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A PALEOECOLOGIC RECONSTRUCTION OF THE HISTORY OF FEATHERBED BANK, BISCAYNE NATIONAL PARK, BISCAYNE BAY, FLORIDA

By

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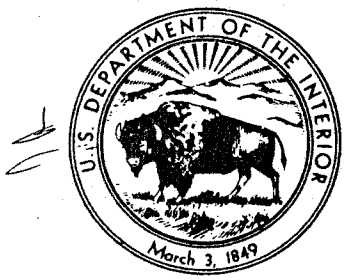
ABSTRACT

Using multiple-proxy biological indicators, a paleoecological history of the past 550 years of Featherbed Bank, Biscayne Bay, has been reconstructed from a short (2.26 m) sediment core. Paleoecological changes in ostracode, mollusc, and foraminifer assemblages show that core SEI297-FB-1 can be divided into three distinctly different zones, which together provide evidence for distinct changes in historical environmental conditions at Featherbed Bank.

Assemblages from fossil biotic communities within zone 1, representing approximately 1440 to 1550 AD, are characterized by open-marine biota with relatively limited numbers of epiphytic biota. Molluscan faunal indicators suggest the sediment was capable of supporting infaunal organisms and that faunal richness was relatively limited during this time period.

A change in the biotic community occurred around 1550 AD and continued until the late 1800's distinguishing zone 2. Fossil biotic indicators from zone 2 show a strong dominance of epiphytic organisms within all of the biotic communities examined. Foraminifers, molluscs, and ostracodes capable of subsisting in salinities slightly lower than normal marine begin to flourish in this time period, and there is a marked decline in infaunal molluscs.

Zone 2 assemblages are replaced around 1900 AD by increased numbers of organisms that typify open-marine conditions and a return to decreased epiphytic assemblages, similar to zone 1. Zone 3 assemblages, however, show some strong dissimilarities from zone 1, including limited infaunal molluscs, increased abundances of the ostracode *Malzella floridana*, and a significant increase in molluscan faunal richness.



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An overview of coral reef research in southern Florida is provided as a prelude to a genuine description of the coral reef ecosystem in the Florida Keys and surrounding environments. Coral reef community types, reef benthos, plankton and reef fish are given specific treatment. Coral reef ecology and management are described.

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INTRODUCTION

Ecosystems and Ecosystem History

Coastal marine environments may change in response to both natural and anthropogenic forces. Natural forces, such as seasonal rainfall variation, hurricanes, climatic variation, and sea-level fluctuation, can dramatically affect substrate and water quality for organisms living within an ecosystem. Human alteration of an environment, such as urbanization, modification of the flow of water and circulation patterns, dredging of natural channels, and introduction of additional nutrients, affect the stability and natural variability of an ecosystem. As a result of tolerances, preferences, and ecological balance, change in the conditions of an ecosystem will result in a concomitant change in biotic assemblages. Therefore, using biota as proxies, historical environmental conditions can be reconstructed from fossil assemblages preserved in short sediment cores.

In 1994, the Everglades Forever Act was passed to help stem the effects of anthropogenic influences upon the Florida Everglades, Florida Bay, and Biscayne Bay. Increasing evidence of changes in the ecosystem attributed to anthropogenic forces, such as industrial pollution, over-harvesting of fisheries, and alteration of natural water circulation patterns, sparked an effort to restore the environment to a more natural condition. However, the impact of natural hydrological and climatic forces had not been adequately investigated. The 'Ecosystem History of Biscayne Bay and the Southeast Coast' project of the USGS was designed to help water management agencies with decisions regarding water and land-use management in south Florida by producing a model for recognizing human-induced and natural ecosystem variation using biological proxies. Documenting and correlating historical trends in the ecosystem's variation with the timing of man-made, hydrological, and climatic events can be used to help determine what

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aspect of the ecosystem has been affected and help distinguish between the factors influencing environmental change.

Setting

Featherbed Bank is located on the margin between central Biscayne Bay and southern Biscayne Bay, off the western coast of Sands Key (fig. 1). The Bank is composed of Holocene sediments that may be greater than 4 meters thick in areas and may represent more than 5000 years of sediment accumulation (Wanless & others, 1995). Monthly salinity readings from sites near Featherbed Bank ranged from 30 to 43.2 ppt between July 1988 and December 1998, averaging around 35.4 ppt (Metro-Dade Department of Environmental Resources Management monthly monitoring of Biscayne Bay, unpublished data).

Multiple-proxy Approach

Ostracodes, foraminifers, and molluscs are small calcareous organisms whose fossil assemblages and shell chemical composition are commonly used in quantitative paleoclimatic reconstruction in deep-sea, coastal, estuarine, and lacustrine environments. These organisms are a major part of the benthic community in Biscayne and Florida Bay, with more than 50 ostracode species, 70 foraminifer species, and over 240 molluscan species (Lyons, 1999). Several studies in Florida Bay and Biscayne Bay have been published that use these biota as a proxy to show changes in a variety of environmental conditions (Turney and Perkins, 1972; Lyons, 1996; Bock & others, 1971; Lidz and Rose, 1989). Analyses of modern flora and fauna within Biscayne Bay (Ishman & others, 1998; Ishman and D'Ambrosio, 1997; Ishman, in press) and the surrounding environments (Brewster-Wingard and Ishman, 1999; Brewster-Wingard & others, 1996; Brewster-Wingard, Stone, and Holmes, in press) have been used to help calibrate modern analogues for foraminifer, mollusc, and ostracode assemblages. In the present study, a multiple-proxy approach was taken to reconstruct the

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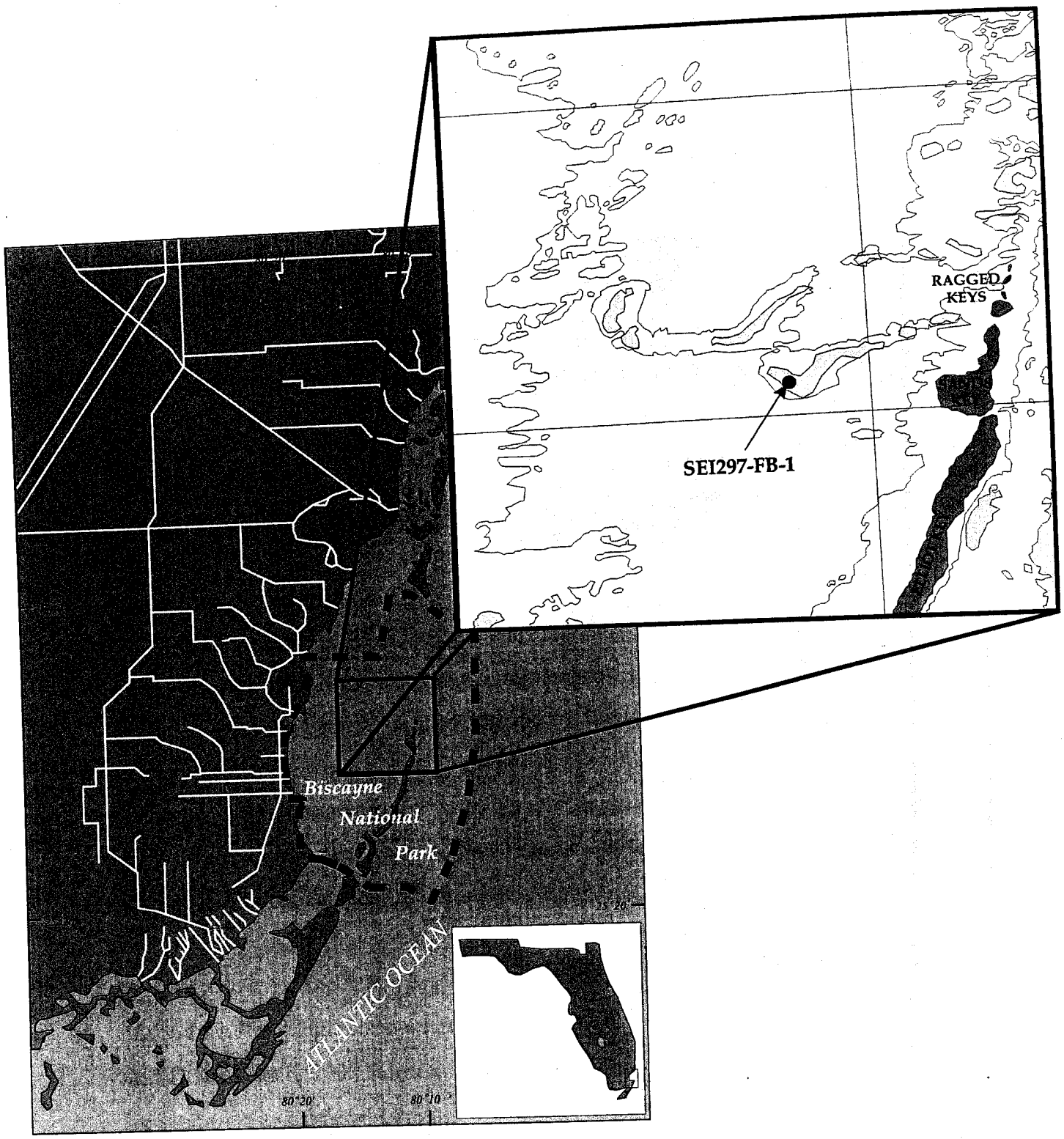


Figure 1. The location of Featherbed Bank within Biscayne National Park, Florida. The dot indicates the location where core SEI297-FB-1 was taken in February 1997.

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METHODS

Core Collection

Core SEI297-FB-1, a 2.26 m long sediment core (25 °31.31'N, 80 °15.39' W), was collected in February 1997 using a large (approximately 4 inches in diameter) piston core. The base of the core did not reach the underlying limestone bedrock (Ishman, 1997). The core was collected in water 63 cm deep, using the USGS pontoon barge. A tripod suspended the core tube through a moon pool in the center of the barge. A piston, placed at the surface-water interface within the core tube, was used to maintain a vacuum that prevented compaction of the sediments as the core tube was being inserted into the sediment. Steel cables attached to the tripod were used to hoist the core tube out of the sediment when the core tube could no longer penetrate the sediment. The recovered core tube was then capped to prevent loss of sediment and to maintain stability in the upper portion of the core before processing (Ishman, 1997). The core

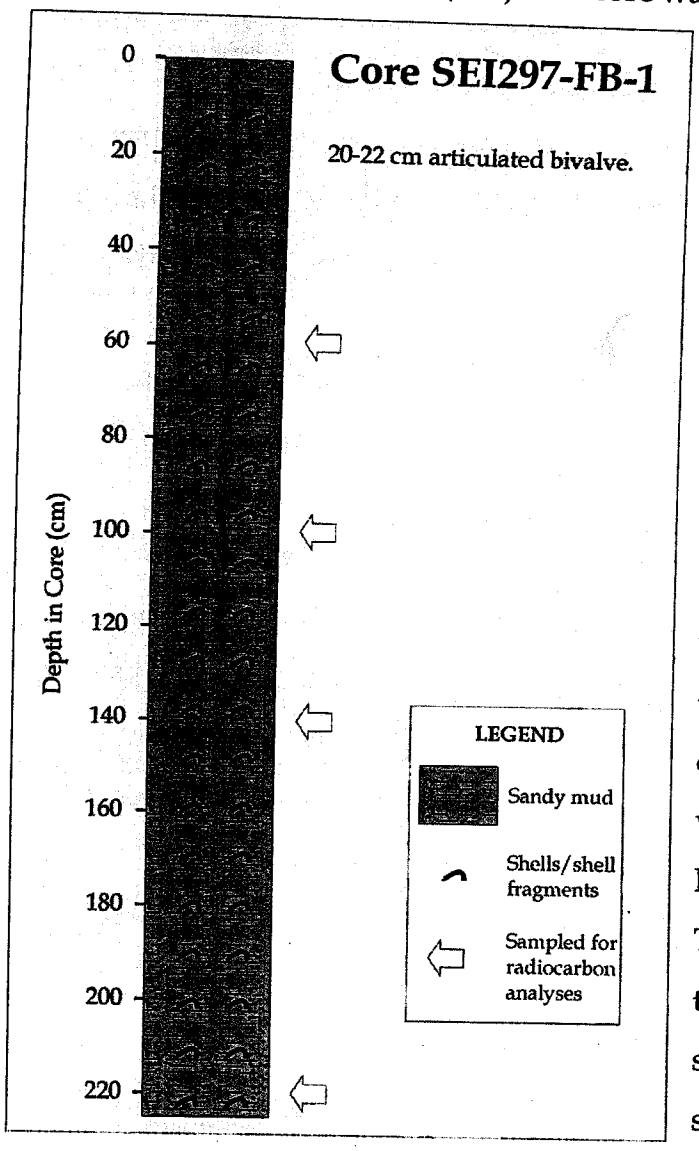


Figure 2. Description of core SEI297-FB-1 (Modified from Ishman, 1997).

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composition is primarily a homogeneous, light-olive-gray, fine sandy mud with plant debris and shell material (fig. 2).

Core Processing

The core was sampled every 2 centimeters, from the top of the core to the base, for faunal and geochemical analysis. All samples were washed through a set of nested 63 μm and 850 μm sieves. Sample components from less than 63 μm were dried at 50°C and weighed for ^{210}Pb analyses. The fractions of the sample greater than 63 μm were dried at 50°C and analyzed for ostracodes, foraminifers, and molluscs. All identifiable molluscs (ranging between 5 and 184 specimens), between 97 and 152 ostracode specimens, and 300 foraminifers (when attainable) were picked from each sample with a fine brush. Samples yielding less than 300 foraminifers were picked in their entirety.

Every other sample from the core was examined. Faunal groups and species were identified, counted, and standardized by calculating percent abundance within each sample. Ostracode species were identified using the taxonomy of Teeter (1975), Keyser (1975, 1976, 1977), and Garbett and Maddocks (1978). Cronin & others (in press) reviewed the ecology of ostracode species. Molluscs were identified primarily using Abbott (1974), Warmke and Abbott (1961), Perry and Schwengel (1955), and Andrews (1971), and taxonomic nomenclature was updated following Turgeon et al (1998). Taxonomy of the benthic foraminiferal species were identified using Loeblich and Tappan (1988). Faunal slides are housed in the Eastern Earth Surface Processes Team, U.S. Geological Survey, Reston, Virginia.

Chronology

A provisional age model (fig. 3) for SEI297-FB-1 was developed from ^{210}Pb (lead) dating for the uppermost 90 cm (Robbins & others, in press), and ^{14}C (radiocarbon) dating by John McGeehin (USGS, Reston) for the interval from 60

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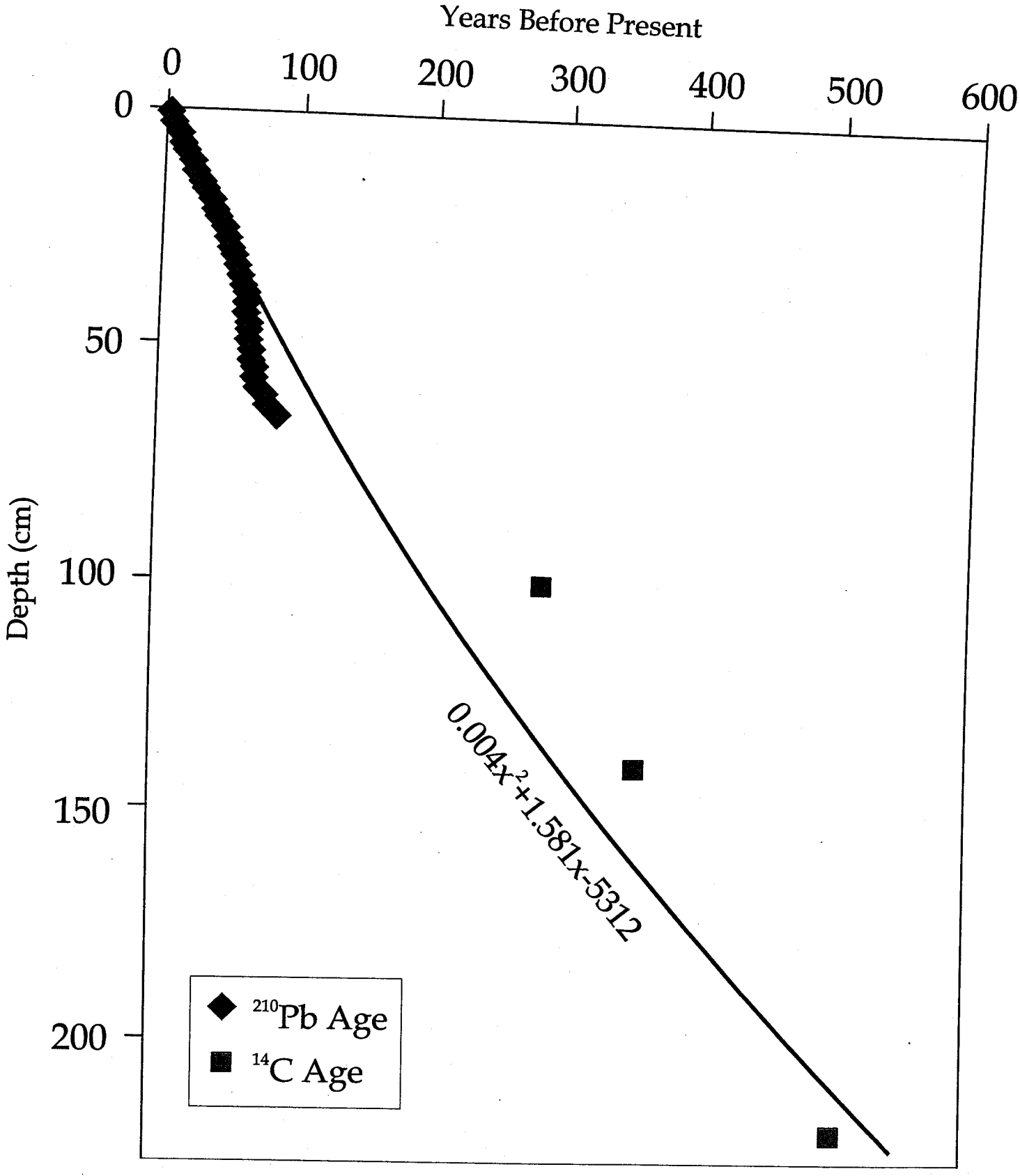


Figure 3. Age model for core SEI297-FB-1.

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to 222 cm (table 1). Using the ^{210}Pb ages and lower three radiocarbon dates (101, 141, and 221 cm) as tie-points (fig. 2), a preliminary age model was obtained with a second order polynomial line yielding the following depth age relationship:

$$Age = 0.004(depth^2) + 1.581\ (depth) - 5.312\ (r^2 = 0.944)$$

Ages for each faunal sample were computed using this equation and are given in Tables 2 - 4.

One can obtain a slightly different age model by using the original age estimates from the ^{210}Pb analyses for the upper 87 cm and a separate age-depth equation for the interval 65-225 cm. This interval can be dated by fitting a line to the oldest ^{210}Pb age of 88 years at 65 cm and lowermost three radiocarbon dates. Ages in this latter model are 20-60 years older in the interval from ~65 to 190 cm; thus it is important to keep in mind the age uncertainty.

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RESULTS

Ostracodes

Core SEI297-FB-1 can be divided into three informal faunal zones based on changes in the relative frequencies of various environmentally sensitive ostracode taxa (fig. 4, table 2). The lowermost zone (zone 1) from 226-175 cm is dominated by the species of the genera *Neonesidea* and *Paranesidea* (lumped into the family Bairdiidae), *Radimella* and *Hermanites* (plotted together), *Neocaudites* and *Actinocythereis*. These species typically live exclusively in waters of normal marine salinity on carbonate platforms in tropical and transitional subtropical regions. The age of this zone is estimated to be about 1450-1600 AD (400-550 yr BP).

The second zone (zone 2) occurs from 175 to 65 cm and is characterized by common *Loxoconcha matagordensis* (20-50 %) and *Xestoleberis* spp. (20-40 %). *Loxochoncha. matagordensis* is an epiphytal species that lives along Atlantic and Gulf of Mexico coasts of North America on *Thalassia, Zostera* (in mid-latitudes), and other marine seagrasses (Cronin & others, in press). Many species of *Xestoleberis* inhabit various types of marine algae in tropical and subtropical regions. In addition to their preference for sub-aquatic vegetation habitats, *L. matagordensis* and several species of *Xestoleberis* thrive in environments of reduced salinity, such as those found in coastal bays and lagoons. Therefore, the dominance of epiphytal euryhaline ostracode species in this zone suggests a period of both abundant seagrass and marine algal habitats and also fluctuating salinity between about 20-35 ppt. The age of this zone is estimated to be about 1600-1850 AD (150-400 yr BP).

The third zone (zone 3) occurs in the interval from 65 cm to the top of the core and represents the period from 1850 to 1997. The ostracode assemblages consist mostly of carbonate platform species as were found in zone 1, and in addition, 10% or more of *Malzella floridana*. This latter species is a dominant form

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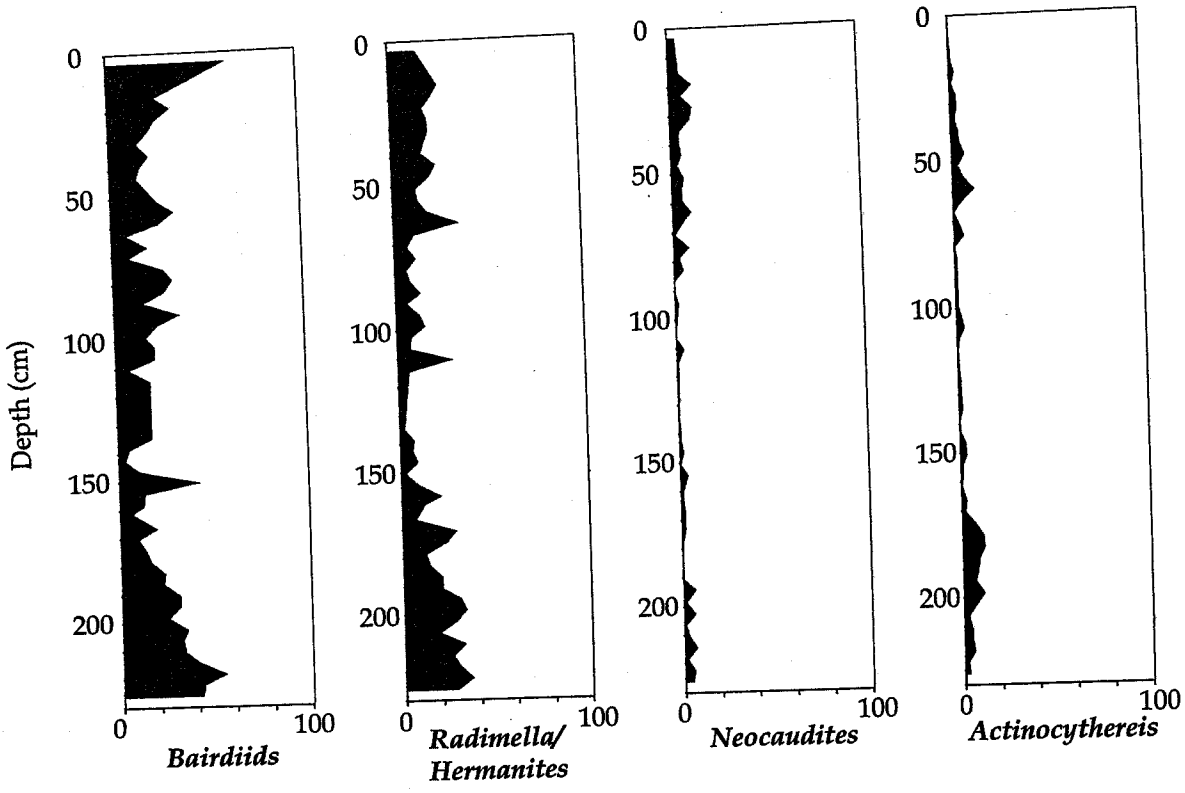
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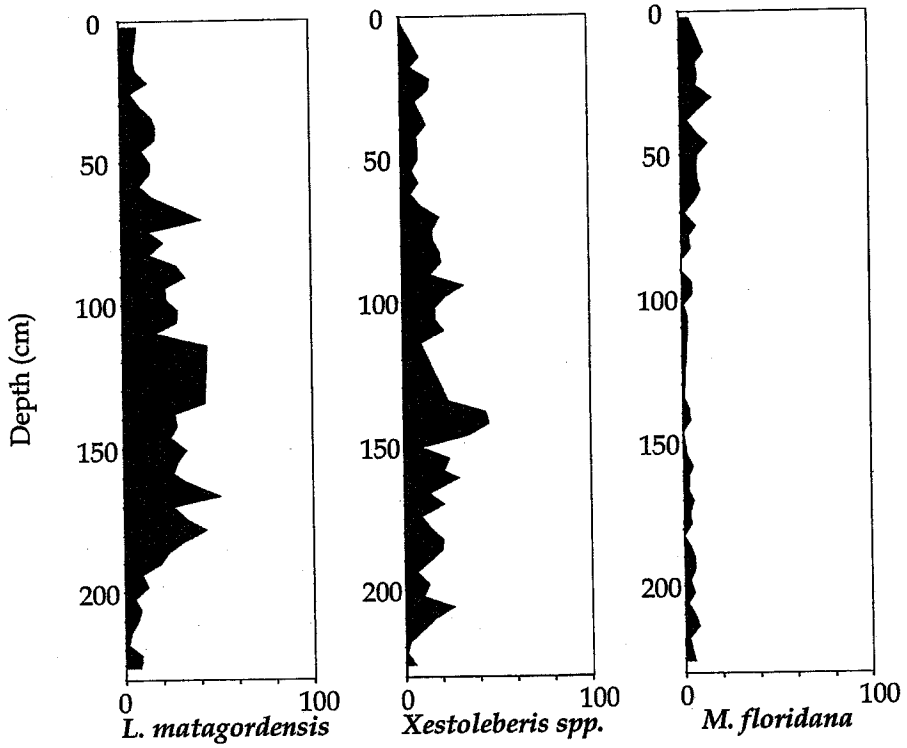
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Figure 4. Ostracodes (in percent abundance) from Featherbed Bank Core, Biscayne Bay.





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in Florida Bay in regions that experience periodic hypersalinity. While its presence in Biscayne Bay during the last 150 years does not necessarily indicate hypersalinity, it does distinguish the assemblages of zone 3 from zone 1. Epiphytal species also decrease significantly in the transition from zone 2 to zone 1.

Molluscs

Examination of the molluscan fauna in Core SEI297-FB-1 resulted in the identification of 96 faunal groups. The dominant species include *Bittiolum varium, Turbo castaneus, Eulithidium* sp., *Tegula fasciata,* and *Vermicularia spirata.* The assemblages and the molluscan faunal richness and abundance throughout the core indicate open-bay to open-marine conditions. On the basis of the molluscan assemblages, the salinity never dropped below 20 ppt, and was probably greater than 25 ppt throughout the time of deposition at this site. There are no molluscan indicators of proximity to land at this site.

The lower portion of Core SEI297-FB-1, from 226 to 175 cm (zone 1), is characterized by the presence of infaunal pelecypods (*Pitar* sp., *Parastarte triquetra, Gouldia* sp., *Nucula proxima*), perhaps indicating softer sediment available for habitation. Epiphytic and epibenthic gastropods (*Eulithidium* sp., *Cerithium* spp., *Tegula fasciata, Vermicularia spirata, Modulus modulus,* and *Turbo castaneus*) are also present in the lower portion of the core (fig. 5, table 3). *Bittiolum varium,* a dominant epiphytic species in the upper portion of the core, is nearly absent from zone 1. Average molluscan faunal richness[1] is 13 and average abundance is 23 in the lower portion of the core; these numbers do not fluctuate significantly in this portion of the core, suggesting a relatively stable ecosystem. The molluscan fauna indicate near normal marine salinities for zone 1. Samples between 190 and 175 cm mark a transition from zone 1 to zone 2.

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[1] Faunal richness is a measure of the number of faunal groups present in a given sample. In some cases, the fauna are grouped into genera and occasionally broader categories (e.g. marginellids), so this is not "species" richness in the usual sense.

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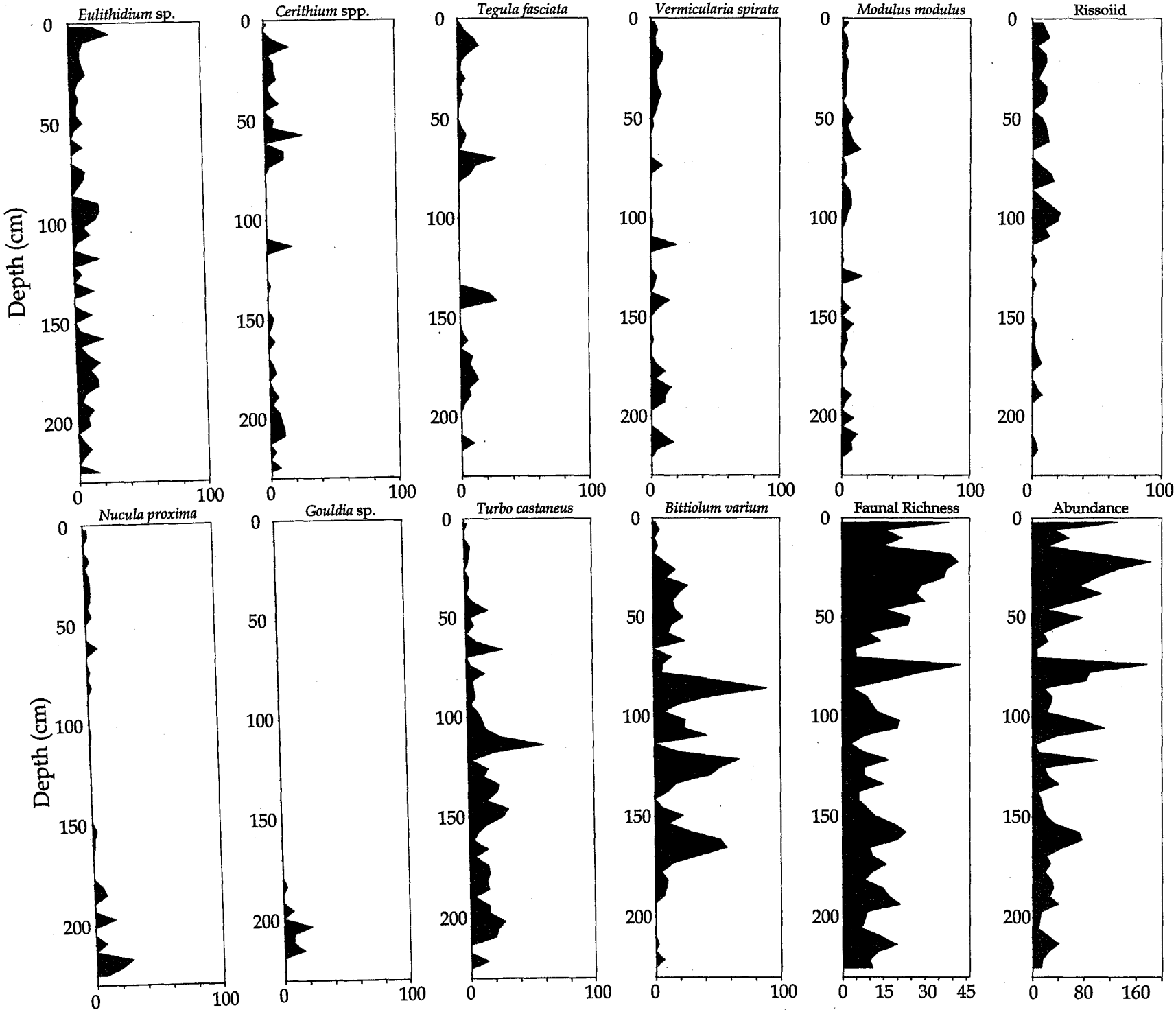
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Figure 5. Molluscs (in percent abundance) from Featherbed Bank Core, Biscayne Bay.



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The middle portion of the core, from 175-65 cm (zone 2), is dominated by the presence of *Bittiolum varium; Turbo castaneus* also is relatively abundant. Burrowing pelecypods are sparse in zone 2 and almost completely absent from 118-90 cm, indicating the substrate may not have been suitable for habitation; this corresponds to an increase in organisms that live on hard substrates and/or sub-aquatic vegetation. Average molluscan faunal richness in the middle portion of the core is 12, nearly the same as the lower portion, but abundance is highly variable compared to zone 1, averaging 39 individuals per sample. The molluscan fauna indicate the salinity in this portion of the core may have been reduced periodically (perhaps as low as 25 ppt) compared to zone 1; the presence of several species that require near normal marine salinities, however, discounts sustained periods of lower salinities. Samples between 90 and 65 cm mark a transition from zone 2 to zone 3, sharing characteristics of both.

The upper portion of the core, from 65 to 0 cm (zone 3), is marked by a decline in the dominance of *Bittiolum varium,* and a dramatic increase in faunal richness to an average of 25 faunal groups per sample. *Cerithium* spp., *Tegula fasciata, Vermicularia spirata, Modulus modulus,* rissoinids, *Nucula proxima,* and *Transenella* sp. increase in numbers in the upper portion of the core. This portion of the core contains a distinct assemblage very similar to the western margin of Florida Bay. The assemblage is dominated by *Turbo castaneus* and *Tegula fasciata* with minor percentages of *Brachidontes exustus, Pteria longisquamosa, Cerithium muscarum, Chione cancellata,* and other species more common in eastern and central Florida Bay. The assemblage requires relatively stable, near-normal marine salinities (Brewster-Wingard, Stone, and Holmes, in press). This evidence is supported by the presence of *Halimeda* in the upper 80cm of the core. *Halimeda* is a green algae common in normal marine conditions and found along the western margin of Florida Bay. Faunal abundance, which fluctuates dramatically in zone 3, ranging from 7 to 184 individuals per sample (averaging 74), distinguishes this assemblage from the molluscan assemblage in zone 1.

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Foraminifers

The foraminiferal analyses resulted in the identification of 41 species (table 4). The assemblages are dominated by miliolid forms, with calcareous hyaline taxa common, and agglutinated taxa rare. The dominant species include *Quinqueloculina bosciana, Q. poeyana, Q. polygona, Q. seminula, Q. tenagos, Triloculina trigonula, Miliolinella circularis, Elphidium delicatulum, Archaias angulatus, Articulina mucronata, Rosalina floridana,* and *R. globularis*. Other subsidiary species include the rotaliids *Ammonia parkinsoniana tepida, A. parkinsoniana typica,* and *Florilus auriculus,* and the textulariid *Clavulina tricarinata* (Fig. 6).

Ishman (in press) recognized four benthic foraminiferal assemblages from surficial sediment samples collected in Biscayne Bay. The foraminiferal faunas from Core SE1297-FB-1 represent a mixture of the open-bay grass assemblage and the open-bay coarse sediment assemblage, indicating open-bay normal circulation throughout the deposition of this core.

From the core bottom to 175 cm (zone 1), an open-bay seagrass form *Elphidium delicatulum* dominates to the near exclusion of other members of the seagrass assemblage. Within this interval, a variety of open-bay coarse sediment forms of the genera *Quinqueloculina* (*Q. tenagos, Q. poeyana, Q. polygona*) and *Triloculina* (*T. triacarinata*) and *Rosalina* (*R. floridana*) are present to common, suggesting a patchy seagrass-bare substrate environment.

From 175 cm to 65 cm (zone 2), *Elphidium delicatulum* still dominates, but other representatives of the seagrass assemblage, such as *Quinqueloculina bosciana, Articulina mucronata,* and *Miliammina circularis,* are present to common, and forms of the open-bay coarse sediment assemblage are still present but less abundant, indicating an environment with fairly healthy seagrass and sparse, patchy bare sediment. Samples between 100 and 65 cm mark a transition from zone 2 to zone 3 assemblages. Foraminifer assemblages, commonly found in minor relative percentages in salinities that range as low as 30 ppt, are present

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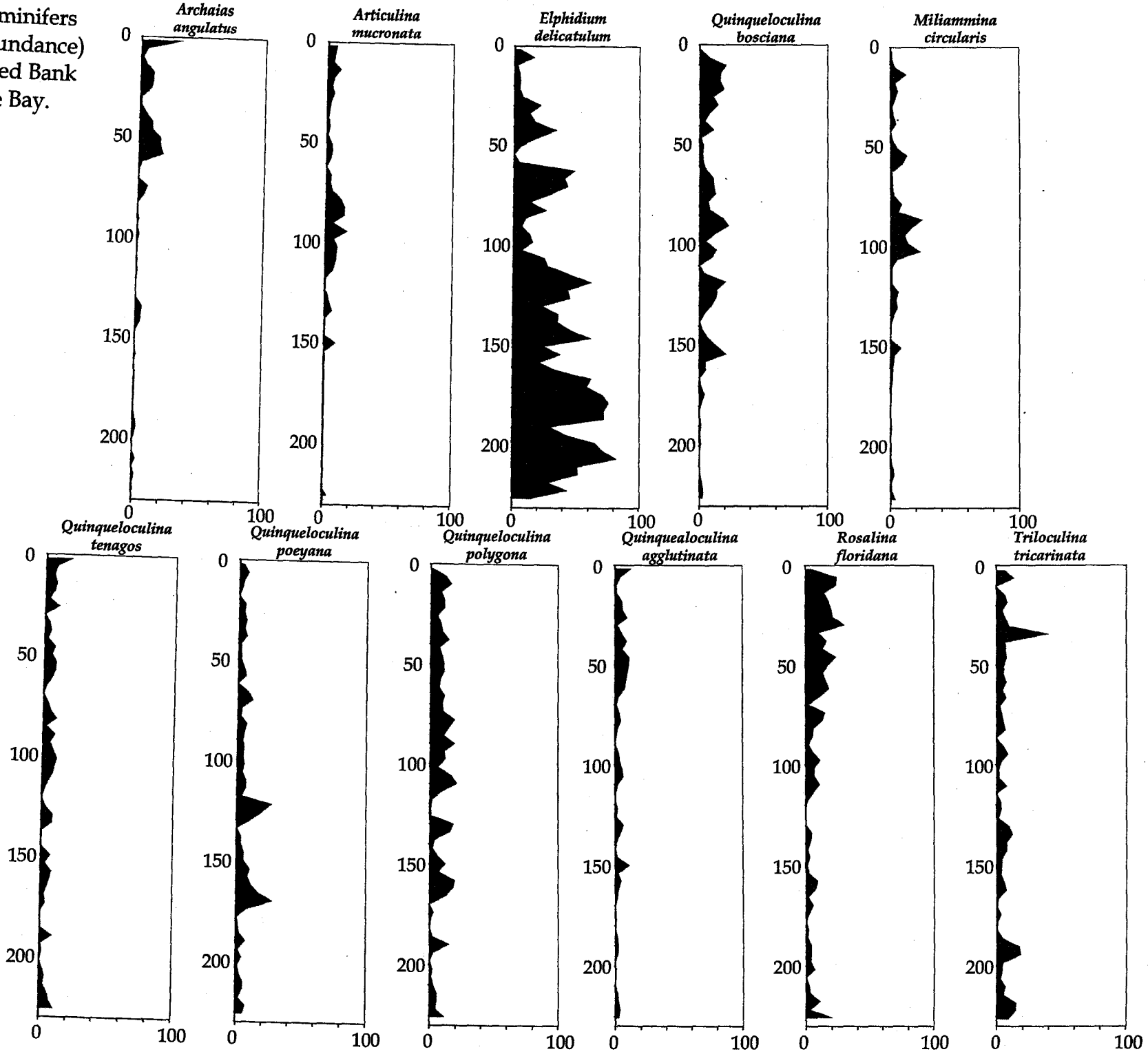
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Figure 6. Foraminifers (in percent abundance) from Featherbed Bank Core, Biscayne Bay.



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within zone 2, suggesting that salinity conditions may have been slightly reduced when compared with zone 1.

From 65 cm to the top of the core (zone 3), the open-bay coarse sediment foraminiferal assemblage attains dominance. There is an increased abundance of most members of the open-bay coarse sediment assemblage in zone 3 and *Elphidium delicatulum* is greatly reduced, only dominating in a few horizons; other forms of the seagrass indicators remain unchanged or show only a modest increase in abundance. This suggests a bare sediment environment with patchy seagrass gradually replacing the lush sub-aquatic vegetation from zone 2 in the upper part of the core.

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DISCUSSION

Regional Model for Featherbed Bank

The results of faunal analyses in this study have produced a model for Core SEI297-FB-1 that divides the fossil assemblages into three informal faunal zones. Although preliminary in nature, the results suggest distinct environmental changes have characterized deposition at Featherbed Bank over the past 5 centuries (fig. 7).

The data from zone 1 (base to 175 cm) indicate that during the 15th and 16th centuries Featherbed Bank had an open-marine carbonate environment. The substrate during this period was patchy sub-aquatic vegetation, with a strong infaunal presence. Key biotic indicators suggest that salinity within zone 1 remained relatively stable and near to normal marine throughout deposition.

Zone 2 (175 – 65 cm) deposited during the 17th, 18th, and 19th centuries, had a thriving bottom community living on seagrasses (probably abundant *Thalassia*) and marine algae. The presence of some taxa capable of tolerating lowered salinities in zone 2 indicate that this period may have experienced a wetter regional climate and/or experienced greater influx of freshwater. However, relatively high abundances of biotic indicators, which require near normal marine salinities within zone 2, limits the potential that salinity conditions were lowered for a sustained period.

Zone 3 (65 – 0 cm) represents the last 150 years of Biscayne Bay history when open-marine species re-colonized and sub-aquatic vegetation decreased. For the first time, the ostracode *Malzella floridana* became common, indicating possible episodes of hypersalinity and a molluscan assemblage similar to the western margin of Florida Bay appeared. The dramatic change in molluscan faunal richness and abundance in the upper portion of the core is striking (fig. 7). It is possible that this is a taphonomic effect, but preservation quality of

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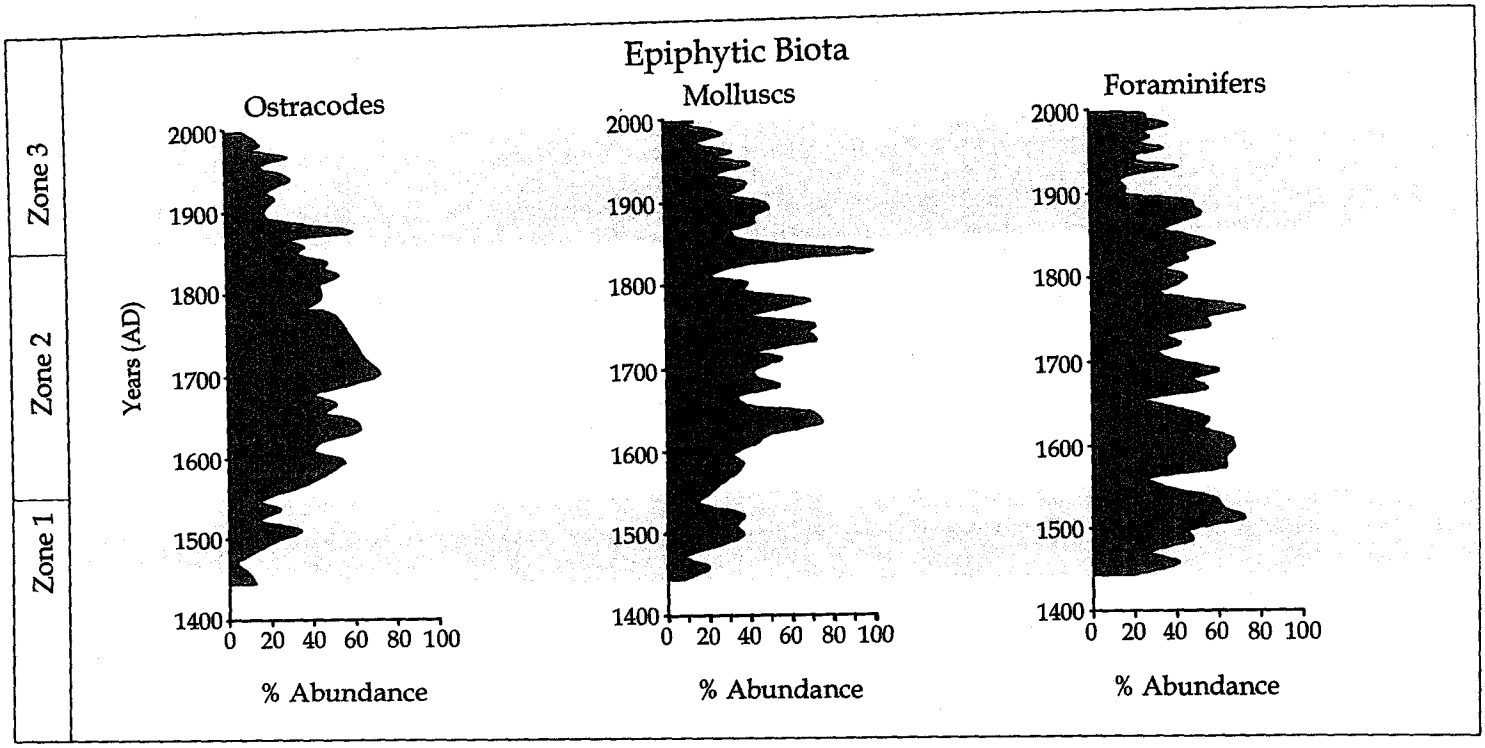
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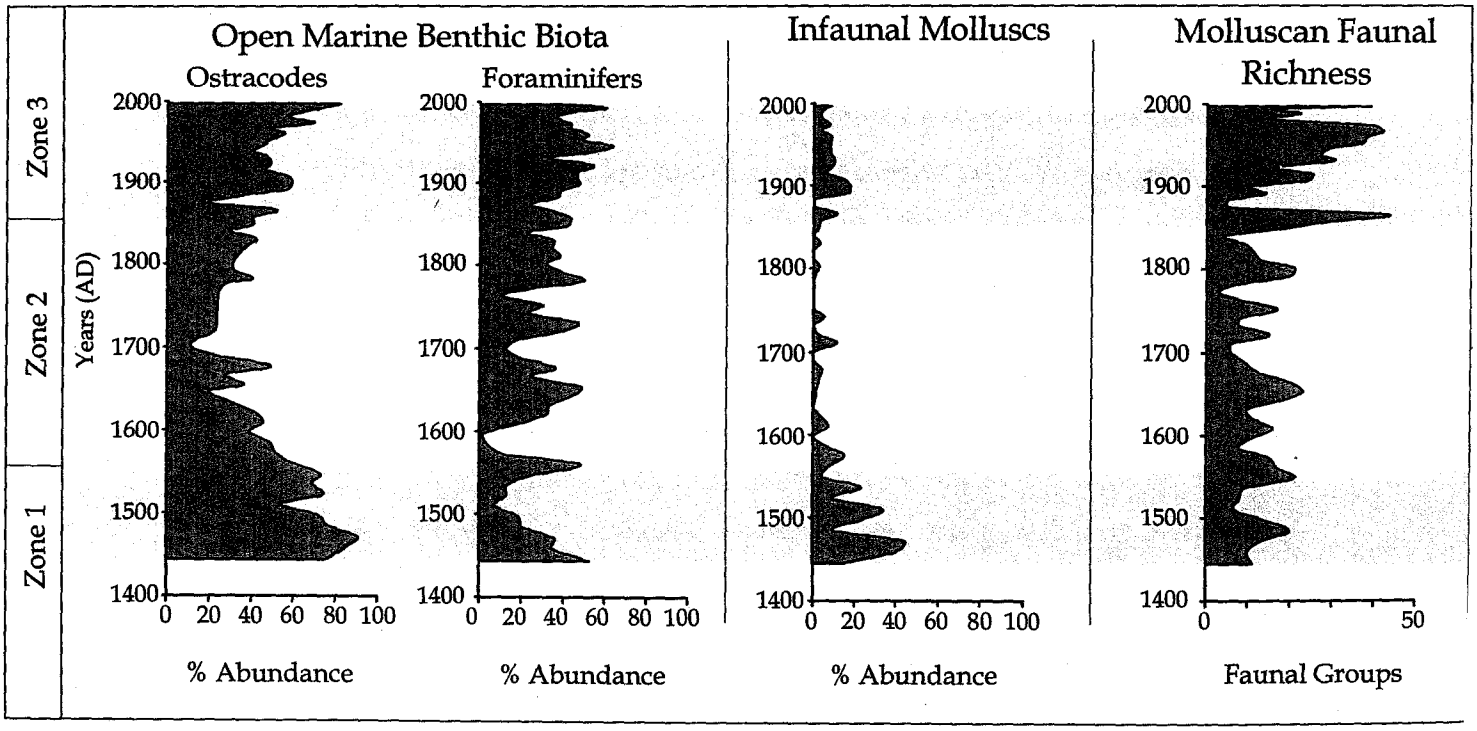
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Figure 7. SEI297-FB-1 Key Down-core Indicators Plotted Against Time.





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molluscan fossil shells is generally the same throughout the core; for example, the lowest portion of the core contains very delicate specimens that are well preserved, and color patterns are still present. These observations indicate that the variation in faunal richness and abundance is real and not a taphonomic bias. The increase in molluscs may be related to the variability in substrate heterogeneity, to fluctuating salinities, or to some other factor such as productivity or increased nutrients.

Bank Migration Model

While distinct, the changes within core SEI297-FB-1 are dominated by assemblages that primarily indicate different substrates. Variation in the fossil biotic communities throughout the core indicate limited variation in salinity conditions, possibly ranging as low as 25 ppt in zone 2; biological proxy indicators suggest that salinity conditions at Featherbed Bank remained stable and near normal marine throughout most of the deposition of the core.

The transition from infaunal and coarse-sediment dwelling biota (zone 1) to prominent epiphytic communities (zone 2) to variable substrates and potentially increased salinity fluctuations (zone 3) is consistent with a model for bank migration; the transition from zone 1 to zone 3 may be explained by gradual shallowing of the environment of deposition, with lush sub-aquatic vegetation (zone 2) representing the side of a migrating bank. Without further investigation, it would be difficult to determine if the changes seen in core SEI297-FB-1 are the result of local bank migration or if they represent regional changes within central Biscayne Bay over the past 5 centuries.

Suggestions for Future Work

To date, short cores, like the core analyzed in this paper, have been taken from six different regions of Biscayne Bay for the USGS 'Ecosystem History of Biscayne Bay and the Southeast Coast' project (Ishman, 1997). Faunal analyses of

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the cores from Manatee Bay and Featherbed Bank have now been completed, and modern analog data exist that allow a more accurate interpretation of historical trends in faunal assemblages. Results from this study suggest that environmental trends within Biscayne Bay show three distinct faunal zones, representing a shift in environmental conditions at Featherbed Bank. To understand whether these changes are a result of bay-wide changes or simply a local phenomenon produced by the migration of Featherbed Bank, additional cores must be analyzed from other regions within Biscayne Bay.

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CONCLUSIONS

Ostracode, molluscan, and foraminiferal biological proxy indicators demonstrate that Featherbed Bank experienced three distinct environments. From approximately 1440–1550AD (zone 1), biotic assemblages show that open-bay, relatively stable marine, carbonate deposition dominated the environment. Patchy to limited sub-aquatic vegetation was present. Between 1550 and 1850 AD (zone 2), this environment gave way to open-bay conditions with lush sub-aquatic vegetation with only limited bare substrate. Salinity conditions may have reached as low as 25 ppt within this zone, but probably not for sustained periods. Between 1850 and 1997 AD (zone 3), biotic assemblages, representing open-bay deposition with patchy sub-aquatic vegetation and increasing bare substrate, re-colonize the environment. However, assemblages after 1850 display distinct differences from those in zone 1, suggesting modest changes in salinity regimes and substrate. There is no evidence for proximity to land or sustained periods of lowered salinity throughout core SEI297-FB-1. Although distinct, the changes in biotic assemblages down-core are dominantly substrate-controlled and may represent either bay-wide or local variations in the biological communities at Featherbed Bank.

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Table 1. Age model for core SEI297-FB-1 samples

Depth (cm)	Method	Age#	2 Sigma Range	Uncorrected C-14 Age	+/-
0-2	lead-210	1.66			
2-4	lead-210	5.04			
4-6	lead-210	8.49			
6-8	lead-210	12.00			
8-10	lead-210	15.57			
10-12	lead-210	19.20			
12-14	lead-210	22.86			
14-16	lead-210	26.55			
16-18	lead-210	30.24			
18-20	lead-210	33.90			
20-22	lead-210	37.52			
22-24	lead-210	41.06			
24-26	lead-210	44.47			
26-28	lead-210	47.71			
28-30	lead-210	50.75			
30-32	lead-210	53.54			
32-34	lead-210	56.05			
34-36	lead-210	58.25			
36-38	lead-210	60.15			
38-40	lead-210	61.74			
40-42	lead-210	63.05			
42-44	lead-210	64.13			
44-46	lead-210	65.05			
46-48	lead-210	65.85			
48-50	lead-210	66.64			
50-52	lead-210	67.49			
52-54	lead-210	68.51			
54-56	lead-210	69.81			
56-58	lead-210	71.52			
58-60	lead-210	73.83			
60-62	lead-210	76.99			
62-64	lead-210	81.40			
64-68	lead-210**	87.77			
60-62	radiocarbon*	295	350-0 yr BP	570	55
100-102	radiocarbon**	286	342-0 yr BP	555	55
140-142	radiocarbon**	359	503-303 yr BP	695	55
220-222	radiocarbon**	505	567-363 yr BP	810	55

*not used in age-depth model

**used to derive age model for interval 65-225 cm
age = 0.004 (depth*depth) + (1.581*depth) - 5.312
#Radiocarbon ages are calibrated using program in Stuvier and Reimer (1993)

COLOR PLATES

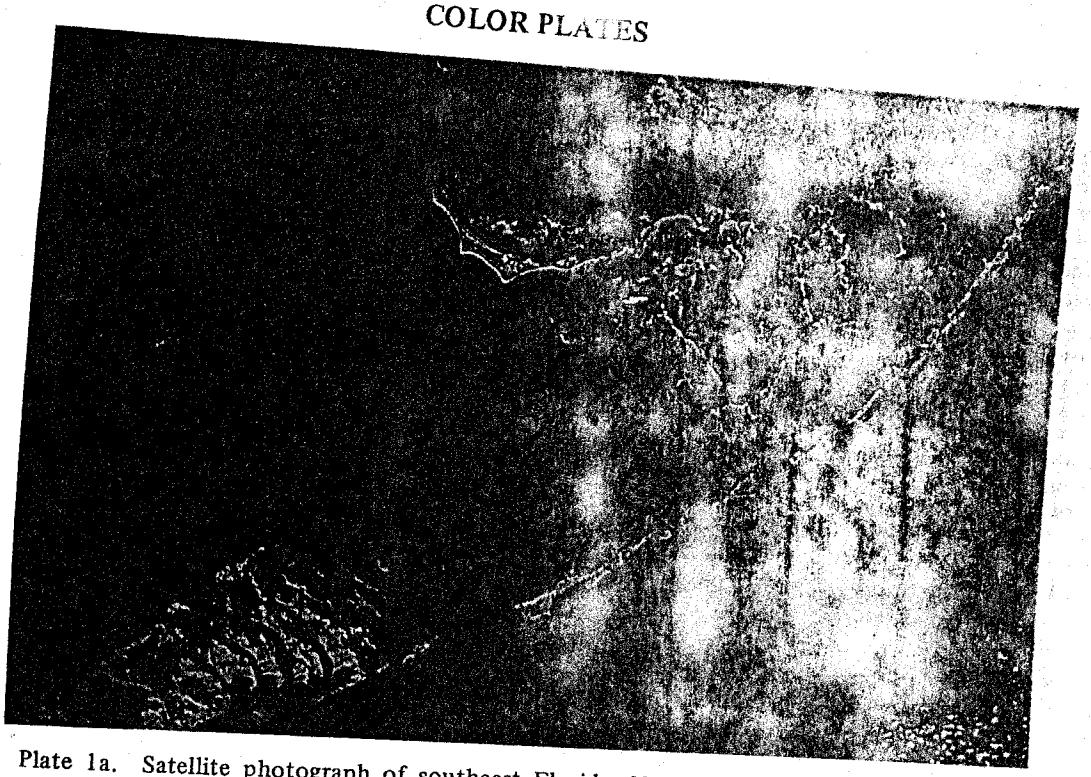


Plate 1a. Satellite photograph of southeast Florida. Note large passes between islands in the middle Keys. Florida Bay lies between the mainland and the Keys.

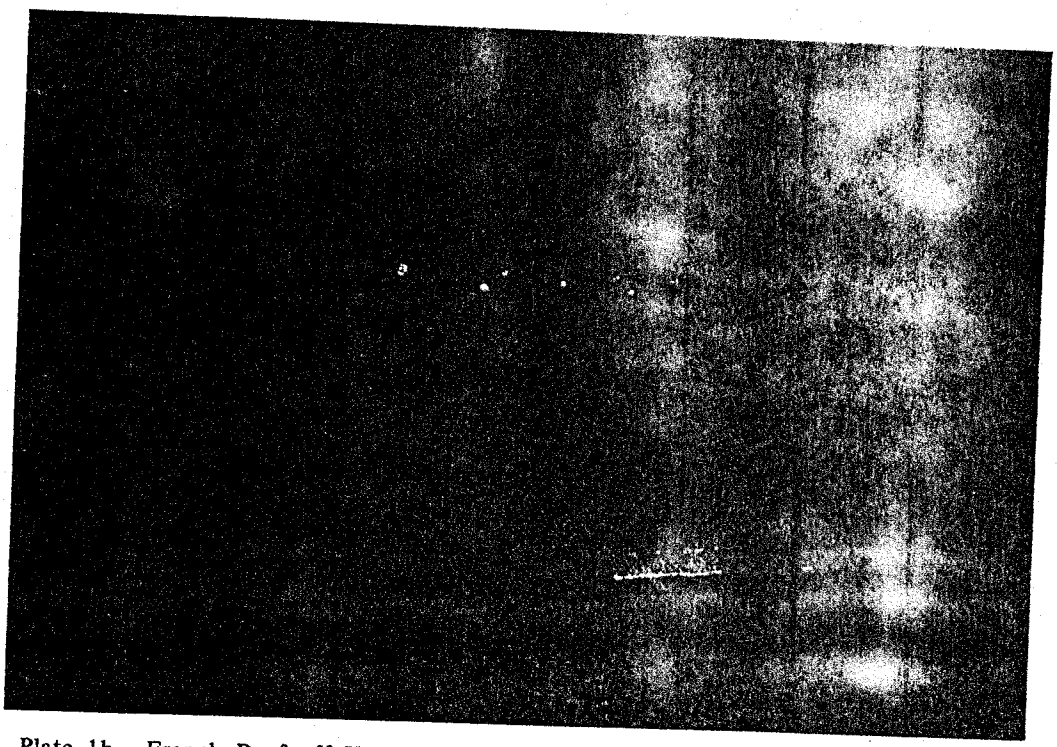


Plate 1b. French Reef off Key Largo. Waves breaking on the reef flat; dive boats anchored on the deeper spur and groove zone.

Table 2: Ostracode Percent Abundance Data for SEI297-FB-1

Depth (cm)	Years (B.P.)	Age Model Year	*P. setipunctata*	*Loxoconcha*	*Malzella*	*Xestoleberis*	Bairdiids	*Puriana*	*Jug/Hermanites/Radimella*	*Neocaudites/Caudites*	*Actinocythereis*	Other	Total Picked
0-2	0.00	1997	0.00	8.65	4.81	0.00	63.46	0.00	14.42	3.85	0.00	4.81	104
12-14	15.92	1981	0.00	6.36	11.82	10.00	25.45	0.00	25.45	5.45	0.91	14.55	110
16-18	22.72	1974	0.00	7.50	7.50	5.00	33.33	0.00	21.67	11.67	2.50	10.83	120
20-22	29.65	1967	0.85	13.68	8.55	15.38	24.79	0.85	17.09	5.98	0.85	11.97	117
24-26	36.71	1960	0.00	4.85	7.77	14.56	21.36	0.97	19.42	11.65	2.91	16.50	103
28-30	43.90	1953	0.00	9.28	15.46	7.22	15.46	4.12	19.59	10.31	3.09	15.46	97
32-34	51.22	1946	0.00	15.38	8.65	10.58	21.15	3.85	17.31	4.81	1.92	16.35	104
36-38	58.66	1938	0.00	17.39	3.48	13.04	16.52	4.35	15.65	4.35	3.48	21.74	115
40-42	66.23	1931	0.79	16.67	7.94	7.94	14.29	4.76	23.02	5.56	3.97	15.08	126
44-46	73.93	1923	1.56	10.16	13.28	8.59	19.53	2.34	19.53	3.13	6.25	15.63	128
48-50	81.76	1915	0.72	14.49	7.97	8.70	24.64	1.45	12.32	6.52	2.90	20.29	138
52-54	89.72	1907	0.00	14.04	7.89	5.26	33.33	0.88	13.16	5.26	5.26	14.91	114
56-58	97.80	1899	0.89	8.93	8.04	8.93	25.00	2.68	17.86	5.36	10.71	11.61	112
60-62	106.01	1891	0.81	15.32	9.68	4.84	8.06	0.81	33.87	9.68	4.84	12.10	124
64-66	114.35	1883	0.87	28.70	6.09	10.43	19.13	2.61	10.43	4.35	0.00	17.39	115
68-70	122.82	1874	5.36	40.18	1.79	19.64	8.93	0.89	7.14	0.89	2.68	12.50	112
72-74	131.42	1866	1.60	13.60	7.20	16.00	27.20	0.00	11.20	8.00	4.80	10.40	125
76-78	140.14	1857	0.00	20.72	3.60	16.22	31.53	0.90	6.31	2.70	0.00	18.02	111
80-82	148.99	1848	0.00	13.51	4.50	19.82	27.03	0.00	8.11	4.50	0.90	21.62	111
84-86	157.97	1839	0.00	27.05	0.00	20.49	15.57	2.46	13.11	0.00	0.82	20.49	122
88-90	167.08	1830	0.00	31.62	0.00	14.53	35.04	0.00	5.98	0.00	0.85	11.97	117
92-94	176.32	1821	0.82	21.31	4.92	31.97	22.95	0.00	12.30	1.64	0.82	3.28	122
96-98	185.68	1811	0.00	21.93	5.26	21.93	16.67	0.88	14.91	0.88	0.88	16.67	114
100-102	195.17	1802	0.00	28.03	0.76	16.67	21.21	0.00	7.58	0.00	2.27	23.48	132
104-106	204.79	1792	0.00	27.03	2.70	17.12	20.72	1.80	7.21	0.00	3.60	19.82	111
108-110	214.54	1782	1.74	16.52	2.61	21.74	6.96	0.00	28.70	3.48	0.87	17.39	115
112-114	224.42	1773	0.00	42.31	2.31	9.23	18.46	0.77	6.15	0.77	0.00	20.00	130
132-134	275.72	1721	0.74	41.18	0.74	23.53	18.38	0.00	2.94	0.00	1.47	11.03	136
136-138	286.36	1711	1.52	25.76	3.03	43.18	6.06	0.00	7.58	0.76	0.00	12.12	132
140-142	297.13	1700	0.00	26.87	3.73	44.78	3.73	2.24	6.72	0.75	0.00	11.19	134
144-146	308.03	1689	0.00	23.73	0.00	34.75	11.02	1.69	9.32	1.69	2.54	15.25	118
148-150	319.06	1678	1.02	31.63	1.02	9.18	42.86	0.00	3.06	0.00	3.06	8.16	98
152-154	330.22	1667	0.00	27.52	1.83	23.85	13.76	0.92	9.17	3.67	0.92	18.35	109
156-158	341.50	1655	0.81	25.00	4.84	20.97	12.90	0.00	20.97	1.61	0.81	12.10	124
160-162	350.05	1647	1.85	30.56	2.78	28.70	6.48	0.00	12.04	0.93	0.00	16.67	108
164-166	364.45	1633	1.65	48.76	2.48	13.22	19.83	0.00	7.44	1.65	2.48	2.48	121
168-170	376.12	1621	0.00	25.00	5.00	20.83	10.00	0.00	28.33	1.67	1.67	7.50	120
172-174	387.92	1609	0.00	31.34	2.99	8.96	14.18	0.00	23.13	1.49	6.72	11.19	134
176-178	399.84	1597	0.00	41.51	3.77	13.21	16.04	0.00	12.26	0.00	10.38	2.83	106
180-182	411.89	1585	0.00	29.69	0.00	20.31	23.44	0.00	14.06	0.00	10.94	1.56	128
184-186	424.07	1573	0.00	21.97	3.03	19.70	22.73	0.00	20.45	0.00	8.33	3.79	132
188-190	436.38	1561	0.00	17.69	5.44	12.93	31.29	0.00	20.41	0.00	7.48	4.76	147
192-194	448.82	1548	0.00	8.53	5.43	6.20	31.01	0.00	29.46	6.20	6.20	6.98	129
196-198	461.38	1536	0.00	11.72	2.76	12.41	24.83	0.00	32.41	1.38	10.34	4.14	145
200-202	474.07	1523	0.00	4.85	4.85	9.71	34.95	0.00	27.18	5.83	5.83	6.80	103
204-206	486.89	1510	0.00	8.06	1.61	25.81	32.26	0.00	18.55	0.81	2.42	10.48	124
208-210	499.84	1497	0.00	5.92	5.26	15.13	33.55	0.00	31.58	2.63	3.95	1.97	152
212-214	512.92	1484	0.00	2.82	7.04	9.15	40.85	0.00	25.35	6.34	4.23	4.23	142
216-218	526.12	1471	0.00	1.45	2.17	2.17	55.07	0.00	28.99	1.45	5.07	3.62	138
220-222	539.45	1458	0.00	8.40	3.36	0.84	42.86	0.00	35.29	5.04	1.68	2.52	119
224-226	552.91	1444	0.00	7.32	4.88	4.88	42.28	0.00	26.83	4.07	2.44	7.32	123

complete an in-depth field study (not a literature survey) in the preparation of an environmental impact statement. Field scientists should have local experience in the area and know the biota. All coral reef communities within 1 nmi of the proposed project should be identified and documented so that monitoring can be accomplished. Dredging operations close to a coral reef should be required to use turbidity curtains. Turbidity and sediment fallout should be monitored; the overall rate should not exceed 200 g/cm^2/day (Griffin 1974). Mechanical dredging equipment should not come in physical contact with the reef. Dredged spoils should not be disposed of on or near reef communities.

Oil spills, vessel groundings, shipwrecks, and sinkings are the responsibility of the Marine Patrol in Florida waters and the Coast Guard in Federal waters. There should be rapid resource evaluation and analysis by competent reef scientists shortly after such accidents. The enforcement agencies should call in reef scientists as soon as possible to evaluate and to offer advice to minimize resource damage in the salvaging efforts.

Each oil spill incident must be evaluated on its own merits. General guidelines are offered here, but local conditions may require taking alternative measures. When major damage occurs, the most expedient way to promote recovery is to let natural recruitment of reef biota recolonize the area. Remedial action should only be taken after it becomes evident that natural recruitment is not occurring or is very slow. Transplanting corals is a slow and costly activity. If it is done, it should be supervised by reef scientists. Hydraulic cement should be used to attach the organisms to the bottom. It will require permits to harvest stock to transplant.

In the case of vessel groundings, if the vessel is afloat or aground it should be removed from the reef as soon as possible in a manner that minimizes reef impact. Explosives should not be used. If the vessel is sunk in depths of less than 5 m, it should be salvaged. Sinkings in deeper water should be evaluated to see what sort of potential harm might occur. They might be left in place if they have no salvage value. In all vessel accidents, care should be taken to minimize fuel and cargo discharge.

Fishing-related problems are the responsibility of DNR in State waters and NMFS in the Federal zone. These agencies should take necessary action to minimize habitat destruction by sport or commercial fishing activities. Action is being taken in some fisheries at the present time. In some areas between Miami and Dry Tortugas it would be beneficial to prohibit the harvest of all fish and invertebrates. This would provide a refuge for those species under intense fishing pressure; in many cases they are harvested before they attain sexual maturity. These refuges would increase reproductive potential and return communities to a more natural state. Several existing marine parks should consider this possibility on an experimental basis for all or portions of their reef areas.

Coral reef communities found off southeast Florida are the northernmost distribution of shallow coral reefs within the tropical Atlantic biogeographical region (exception being Bermuda). Located this far north, they endure natural physical stresses not encountered in more southerly Caribbean areas. Human interferences, as noted, are not individually as harmful to the reef community as natural events (hurricanes); however, it is the chronic and synergistic effect of the human impact that causes problems. These coral reefs are a natural resource similar to California's redwood forests or the Grand Canyon, and they should be viewed as a national treasure worth conserving for future generations. Their fisheries resources are significant and yields could be increased with better management. The economics are very important to southeast Florida. Fishing, diving, boating, and tourism in general are dependent on the vitality of these coral reefs.

Table 3: Molluscan (Bivalve) Percent Abundance Data for SEI297-FB-1

Depth (cm)	Years (B.P.)	Age Model Year	*Arcopsis adamsi*	*Brachidontes exustus*	*Caradium*	*Chione cancellata*	*Chione granulata ?*	*Chione sp. FB1*	*Codakia orbicularis*	*Codakia orbiculata*	*Cumingia tellinoides*	*Cyrenoida floridana*	*Glycymeris pectinata ?*	*Gouldia sp.*	*Laevicardium sp.*	*Laevicardium spp.*	*Linaria sp. cf. L. pellucida*	*Lingula amiantus*
0-2	0.00	1997	0.00	0.00	0.00	0.75	0.00	3.76	0.00	5.26	0.75	0.00	3.76	0.00	0.75	0.00	1.50	0.00
4-6	2.69	1994	2.78	0.00	0.00	0.00	0.00	2.78	0.00	5.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8-10	9.24	1988	1.72	0.00	0.00	0.00	0.00	0.00	6.90	5.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.72
12-14	15.92	1981	0.00	0.00	0.00	4.00	0.00	0.00	12.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	4.00	0.00
16-18	22.72	1974	0.00	0.95	0.00	1.90	0.00	0.95	0.95	3.81	0.95	0.00	0.00	0.00	0.95	0.00	1.90	0.00
20-22	29.65	1967	0.00	0.54	0.00	0.00	0.00	0.54	2.17	3.26	1.09	0.00	0.00	0.00	0.00	0.00	0.54	0.00
24-26	36.71	1960	0.76	0.00	0.00	0.76	0.00	1.52	0.00	0.76	0.76	0.00	0.00	0.00	1.52	0.00	1.52	0.00
28-30	43.90	1953	0.00	0.99	0.00	2.97	0.00	0.99	0.99	0.99	0.99	0.99	0.99	0.00	0.00	0.00	0.00	0.00
32-34	51.22	1946	0.00	1.33	0.00	2.67	0.00	0.00	4.00	1.33	0.00	0.00	0.00	0.00	2.67	0.00	2.67	0.00
36-38	58.66	1938	0.00	1.85	0.00	0.00	0.00	2.78	0.00	3.70	1.85	0.00	0.00	0.00	0.00	0.00	0.93	0.00
40-42	66.23	1931	0.00	1.41	0.00	2.82	0.00	2.82	0.00	0.00	1.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00
44-46	73.93	1923	0.00	4.35	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
48-50	81.76	1915	0.00	0.00	0.00	2.53	0.00	1.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
52-54	89.72	1907	0.00	0.00	0.00	6.25	0.00	8.33	0.00	2.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
56-58	97.80	1899	0.00	0.00	0.00	5.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
60-62	106.01	1891	0.00	4.17	0.00	4.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
64-66	114.35	1883	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
68-70	122.82	1874	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
72-74	131.42	1866	1.69	1.12	0.00	0.56	0.56	4.49	0.56	2.25	0.56	0.00	0.56	0.00	0.56	0.00	0.56	0.00
76-78	140.14	1857	0.00	1.11	0.00	0.00	0.00	1.11	1.11	4.44	1.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00
80-82	148.99	1848	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
84-86	157.97	1839	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
88-90	167.08	1830	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
92-94	176.32	1821	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
96-98	185.68	1811	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
100-102	195.17	1802	0.00	0.00	0.00	0.00	0.00	2.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
104-106	204.79	1792	0.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00	1.77	0.00
108-110	214.54	1782	2.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
112-114	224.42	1773	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
116-118	234.42	1763	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
120-122	244.55	1752	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.96	0.00	0.00
124-126	254.81	1742	0.00	0.00	0.00	5.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
128-130	265.20	1732	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
132-134	275.72	1721	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
136-138	286.36	1711	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
140-142	297.13	1700	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
144-146	308.03	1689	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.25	0.00
148-150	319.06	1678	0.00	0.00	0.00	4.55	0.00	0.00	0.00	0.00	4.55	0.00	0.00	0.00	4.55	0.00	0.00	0.00
152-154	330.22	1667	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
156-158	341.50	1655	0.00	2.78	0.00	0.00	0.00	0.00	0.00	0.00	5.56	0.00	0.00	0.00	0.00	2.78	0.00	0.00
160-162	350.05	1647	0.00	2.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
164-166	364.45	1633	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.26	0.00	0.00	0.00
168-170	376.12	1621	0.00	0.00	0.00	0.00	0.00	4.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
172-174	387.92	1609	0.00	0.00	0.00	0.00	0.00	7.14	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
176-178	399.84	1597	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
180-182	411.89	1585	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
184-186	424.07	1573	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.03	0.00	0.00	0.00	0.00
188-190	436.38	1561	0.00	0.00	0.00	7.41	0.00	0.00	3.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
192-194	448.82	1548	0.00	0.00	2.50	0.00	0.00	0.00	0.00	2.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
196-198	461.38	1536	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.69	0.00	0.00	0.00	0.00
200-202	474.07	1523	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
204-206	486.89	1510	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.22	0.00	0.00	0.00	0.00
208-210	499.84	1497	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.00	0.00	0.00	0.00	0.00
212-214	512.92	1484	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.32	0.00	0.00	0.00	0.00
216-218	526.12	1471	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.00	0.00	0.00	0.00	0.00
220-222	539.45	1458	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00
224-226	552.91	1444	0.00	0.00	0.00	7.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

and displayed for public benefit.

Federal

Office of Coastal Zone Management, Marine Sanctuaries Program, NOAA. Specifically, this program manages and funds the program at KLNMS and LKNMS. On-site management and enforcement are delegated to DNR through special agreements. Funding for research and management is arranged through grants. A management plan for KLNMS was published in 1979; the management plan for LKNMS was published in 1984.

National Marine Fisheries Service (NMFS), NOAA. The enactment of the Fishery Management Act of 1976 (P. L. 94-265) provides for exclusive management of fisheries seaward of State jurisdiction. This includes both specific fishery stocks and habitat. The process for developing "fishery management plans" (FMP) is highly complex. It includes plan development by various procedures through a fisheries management council. NMFS implements approved plans. The Coast Guard, NMFS, and Florida Marine Patrol enforce reef related FMP's. Presently, FMP's for corals and coral reefs, reef fish, grouper and snapper, and spiny lobster are in the developmental stages or already in force.

National Park Service (NPS), Department of the Interior (DOI). National parks and monuments, including Biscayne National Park and Ft. Jefferson National Monument, are under the jurisdiction of NPS. Management, enforcement, and research are accomplished in-house. In some cases research projects are contracted out or made through interagency agreements.

Minerals Management Service (MMS), DOI. This agency has jurisdiction over mineral and petroleum resources on the continental shelf. Management has included specific lease regulations and mitigation of exploration and production activities in areas where coral resources are known to exist. Specifically, the agency helped to fund a coral reef mapping project from Miami to Key West.

Fish and Wildlife Service (FWS), DOI. FWS assists with environmental impact review, develops biological resource evaluations, and administers the endangered species program. In the Keys area the FWS manages several national refuges for wildlife. The Great White Heron and Key West Refuges include Sand Key Reef off Key West. Importing of exotic biota is monitored and controlled by FWS. The Lacey Act was amended in 1981 to include all coral. This should curtail all commercial imports.

Geological Survey (GS), DOI. In the coral reef areas GS has conducted considerable reef research and assisted or cooperated with other institutions and agencies to facilitate logistics and support of coral reef research. The mapping program was partially supported through GS funding.

Coast Guard (CG), Department of Transportation. The 1978 Waterways Safety Act charges the CG with marine environmental protection. The CG is the general enforcement agency for all marine activity in the Federal zone. Among the duties are enforcement of sanctuary and fishery management regulations, managing vessel salvage, coordinating oil spill cleanup operations at sea and search and rescue operations, interdicting illegal alien and drug traffic, and maintenance of navigational aids such as buoys and lighthouses.

U.S. Army Corps of Engineers (USACE). USACE contracts and regulates coastal engineering projects, particularly harbor dredging and beach renourishment projects. USACE also reviews and is the permitting agency for coastal development projects and artificial reefs.

Environmental Protection Agency (EPA). This agency has a general responsibility in the air and water pollution area. Disposal of hazardous wastes and sewage plant outfall permitting are EPA functions. Certain mineral and petroleum exploration and production activities are managed by EPA. Environmental research germane to waste disposal and pollution are funded by EPA.

8.3 MANAGEMENT AND MITIGATION RECOMMENDATIONS

This document has detailed the complexity of coral reef communities: their biota, their physical and chemical determinants, the multi-user nature of their resources, their significance as fishery and aesthetic-tourist resources to southeast Florida and the United States, and the conflicts and human impact problems that currently exist. The wisdom of Solomon would be put to the test to devise a management plan for these resources that would satisfy all the users and management and enforcement agencies. Decisions will have to be made that do not satisfy some users. The main criteria that should be used in judging any particular decision should be: (1) does it significantly impact the resource and/or (2) will it cause undue economic hardship on a large segment of the population. It is literally impossible not to cause some impact and some economic hardship. Overall, the goal should be prudent stewardship of the coral reef resources.

While we can do nothing to mitigate natural events, we should make every effort to minimize human insults. Major emphasis toward achieving this goal should include improved communication between the various responsible State and Federal agencies, improved enforcement, and a meaningful public information and education program. Since it is impossible to place enforcement officers on every reef, public education is the most efficient way to obtain cooperation, especially in terms of chronic boating and diving accidents. Signs, brochures, television, and user group workshops are ways to get the message across.

In terms of specific recommendations, the age-old adage that a gram of prevention is worth a kilogram of cure holds true in coral reef communities. It is far easier to prevent most human interference beforehand than to correct the damage after it occurs. This is particularly true in the case of major coastal engineering projects (e.g., dredging, pipeline excavation) in southeast Florida. Any proposed project should be required to

Table 3: Molluscan (Bivalve) Percent Abundance Data for SEI297-FB-1

Depth (cm)	Years (B.P.)	Age Model Year	*Lucina multilineata*	*Lucina muricata ?*	*Macoma ?*	*Mysella ? sp.*	*Mysella sp.*	*Nucula proxima*	*Parastarte triquetra*	Pectinid	*Pitar sp.*	*Pleuromeris tridenta*	*Polymesoda sp.*	*Pteria longisquamosa*	*Semele sp.*	*Tellina spp.*	*Transennella sp.*	Unidentified Pelecypods	*Dentalium sp.*	Total # gastropod specimens
0-2	0.00	1997	0.00	0.00	0.00	1.50	0.00	2.26	0.00	0.00	0.00	0.00	0.00	2.26	0.00	0.00	1.50	0.00	0.00	133
4-6	2.69	1994	0.00	0.00	0.00	0.00	0.00	2.78	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.78	0.00	36
8-10	9.24	1988	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.45	0.00	1.72	3.45	0.00	0.00	58
12-14	15.92	1981	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	25
16-18	22.72	1974	0.00	0.00	0.00	5.71	0.00	3.81	0.00	0.00	0.00	0.00	0.00	0.95	0.00	0.00	0.95	0.00	0.00	105
20-22	29.65	1967	0.00	0.00	0.54	0.54	0.00	0.54	0.00	0.00	2.72	0.00	0.00	1.09	0.00	0.00	0.00	0.00	0.00	184
24-26	36.71	1960	0.76	0.00	3.03	0.00	0.00	3.03	0.00	0.00	3.03	0.00	0.00	2.27	0.00	0.76	0.00	1.52	0.00	132
28-30	43.90	1953	0.00	0.00	3.96	0.00	0.99	3.96	0.00	0.00	0.00	0.00	1.98	1.98	0.00	2.97	0.00	0.99	0.00	101
32-34	51.22	1946	0.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00	5.33	1.33	0.00	1.33	0.00	0.00	75
36-38	58.66	1938	0.00	0.00	5.56	0.00	0.00	3.70	0.00	0.93	0.00	0.00	0.00	0.00	0.00	3.70	1.85	3.70	0.00	108
40-42	66.23	1931	0.00	0.00	0.00	0.00	0.00	1.41	0.00	0.00	0.00	0.00	0.00	1.41	0.00	2.82	2.82	7.04	0.00	71
44-46	73.93	1923	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	4.35	0.00	23
48-50	81.76	1915	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.27	0.00	2.53	8.86	0.00	79
52-54	89.72	1907	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.17	0.00	4.17	0.00	48
56-58	97.80	1899	11.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.76	0.00	0.00	0.00	0.00	0.00	0.00	5.88	0.00	17
60-62	106.01	1891	0.00	0.00	0.00	0.00	0.00	8.33	0.00	0.00	4.17	0.00	0.00	4.17	0.00	0.00	0.00	4.17	0.00	24
64-66	114.35	1883	14.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.57	0.00	7
68-70	122.82	1874	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7
72-74	131.42	1866	0.00	0.00	0.00	0.00	1.12	1.69	0.00	0.00	3.93	0.00	0.00	2.25	0.00	2.81	0.00	1.12	0.00	178
76-78	140.14	1857	0.00	0.00	0.00	0.00	1.11	0.00	0.00	0.00	2.22	0.00	0.00	1.11	0.00	0.00	0.00	0.00	0.00	90
80-82	148.99	1848	2.38	0.00	0.00	0.00	0.00	2.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.19	0.00	0.00	0.00	84
84-86	157.97	1839	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	19
88-90	167.08	1830	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.23	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	31
92-94	176.32	1821	0.00	0.00	3.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	29
96-98	185.68	1811	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	23
100-102	195.17	1802	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	76
104-106	204.79	1792	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	113
108-110	214.54	1782	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	38
112-114	224.42	1773	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5
116-118	234.42	1763	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10
120-122	244.55	1752	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.96	0.00	0.00	0.00	102
124-126	254.81	1742	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.26	0.00	19
128-130	265.20	1732	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.00	0.00	25
132-134	275.72	1721	0.00	0.00	0.00	0.00	0.00	0.00	2.44	0.00	0.00	2.44	0.00	0.00	0.00	4.88	0.00	0.00	0.00	41
136-138	286.36	1711	0.00	0.00	0.00	0.00	0.00	0.00	11.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9
140-142	297.13	1700	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.29	0.00	14
144-146	308.03	1689	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.25	0.00	16
148-150	319.06	1678	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.09	0.00	22
152-154	330.22	1667	0.00	0.00	0.00	0.00	2.86	2.86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.43	0.00	35
156-158	341.50	1655	0.00	0.00	0.00	0.00	1.39	1.39	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.17	0.00	72
160-162	350.05	1647	0.00	0.00	0.00	0.00	0.00	1.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.56	0.00	2.56	0.00	78
164-166	364.45	1633	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	47
168-170	376.12	1621	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22
172-174	387.92	1609	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28
176-178	399.84	1597	10.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.26	0.00	19
180-182	411.89	1585	0.00	0.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30
184-186	424.07	1573	0.00	0.00	0.00	0.00	0.00	9.09	0.00	0.00	3.03	0.00	0.00	0.00	0.00	0.00	0.00	9.09	0.00	33
188-190	436.38	1561	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.70	0.00	27
192-194	448.82	1548	0.00	2.50	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	2.50	0.00	0.00	0.00	0.00	7.50	0.00	40
196-198	461.38	1536	0.00	0.00	0.00	0.00	0.00	15.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.69	0.00	13
200-202	474.07	1523	9.09	0.00	0.00	0.00	0.00	0.00	0.00	18.18	9.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11
204-206	486.89	1510	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.11	0.00	0.00	0.00	0.00	0.00	0.00	11.11	0.00	9
208-210	499.84	1497	0.00	0.00	0.00	0.00	0.00	8.00	0.00	4.00	8.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	25
212-214	512.92	1484	2.44	2.44	0.00	0.00	2.44	0.00	0.00	2.44	2.44	0.00	0.00	2.44	0.00	0.00	0.00	4.88	2.44	41
216-218	526.12	1471	0.00	0.00	0.00	0.00	0.00	28.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	25
220-222	539.45	1458	0.00	0.00	0.00	0.00	0.00	20.00	0.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00	6.67	0.00	15
224-226	552.91	1444	7.69	0.00	0.00	0.00	7.69	7.69	0.00	0.00	0.00	0.00	0.00	7.69	0.00	0.00	0.00	7.69	0.00	13

management plan for the coral reefs and corals from North Carolina to Texas. The coral reef fishery management plan will be effective as of August 22, 1984. This would extend to all the coral species found within the Federal jurisdiction (the 200-mi zone). Proposed Federal regulations would parallel Florida statutes. There would be allowable bycatch in certain fishing activities. Some areas would receive special considerations as Habitat Areas of Particular Concern (HAPC). Limitations on fishing gear and anchoring are proposed to conserve habitat (Gulf of Mexico and South Atlantic Fishery Management Councils 1981).

8.2 CORAL REEF RESOURCE MANAGEMENT

Coral reef parks and other sanctuaries represent a unique management for subsea resources.

Parks, Sanctuaries, and Monuments

Biscayne National Park (BNP) (70,822 ha; Figure 1). Located off southeast Florida, including nonreef areas in Biscayne Bay. Reef areas are seaward of Elliott and the Ragged Keys to a 60-ft (18.3-m) depth. To the southwest this park adjoins John Pennekamp Coral Reef State Park and Key Largo National Marine Sanctuary. To the north the BNP adjoins Biscayne Bay. The park is administered by the U.S. National Park Service with headquarters at Convoy Point. All coral is protected. Rangers enforce regulations.

John Pennekamp Coral Reef State Park (JPCRSP) (21,741 ha; Figure 1). Located off north and central Key Largo. It includes the mangrove communities to the 3-nmi limit. It is administered by the Florida Department of Natural Resources (FDNR) with headquarters located on Key Largo. Park rangers and the Florida Marine Patrol enforce statutes that protect coral and other living resources.

Key Largo National Marine Sanctuary (KLNMS) (25,901 ha; Figure 1). Continues from the seaward boundary of John Pennekamp Coral Reef State Park to the 300-ft (91-m) isobath. It is administered, by special agreement with the National Oceanic and Atmospheric Administration (NOAA). On site inspection is by the Florida Department of Natural Resources (DNR). Enforcement is by park rangers, U.S. Coast Guard, and Florida Marine Patrol.

Looe Key National Marine Sanctuary (LKNMS) (11,144 ha; Figure 1 and Plate 2). Recently established; located seaward of Big Pine Key. Unlike the previously mentioned parks, it does not include any coastal seafloor in its boundaries but is a discrete area of reef. Administration is by NOAA, with the Florida DNR rangers and Marine Patrol enforcing regulatory statutes on-site.

Dry Tortugas, Ft. Jefferson National Monument (19,021 ha). Located in the Dry Tortugas, 60 mi west of Key West. It is administered by U.S. National Park Service with headquarters on Garden Key, Dry Tortugas. Park rangers enforce regulations.

The following summarizes the various county, State, and Federal regulations governing portions of the resource. Shinn (1979) detailed permitting regulations and agency responsibility for collecting biological and geological specimens. In the coral reef environments a patchwork of regulations and jurisdiction exists that is inefficient and often a duplication of effort. It is beyond the scope of this treatise to review and offer ways to correct this problem. The reader may use the following outline to determine jurisdiction and enforcement responsibilities. Damage mitigation and management recommendations will be presented in 8.3.

Monroe County

Monroe County prohibits use of spearguns for the harvesting of marine protein in and around bridges and piers and in State waters from the Dade County border to Long Key.

State of Florida

Department of Natural Resources (DNR). DNR is responsible for management of all marine fisheries and resources in State waters. In the area of consideration, this includes lobster, snook, snapper, grouper, other commercial and sport species, mangrove, seagrass, and coral reef communities. DNR has specific police powers through the Florida Marine Patrol to enforce State and some Federal statutes. In the area of specific regulations for reef management, the department enforces statute 370.110 (prohibition of harvest, damage, or sale of fire coral, sea fans, and the true stony corals), 370.114 (protection of all corals in John Pennekamp Coral Reef State Park), 370.08 (management of fish collecting chemicals), and 370.15 (fishery gear regulation). The Division of Recreation and Parks manages and operates State parks and Federal marine sanctuaries through agreements with NOAA. The Division of Marine Research conducts scientific research to support management in the areas of coral reef ecology and fisheries.

Department of Environmental Regulation (DER). Within State waters DER has management powers over environmental change caused by human activity. All major engineering projects must be reviewed prior to permitting. Both environmental monitoring and research are conducted. In the area of permitting, DER reviews permits for any human activity that affects the marine environment. Coastal dredging is managed through statute 370.03 and marine pollution under statute 370.09.

Department of Administration (DOA). Under special powers the DOA can enact "State Areas of Critical Concern" and decree special regulations for indefinite periods if growth or other activities overload the capacity of local government to adequately manage the resources.

Department of State (DOS). DOS manages salvage of historical artifacts in State waters. In the Keys area this includes numerous vessels sunk offshore. The activity is managed through the licensing of salvagers and monitoring of operations. Many historical artifacts are recovered for the State. These are archived in museums

Table 3: Molluscan (Gastropod) Percent Abundance Data for SEI297-FB-1

Depth (cm)	Years (B.P.)	Age Model Yea	*Acmaea leucopleura ?*	*Acmaea pustulata*	*Acteocina canaliculata*	*Alvania ? sp.*	*Amaea retifera*	*Anachis avara*	*Astraea phoebia*	*Bittiolum varium*	*Bulla striata*	*Caecum cornucopiae*	*Caecum pulchellum*	*Calliostoma sp.*	*Cerithidea spp.*	*Cerithiopsis greeni*
0-2	0.00	1997	0.75	0.00	0.00	0.00	0.00	0.00	1.50	2.26	0.00	0.75	1.50	0.00	0.00	0.00
4-6	2.69	1994	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.56	0.00	5.56	0.00	0.00	0.00	0.00
8-10	9.24	1988	0.00	1.72	0.00	0.00	3.45	0.00	1.72	1.72	0.00	1.72	0.00	0.00	0.00	0.00
12-14	15.92	1981	0.00	0.00	0.00	0.00	4.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00
16-18	22.72	1974	0.00	4.76	0.00	0.00	0.95	0.95	0.00	0.95	0.00	0.95	0.95	0.00	0.00	0.00
20-22	29.65	1967	0.54	1.63	0.00	0.54	0.00	0.54	1.09	9.78	0.00	0.54	0.00	0.00	0.00	0.00
24-26	36.71	1960	1.52	0.00	0.00	0.00	0.00	0.00	1.52	18.18	0.00	0.00	0.00	0.00	0.00	0.76
28-30	43.90	1953	1.98	0.00	0.00	0.00	0.00	1.98	0.00	10.89	0.00	6.93	0.00	0.00	0.00	0.00
32-34	51.22	1946	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.00	0.00	0.00	0.00	0.00	0.00	0.00
36-38	58.66	1938	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.37	0.00	0.00	0.00	0.00	0.00	1.85
40-42	66.23	1931	0.00	0.00	0.00	0.00	1.41	1.41	0.00	15.49	0.00	0.00	0.00	0.00	0.00	2.82
44-46	73.93	1923	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.39	0.00	0.00	0.00	0.00	0.00	4.35
48-50	81.76	1915	0.00	0.00	1.27	0.00	1.27	0.00	0.00	24.05	0.00	1.27	0.00	0.00	0.00	2.53
52-54	89.72	1907	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.58	0.00	0.00	0.00	0.00	0.00	0.00
56-58	97.80	1899	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.76	0.00	0.00	0.00	0.00	0.00	0.00
60-62	106.01	1891	0.00	0.00	0.00	0.00	0.00	0.00	0.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00
64-66	114.35	1883	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
68-70	122.82	1874	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.29	0.00	0.00	0.00	0.00	0.00	0.00
72-74	131.42	1866	0.56	0.00	0.00	0.00	0.00	1.69	0.00	7.30	0.00	0.56	0.00	0.00	0.00	1.12
76-78	140.14	1857	2.22	0.00	0.00	0.00	0.00	0.00	0.00	6.67	0.00	3.33	0.00	0.00	0.00	0.00
80-82	148.99	1848	0.00	0.00	0.00	0.00	0.00	0.00	0.00	52.38	0.00	1.19	0.00	0.00	0.00	0.00
84-86	157.97	1839	0.00	0.00	0.00	0.00	0.00	0.00	0.00	89.47	0.00	0.00	0.00	0.00	0.00	0.00
88-90	167.08	1830	0.00	0.00	0.00	0.00	0.00	0.00	0.00	48.39	0.00	0.00	0.00	0.00	0.00	0.00
92-94	176.32	1821	3.45	0.00	0.00	0.00	0.00	0.00	0.00	20.69	0.00	0.00	0.00	0.00	0.00	0.00
96-98	185.68	1811	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.70	0.00	4.35	0.00	0.00	0.00	13.04
100-102	195.17	1802	0.00	0.00	0.00	0.00	0.00	0.00	0.00	25.00	0.00	11.84	0.00	0.00	0.00	1.32
104-106	204.79	1792	0.00	0.00	0.00	0.00	0.00	0.00	0.00	23.89	0.00	10.62	0.00	0.00	0.00	6.19
108-110	214.54	1782	0.00	0.00	0.00	0.00	0.00	0.00	0.00	42.11	0.00	0.00	0.00	0.00	0.00	0.00
112-114	224.42	1773	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
116-118	234.42	1763	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00
120-122	244.55	1752	0.00	0.00	0.00	0.00	0.00	0.00	0.00	67.65	0.00	4.90	0.00	0.00	0.00	0.00
124-126	254.81	1742	0.00	0.00	0.00	0.00	0.00	0.00	0.00	52.63	0.00	0.00	0.00	0.00	0.00	0.00
128-130	265.20	1732	0.00	0.00	0.00	0.00	0.00	0.00	0.00	44.00	0.00	0.00	0.00	0.00	0.00	0.00
132-134	275.72	1721	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.07	0.00	0.00	0.00	0.00	4.88	0.00
136-138	286.36	1711	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.11	0.00	0.00	0.00	0.00	11.11	0.00
140-142	297.13	1700	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
144-146	308.03	1689	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.25	0.00	6.25	0.00	0.00	0.00	0.00
148-150	319.06	1678	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.73	0.00	9.09	4.55	0.00	0.00	0.00
152-154	330.22	1667	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.43	0.00	5.71	0.00	2.86	0.00	0.00
156-158	341.50	1655	0.00	0.00	0.00	0.00	0.00	0.00	0.00	27.78	0.00	0.00	0.00	0.00	0.00	2.78
160-162	350.05	1647	1.28	0.00	0.00	0.00	0.00	0.00	0.00	52.56	0.00	0.00	0.00	0.00	0.00	2.56
164-166	364.45	1633	0.00	0.00	0.00	0.00	0.00	0.00	0.00	57.45	0.00	0.00	0.00	0.00	0.00	0.00
168-170	376.12	1621	0.00	0.00	0.00	0.00	0.00	0.00	0.00	36.36	0.00	0.00	0.00	0.00	0.00	4.55
172-174	387.92	1609	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.29	0.00	7.14	0.00	0.00	0.00	3.57
176-178	399.84	1597	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.26	0.00	0.00	0.00	5.26	0.00	0.00
180-182	411.89	1585	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	0.00	0.00	0.00	0.00
184-186	424.07	1573	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.09	0.00	0.00	0.00	0.00	0.00	0.00
188-190	436.38	1561	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.41	0.00	3.70	0.00	0.00	0.00	7.41
192-194	448.82	1548	2.50	0.00	0.00	0.00	0.00	0.00	2.50	0.00	0.00	0.00	0.00	0.00	0.00	5.00
196-198	461.38	1536	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
200-202	474.07	1523	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.09
204-206	486.89	1510	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.11	0.00	0.00	0.00	0.00	0.00
208-210	499.84	1497	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
212-214	512.92	1484	7.32	0.00	0.00	0.00	0.00	0.00	0.00	2.44	0.00	2.44	0.00	0.00	0.00	0.00
216-218	526.12	1471	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
220-222	539.45	1458	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00	0.00	0.00	0.00
224-226	552.91	1444	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

period of years, disposed of spent batteries by throwing them into the sea; subsequently, acids are released into the area.

Southeastern Florida is a major truck farm area for vegetables and fruit. Use of agricultural chemicals (fertilizers, herbicides, pesticides, etc.) is intense. Porous soils, canal systems leading to the bays, and rapid runoff of surface materials following rains and irrigation are causes for concern. McCloskey and Chesher (1971) reported that organochloride compounds reduced productivity (photosynthesis:respiration ratios) in *Acropora cervicornis*. The methodology and concentrations of the study were not realistic compared to what is the normal concentration of such compounds in the reef environment. The effect of chronic low level concentrations over a long period has not been studied. Pollution research into chronic low level concentrations of hydrocarbon pollutants documents that reproduction is the most severely affected biological process (Loya and Rinkevich 1980).

Petroleum Hydrocarbons

The effect of petroleum hydrocarbons (PHC) on coral reefs is poorly understood. Reviews summarizing the information include Johannes (1975), Loya and Rinkevich (1980), Ray (1981), and Bright et al. (1981). Gunkel and Gassmann (1980) reviewed oil pollution in the marine environment.

A diversity of methods has been used to evaluate the effects of PHC on corals; many of the procedures used represent exposures or concentrations that are difficult to relate to field conditions. Some situations on a coral reef tend to magnify exposure, while others would lessen impact; laboratory tests often are unrealistic compared with the actual environment. Shallow reef flats, lagoons, and other reef environments with poor circulation expose organisms to higher concentrations than open ocean conditions, while spur and groove formations with high turbulence probably reduce exposure. Experiments have documented response of coral tissue to coating by PHC. Static and flow through bioassay tests are poor because of prolonged exposure, unrealistic concentrations, and unknown real concentration of PHC (detailed as oil added with unknown solubility). Quantitative field research has advanced knowledge on the ecological consequences of PHC in coral reef communities (Loya 1972, 1975, 1976b; Loya and Rinkevich 1980). Quantitative chemical data on uptake, as well as flux between organisms, water column, and sediments are presently the missing links in field studies.

Recent studies documented that detrimental effects of PHC on corals included feeding, reproduction, recruitment, and growth. The environmental parameters make each oil spill a unique ecological problem; temperature, wind, tide, etc., all contribute to overall consequences. Heavier grades of oil that float are less likely to cause negative impact. Jaap (1975, unpublished) and Chan (1976) reported on the 1975 oil spill in the Florida Keys. The spill was of an estimated magnitude of 20,000-50,000 gallons. Diving observations and histopathology revealed little or no damage to the reefs or corals. Lighter fraction PHC that has high solubility poses a greater threat.

Rinkevich and Loya (1977) reported damage to gonadal tissues and no coral recruitment in shallow reef areas off Eilat, Israel, that were chronically polluted by PHC. Other field observations reported that *Acropora* spp. possessed a greater affinity for oil than *Agaricia* (Lewis 1971). Oil mixed with sediments also caused morbidity in corals (Bak and Elgershuzen 1976). Oil dispersant in concentrations of 100-500 ppm was harmful to corals (Lewis 1971). Oil and its effect on reproduction is of prime concern. Recent studies by Rinkevich and Loya (1977) show a strong relationship between reduced coral fecundity and PHC exposure. Lewis (1971) reported reduced feeding responses in corals exposed to PHC.

Corals respond or protect themselves from foreign materials by secretion of mucus, ciliary water currents, and pulsation. Growth and calcification studies indicate various responses to PHC exposure. Neff (1981) tested several species and found both increased and decreased calcification rates.

At this point the evidence indicates that chronic PHC pollution is harmful to coral reef communities. The stenotopic nature of many reef dwelling organisms, and the fact that many are sessile, leads to the conclusion that while most of the research in coral reefs on PHC pollution has dealt with corals, chronic or massive concentrations of PHC would also harm the other organisms. Population dynamics (reproduction, development, larval recruitment, settlement, and juvenile growth) appears to be the biological process most affected by PHC pollution.

Potential oil pollution sources include tanker cleaning and cargo discharge, vessel sinkings and accidents, and accidental discharges from petroleum production and transportation activities. The Minerals Management Service (MMS) (Department of the Interior) controls leasing and operational aspects of offshore oil exploration and development in federal waters.

Although there are numerous reports of other acts that have damaged coral reefs in other areas of the world, they are not germane to Florida at this time; hence, the reader is referred to Johannes (1975) and Bright et al. (1981) for documentation.

Coral Collection

Collection, damage, or sale of stony corals (*Millepora* spp. and Scleractinia) and two species of sea fan (*Gorgonia ventalina* and *G. flabellum*) in Florida waters is prohibited by Florida statute 370.110. Florida waters extend to 3 nmi on the Atlantic and approximately 10.3 nmi on the gulf coast. Corals and other biota within specially designated parks, marine monuments, and sanctuaries are protected by special Federal and State regulations. The area under Federal regulation is currently without protection. However, at the time of this writing the Gulf of Mexico and South Atlantic Fishery Management Councils are developing a fishery

Table 3: Molluscan (Gastropod) Percent Abundance Data for SEI297-FB-1

Depth (cm)	Years (B.P.)	Age Model Yea	*Cerithium muscarum*	*Cerithium* sp.	*Cerithium* spp.	*Cerodrillia* sp.	*Columbella* sp.	Conidae juvenile	*Crassispira leucocyma*	*Crassispira* sp.	*Crepidula* spp.	*Cyclostremiscus* sp.	*Diodora* sp.	*Epitonium* sp.	Eulimidae	*Eulithidium* sp.	*Fasciolaria* sp.	*Finella* sp.	*Latirus ?*	*Lithopoma americanum*
0-2	0.00	1997	2.26	0.00	0.00	0.00	0.75	0.00	0.00	0.00	2.26	0.75	0.00	0.00	0.00	18.05	0.75	0.00	0.00	0.00
4-6	2.69	1994	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30.56	0.00	0.00	0.00	0.00
8-10	9.24	1988	0.00	0.00	6.90	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.45	0.00	10.34	0.00	0.00	0.00	0.00
12-14	15.92	1981	0.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	8.00	0.00	0.00	0.00	0.00
16-18	22.72	1974	1.90	0.00	1.90	0.00	0.00	0.00	1.90	0.00	0.00	0.00	0.00	0.00	2.86	7.62	0.00	0.00	0.00	0.00
20-22	29.65	1967	0.00	0.00	7.61	0.00	0.00	0.00	1.63	0.00	0.54	0.54	0.00	0.00	2.72	9.24	0.00	0.00	0.00	0.54
24-26	36.71	1960	7.58	0.00	0.00	0.00	0.76	0.00	0.76	0.00	2.27	0.00	0.00	0.00	0.00	12.12	0.00	0.00	0.00	0.00
28-30	43.90	1953	0.00	0.00	9.90	0.99	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.99	5.94	0.00	0.00	0.00	0.00
32-34	51.22	1946	1.33	0.00	1.33	0.00	0.00	0.00	2.67	0.00	2.67	0.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00
36-38	58.66	1938	1.85	0.00	3.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.48	0.00	0.00	0.00	0.00
40-42	66.23	1931	1.41	9.86	0.00	0.00	0.00	0.00	0.00	0.00	2.82	0.00	0.00	0.00	0.00	4.23	0.00	0.00	0.00	0.00
44-46	73.93	1923	0.00	0.00	0.00	0.00	0.00	0.00	8.70	0.00	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00
48-50	81.76	1915	1.27	0.00	6.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.86	0.00	0.00	0.00	0.00
52-54	89.72	1907	4.17	0.00	2.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.08	2.08	0.00	0.00	0.00	0.00
56-58	97.80	1899	23.53	5.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
60-62	106.01	1891	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.33	0.00	0.00	0.00	0.00
64-66	114.35	1883	0.00	0.00	14.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
68-70	122.82	1874	0.00	0.00	14.29	0.00	0.00	0.00	14.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
72-74	131.42	1866	2.81	0.00	0.56	1.69	0.00	0.56	0.00	0.00	0.56	0.00	0.00	0.00	0.00	10.11	0.00	0.00	0.00	0.00
76-78	140.14	1857	0.00	0.00	0.00	0.00	0.00	0.00	1.11	0.00	2.22	0.00	0.00	0.00	0.00	8.89	2.22	0.00	1.11	0.00
80-82	148.99	1848	0.00	0.00	0.00	0.00	0.00	0.00	1.19	0.00	0.00	0.00	0.00	0.00	0.00	4.76	0.00	0.00	1.19	0.00
84-86	157.97	1839	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
88-90	167.08	1830	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	19.35	0.00	0.00	0.00	0.00
92-94	176.32	1821	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.69	0.00	0.00	0.00	0.00
96-98	185.68	1811	0.00	0.00	0.00	0.00	0.00	0.00	4.35	0.00	4.35	0.00	0.00	0.00	0.00	17.39	0.00	0.00	0.00	0.00
100-102	195.17	1802	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.32	1.32	0.00	0.00	0.00	1.32	7.89	0.00	1.32	0.00	0.00
104-106	204.79	1792	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	0.88	0.00	0.00	12.39	0.00	0.00	0.00	0.00
108-110	214.54	1782	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.63	0.00	0.00	0.00	0.00
112-114	224.42	1773	0.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
116-118	234.42	1763	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	20.00	0.00	0.00	0.00	0.00
120-122	244.55	1752	0.00	0.00	0.00	0.00	0.00	0.00	1.96	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
124-126	254.81	1742	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.26	0.00	0.00	0.00	0.00
128-130	265.20	1732	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
132-134	275.72	1721	2.44	0.00	0.00	0.00	0.00	0.00	0.00	2.44	0.00	0.00	0.00	0.00	0.00	14.63	0.00	0.00	0.00	0.00
136-138	286.36	1711	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
140-142	297.13	1700	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
144-146	308.03	1689	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.50	0.00	0.00	0.00	0.00
148-150	319.06	1678	4.55	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
152-154	330.22	1667	0.00	0.00	2.86	0.00	0.00	2.86	0.00	5.71	0.00	0.00	0.00	0.00	0.00	2.86	0.00	0.00	2.86	0.00
156-158	341.50	1655	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.78	0.00	0.00	0.00	0.00	0.00	20.83	0.00	0.00	1.39	0.00
160-162	350.05	1647	5.13	0.00	0.00	0.00	0.00	0.00	0.00	1.28	0.00	0.00	0.00	0.00	0.00	3.85	0.00	0.00	0.00	0.00
164-166	364.45	1633	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.51	0.00	0.00	0.00	0.00
168-170	376.12	1621	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.55	0.00	0.00	0.00	0.00	18.18	0.00	0.00	0.00	0.00
172-174	387.92	1609	3.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.71	0.00	0.00	0.00	0.00
176-178	399.84	1597	0.00	0.00	5.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.79	0.00	0.00	0.00	0.00
180-182	411.89	1585	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	16.67	0.00	0.00	0.00	0.00
184-186	424.07	1573	3.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.06	0.00	0.00	0.00	0.00
188-190	436.38	1561	0.00	0.00	7.41	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.70	0.00	0.00	0.00	0.00
192-194	448.82	1548	0.00	0.00	2.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.50	12.50	0.00	0.00	0.00	0.00
196-198	461.38	1536	0.00	0.00	7.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.69	0.00	0.00	0.00	7.69
200-202	474.07	1523	0.00	0.00	9.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.09	0.00	0.00	0.00	0.00
204-206	486.89	1510	11.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
208-210	499.84	1497	4.00	0.00	8.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00	4.00	0.00
212-214	512.92	1484	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.76	0.00	0.00	0.00	0.00
216-218	526.12	1471	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00
220-222	539.45	1458	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.67
224-226	552.91	1444	0.00	0.00	7.69	0.00	0.00	0.00	0.00	7.69	0.00	0.00	0.00	0.00	0.00	15.38	0.00	0.00	0.00	0.00

by physical impact during setting and recovery. National Marine Fisheries Service laboratory studies show that some reef fish species can enter and escape from fish traps at will.

Spearfishing is the major means divers employ to harvest finfish. Spearpoints damage coral if they are fired into the reef. Some divers use a "bangstick" (explosive head on the end of a spear or a stick) to harvest large fish or for confidence. When exploded on the surface of a stony coral, it creates a concave crater about 0.5 ft in diameter and of equal depth. It is illegal to use spearguns in several of the marine parks, and within much of Monroe County.

Diving Activities

Diving as a sport and hobby has increased and developed into a major industry in the Keys area. As reported earlier, it is a major economic contributor in some parts of Monroe County. With the numbers of persons involved, it is not surprising that negative impacts occur. Unskilled divers grab coral for stabilization. The dive guides try to enforce and instill an axiom of don't touch or collect anything. The efforts are for the most part successful; however, there are so many people to monitor that it is difficult to police everyone. Those persons who visit the reefs in private boats are not governed by similar restraint. A small number of coral collection violations occur within the parks and sanctuaries. Enforcement is spread very thinly; hence many persons probably do collect coral as a souvenir.

Marine collecting as a hobby includes both live and dead material for aquariums. Some individuals harvest mollusk shells and other curio items for collections. For the most part, these specimens are dead; however, some live material is taken. Collection pressure is quite heavy on colorful and distinctive species such as helmet shells (*Cassis* spp.), thorny oyster (*Spondylus* spp.), and the flamingo tongue (*Cyphoma gibbosum*). Queen conch (*Strombus gigas*) is harvested for food and for its shell.

Live marine specimen collecting has developed as a minor industry and popular hobby in southeast Florida. The collection of attractive fish and invertebrates is focused in the coral reef areas primarily between Palm Beach and Key West. Brightly colored fish, crustaceans, mollusks, and other species are collected and sold to pet shops and aquarium stores.

Specimens are collected by divers using various techniques and transported in tanks aboard their boats. Professional collectors use nets, traps, and in some cases narcotizing chemicals to collect target species. Damage is inevitable; in the quest to harvest illusive fish and invertebrates, certain amounts of physical damage are bound to occur. Frequency and magnitude of damage are correlated with the experience and conservation ethic of the collector. Part-time amateur and hobby collectors with limited experience and time pose a greater threat than a professional collector with several years of experience.

Chemical collecting agents threaten corals if used indiscriminately or in strong concentration (Plate 25b). The most frequently employed chemical is Quinaldine (Jaap and Wheaton 1975). The State of Florida requires a permit for its use. When used in a restrained manner, it poses a minimal threat to corals. In strong concentration it may cause zooxanthellae expulsion and stun cryptic microfauna which are rapidly consumed by certain fish (e.g., the bluehead wrasse) that are immune to the chemical. The use of Quinaldine is minimal; hence, it does not pose a great threat. Other chemicals cited as major threats to coral reef communities include a great list of materials (Johannes 1975). The use of commercial laundry bleach (sodium hypochlorite) is a potential threat. It has been cited as a fish and invertebrate collecting chemical, but it also does severe damage (mortality) to sessile benthic invertebrates (Johannes 1975).

Pollution

General reviews of the effects of pollution on coral reefs are Johannes (1975) and Endean (1976). Weiss and Goddard (1977) reviewed a case history of coastal pollution and its effect on coral reefs off the coast of Venezuela. Bright et al. (1981) added additional references on the subject. Loftas (1970), McCloskey and Chesher (1971) and Smith et al. (1973) documented the effects of pollution on coral reefs. Many of the previous studies were either unrealistic field and laboratory experiments or from Kaneeohe Bay, Hawaii. Certainly there is cause for concern in Florida coastal waters as the population continues to grow and municipal sanitary sewage systems use ocean outfalls as an expedient means of disposal of sewage effluent. Kaneeohe Bay, Hawaii, is a classic case of what can go wrong when untreated sewage and siltation from poor land management impact a semi-closed ecosystem. Eutrophication and siltation of the sea bottom extirpated a large number of the reefs (Smith et al. 1973). Florida coral reefs represent an open ecosystem where eutrophication is less likely to occur.

Much of urban Monroe County uses septic tank sewage disposal; therefore, input into the marine environment is likely. Bright et al. (1981) reported that the porous limestone strata in the Florida Keys did not retain the sewage effluent for sufficient time to allow for decompositon. The aforementioned article also reported on the massive amount of liquid wastes pumped into the ocean by southeast Florida coastal communities. As growth in coastal southeast Florida continues, potential for pollution impact on coral reef communities also increases. Dilution in the ocean is not the solution for sewage disposal.

Manker (1975) reported on heavy metal accumulations in the sediments and corals off southeast Florida; he noted higher concentrations of mercury, zinc, lead, and cobalt adjacent to population centers.

Disposal of wastes from existing lighthouse navigational aids may be a minor problem, yet is clearly a cause for concern. Plate 30b shows batteries and other refuse disposed of on the reef flat at Carysfort lighthouse. Coast Guard maintenance crews have, over a

Table 3: Molluscan (Gastropod) Percent Abundance Data for SEI297-FB-1

Depth (cm)	Years (B.P.)	Age Model Yea	Marginellid	*Marshallora nigrocincta*	*Mitra nodulosa*	*Modiolus ? sp.*	*Modulus modulus*	Muricidae sp. B	*Muricopsis ?*	*Nassarius albus*	*Nassarius sp.*	*Natica ? sp.*	*Nitidella sp.*	*Odostomia spp.*	*Olivella pusilla*	Opercula - calc folded/hooked	Opercula - calc other	Opercula - calc pearly	Opercula - chitonous	*Pusia hanleyi ?*
0-2	0.00	1997	2.26	0.00	0.00	0.00	4.51	0.00	0.00	0.75	0.00	0.00	0.75	0.75	0.00	6.02	0.00	0.75	0.00	0.00
4-6	2.69	1994	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.78	0.00	5.56	0.00	5.56	0.00	0.00
8-10	9.24	1988	0.00	0.00	0.00	0.00	3.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.90	0.00	0.00	0.00
12-14	15.92	1981	0.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00
16-18	22.72	1974	0.95	0.00	0.00	0.00	1.90	0.00	0.95	1.90	0.00	0.00	0.95	3.81	1.90	0.00	3.81	0.00	0.00	0.00
20-22	29.65	1967	1.09	0.00	0.54	0.00	4.35	0.00	0.00	0.00	0.00	0.00	3.26	1.63	0.00	0.00	4.35	0.00	0.00	1.09
24-26	36.71	1960	3.03	0.00	0.00	0.00	3.03	0.76	0.76	0.00	0.00	0.00	2.27	3.79	0.00	0.00	0.00	0.76	0.00	0.00
28-30	43.90	1953	0.00	0.00	0.00	0.00	2.97	0.00	0.00	0.00	0.00	0.00	1.98	0.00	0.00	0.00	1.98	1.98	0.00	0.00
32-34	51.22	1946	4.00	1.33	0.00	0.00	2.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.33	1.33	0.00	0.00
36-38	58.66	1938	4.63	0.00	0.00	0.00	2.78	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.93	0.00	0.00
40-42	66.23	1931	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.82	1.41	0.00	0.00	2.82	1.41	0.00	0.00
44-46	73.93	1923	4.35	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.70	0.00	0.00
48-50	81.76	1915	2.53	0.00	0.00	0.00	7.59	1.27	0.00	0.00	0.00	0.00	1.27	0.00	1.27	0.00	0.00	0.00	0.00	0.00
52-54	89.72	1907	4.17	0.00	0.00	0.00	4.17	0.00	0.00	0.00	0.00	0.00	4.17	8.33	0.00	0.00	0.00	2.08	0.00	2.08
56-58	97.80	1899	0.00	0.00	0.00	0.00	5.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
60-62	106.01	1891	0.00	0.00	0.00	0.00	8.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.17	0.00	0.00
64-66	114.35	1883	0.00	0.00	0.00	0.00	14.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
68-70	122.82	1874	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.57	0.00	0.00
72-74	131.42	1866	1.69	0.00	0.00	0.00	2.81	0.56	0.00	0.00	0.00	0.00	0.00	1.12	0.00	0.00	0.00	3.37	0.00	0.00
76-78	140.14	1857	0.00	0.00	0.00	0.00	3.33	0.00	0.00	0.00	1.11	0.00	1.11	2.22	0.00	1.11	0.00	10.00	0.00	0.00
80-82	148.99	1848	0.00	1.19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.19	1.19	0.00	2.38	0.00	5.95	0.00	0.00
84-86	157.97	1839	0.00	0.00	0.00	0.00	5.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
88-90	167.08	1830	0.00	0.00	0.00	0.00	6.45	0.00	0.00	0.00	0.00	0.00	0.00	6.45	0.00	0.00	3.23	0.00	0.00	0.00
92-94	176.32	1821	0.00	0.00	3.45	0.00	6.90	0.00	0.00	0.00	0.00	0.00	0.00	3.45	0.00	0.00	6.90	13.79	0.00	0.00
96-98	185.68	1811	0.00	0.00	0.00	0.00	4.35	0.00	0.00	0.00	0.00	0.00	0.00	4.35	0.00	0.00	4.35	0.00	0.00	0.00
100-102	195.17	1802	0.00	0.00	1.32	0.00	2.63	0.00	0.00	0.00	1.32	0.00	1.32	1.32	0.00	2.63	0.00	2.63	0.00	0.00
104-106	204.79	1792	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	0.00	5.31	0.00	5.31	0.00	0.00
108-110	214.54	1782	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.26	0.00	7.89	0.00	0.00
112-114	224.42	1773	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
116-118	234.42	1763	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	0.00	10.00	0.00
120-122	244.55	1752	0.00	0.98	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	0.00	1.96	0.00	0.98	0.00	6.86	0.98	0.00
124-126	254.81	1742	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.26	0.00	10.53	0.00	0.00
128-130	265.20	1732	0.00	0.00	0.00	0.00	16.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00
132-134	275.72	1721	0.00	9.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.32	0.00	0.00
136-138	286.36	1711	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.22	0.00	0.00
140-142	297.13	1700	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.29	0.00	14.29	0.00	0.00
144-146	308.03	1689	0.00	0.00	0.00	0.00	6.25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	18.75	0.00	0.00
148-150	319.06	1678	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.55	0.00	4.55	0.00	0.00
152-154	330.22	1667	0.00	0.00	0.00	0.00	8.57	0.00	0.00	0.00	0.00	0.00	0.00	2.86	0.00	5.71	0.00	8.57	0.00	0.00
156-158	341.50	1655	0.00	1.39	1.39	0.00	2.78	0.00	0.00	0.00	0.00	0.00	0.00	5.56	0.00	1.39	0.00	1.39	0.00	1.39
160-162	350.05	1647	0.00	0.00	0.00	0.00	3.85	0.00	0.00	0.00	0.00	0.00	0.00	5.13	0.00	1.28	0.00	1.28	0.00	0.00
164-166	364.45	1633	0.00	0.00	0.00	0.00	2.13	0.00	0.00	0.00	0.00	0.00	0.00	2.13	0.00	2.13	0.00	6.38	0.00	0.00
168-170	376.12	1621	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.09	0.00	0.00	0.00	0.00
172-174	387.92	1609	0.00	0.00	0.00	0.00	3.57	0.00	0.00	0.00	0.00	0.00	0.00	3.57	0.00	3.57	0.00	7.14	0.00	0.00
176-178	399.84	1597	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.26	0.00	0.00	0.00	0.00	0.00	10.53	0.00	0.00
180-182	411.89	1585	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	10.00	0.00	26.67	0.00	0.00
184-186	424.07	1573	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.06	0.00	6.06	0.00	0.00
188-190	436.38	1561	0.00	0.00	0.00	0.00	7.41	0.00	0.00	0.00	0.00	0.00	0.00	11.11	0.00	3.70	0.00	3.70	0.00	0.00
192-194	448.82	1548	0.00	0.00	0.00	0.00	2.50	0.00	0.00	0.00	0.00	0.00	0.00	2.50	2.50	5.00	0.00	0.00	0.00	0.00
196-198	461.38	1536	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	23.08	0.00	0.00
200-202	474.07	1523	0.00	0.00	0.00	0.00	9.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
204-206	486.89	1510	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
208-210	499.84	1497	0.00	0.00	0.00	0.00	12.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	4.00	0.00	0.00
212-214	512.92	1484	0.00	0.00	0.00	0.00	7.32	0.00	0.00	0.00	0.00	0.00	0.00	4.88	0.00	2.44	0.00	4.88	0.00	0.00
216-218	526.12	1471	0.00	0.00	0.00	0.00	8.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	0.00	4.00	0.00	0.00	0.00
220-222	539.45	1458	0.00	0.00	0.00	6.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	6.67	0.00	0.00	0.00	0.00	0.00	0.00
224-226	552.91	1444	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.38	0.00	0.00	0.00	0.00	0.00	7.69

The threat of a major shipwreck is quite real. Much of the ship traffic into and out of the Gulf of Mexico is concentrated just seaward of the reef tract. Traffic into the gulf is between the coral reefs and the Gulf Stream; outbound vessels travel inside the Gulf Stream to take advantage of the current. Large tankers or freighters grounded on a reef because of mechanical difficulties or navigational errors would cause greater damage than small vessels. The 400-ft vessel *MV Wellwood* grounded on Molasses Reef on 5 August 1984, causing severe damage to the reef.

The collisions of large vessels is like a bulldozer blade leveling the top of the reef. Other negative effects of shipwrecks and groundings include fuel leakage and cargo and other materials lost or thrown overboard. An example of a vessel grounding incident was the wreck of the 110-ft motor vessel *Lola* on Looe Key Reef on 5 January 1976 (Plates 26b and 27a). The vessel was loaded with construction steel when it began taking on water. The captain ran the ship aground to avoid sinking. The vessel ended up on a spur and remained aground on the reef for 18 days. Approximately 344 m^2 of reef were impacted. The crew remained aboard ship while the vessel was aground and disposed of garbage, sewage, damaged steel cargo, and other junk including batteries and tools onto the reef. Several weeks after grounding, the ship was lightened by the removal of cargo onto a barge and towed to Key West for repairs. The *Lola* was foreign owned, and no legal action was taken.

Salvage operations pose a threat when they occur around a coral reef. Techniques used to free grounded or sunken vessels are often counter to reef conservation. Explosives, large anchors, and ground tackle pose a threat to the reef. In 1976 the *Robby Dale* carrying contraband drugs was wrecked at Looe Key Reef. A salvager used explosives to remove the ship from the reef, despite warnings by the Bureau of Land Management that unwarranted reef damage would result in legal prosecution under the Outer Continental Shelf Lands Act. The salvage firm of Alexander was brought to court and found guilty on two accounts. However, the Fifth Circuit Court of Appeals ruled that the Outer Continental Shelf Lands Act could only be invoked in cases where mineral or petroleum exploration or production activities were threatening coral reefs.

In cases where tugboats are used to tow the grounded vessel off the reef, care should be exercised to keep towing cables off the bottom. During the *Wellwood* salvage, towing cables caused a great deal of damage to the reef (corals were turned over, broken, and abraded by the towing cables). This could have been avoided. More stringent regulations should be enforced when salvage operations are close to coral reef habitats. Coast Guard cooperation and reef scientists' advice would aid in moderating the severity of negative impacts.

Numerous other incidents could be cited. The results have a general pattern that includes initial damage; sinking or salvaging of vessel; and development of successional communities in the disturbed area. If the structural integrity of the reef platform is not adversely affected, the community will recover; after 5-10 years or more the impact will be unnoticeable (Pearson 1981).

Fishing

Coral reefs concentrate marine protein in a localized area, attracting both commercial and sport fishing interests that use various techniques to harvest fish and invertebrate stocks. Negative impacts occur as a result of gear deployment and harvesting.

Lobster fishing is the largest commercial fishery located in and adjacent to the coral reef habitat area. This fishery was worth over $10 million in 1980 (Table 1). The commercial fishery uses traps or pots to harvest the spiny lobster *Panulirus argus*. Traps are set in waters inshore and offshore of the reefs, and on occasion close to the reefs. Damage occurs when the traps are set on corals, as well as during recovery. Trap recovery takes place while the boat is underway; the hydraulic puller retrieves the trap while the boat motors to the next trap. The trap is pulled along the bottom for a short distance before it clears the bottom. When the lobster trap is on coral, the sliding trap breaks and damages coral and other sessile benthos. Large numbers of traps are lost when buoy lines are cut by boat propellers. Lost lobster traps decompose in time, but cement bottoms do not rapidly degrade. To eliminate this negative impact, fishermen should be required to keep their traps out of the reef environment proper.

Sport divers who harvest lobster damage the reef through their efforts to dislodge lobsters from ledges and caves. The author has seen moderately large (1.5-m diameter) brain coral heads (*D. strigosa*) dislodged and turned over by enthusiastic lobster divers. Smaller fragile corals and other benthic organisms are damaged in the process of lobster hunting. The lobster divers often become so engrossed in their quest to obtain lobster that they break off coral that is in their way to get at the lobster.

Hook-and-line fishing methods are employed by commercial and sportfishermen in the coral reef habitat. There is considerable loss of line, leaders, hooks, sinkers, lures, and other paraphernalia on the reefs. When diving on any reef, it is common to find line, hooks, etc., caught in the coral. The hooks and line impact when the hook is dragged across the coral face, causing lesions or scars. Monofilament line wraps around corals and other organisms, often causing abnormal growth. Net fishing is not common around coral reef habitats; however the author found a net entangled in the coral at Eastern Sambo reef in 1973. Shrimp vessels anchoring at Pulaski Shoal near Dry Tortugas have made a habit of disposing junk on the reef. The area resembles a garbage dump, with all manner of fishing-related gear on the bottom.

Fish traps are a controversial issue with polarized constituents expounding their viewpoint. Traps are not selective, but catch all manner of biota, much of which is not consumed because of cultural biases or lack of a market. The trap is made of steel mesh and is marked with a buoy. If the buoy is lost, the trap continues to harvest fish, many of which die in the trap (Plate 29b). The fish trap, like the lobster trap, can damage the coral

Table 3: Molluscan (Gastropod) Percent Abundance Data for SEI297-FB-1

Depth (cm)	Years (B.P.)	Age Model Yea	*Pyramidella crenulata*	*Pyramidella* sp.	*Rissoina cancellata*	*Rissoina decussata*	*Schwartziella catesbyana*	*Tegula fasciata*	*Triptychus niveus*	*Trivia* sp.	*Truncatella* sp.	*Turbo castaneus*	*Turbonilla* sp.	Turridae sp. A	Unidentified Gastropods	*Vermicularia spirata*	*Vexillum* sp.	Vitrinellid	*Zebina browniana*
0-2	0.00	1997	0.75	0.00	0.75	0.75	6.77	0.75	0.00	0.00	0.00	2.26	0.00	0.75	11.28	2.26	0.00	0.00	2.26
4-6	2.69	1994	0.00	0.00	0.00	0.00	11.11	5.56	0.00	0.00	0.00	0.00	0.00	0.00	2.78	5.56	0.00	0.00	2.78
8-10	9.24	1988	0.00	0.00	0.00	0.00	13.79	12.07	1.72	0.00	0.00	0.00	0.00	0.00	0.00	3.45	0.00	0.00	3.45
12-14	15.92	1981	0.00	0.00	0.00	0.00	4.00	16.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00
16-18	22.72	1974	0.95	0.00	0.95	0.00	9.52	7.62	1.90	0.00	0.00	2.86	0.00	0.00	0.00	9.52	0.95	0.00	0.00
20-22	29.65	1967	0.00	0.00	2.17	0.00	8.70	2.17	3.26	0.54	0.00	2.17	0.00	0.00	4.35	8.70	0.00	0.00	0.54
24-26	36.71	1960	0.00	0.00	2.27	0.00	5.30	1.52	3.03	0.00	0.76	0.00	0.00	0.00	0.00	4.55	0.00	0.00	0.76
28-30	43.90	1953	0.99	0.00	1.98	0.00	2.97	5.94	1.98	0.00	0.00	2.97	0.00	0.00	0.00	4.95	0.00	0.00	1.98
32-34	51.22	1946	0.00	0.00	8.00	0.00	2.67	1.33	0.00	0.00	0.00	2.67	0.00	1.33	0.00	5.33	0.00	0.00	1.33
36-38	58.66	1938	0.00	0.00	0.93	0.00	10.19	3.70	0.00	0.00	0.00	0.93	0.00	0.00	0.93	8.33	0.00	0.00	1.85
40-42	66.23	1931	1.41	0.00	5.63	0.00	2.82	1.41	1.41	0.00	0.00	5.63	0.00	0.00	4.23	5.63	0.00	0.00	0.00
44-46	73.93	1923	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.39	0.00	0.00	4.35	4.35	0.00	0.00	0.00
48-50	81.76	1915	0.00	0.00	3.80	0.00	3.80	0.00	0.00	0.00	0.00	3.80	0.00	2.53	7.59	1.27	0.00	0.00	0.00
52-54	89.72	1907	0.00	0.00	6.25	0.00	4.17	2.08	0.00	0.00	0.00	6.25	2.08	2.08	0.00	2.08	0.00	0.00	0.00
56-58	97.80	1899	0.00	0.00	0.00	0.00	11.76	5.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
60-62	106.01	1891	0.00	0.00	0.00	0.00	12.50	4.17	0.00	0.00	0.00	8.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00
64-66	114.35	1883	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	28.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00
68-70	122.82	1874	0.00	0.00	0.00	0.00	0.00	28.57	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
72-74	131.42	1866	0.00	0.56	2.25	0.00	4.49	12.92	1.12	0.00	0.00	3.37	0.00	0.00	0.56	8.99	0.00	0.00	2.25
76-78	140.14	1857	0.00	0.00	5.56	0.00	8.89	8.89	0.00	0.00	0.00	14.44	0.00	0.00	0.00	1.11	1.11	0.00	0.00
80-82	148.99	1848	0.00	0.00	8.33	0.00	8.33	0.00	0.00	0.00	0.00	4.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00
84-86	157.97	1839	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.26	0.00	0.00	0.00	0.00	0.00	0.00	0.00
88-90	167.08	1830	0.00	0.00	6.45	0.00	0.00	0.00	0.00	0.00	0.00	6.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00
92-94	176.32	1821	0.00	0.00	13.79	0.00	0.00	0.00	0.00	0.00	0.00	3.45	0.00	0.00	0.00	0.00	0.00	0.00	0.00
96-98	185.68	1811	0.00	0.00	13.04	0.00	8.70	0.00	4.35	0.00	0.00	8.70	0.00	0.00	0.00	0.00	0.00	0.00	0.00
100-102	195.17	1802	0.00	0.00	14.47	0.00	5.26	0.00	0.00	0.00	0.00	11.84	0.00	0.00	0.00	1.32	0.00	0.00	0.00
104-106	204.79	1792	0.00	0.00	6.19	0.00	3.54	0.00	0.00	0.00	0.00	14.16	0.00	0.00	0.88	0.88	0.00	0.00	3.54
108-110	214.54	1782	0.00	0.00	13.16	0.00	0.00	0.00	0.00	0.00	0.00	26.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00
112-114	224.42	1773	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	60.00	0.00	0.00	0.00	20.00	0.00	0.00	0.00
116-118	234.42	1763	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
120-122	244.55	1752	0.00	0.00	0.98	0.00	1.96	0.00	0.00	0.00	0.00	2.94	0.98	0.00	1.96	0.00	0.00	0.00	0.00
124-126	254.81	1742	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00
128-130	265.20	1732	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.00	0.00	0.00	0.00	4.00	0.00	0.00	0.00
132-134	275.72	1721	0.00	0.00	0.00	0.00	2.44	0.00	0.00	0.00	0.00	24.39	0.00	0.00	0.00	2.44	0.00	0.00	2.44
136-138	286.36	1711	0.00	0.00	0.00	0.00	0.00	22.22	0.00	0.00	0.00	22.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00
140-142	297.13	1700	0.00	0.00	0.00	0.00	0.00	28.57	0.00	0.00	0.00	14.29	0.00	0.00	0.00	14.29	0.00	0.00	0.00
144-146	308.03	1689	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	31.25	0.00	0.00	0.00	6.25	0.00	0.00	0.00
148-150	319.06	1678	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	27.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00
152-154	330.22	1667	0.00	0.00	2.86	0.00	0.00	0.00	0.00	0.00	0.00	14.29	0.00	0.00	2.86	0.00	0.00	0.00	0.00
156-158	341.50	1655	0.00	0.00	1.39	0.00	0.00	1.39	0.00	0.00	0.00	6.94	0.00	1.39	0.00	0.00	0.00	0.00	0.00
160-162	350.05	1647	0.00	0.00	0.00	0.00	1.28	5.13	0.00	0.00	0.00	3.85	0.00	1.28	0.00	1.28	0.00	0.00	0.00
164-166	364.45	1633	0.00	0.00	0.00	0.00	2.13	0.00	0.00	0.00	0.00	14.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00
168-170	376.12	1621	0.00	0.00	4.55	0.00	0.00	9.09	0.00	0.00	0.00	4.55	0.00	0.00	4.55	0.00	0.00	0.00	0.00
172-174	387.92	1609	0.00	0.00	7.14	0.00	0.00	7.14	0.00	0.00	0.00	14.29	0.00	0.00	3.57	3.57	0.00	0.00	0.00
176-178	399.84	1597	0.00	0.00	0.00	0.00	0.00	10.53	0.00	0.00	0.00	15.79	0.00	0.00	0.00	10.53	0.00	0.00	0.00
180-182	411.89	1585	0.00	0.00	0.00	0.00	0.00	13.33	0.00	0.00	0.00	13.33	0.00	0.00	0.00	3.33	0.00	0.00	0.00
184-186	424.07	1573	0.00	0.00	3.03	0.00	0.00	6.06	0.00	0.00	0.00	15.15	0.00	0.00	6.06	15.15	0.00	0.00	0.00
188-190	436.38	1561	0.00	0.00	3.70	0.00	3.70	7.41	0.00	0.00	0.00	3.70	0.00	0.00	0.00	11.11	0.00	0.00	0.00
192-194	448.82	1548	0.00	0.00	0.00	0.00	0.00	2.50	0.00	0.00	0.00	15.00	0.00	0.00	5.00	10.00	0.00	0.00	5.00
196-198	461.38	1536	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.38	0.00	0.00	7.69	0.00	0.00	0.00	0.00
200-202	474.07	1523	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	27.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00
204-206	486.89	1510	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	22.22	0.00	0.00	11.11	0.00	0.00	0.00	0.00
208-210	499.84	1497	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	20.00	0.00	0.00	0.00	8.00	0.00	0.00	0.00
212-214	512.92	1484	0.00	0.00	0.00	0.00	2.44	9.76	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.07	0.00	0.00	0.00
216-218	526.12	1471	0.00	0.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	12.00	4.00	0.00	0.00	0.00
220-222	539.45	1458	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.33	0.00	0.00	0.00	0.00	0.00	6.67	0.00
224-226	552.91	1444	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Another activity affecting reefs that is somewhat similar to dredging is salvaging of ancient shipwrecks for treasure and artifacts. If the activity is near a coral reef, turbidity may increase. Many of these salvage operations employ the "mailbox" technique. A tubular elbow-shaped device surrounding a propeller forces the thrust downward to remove overburden from the shipwreck. Air lifts used to vacuum up material from the bottom for shipboard inspection also increase turbidity. A sufficient buffer zone should be established to protect any reef from the impacts of this activity. Restraints similar to dredging recommendations should be enforced.

Anchor Damage

Anchor damage was a significant negative human impact on coral reefs at Dry Tortugas (Davis 1977a). Carelessly deployed anchors break fragile corals, dislodge reef framework, and scar corals, opening lesions for infection (Plate 27b). Increased visits increase the number of anchorings and the potential for impact. Anchor ground tackle, lines, and chains also are documented as destructive agents (Davis 1977a). Anchor buoys were established at Biscayne National Park in 1977 as a means of mitigating this negative impact on four reefs. During the summer of 1981 anchor buoys were established at French Reef, JPCRSP-KLNMS, as a test (Plate 28b; also see Plate 28a). Anchor buoys, designated anchorages, and better public education are the best way to mitigate this problem. Halas (in preparation) documents the techniques for installing anchorless mooring buoys in the JPCRSP-KLNMS.

Groundings and Shipwrecks

Since the time of the Spanish and English explorations along the Florida coast, shipwrecks and groundings on reefs have been common. As reported in Chapter 1, luring ships onto a reef was a major economic enterprise during the 19th century, a practice that ended with the building of lighthouses. In the recent past small boat shipwrecks and groundings have increased. Table 31 summarizes recent reef shipwrecks. Pleasure and commercial craft of $<$ 100-ft ($<$ 30-m) length have run aground or sunk on many reefs. These occurrences are the result of poor navigational skills, accidents, drug-related incidents, and in some cases, purposeful grounding to avoid sinking. Whatever the reason, the vessels cause physical damage to the reef. In some cases the negative impact is very severe; corals and other organisms are dislodged from the reef platform.

The greatest potential for groundings and shipwrecks is on the reef flat and in barely submerged patch reefs. It would be impossible to buoy all the reefs that are potentially threatened. While conducting research in Biscayne National Park (BNP) during 1979, the author witnessed the grounding of a motor yacht *High Life* on Elkhorn Reef. The vessel captain was confused by the anchor buoy and ran hard aground on the reef flat. The vessel's path was strewn with broken fragments of elkhorn and staghorn coral (Plate 29a). Toxic antifouling paint was driven into several heads of *Siderastrea siderea*. Another patch reef in BNP suffered when a boat struck a large buttress of *Montastraea annularis*, splitting and toppling the coral. Toxic antifouling paint was again driven into the corallites.

Table 31

Recent reef shipwrecks.

Vessel	Size (ft)	Date	Location	Impact
Ice Fog and barge	70	1973	Molasses Reef	Tug sank in deep water; barge grounded on reef; both salvaged.
Capt. Allen (Plate 26a)	60	1973-1974	Middle Sambo	Abandoned on reef flat.
Lola (Plate 26b and 27a)	110	1976	Looe Key	Aground on a spur for 18 days.
Robby Dale	60-75	1977	Looe Key	Aground; spilled fuel.
Morania		1979	Fort Lauderdale	Damaged 5,600 m^2 of live bottom.
2 shrimp boats		November 1982	Looe Key Reef	Extensive damage to a spur.
Wellwood	397	August 1984	Molasses Reef	18.6 acres impacted.

Table 4: Foraminifer Percent Abundance Data for SEI297-FB-1

Depth (cm)	Years (B.P.)	Age Model Year	*Ammonia parkinsoniana tepida*	*Ammonia parkinsoniana typica*	*Archaias angulatus*	*Articulina mucronata*	*Bolivina lowmani*	*Bolivina pseudoplicata*	*Buccella hannai*	*Cibicides sp.*	*Clavulina tricarinata*	*Cycloggra involvens*	*Elphidium advenum*	*Elphidium delicatulum*	*Elphidium discoidale*	*Elphidium excavatum*	*Elphidium mexicanum*	*Elphidium sp.*	*Florilus auriculus*	*Fursenkoina sp.*	*Hanzawaia concentrica*
0-2	0.00	1997	0.00	0.00	32.69	6.47	0.00	0.00	0.00	0.00	0.65	0.00	0.00	3.56	0.00	0.00	0.00	0.00	0.00	0.00	0.00
4-6	2.69	1994	0.00	0.00	4.88	5.49	0.00	0.00	0.00	0.00	0.30	0.00	0.00	13.72	2.13	0.00	0.00	0.30	0.00	0.00	0.00
8-10	9.24	1988	0.00	0.00	1.95	4.55	0.00	0.00	0.00	0.00	1.30	0.00	0.00	1.95	0.00	0.00	0.00	0.00	1.62	0.00	0.00
12-14	15.92	1981	0.00	0.00	4.93	9.28	0.00	0.00	0.00	0.00	2.32	0.00	0.29	3.19	0.00	0.00	0.00	0.87	2.03	0.00	0.00
16-18	22.72	1974	0.00	0.00	10.26	4.97	0.00	0.00	0.00	0.00	1.66	0.00	0.00	3.97	0.66	0.00	0.00	0.00	0.00	0.00	0.00
20-22	29.65	1967	0.00	0.00	10.14	3.77	0.00	0.00	0.00	0.00	0.87	0.00	0.00	3.48	0.29	0.00	0.00	0.29	0.87	0.00	0.00
24-26	36.71	1960	0.00	0.00	9.01	4.94	0.00	0.00	0.00	0.00	1.74	0.00	0.00	5.81	0.87	0.00	0.00	0.00	1.45	0.00	0.00
28-30	43.90	1953	0.00	0.00	1.44	2.87	0.00	0.00	0.00	0.00	0.29	0.00	0.86	18.68	0.29	0.00	0.00	0.00	1.44	0.00	0.00
32-34	51.22	1946	0.00	0.00	1.34	2.10	0.00	0.00	0.00	0.00	0.57	0.00	0.38	10.88	0.00	0.00	0.00	0.00	0.00	0.00	0.00
36-38	58.66	1938	0.00	0.00	5.29	1.39	0.00	0.00	0.00	0.00	2.51	0.00	0.84	14.48	0.28	0.00	0.00	0.00	0.84	0.00	0.00
40-42	66.23	1931	0.00	0.00	10.03	2.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	29.77	0.00	0.00	0.00	0.32	0.97	0.00	0.00
44-46	73.93	1923	0.00	0.28	10.36	1.12	0.00	0.00	0.00	0.00	1.12	0.00	1.40	15.69	0.56	0.00	0.00	0.00	1.96	0.00	0.00
48-50	81.76	1915	0.29	0.00	16.86	3.43	0.00	0.00	0.00	0.00	3.71	0.00	1.14	4.57	0.29	0.00	0.00	0.86	0.86	0.00	0.00
52-54	89.72	1907	0.00	0.00	16.71	4.38	0.00	0.00	0.00	0.00	3.29	0.00	0.00	0.00	0.27	0.00	0.00	0.00	0.00	0.00	0.00
56-58	97.80	1899	0.00	0.00	19.05	3.17	0.00	0.00	0.00	0.00	2.91	0.00	0.26	3.70	0.26	0.00	0.00	0.00	0.26	0.00	0.00
60-62	106.01	1891	0.00	0.00	2.65	0.33	0.00	0.00	0.00	0.00	0.33	0.00	1.66	42.38	0.00	0.00	0.00	0.00	0.00	0.00	0.00
64-66	114.35	1883	0.00	0.00	0.64	3.53	0.00	0.00	0.00	0.00	0.00	0.00	0.96	35.58	1.92	0.00	0.00	0.00	2.56	0.00	0.00
68-70	122.82	1874	0.00	0.00	0.00	3.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	37.96	0.00	0.00	0.00	0.00	0.31	0.00	0.00
72-74	131.42	1866	0.00	0.00	7.37	4.81	0.00	0.00	0.00	0.00	0.32	0.00	1.28	25.64	1.60	0.00	0.00	0.00	0.96	0.00	0.00
76-78	140.14	1857	0.00	0.00	5.16	10.60	0.00	0.00	0.00	0.00	0.57	0.00	0.29	11.17	1.15	0.00	0.00	0.00	0.00	0.00	0.00
80-82	148.99	1848	0.00	0.00	0.33	13.29	0.00	0.00	0.00	0.00	0.00	0.00	1.00	22.92	1.00	0.00	0.00	0.00	0.00	0.00	0.00
84-86	157.97	1839	0.00	0.00	0.28	13.30	0.00	0.00	0.00	0.00	0.00	0.00	0.00	8.03	0.00	0.00	0.00	0.00	1.39	0.00	0.00
88-90	167.08	1830	0.00	0.32	1.28	5.13	0.00	0.00	0.00	0.00	1.28	0.00	0.00	5.45	0.64	0.00	0.00	0.00	1.28	0.00	0.00
92-94	176.32	1821	0.00	0.00	0.00	15.05	0.00	0.00	0.00	0.00	1.00	0.00	0.67	11.04	1.34	0.00	0.00	0.00	4.68	0.00	0.33
96-98	185.68	1811	0.00	0.00	1.85	6.17	0.00	0.00	0.00	0.00	0.62	0.00	0.93	13.27	0.00	0.00	0.00	0.00	1.85	0.00	0.00
100-102	195.17	1802	0.00	0.00	0.70	8.36	0.00	0.00	0.00	0.00	2.44	0.00	0.70	5.23	0.00	0.00	0.00	0.00	2.09	0.00	0.00
104-106	204.79	1792	0.00	0.00	0.68	7.88	0.00	0.00	0.00	0.00	1.03	0.00	1.03	21.58	0.00	0.00	0.00	0.00	0.68	0.00	0.00
108-110	214.54	1782	0.00	0.00	0.00	7.34	0.00	0.00	0.00	0.00	0.00	0.00	1.40	24.13	2.80	0.00	0.00	0.00	0.70	0.00	0.00
112-114	224.42	1773	0.00	0.00	0.00	5.39	0.00	0.00	0.00	0.00	0.00	0.00	2.40	38.92	0.60	0.00	0.00	0.00	5.39	0.00	0.00

CHAPTER 8

MANAGEMENT

8.1 HUMAN IMPACTS

Coral reefs off southeast Florida are multi-user resources, experiencing increased exploitation that results in some negative human impact on the resource. Although natural events are far more severe than man's individual acts, human impact on the reefs must be multiplied by the number and the frequency of occurrence, which in total may not allow the reef resources sufficient time for recovery. Some negative impact is focused on spatially small areas and is chronic. In recent years a number of publications dealing with coral reef pollution, stress, and death have documented or portrayed these subjects in some detail. Loftas (1970), McCloskey and Chesher (1971), Smith et al. (1973), Johannes (1975), Endean (1976), and Weiss and Goddard (1977) detailed pollution and human impact on coral reef communities. Voss (1973) and Dustan (1977b) reviewed problems in Florida reefs. Currently a number of controls are in force to mitigate human impact. In some cases controls have worked; in others, the negative impact has continued, and increased damage has occurred. Mitigation is difficult because activities are continuous and human impact on coral reefs is controversial. User groups are often polarized, frequently making the possibility of compromise or acceptance of alternative viewpoints difficult.

Dredging and Treasure Salvage

In terms of severity, dredging is the most damaging human activity in and around coral reefs. Poorly planned and managed dredging operations have caused the demise of many reefs. The physical impact of dredge gear (anchors, cables, chains, pipes, suction and cutting heads) dislodge corals or cause lesions or scars that lead to infection and mortality. Reef organisms increase respiration to remove silt resulting in reduced dissolved oxygen levels. Coupled with increased respiration is reduced photosynthesis and oxygen production due to lowered light levels. High turbidity generated by dredging reduces light penetration through the water column (Johannes 1975). Sediments excavated by dredging are often anaerobic and bind up available dissolved oxygen. Silt created by dredging remains in the local area for long periods and is resuspended during storms. Johannes (1975), Levin (1970), Endean (1976), and Bright et al. (1981) reviewed dredging impacts on coral reefs. A coral's ability to remove sediments was reported by Hubbard and Pocock (1972) and Hubbard (1973). Bak (1978) reported on lethal and sublethal effects of dredging on reef corals in Curacao, Netherlands West Indies. Corals that were poor sediment removers expelled zooxanthellae and died. Two species had extremely reduced calcification rates (Bak 1978).

Two types of dredging occur off southeast Florida; most of this activity is located from Miami northward. One kind results in spoil from deepening and maintenance dredging of navigational channels; it is disposed of on land and at sea. When disposed at sea there is potential for reef burial and increased turbidity. Occasionally, dredging operations will cut through living reefs. Sewage outfall pipe burial has also cut through reefs (Shinn et al. 1977). The other form of dredging off the southeast coast is done for beach renourishment. Sedimentary deposits are mined and brought ashore by pipes or barges and deposited on the beach. The material is a slurry; the silty runoff leaches back to sea causing increased sediment loading of the water column. During the fall of 1981, a beach renourishment project on South Miami Beach threatened a small linear hardground community composed of significant numbers of octocorals and stony corals. Dade County Pollution Control, Dade County Marine Institute, U.S. Geological Survey, and Florida DNR personnel transplanted about 200 stony coral colonies that were threatened by burial.

A critical part of all dredging activities should be a coherent field study to insure that reef communities are not endangered by dredging. Occasionally tradeoffs must be made, but should be minimized. Straughan (1972) condemned dredging for the demise of Florida Keys reefs. Courtney et al. (1974) documented reef burial and water quality problems at a beach renourishment dredging project off Hallendale; poor planning resulted in reef burial. Griffin (1974) studied a dredge operation on coastal Key Largo, and reported localized water quality problems. Aller and Dodge (1974), Dodge et al. (1974), and Dodge and Vaisnys (1977) reported that coral growth was retarded by dredge-created sediments. Loya (1976b) reported that Puerto Rican coral reefs impacted naturally by heavy sedimentation had lower species diversity than protected reefs.

Griffin (1974) and Courtney et al. (1974) recommended that all dredge operations in the vicinity of coral reef communities be closely monitored to insure that the community's vitality was not adversely affected. Specifically, Griffin proposed the following guidelines. A buffer zone of at least 0.5 nmi should separate the coral reef community from dredge operations. The magnitude of the buffer zone should be determined by local hydrographic conditions (wave and current patterns). Water column turbidity and sedimentation rates should be closely monitored. The water column sediment load deposition rate should not exceed 200 mg/cm^2/day, averaged over a 7-day period; if fall out exceeds this rate, a pause in dredging should be imposed to allow the benthic community to adjust. Because coral transplanting is a time consuming, labor intensive activity, it should not be considered a routine technique for restoration or mitigation. Natural stocks must be used; hence it becomes a matter of removing corals from an existing reef to restore a damaged reef. Survival of transplants may or may not be successful. Insufficient research has been accomplished to rationally judge this.

Table 4: Foraminifer Percent Abundance Data for SEI297-FB-1

Depth (cm)	Years (B.P.)	Age Model Year	*Ammonia parkinsoniana tepida*	*Ammonia parkinsoniana typica*	*Archaias angulatus*	*Articulina mucronata*	*Bolivina lowmani*	*Bolivina pseudoplicata*	*Buccella hannaii*	*Cibicides sp.*	*Clavulina tricarinata*	*Cyclogyra involvens*	*Elphidium advenum*	*Elphidium delicatulum*	*Elphidium discoidale*	*Elphidium excavatum*	*Elphidium mexicanum*	*Elphidium sp.*	*Florilus auriculus*	*Fursenkoina sp.*	*Hanzawaia concentrica*
116-118	234.42	1763	0.00	0.00	0.00	0.00	0.80	0.00	0.00	0.00	0.00	0.00	0.00	54.18	0.40	0.00	0.00	0.00	4.78	1.20	0.00
120-122	244.55	1752	0.00	0.00	0.31	0.00	0.93	0.00	3.43	0.00	0.00	0.31	0.00	38.01	0.00	0.00	0.00	0.00	1.25	0.31	0.00
124-126	254.81	1742	0.00	0.00	0.33	1.99	2.99	1.00	3.32	0.00	0.00	0.00	0.00	39.53	0.33	0.00	0.33	0.00	0.00	1.66	0.00
128-130	265.20	1732	0.00	0.00	0.61	3.34	0.61	0.00	5.78	0.00	0.00	0.00	1.22	20.36	0.61	0.00	0.30	0.00	0.61	0.00	0.00
132-134	275.72	1721	0.00	2.57	5.15	5.51	0.00	0.00	0.00	0.00	0.74	0.00	0.00	31.62	0.00	0.00	1.47	0.00	0.37	0.00	0.00
136-138	286.36	1711	0.00	9.20	4.60	0.00	0.00	0.00	0.00	0.00	0.00	0.00	9.20	31.03	10.92	0.00	4.02	0.00	1.72	0.00	0.00
140-142	297.13	1700	0.00	4.88	3.66	0.00	0.00	0.00	0.00	0.00	2.44	0.00	4.27	40.24	6.10	0.00	0.61	0.00	5.49	0.00	0.00
144-146	308.03	1689	0.00	0.32	0.63	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.63	54.29	0.63	0.00	0.63	0.00	5.71	0.00	0.00
148-150	319.06	1678	0.00	0.00	0.35	8.36	0.00	0.00	0.00	0.00	0.00	0.00	0.35	21.25	0.00	0.00	0.35	0.00	2.79	0.00	0.00
152-154	330.22	1667	0.00	0.00	0.00	0.63	0.00	0.00	0.00	0.00	0.00	0.00	0.00	33.02	0.00	0.00	0.31	0.00	4.40	0.00	0.31
156-158	341.50	1655	0.00	0.00	1.21	1.21	0.00	0.00	0.00	0.00	0.00	0.00	0.00	18.13	0.30	0.00	0.00	0.00	2.72	0.00	0.00
160-162	350.05	1647	0.00	0.00	0.31	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30.72	0.00	0.00	0.31	0.00	3.45	0.00	0.00
164-166	364.45	1633	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.32	54.28	0.99	0.00	0.00	0.00	0.99	0.00	0.00
168-170	376.12	1621	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.65	51.46	0.65	0.00	0.00	0.00	4.53	0.00	0.00
172-174	387.92	1609	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	62.46	1.66	0.00	0.00	0.00	7.97	0.00	0.00
176-178	399.84	1597	0.00	0.00	0.00	0.00	15.73	3.15	0.00	0.00	0.00	0.00	0.00	66.43	2.10	0.00	0.00	0.00	4.55	0.00	0.70
180-182	411.89	1585	0.00	0.00	0.31	0.00	16.51	1.22	0.00	0.31	0.00	0.00	1.22	63.30	0.61	0.00	0.61	0.00	4.28	0.31	0.00
184-186	424.07	1573	0.00	0.85	0.57	0.00	4.53	0.85	0.00	0.00	0.00	0.00	1.98	63.17	4.25	0.00	0.28	0.00	3.97	0.85	0.00
188-190	436.38	1561	0.00	0.30	1.81	0.30	0.00	0.90	0.00	0.00	0.00	0.00	1.51	26.20	7.23	0.00	0.30	0.00	0.90	0.00	0.00
192-194	448.82	1548	0.00	2.57	2.57	0.00	1.93	0.96	0.00	0.00	0.00	0.00	9.97	36.33	15.43	0.00	0.00	0.00	0.00	0.00	0.00
196-198	461.38	1536	0.00	0.00	1.46	0.00	4.09	0.88	0.00	0.00	0.00	0.00	4.97	56.73	6.14	0.00	0.58	0.00	2.92	0.58	0.00
200-202	474.07	1523	0.00	0.00	0.00	0.00	3.18	1.27	0.00	0.00	0.00	0.00	4.14	62.42	6.05	2.55	0.00	0.00	1.91	0.96	0.00
204-206	486.89	1510	0.00	0.30	0.30	0.00	2.11	0.60	0.00	0.00	0.00	0.00	4.22	71.99	8.13	0.00	0.90	0.00	3.01	0.00	0.00
208-210	499.84	1497	0.00	0.29	2.62	0.00	0.58	0.29	0.00	0.29	0.29	0.00	4.65	44.77	18.31	0.00	0.00	0.00	0.87	0.00	0.00
212-214	512.92	1484	0.00	1.72	0.57	0.00	0.00	0.00	0.00	0.00	0.57	0.00	4.58	45.27	15.19	0.00	0.00	0.00	2.29	0.29	0.00
216-218	526.12	1471	0.00	0.56	1.94	0.56	0.00	0.00	0.00	0.00	0.28	0.00	8.06	24.72	19.44	0.00	0.00	0.00	1.67	0.00	0.00
220-222	539.45	1458	0.00	0.00	0.96	0.32	0.32	0.32	0.00	0.00	0.96	0.00	0.00	37.90	17.20	0.00	0.00	0.00	0.00	0.32	0.00
224-226	552.91	1444	0.00	0.90	1.36	3.17	0.00	0.00	0.00	0.00	1.36	0.00	0.00	13.12	6.79	0.00	0.00	0.00	0.90	0.00	0.00

years after the passing of Betsy. Ball et al. (1967) and Perkins and Enos (1968) also discussed the effect Hurricanes Donna and Betsy had on the reefs from a geological standpoint. Jindrich (1972) postulated that hurricanes were one of the controls on reef development at Dry Tortugas.

The nature of hurricane impact has several interesting aspects. First, the hurricane causes considerable physical alteration of habitat. Sessile biota are often dislodged and transported considerable distances from their original growth positions. Fish are dislocated some distance from the resident reefs (Springer and McErlean 1962a). Smaller cryptic organisms are often left homeless, the resident coral or sponge being fragmented or possibly destroyed. When the mobile organism is an obligate commensal (having specialized niche requirements), it is quite likely that it will be difficult for it to locate alternative housing. Following the initial impact, turbidity may remain high for a week or more before water column transparency returns to normal conditions. After several more weeks, those corals that did survive will either exhibit growth over the scars and lesions and reattach to the bottom or they will die. Several recent reports described in detail the process of healing and secondary mortality. Highsmith et al. (1980), Woodley et al. (1981), and Rodgers et al. (1982) reported on the effects of several Caribbean hurricanes. *Acropora cervicornis* and *A. palmata* displayed impressive recovery in Belize and the U.S. Virgin Islands (Highsmith et al. 1980; Rodgers et al. 1982); however, these same species displayed considerable secondary mortality in Jamaica (Woodley et al. 1981). In Florida rapid recovery was reported following Hurricanes Donna and Betsy (Shinn 1975). The differences relate to the magnitude of impact; those reefs exposed to major hurricanes that pass close to the reef will suffer severe impact, while hurricanes that are of lesser magnitude or a greater distance from the reef are a lesser threat. Pearson (1981) reviewed coral reef recovery; he reported that following severe impact, it requires several decades for recovery. Pearson also reported that larval recruitment was much more significant than fragment propagation in the reef recovery process. This finding reflects recovery of Pacific reefs following the plaguelike predation by *Acanthaster planci* (crown-of-thorns starfish) more than recovery from natural physical impacts. It appears that following major storm damage *Acropora palmata* and *A. cervicornis* may benefit from fragment propagation. In Discovery Bay, Jamaica, however, the few fragments of *A. cervicornis* alive 5 months after the storm still suffered heavy mortality from surviving coral predators (Knowlton et al. 1981). Plate 10b shows fragments of an *A. palmata* colony that has been overturned and is now sprouting new branches. Highsmith (1982) reviewed propagation recruitment.

The other major natural impact on coral reefs is thermal stress. This can occur on either end of the spectrum; both heat and cold stress are reported to cause negative impact. Jaap (1979) reported on a zooxanthellae expulsion (Plate 24b) at Middle Sambo Reef (off Boca Chica Key) related to elevated water temperature that was created by synergistic meteorological and tidal conditions. The overall impact was not significant in that recovery took approximately 6 weeks. Vaughan (1911), Mayer (1918), Porter et al. (1982), and Hudson (in press) reported thermal stress damaged or killed reef biota at Dry Tortugas.

Heat-related stress usually occurs in late summer during solar noon to mid-afternoon. It is usually low tide, and the sea state is calm. Under these conditions, shallow reefs heat rather rapidly. Ambient temperatures are already 30°-31° C. Since the upper lethal temperature for *Acropora palmata* is 35.8° C (Mayer 1914), it does not take a great deal of heating to create stressful temperature levels. Shinn (1966) reported that transplanted *A. cervicornis* expelled zooxanthellae at or near 33.8° C. In contrast to cold stress, most heat stress is localized and is not a transported water mass phenomenon.

Cold stress was discussed in Chapter 2 under seawater temperature. The basic geographic configuration lends itself to the creation of cold water masses in shallow embayments, especially Florida Bay during the passage of winter cold fronts. The shallow bay allows the water mass maximum surface exposure to the polar air mass. After cooling, the water is moved to the Atlantic by tidal pumping, density gradients, and winds. The water mass moves through the passes and across the shelf and into the reef communities. Reef development requires no prolonged exposure to 18° C; however, individual species can tolerate significantly lower temperature (Mayer 1914, 1918). Most reef corals are severely stressed at or near 14° C. Shinn (1975), Hudson et al. (1976), and Roberts et al. (1982) reported that cold water masses originating in Florida Bay caused coral mortality to patch reefs adjacent to the passes. Most major offshore reefs do not suffer due to mixing of the cold water with resident water masses and the moderating effect of the Florida Current. Dry Tortugas has suffered significant mortality of staghorn coral populations as reported earlier due to cold stress.

Red tide (toxic phytoplankton blooms) are not common off the east coast, but entrained water masses occasionally carry a red tide into the Atlantic.

Natural events are a major factor controlling coral reef development, community structure, and species diversity. Connell (1978) reported that high diversity in tropical rain forests and coral reefs was related to intermediate frequency and magnitude of interference by natural events. Without negative impact by these agents, dominant organisms outcompete other organisms for resources, and species diversity is reduced. The hurricane or other natural agent opens new spatial habitat to pioneering organisms that can successfully exploit new territories. In a benign environment, one or a few species can potentially dominate, thus reducing diversity and the overall ability of the community to respond to outside stress.

Table 4: Foraminifer Percent Abundance Data for SEI297-FB-1

Depth (cm)	Years (B.P.)	Age Model Year	*Haynesina germanica*	*Miliammina circularis*	*Miliammina labiosa*	*Nodobacularia sp.*	*Peneroplis proteus*	*Pyrgo sp.*	*Quinqueloculina agglutinata*	*Quinqueloculina bosciana*	*Quinqueloculina poeyana*	*Quinqueloculina polygona*	*Quinqueloculina seminula*	*Quinqueloculina tenagos*	*Rosalina floridana*	*Rosalina globularis*	*Sorites sp.*	*Spiroloculina antillarum*	*Spirosigmoilina*	*Triloculina rotunda*	*Triloculina striatula*	*Triloculina tricarinata*	*Triloculina variolata*	*Valvulina oviedoina*
0-2	0.00	1997	0.00	0.65	4.53	0.00	0.97	3.24	11.00	0.32	2.91	0.00	0.00	17.48	3.24	0.32	0.32	0.00	0.00	0.00	0.00	5.83	5.83	0.00
4-6	2.69	1994	0.00	0.91	2.74	0.00	0.00	1.22	3.66	6.10	6.10	10.06	0.00	7.62	21.04	0.00	0.00	0.00	0.00	0.00	0.30	11.59	0.91	0.91
8-10	9.24	1988	0.00	2.60	5.84	0.00	0.00	0.97	0.97	18.18	3.25	14.29	2.92	5.52	20.78	4.55	0.00	1.30	2.92	1.95	0.00	0.00	1.30	1.30
12-14	15.92	1981	0.00	10.43	2.03	0.00	0.00	0.87	1.16	14.49	2.03	7.54	2.90	7.25	12.46	3.48	0.00	2.90	1.74	0.00	0.29	5.51	0.58	1.45
16-18	22.72	1974	0.00	2.98	0.66	0.00	0.33	4.97	4.64	14.24	0.00	9.27	0.00	6.29	15.56	0.66	1.99	5.96	0.99	0.00	0.00	7.28	2.65	0.00
20-22	29.65	1967	0.00	4.64	0.00	0.00	0.00	0.58	5.22	16.81	4.35	9.57	2.03	2.61	17.39	3.19	0.00	1.74	2.32	0.00	0.00	4.06	4.93	0.87
24-26	36.71	1960	0.00	2.91	0.58	0.00	0.00	0.00	8.43	9.30	3.78	4.94	0.00	9.30	18.60	3.20	0.00	2.03	2.33	0.00	0.00	6.10	2.91	1.74
28-30	43.90	1953	0.00	0.86	0.86	0.00	0.00	0.00	1.44	12.64	5.17	7.18	1.15	0.00	26.44	2.59	0.00	3.74	0.57	0.00	0.00	8.62	2.59	0.29
32-34	51.22	1946	0.00	1.72	1.34	0.00	0.00	0.00	4.39	7.25	3.82	8.21	2.67	2.86	8.78	3.63	0.00	0.76	1.53	0.00	0.38	35.31	1.34	0.76
36-38	58.66	1938	0.00	3.34	3.34	0.00	0.00	0.00	8.08	3.34	5.57	12.81	1.95	4.18	14.21	3.62	0.00	0.56	0.28	0.00	3.34	6.13	1.95	1.67
40-42	66.23	1931	0.00	0.00	1.62	0.32	0.00	1.29	4.85	9.71	1.62	6.15	4.53	2.27	11.33	3.56	0.32	0.65	0.00	0.00	0.00	6.15	2.27	0.00
44-46	73.93	1923	0.00	1.12	0.00	0.00	0.00	0.00	9.52	1.12	1.68	8.12	0.84	7.00	20.73	3.64	0.00	0.84	0.28	0.00	1.12	6.72	4.20	0.56
48-50	81.76	1915	0.00	3.71	0.57	0.00	0.00	0.29	9.43	2.29	2.00	9.43	0.57	5.14	15.43	5.43	0.00	1.71	0.86	0.00	0.00	5.14	2.57	3.43
52-54	89.72	1907	0.00	10.68	4.66	0.00	0.27	0.00	8.22	1.92	4.11	9.32	0.82	8.22	11.51	3.01	0.00	0.82	0.00	0.00	0.00	4.66	2.74	4.38
56-58	97.80	1899	0.00	7.94	6.61	0.00	0.00	0.00	7.41	2.38	5.29	6.88	0.26	7.41	13.49	1.32	0.00	1.06	0.26	0.00	0.00	6.61	2.38	1.06
60-62	106.01	1891	0.00	0.66	1.32	0.00	0.00	0.66	6.62	4.30	0.00	6.29	0.00	5.30	15.89	3.31	0.00	0.00	0.00	0.00	0.66	4.30	3.31	0.00
64-66	114.35	1883	0.00	0.96	0.64	0.00	0.32	0.00	2.24	9.29	7.05	9.62	0.00	1.92	9.62	3.21	0.00	0.32	0.32	0.00	1.60	6.41	1.28	0.00
68-70	122.82	1874	8.33	1.23	0.31	0.00	0.00	0.00	0.93	9.88	10.19	8.33	7.10	0.00	1.85	4.01	0.00	1.54	0.62	0.31	0.93	2.47	0.31	0.00
72-74	131.42	1866	0.00	1.92	3.21	0.00	0.00	0.00	2.88	10.90	2.88	8.97	0.00	2.88	13.14	4.49	0.00	0.00	0.96	0.00	0.64	3.85	1.28	0.00
76-78	140.14	1857	0.00	7.16	3.72	0.00	0.00	0.00	3.72	5.73	2.29	16.62	5.44	4.87	11.17	3.44	0.00	0.57	0.00	0.00	0.57	4.58	0.86	0.29
80-82	148.99	1848	0.00	4.98	3.65	0.00	0.00	1.33	1.66	6.98	5.98	12.96	0.00	8.97	5.32	0.00	0.00	1.33	0.00	0.00	2.33	5.98	0.00	0.00
84-86	157.97	1839	0.00	21.33	3.32	0.00	0.00	0.00	0.83	15.79	4.71	9.42	5.54	2.22	4.71	6.09	0.00	0.83	0.00	0.55	1.11	0.00	0.28	0.28
88-90	167.08	1830	0.00	14.10	0.96	0.00	0.00	0.00	0.00	19.87	3.85	16.67	6.09	8.33	1.92	5.45	0.00	1.28	0.00	0.00	0.00	4.49	1.28	0.32
92-94	176.32	1821	0.00	9.36	1.34	0.00	0.00	0.00	2.34	10.70	4.35	9.70	3.01	5.02	5.02	5.02	0.00	1.34	0.00	0.00	0.00	7.69	1.00	0.00
96-98	185.68	1811	0.00	11.42	0.93	0.00	0.00	0.00	3.09	4.32	4.01	10.49	3.40	7.10	9.88	11.42	0.00	2.16	0.31	0.00	1.23	3.40	2.16	0.00
100-102	195.17	1802	0.00	19.86	3.48	0.00	0.00	0.00	4.53	11.50	4.88	5.57	5.23	9.76	5.57	5.92	0.00	0.70	0.00	1.39	0.35	1.39	0.00	0.35
104-106	204.79	1792	2.40	4.11	4.11	0.00	0.00	0.00	5.48	8.56	3.42	14.38	1.03	8.22	5.82	2.40	0.00	1.03	0.00	0.00	2.05	1.71	2.40	0.00
108-110	214.54	1782	0.00	0.70	4.20	0.00	0.00	0.00	1.75	0.00	5.94	18.53	1.75	6.64	9.44	2.80	0.00	0.00	0.00	2.10	0.00	6.99	2.80	0.00
112-114	224.42	1773	3.59	0.60	0.00	0.00	0.00	0.00	0.60	2.99	5.99	8.38	7.78	3.59	5.39	5.99	0.00	0.60	0.00	0.00	0.00	0.00	1.80	0.00

5. *Detritus/Nutrient*
   a. Nitrate, NO_3 dissolved
   b. Nitrite, NO_2 dissolved
   c. Ammonia, NH_3 dissolved
   d. Organic carbon, C dissolved
   e. Suspended detritus, <10 microns
   f. Suspended detritus, 10-100 microns
   g. Suspended detritus, >100 microns
   h. Trapped detritus
   i. Organic nitrogen, N dissolved
   j. Inorganic phosphate, PO_4
   k. Organic phosphorus, P dissolved
   l. Oxygen, O_2
   m. Interstitial NO_3, dissolved
   n. Interstitial NO_2, dissolved
   o. Interstitial NH_4, dissolved
   p. Interstitial C, dissolved
   q. Interstitial particulate organic C (dead)
   r. Interstitial organic N, dissolved
   s. Interstitial organic P, dissolved
   t. Interstitial PO_4, dissolved
   u. Interstitial O_2, dissolved

6. *Geology*
   a. Dissolved inorganic C (CO_2, HCO_3, and CO_3)
   b. Suspended inorganic C (fine $CaCO_3$)
   c. Bedload inorganic C (coarse $CaCO_3$ sediments on the sea floor)
   d. Frame inorganic C (reef frame)
   e. Organism inorganic C ($CaCO_3$ in living non-frame organisms)
   f. Rubble inorganic C (large talus)
   g. Inorganic C in sand ($CaCO_3$, 62 microns-4 mm)
   h. Inorganic C in mud ($CaCO_3$, <62 microns)
   i. Interstitial dissolved C (CO_2, HCO_3, and CO_3 dissolved in interstitial sediment water)

7. *Input From Outside the Reef Community*
   a. Autotrophic plants, C
   b. Nitrogen-fixing plants, N
   c. Nitrogen-transforming plants, oxidize and reduce N compounds
   d. Decomposing plants, convert organism biomass to simpler organic material, nutrients, CO_2, and water
   e. Birds, remove fish and invertebrates, contribute feces containing N and P compounds
   f. Decomposing organisms, contribute to organic and inorganic chemical pool
   g. Sea turtles, feed on benthos and floating organisms, contribute chemicals from feces
   h. Talus islands adjacent to the reefs, may contribute organic and inorganic chemicals and sediments to the reef.

The Dahl et al. model contained 104 compartments. A matrix of the interrelationships implied about 2,000 of the 10,816 potential interactions were active, and a material and energy flow exists between these categories. In terms of modeling coral reefs, Smith et al. (1978) reported that until the modeling technique advances to the point that it is realistic, the budget analysis method offers better insight into ecosystem dynamics by focusing on an element within the ecosystem (e.g., carbon budget, nitrogen budget). Smith et al. (1978) reported on several budgets from a hypothetical atoll in the Pacific. Figure 15 provided a qualitative graphic representation of a calcium carbonate budget from Barbados.

7.9 NATURAL IMPACTS

Hurricanes are the most severe natural impact faced by coral reef communities. Mega-hurricanes (those with 200-mi/hr or greater winds) have devastated reef areas, and either recovery has been slow or the coral reef community has been replaced by another community. Stoddart (1962, 1963, 1974) reported that Hurricane Hattie destroyed reefs off the coast of British Honduras (Belize) and that recovery was negligible. Woodley et al. (1981) reported that Hurricane David decimated shallow reefs near Discovery Bay, Jamaica, and post-hurricane mortality of damaged organisms was significant (Knowlton et al. 1981).

In considering the effect of hurricanes, two major areas of negative impact are reported. Physical damage occurs as a result of the huge seas generated by the hurricane winds. Shallow reef zones bear the brunt of the wave forces as they are expended on the spur and groove and reef flat. Smaller corals and other attached organisms are often dislodged, fragmented, and abraded by the severe physical pounding. The other major impact concerns dilution of salinity caused by torrential rains. In regions where mountainous terrestrial land masses abut the coral-lined coast, severe runoff may turn coastal waters hyposaline (Goreau 1964). Erosion of soil and transport by the runoff is also credited with causing coral mortality. Goreau (1964) reported shallow reef mortalities due to salinity stress as well as to burial by terrigenous silt. The passage of the storm also causes churning of the bottom sediments increasing turbidity within the water column.

Hurricane damage to Florida reefs reported from the literature are of a lesser magnitude, and in some respects could be considered beneficial. Springer and McErlean (1962a) reported negative impact on patch reefs off Key Largo from Hurricane Donna. The storm crossed the reef tract about 40 km south of Key Largo, 9-10 September 1960. Windspeed was approximately 161 km/hr, with gusts approaching 242 km/hr (Shinn 1975). High seas dislodged and redistributed corals in the adjacent area of Key Largo Dry Rocks (Shinn 1975). Hurricane Betsy passed within 16 km of Key Largo Dry Rocks on 8 September 1967, with a windspeed of approximately 193 km/hr. Shinn reported that hurricane damage was not evident 5 years following Donna and 2

Table 4: Foraminifer Percent Abundance Data for SEI297-FB-1

DUPLICATE:
Original in
Museum Archives

Depth (cm)	Years (B.P.)	Age Model Year	*Haynesina germanica*	*Miliammina circularis*	*Miliammina labiosa*	*Nodobacularia sp.*	*Peneroplis proteus*	*Pyrgo sp.*	*Quinqueloculina agglutinata*	*Quinqueloculina bosciana*	*Quinqueloculina poeyana*	*Quinqueloculina polygona*	*Quinqueloculina seminula*	*Quinqueloculina tenagos*	*Rosalina floridana*	*Rosalina globularis*	*Sorites sp.*	*Spiroloculina antillarum*	*Spirosigmoilina*	*Triloculina rotunda*	*Triloculina striatula*	*Triloculina tricarinata*	*Triloculina variolata*	*Valvulina oviedoina*
116-118	234.42	1763	0.00	0.80	0.40	0.00	0.00	0.00	0.00	17.93	3.19	1.59	2.39	1.59	1.20	5.98	0.00	0.00	0.00	0.00	0.80	2.79	0.00	0.00
120-122	244.55	1752	0.00	4.67	0.62	0.00	0.00	0.00	1.56	12.15	23.99	0.93	5.61	0.00	0.00	1.87	0.00	0.00	0.00	0.00	0.62	3.12	0.00	0.31
124-126	254.81	1742	0.00	3.32	0.00	0.00	0.00	0.00	1.00	11.30	17.28	1.00	1.99	2.66	0.00	8.31	0.00	0.00	0.00	0.00	0.00	1.33	0.00	0.33
128-130	265.20	1732	0.00	4.26	3.65	0.61	0.00	0.00	5.47	8.21	9.42	15.81	0.91	7.60	0.00	1.52	0.00	0.61	0.00	0.30	0.00	8.21	0.00	0.00
132-134	275.72	1721	1.10	1.84	0.00	0.00	0.00	0.00	3.68	3.31	0.00	13.97	0.00	6.99	4.04	2.21	0.00	0.00	0.00	2.57	1.10	10.66	0.74	0.37
136-138	286.36	1711	5.75	0.00	0.00	0.00	0.00	0.00	1.15	0.00	2.87	3.45	0.00	0.00	3.45	4.60	0.00	0.00	0.00	0.57	0.57	6.90	0.00	0.00
140-142	297.13	1700	12.20	0.00	0.00	0.00	0.00	0.00	0.00	1.83	3.05	1.83	0.61	0.00	1.22	4.27	0.00	0.00	0.00	0.00	0.00	6.71	0.00	0.61
144-146	308.03	1689	0.00	0.00	0.00	0.00	0.00	0.00	1.27	5.71	4.76	5.40	5.08	0.63	2.54	6.67	0.00	0.32	0.00	0.32	0.00	3.81	0.32	0.00
148-150	319.06	1678	0.00	6.62	4.18	0.00	0.35	0.35	9.76	11.50	4.88	10.80	0.00	6.27	1.05	2.79	0.00	0.70	0.00	2.09	0.00	3.48	1.74	0.00
152-154	330.22	1667	0.00	2.20	1.26	0.00	0.00	0.00	1.89	18.24	9.12	5.97	5.03	2.83	1.89	5.97	0.00	0.00	1.57	0.31	1.57	2.83	0.63	0.00
156-158	341.50	1655	0.00	1.81	5.14	0.00	0.00	0.00	3.93	3.93	7.55	16.92	3.63	6.95	7.85	4.53	0.00	0.00	0.00	2.72	6.34	5.14	0.00	0.00
160-162	350.05	1647	0.00	0.94	2.19	0.00	0.00	0.00	2.19	4.08	10.03	15.99	5.33	5.64	6.58	4.08	0.00	0.31	0.00	0.00	0.00	6.58	0.94	0.00
164-166	364.45	1633	0.00	0.99	4.28	0.00	0.00	0.00	1.32	0.00	15.46	10.86	0.00	3.95	1.32	0.66	0.00	0.00	0.00	0.00	2.30	0.99	0.33	0.00
168-170	376.12	1621	0.00	0.32	0.00	0.00	0.00	0.00	0.00	0.97	24.60	0.00	0.97	2.27	4.85	6.47	0.00	0.32	0.00	1.29	0.00	0.00	0.65	0.00
172-174	387.92	1609	0.00	0.00	0.00	0.00	0.00	0.00	0.33	3.32	7.31	2.66	0.33	2.99	2.33	4.98	0.00	0.33	0.00	0.00	0.00	2.99	0.00	0.00
176-178	399.84	1597	0.00	0.00	0.00	0.00	0.00	0.00	0.35	1.40	0.70	0.70	0.00	0.00	0.00	3.50	0.00	0.00	0.00	0.00	0.70	0.00	0.00	0.00
180-182	411.89	1585	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.22	0.31	0.31	0.00	1.53	7.65	0.00	0.00	0.00	0.00	0.00	0.31	0.00	0.00
184-186	424.07	1573	0.00	0.00	0.00	0.00	0.00	0.00	1.42	0.28	2.27	1.98	0.00	0.28	1.13	5.67	0.00	0.57	0.00	0.28	0.00	4.53	0.28	0.00
188-190	436.38	1561	0.00	0.30	0.90	0.00	0.00	0.00	1.81	0.90	6.63	13.25	3.61	8.13	3.31	3.31	0.00	0.00	0.00	0.00	0.00	15.06	2.71	0.60
192-194	448.82	1548	0.00	0.00	0.00	0.00	0.00	0.00	1.61	0.32	1.29	2.57	0.64	0.64	3.22	2.57	0.00	0.00	0.00	0.64	0.00	16.08	0.64	0.00
196-198	461.38	1536	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.88	3.80	0.58	0.00	1.17	3.22	7.02	0.00	0.00	0.00	0.29	0.00	4.39	0.29	0.00
200-202	474.07	1523	0.00	0.00	0.00	0.00	0.00	0.00	0.32	0.00	1.27	1.91	1.27	0.00	5.73	2.87	0.00	0.32	0.00	0.32	0.00	3.50	0.00	0.00
204-206	486.89	1510	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.11	1.20	0.90	1.81	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.41	0.00	0.00
208-210	499.84	1497	0.00	1.16	1.45	0.00	0.00	0.00	0.00	0.00	4.65	2.62	2.03	3.20	2.03	2.33	0.00	0.00	0.29	0.00	0.00	6.10	1.16	0.00
212-214	512.92	1484	0.00	2.01	1.15	0.00	0.00	0.00	1.43	0.00	4.58	4.87	2.58	2.29	2.87	2.58	0.00	0.00	0.00	0.00	0.00	4.58	0.57	0.00
216-218	526.12	1471	0.00	0.28	0.56	0.00	0.00	0.00	1.94	1.39	1.67	4.72	0.28	5.00	9.44	2.22	0.00	0.00	0.00	0.56	0.00	13.06	1.67	0.00
220-222	539.45	1458	0.00	0.64	0.00	0.00	0.00	0.00	3.18	2.23	6.37	4.14	0.64	6.05	2.55	1.91	0.00	0.00	0.00	0.32	0.00	12.74	0.96	0.00
224-226	552.91	1444	0.00	2.71	2.26	0.00	0.00	0.00	2.26	1.81	4.98	9.95	4.07	9.50	17.65	3.62	0.00	0.00	0.00	0.00	2.26	8.14	1.81	1.36

et al. (1974), with some modification in terminology.

1. *Benthic Plants*
   a. Nitrogen-fixing algae, nutrient recycling function
   b. Crustose coralline algae, framework organism, cementing function
   c. Benthic microalgae, primary producer
   d. Turf algae, <2 cm high, autotroph
   e. Carbonate producing macroalgae, sediment production
   f. Boring algae (Ostreobium), filamentous, within the carbonate frame
   g. Detached macroalgae, Sargassum, floating autotrophs
   h. Marine grasses, blades, adjacent to the reef
   i. Marine grasses, roots, alter sediment characteristics

2. *Plankton*
   a. Heterotrophic phytoplankton, <10 microns
   b. Autotrophic phytoplankton, <10 microns
   c. Autotrophic phytoplankton, 10-100 microns
   d. Autotrophic phytoplankton, >100 microns
   e. Microholoplanktonic omnivores, <200 microns
   f. Mesoholoplanktonic omnivores, 200-500 microns
   g. Macroholoplanktonic omnivores, >500 microns
   h. Neuston omnivores, all sizes
   i. Microepibenthic omnivores, <200 microns
   j. Mesoepibenthic omnivores, 200-500 microns
   k. Macroepibenthic omnivores, >500 microns
   l. Mesoholoplanktonic carnivores, 200-500 microns
   m. Macroholoplanktonic carnivores, >500 microns
   n. Neuston carnivores, all sizes
   o. Mesoepibenthic carnivores, 200-500 microns
   p. Macroepibenthic carnivores, >500 microns
   q. Microholoplanktonic detritivores, <200 microns
   r. Mesoholoplanktonic detritivores, 200-500 microns
   s. Macroholoplanktonic detritivores, >500 microns
   t. Neuston detritivores, all sizes
   u. Microepibenthic detritivores, <200 microns
   v. Mesoepibenthic detritivores, 200-500 microns
   w. Macroepibenthic detritivores, >500 microns

3. *Benthos, Invertebrates*
   a. Animal-plant symbionts, energetic support from autotrophs
   b. Invertebrate "scrapers," remove substratum with food
   c. Invertebrate browsers, do not remove substratum
   d. Passive suspension feeders, collect nutrients from water column without physical action on the part of the organism
   e. Active suspension feeders, actively collect nutrients from the water column by creating currents or selective predation
   f. Microbrowsers (meiofauna), nutrition gained from material in sediments, <2 mm
   g. Macro-deposit feeders, nutrition gained from larger (>2 mm) sedimentary fraction
   h. Sedentary micropredators, selectively capture water column prey
   i. Small predators, motile organisms that harvest invertebrates and vertebrates
   j. Medium predators, mobile organisms that harvest medium-sized invertebrates or vertebrates
   k. Meiofauna predators, live in the sediment, harvest meiofauna
   l. Parasites and pathogens, very selective predator that gains nutrients from a limited number of host organisms
   m. Parasite cleaners, mobile organisms, specializing in removing parasites from other organisms
   n. Attached eggs

4. *Nekton, Vertebrates*
   a. Grazers, also remove a portion of the substrate, i.e., parrotfish
   b. Browsers, do not affect substrate
   c. Bottom feeding planktivores, feed on epibenthic plankton
   d. Midwater feeding planktivores, feed on holoplankton and neuston
   e. Small predators, <50 mm standard length (SL)
   f. Medium predators, 50-250 mm SL
   g. Large predators, 250-500 mm SL
   h. Top predators, >500 mm
   i. Parasite pickers, feed on vertebrate ectoparasites
   j. Detritus feeders
   k. Attached eggs

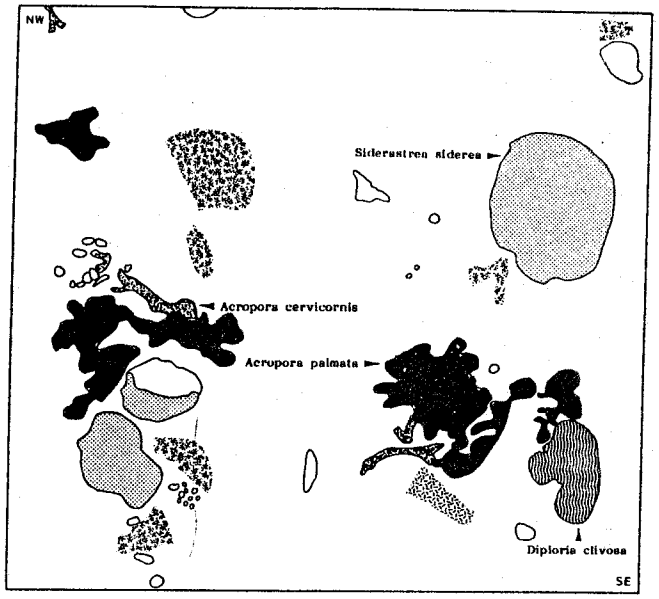


Figure 24. Time series of a 2x2 meter area of Elkhorn Reef, 1978.

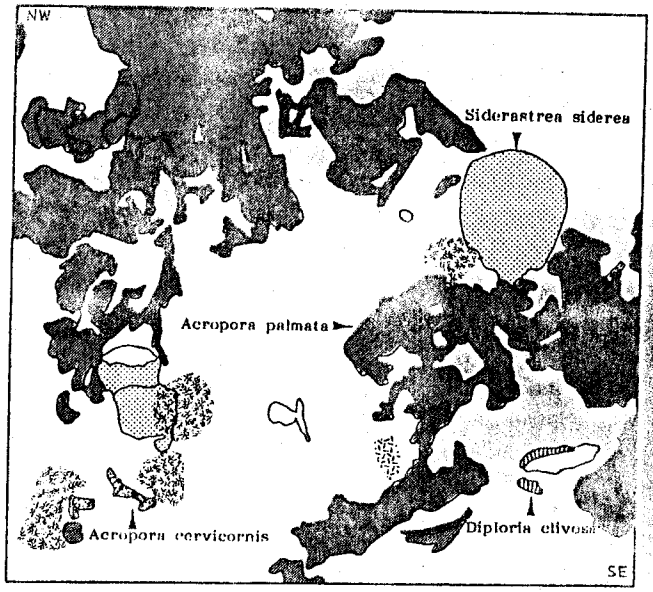


Figure 25. Time series of a 2x2 meter area of Elkhorn Reef, 1979.

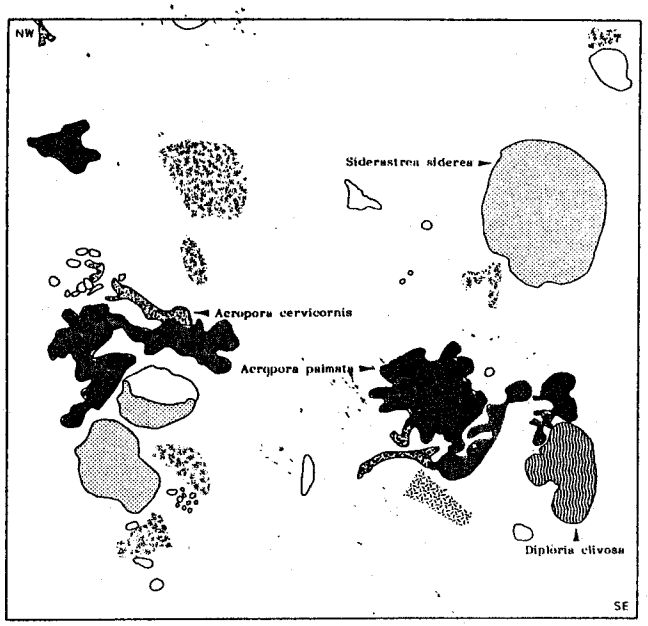


Figure 26. Time series of a 2x2 meter area of Elkhorn Reef, 1980.

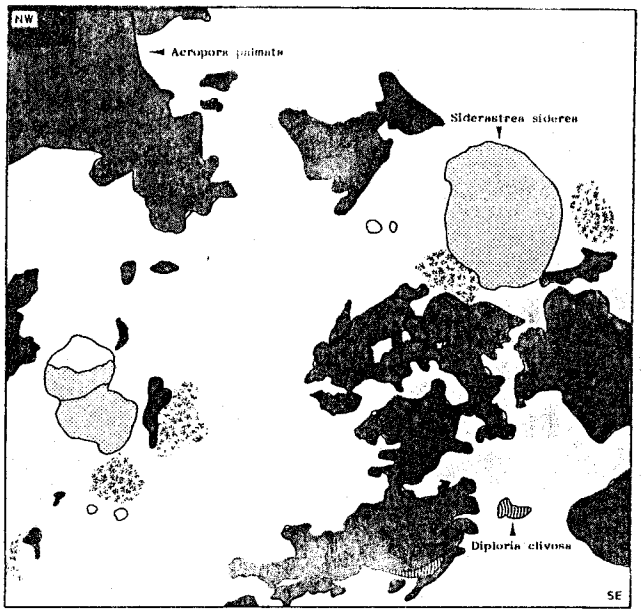


Figure 27. Time series of a 2x2 meter area of Elkhorn Reef, 1981.

gible. Much of this research was accomplished in the Pacific; extrapolation to Florida reefs must be qualified by several facts. The Pacific reefs are usually set in more benign or predictable environments, with negligible seasonal variation in temperature. Because of the difficulty in evaluating community productivity and respiration, few studies have considered total community metabolic budgets. By far, the greatest research emphasis has been on the zooxanthellae and the symbiotic relationship with coral. Trench (1979) and Schoenberg and Trench (1980a, 1980b, 1980c) reviewed the cellular biology of this aspect. Rodgers (1979) studied two 10 x 1 m reef sections at San Cristobal Reef, Puerto Rico; net productivity ranged from 0.03 to 1.85 g $O_2/m^2/hr$. A recent summary-review of coral reef physiology is found in Gladfelter (1983).

7.8 CORAL REEF MODELS

Conceptual models were proposed by Dahl et al. (1974) and improved upon by Smith (1978). The Dahl et al. (1974) model included organism processing units (similar functional elements), pathways, and external driving forces. The following outline is taken from Dahl

organisms live successfully on the coral's upper surface. Some, such as copepods, have developed specialized forms to live in the coral polyps; they are more worm-like than crustacean (Patton 1976). Some organisms have developed unique ways to modify the coral skeleton. The subfamily Pyrogomatinae (barnacles) and the decapod crustacean *Domecia acanthophora* are able to modify the Scleractinian skeleton. *Domecia acanthophora* lives on *A. palmata* branches (Patton 1967) and is able to influence calcification such that the coral builds a skeletal structure around the crab. The process initiates when a crab seeks a position on the branch margins where bifurcation has begun; the crab maintains its position, and the skeleton grows around its den. In time the area resembles a small pit or cave. *Domecia acanthophora* has modified second maxillipeds that allow the crab to feed on suspended material. In this case, the relationship is both shelter- and food-related. Patton (1976) reported that mobile crustaceans living in close association with corals feed on the sediment and detritus from the water column and that which settles on the coral surface. Corals also release energy sustaining materials that other organisms may utilize, e.g, mucus, fecal detritus, zooxanthellae, and metabolic wastes.

Competitive interactions are important in determining community structure on a coral reef. The major area of interaction is in the competition to acquire spatial territory. Successful organisms can defend their territory against intruders. They are also able to expand into the adjacent region at the expense of organisms that are less able to maintain their territory. An example of local habitat manipulation is the effect of the threespot damselfish (*Pomacentrus planifrons*) on the corals *Acropora cervicornis* and *Montastraea annularis*. Kaufman (1977) and Potts (1977) reported that the threespot damselfish was able to garden small areas of reef by killing the corals and defending the area from herbivorous fish, thus allowing a crop of filamentous algae to grow on the dead corals. These small fish are territorial and defend the area against fish, invertebrates, and divers. As a result, the area has an abnormally high algal cover. This result is short term in *A. cervicornis* habitats. Since this species grows rather rapidly, it can grow away from the damselfish territory and develop a new area. In the case of *M. annularis* where growth is slow and propagation is mostly by larval recruitment, the damselfish may have a more significant negative impact on the affected coral colony.

A number of authors have reported on the effect of the black-spined sea urchin, *Diadema antillarum*, on coral reefs. Sammarco et al. (1974) reported that *D. antillarum* controlled coral community structure; Bak and Van Eys (1975) reported that the urchin fed on coral; and Sammarco (1980) reported that *D. antillarum* was important in providing microhabitats for coral larvae to settle. *Diadema antillarum* is a common resident on most coral reefs; hence, its control is probably significant.

Another form of interaction that has been mentioned earlier is the ability of the corals themselves to maintain or advance territorial superiority by extracoelentric feeding behavior with the extension of mesenterial filaments. The more "aggressive" species have the ability to digest the tissues of less "aggressive" adjacent species. Lang (1973) described this form of interaction. It is not a rapid phenomenon; in some cases it may take months for the interaction to be noticed.

7.6 PREDATOR-PREY RELATIONS

Predator-prey relationships are far too great and complex to detail here. One of the more well-known corallivores is the polychaete *Hermodice carunculata* (Plate 18b), a large marine worm that is documented to feed on a number of coral species (Marsden 1960, 1962; Glynn 1962; Ebbs 1966; Antonius 1974b; Lizama and Blanquet 1975. Glynn (1973) reviewed western Atlantic coral predators. Some organisms such as the gastropods *Coralliophila abbreviata, Calliostoma javanicum*, and *Cyphoma gibbosum* are mobile species that move to and from the coral. They feed on the coral, but apparently do not receive protective shelter. Fish within the families Scaridae, Ephippidae, and Pomacentridae feed on coral (Glynn 1973). They are not obligate to a particular coral species; this major difference between Pacific and Atlantic corallivores (lack of obligate species relationships in the Atlantic) may reflect that the time of development for Atlantic reefs and coral species has been relatively short. (Atlantic Scleractinia are only ca. one million years old; Pacific reefs have a much older fauna.) Predation may directly cause mortality and morbidity. Injury caused by predation may lead to the invasion of boring and rasping biota. When the coral is damaged, recovery may occur by regeneration of tissue; but regeneration may be prevented by successful colonization of the injured area by other organisms (filamentous algae, diatoms, sponges, *Millepora*, and zoanthids). This alien growth is detrimental to the coral, which may succumb to the secondary invasion.

Rapidly growing species may grow over and shade out other organisms, denying them resources. There is also evidence that some reef organisms are able to maintain and advance spatial resources through the secretion of toxic chemicals (Jackson and Buss 1975).

Figures 24-27 show the cumulative effect of these interactions through time for a small area on Elkhorn Reef.

7.7 PRODUCTIVITY

The earliest study of overall productivity of a small coral reef was Odum and Odum (1955) at Eniwetok, a Pacific atoll. The comparability with Florida is poor; however, the concept of high productivity is valid. Odum and Odum (1955) reported that mean annual production was 846 gm dry biomass/m^2. On a 24-hour basis there was a net gain of 2 gm C/m^2. Sournia (1977) reviewed coral reef primary production and concluded that gross production in coral reefs yielded the highest productivity of any ecosystem on earth. The magnitude of gross production ranged from 2-10 gm C/m^2/day; however, net production may, in some cases, be negli-

MEETING BRIEFS

Coral Reefs Dominate Integrative Biology Meeting

BOSTON—In addition to the normal contingent of biologists from many disciplines, this year's annual meeting of the Society for Integrative and Comparative Biology, which was held here from 3 to 7 January, attracted hundreds of coral reef scientists. Some highlights follow.

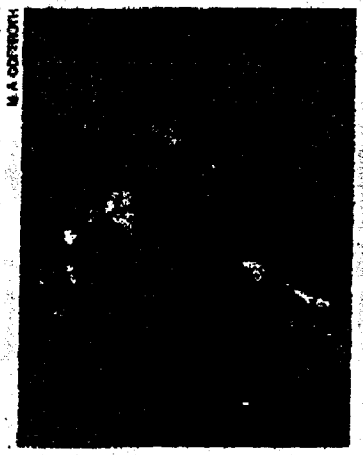
Coral Partners May Enhance Reef Survival, Versatility

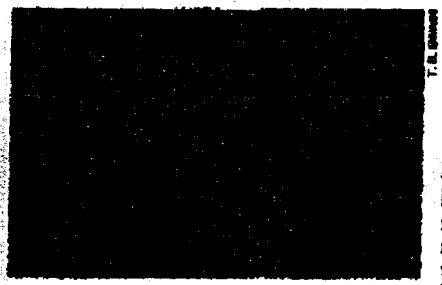
Many visitors to coral reefs are so taken by the beauty and diversity of the colorful fish and other reef inhabitants that they never notice one of the reef's most important components: microscopic algae called zooxanthellae that color reefs greenish gold. But the absence of these algae, which inhabit the tissue of the tiny coral animals and provide the nourishment that enables corals to form large colonies, is impossible to overlook. In the past decade, they have sometimes disappeared from large expanses of reefs throughout the world, leaving them bleached a ghostly white—and apparently dead (*Science*, 25 July 1997, p. 491). As the reefs went white, their departed brown guests caught marine biologists' attention.

No one knows what causes coral bleaching, although biologists have fingered everything from global warming to disease. But the scrutiny the zooxanthellae are now attracting is putting their symbiotic relationship with corals in a new light—and suggesting that the outlook for bleached corals may not be as grim as it had seemed.

Data presented at the meeting indicate, for example, that this symbiosis undergoes seasonal fluctuations in which about three-quarters of the zooxanthellae can be lost from a reef without harming it. Moreover, corals may still retain some of these algae in deep reserve even when they look dead white. And while it was once assumed that each species of coral associates with a particular alga, researchers now find that corals can take in different zooxanthellae depending on circumstances—a hint that when one kind of algae leaves, another might come to the rescue. "There's potential for [corals] to be fairly malleable systems," says Rob Rowan, a marine biologist at the University of Guam.

Signs that zooxanthellae come and go with the seasons emerged in studies of coral reefs off Florida and the Bahamas that marine biologist Bill Fitt of the University of Georgia, Athens, and his colleagues began 3 years ago. The researchers expected that zooxanthellae densities and the corals' reserves of proteins, carbohydrates, and lipids would be highest in the summer, when light is most plentiful. But instead, "the highest densities [are] in the winter, in the coolest part of the year," says Fitt. Their quarterly measurements indicated that by late summer the algal density often plunges to one-fourth or less of peak levels.





Symbiont shuffle. Both hard *(left)* and soft *(above)* corals mix and match algal partners.

This suggested that the high-light, high-temperature conditions of summer somehow disrupt the algae's photosynthetic pathways. Mark Warner of the University of Georgia, working with Georgia botanist Gregory Schmidt and Fitt, has confirmed that idea, showing that a light-sensitive protein, called D1, which helps convert sunlight to chemical energy, breaks down in high water temperatures—above 30 degrees Celsius. As a result, photosynthesis declines and the algae seem to die and be expelled from the coral, perhaps because they are no longer useful. "All reef-building corals bleach every single year even when we don't see it," says Fitt. Only when algal density drops below a million algae per square centimeter, as it does in particularly hot summers with little cloud cover, does the coral begin to pale, and even then it usually recovers.

Indeed, even coral that appears dead may have a secret reserve of algae, Cynthia Hunter, a coral-reef biologist at the University of Hawaii, Honolulu, reported at the meeting. She has studied the ability of corals to withstand sudden immersion in fresh water, a threat to corals that live in estuarine areas where rainfall can cause bursts of freshwater runoff. One branching coral, *Porites compressa*, seems to die in fresh water, as it bleaches and loses all signs of soft tissue. But when Hunter examined the remaining coral skeleton, she found live tissue, including zooxanthellae, underneath. That tissue enables the coral to come back to life eventually.

Another factor may also help bleached corals bounce back: their ability to host a range of different algal guests. Evidence that they can do so first came last year when Rowan's team found that a single coral colony could have a different algal symbiont, depending on whether the coral face was in the sun or shaded. They also found that three closely related corals varied in which of the three recognized groups of algae (designated A, B, and C) they carried, depending on the depth at which the corals lived.

Other researchers are now finding the same type of algal diversity in other types of corals. Coral reef biologist Andrew Baker of the University of Miami in Florida, for example, compared DNA in zooxanthellae collected from a variety of hard corals in locations ranging from the Bahamas and eastern Panama to Australia and western Panama. He too finds that a particular coral species can associate with more than one type of zooxanthellae. Mary Alice Coffroth and Tamar Goulet at the State University of New York at Buffalo have seen similar patterns in soft corals such as sea fans. "Coral can be seen as a landscape in which different populations of zooxanthellae are competing," Baker told the meeting participants.

That diversity may help explain why one coral bleaches while another just a few yards away does not. Different zooxanthellae in those corals may respond differently to the stress that leads to bleaching, Rowan explains. Bleaching may even help the coral switch to an alga better suited to new conditions. Yet he and others caution that they still have much to learn about the ongoing conversation between the algae and the coral. "It's only beginning to come out how complex it is," says Goulet.

Farm-Fresh Corals

Fish and pearls now come from farms, so why not corals? At the meeting, reef scientists reported techniques that may allow aquaculturists to

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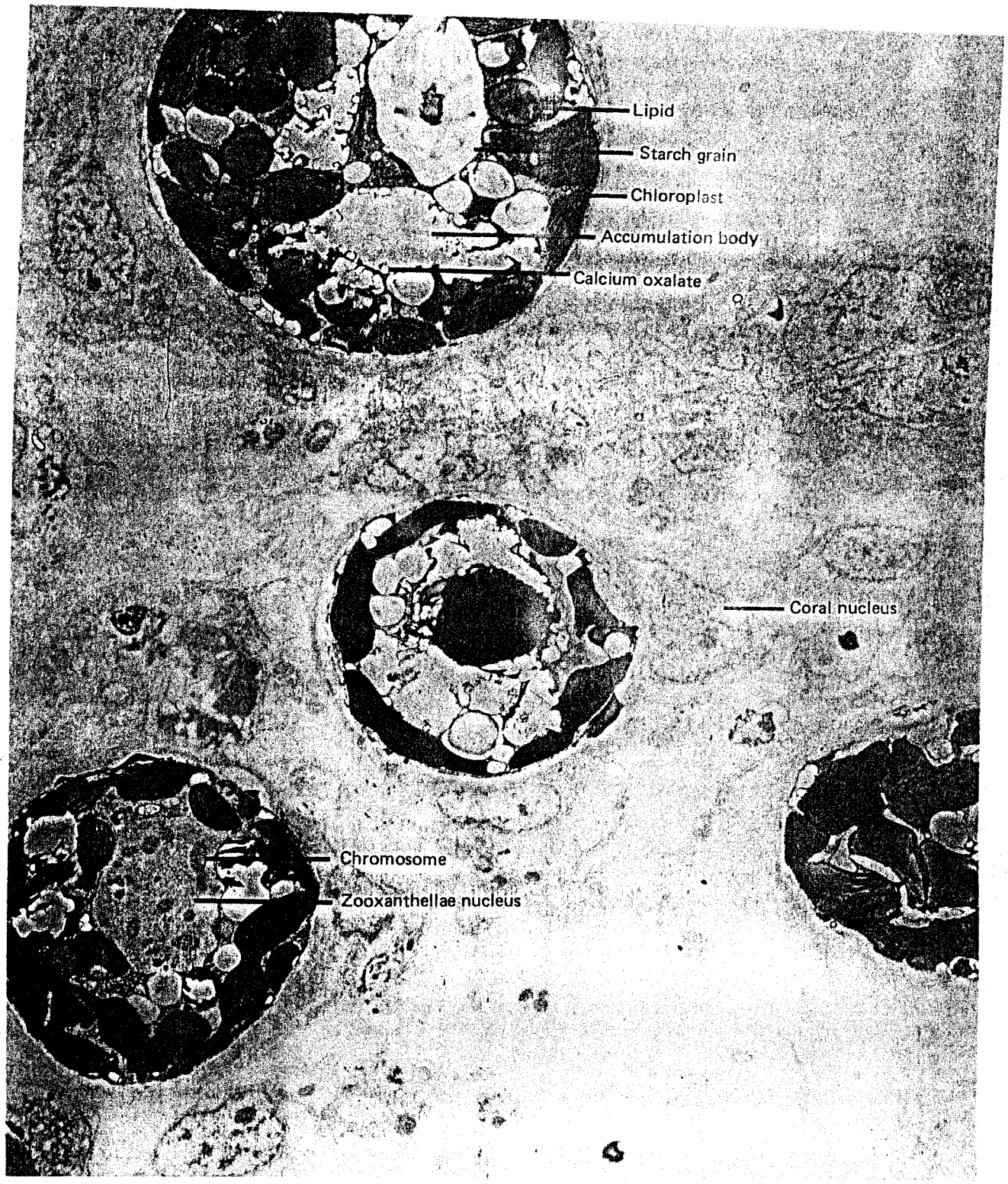


Figure 23. Electron micrograph of *Agaricia fragilis* zooxanthella, 14,660 magnification.

grow coral commercially for sale to tourists or aquarium enthusiasts, reducing the harvesting of natural reefs. The cultivated corals might also be used to reseed small swathes of reef damaged by ships, fishing, or development, says one of the researchers, Robert Richmond of the University of Guam Marine Laboratory in Mangilao.

The idea of growing corals is not new, but with these methods, "the goal is to make the [aquaculture] system simple so that it can be used by the island communities," says Richmond, whose university has been developing the system based on the discoveries he and others have made about coral reproduction.

The culture systems are catching the eye of conservationists as well as entrepreneurs. "It's dangerous to think we will grow back reefs on the kilometers scale," comments reef scientist Howard Lasker of the State University of New York, Buffalo. "But reseeding efforts [with cultivated corals] will be important in specialized cases."

Richmond's initial interest was not in reef restoration or aquaculture but in producing the many dozens of coral specimens he needed to test the toxicity of various chemicals to reefs. Before the corals could be cultured, however, his team first studied them in the wild to determine when the tiny polyp-shaped animals that form coral colonies release their gametes. This turned out to be within a week after the summer full moons.

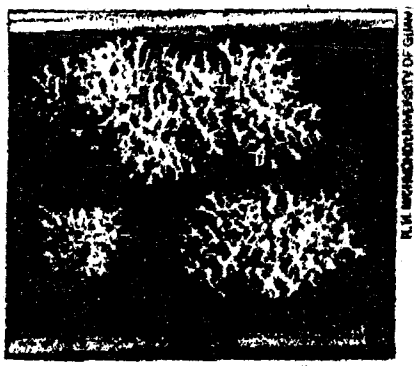
This cycle sets the timetable for coral culturing. The researchers collect adult pieces of reefs just before the full moon and place



R. H. RICHMOND/UNIVERSITY OF GUAM

Head start. Aided by this protective device, "farmed" larvae can reseed a reef.

them in tanks with running seawater. When the gametes are ready, the team siphons off the eggs and sperm released by the corals and mixes those gametes in new containers where the fertilized eggs transform into swimming larvae. After 2 days, the larvae begin to settle on glass plates at the bottom of the containers. At that point, the researchers place a larger coral colony in with the settled larvae to provide a source of the algae that the new corals need to take in if they are to survive. The corals then begin forming calcified nodules—reefs in microcosm.



R. H. RICHMOND/UNIVERSITY OF GUAM

Coral crop. Lasting young corals fuse yields bigger corals faster (top, right).

Thus far, the team in Guam has cultivated 10 species with this technique. Most are branching corals, although others grow into large, rounded colonies. The researchers have learned that because the closely spaced young corals in the containers quickly fuse into a single, larger colony, cultivated corals can reach souvenir and aquarium size—about 10 centimeters around—in just 5 months rather than the year it takes in nature.

Next summer, Richmond's team plans to scale up their operations to demonstrate whether mass production of corals is possible. If all goes well, they expect to hold a workshop by fall to teach potential coral farmers these techniques, but they have already started transferring the technology to Palau, Richmond's colleague Sandra Romano reported at the meeting.

Researchers interested in reconstituting damaged coral reefs are studying the cultured corals to see if they can be used in transplants instead of natural corals. "Transplanting coral is viable, but you always get some mortality," Richmond explains.

In one experiment, Laurie Raymundo, a coral reef biologist at Silliman University in the Philippines, and her colleagues showed that cultured coral colonies can survive when transplanted to natural reefs, provided the transplants are big enough. When they grafted colonies they had cultured using an approach similar to Richmond's onto a healthy reef off Negros Island in the central Philippines, the researchers found that only about 10% of corals with diameters smaller than 6 millimeters survived. But nearly 70% of those with diameters of 10 millimeters or more lived. The team is now monitoring the transplanted corals to see whether they will continue to thrive and to grow.

Throat Pumps for Better Breathing, Longer Run

For years, researchers have argued about whether lizards can run and breathe at the same time. Their anatomy suggests that they can't, at least not well. But when the wide-ranging kind of lizards called monitors run on a treadmill, their blood remains rich in oxygen—suggesting that these animals breathe just fine as they run. "It's been a fairly contentious argument for over a decade," says David Carrier, a functional morphologist at the University of Utah, Salt Lake City. Now it may be over.

New data presented at the meeting by physiologist Elizabeth Brainerd of the University of Massachusetts, Amherst, and her colleagues suggest that monitors are a special case. They have found that the large throat pouches found in these lizards serve as accessory air pumps, forcing air into their lungs and overcoming the anatomical limitations of other lizards. The finding "seems to have resolved the conflict," comments Jaap Hillenius, a physiologist at the College of Charleston in South Carolina. "Some lizards can breathe and some lizards cannot."

Mammals use a specialized muscle—the diaphragm—for breathing, freeing the other muscles for locomotion. But in lizards, the same rib muscles that cause the lungs to expand and contract also make the lizard's body stay upright and wiggle from side to side as it runs. As a result, these animals generally can't breathe hard when they need to most and "would have had a problem with sustained locomotion," says Carrier.

Brainerd got her first clue that monitors might be an exception when she made an x-ray video of a monitor lizard in motion. It revealed that the expandable gular region of the throat was filled with air and seemed to be expanding and contracting.

Others had previously noted that when monitors breathe, they exhale all at once, but they seem to inhale in a series of small breaths. Brainerd found that those breaths feed air to the gular pouch, which acts as a pump. With each inhalation, she found, the gular region would pump several times, pushing air down into the lungs. Another sign that the pouch aids breathing is that its movements correlate with the lizard's degree of activity. "The faster they run, the more they pump; the longer they run, the more they pump," Brainerd says.

And when she, Tomasz Owerkowicz of Harvard University, and Colleen Farmer and James Hicks of the University of California, Irvine, prevented the pouch from pumping by propping the lizards' mouths open, the animals couldn't take in oxygen as well as before. When they ran on the treadmill at 1 kilometer per hour, their oxygen intake dropped 22% at 2 kilometers per hour the decrease was 37%. "The faster they go, the more constrained they get," she adds, just as predicted for lizards

BISC Science Files: Biscayne Section: Corals Reefs: Ecology. DUPLICATE: Original in Museum Archives



Figure 22. Electron micrograph of *Agaricia fragilis* zooxanthella, 6590 magnification.

cated use of information theory to study species diversity, and Hurlburt (1971) responded that species diversity was a nonconcept. Species diversity has been measured in many ways. Some reef workers have favored using plotless sampling techniques and computing diversity with the Shannon Wiener Index H' and its evenness component, J', as well as reporting the number of species (species richness). Sampling adequacy is usually determined by the asymptote of a species area curve. The most striking finding in relation to stony corals is the matter of sample size. In the Red Sea (Loya 1972) and Panama (Porter 1972) the minimum acceptable transect length was 10 m; in Florida reef communities, a 25-m length is necessary to insure adequate sampling. This implies that the reefs off southeast Florida are less diverse in their stony coral fauna than those from other more tropical regions. If one studies the species found on any given reef, however, one will find almost all the species reported from other Caribbean areas. They may be quite rare, but present nevertheless. Table 27 presents the Scleractinia found throughout the Florida Reef Tract, and Figure 21 shows

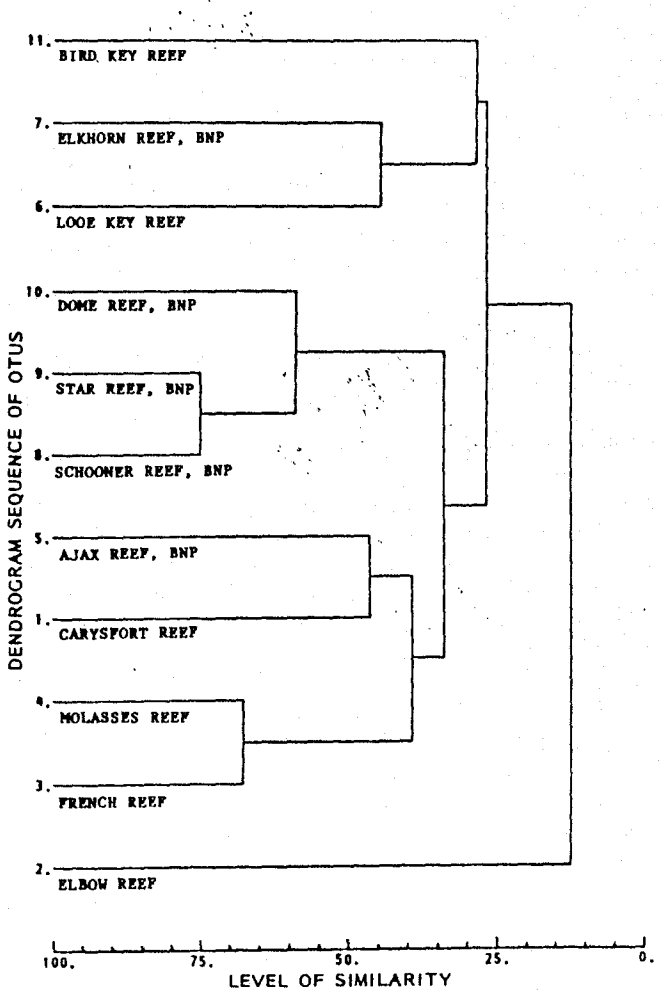


Figure 21. Similarity of coral fauna on Florida reefs using group average sorting and Czekanowski's coefficient.

similarity of coral fauna at various reefs. Some reefs have received much more intensive study than others; therefore, inter-reef comparisons cannot be drawn. For example, in Table 17 sampling was restricted to a specific site within a narrow depth range; hence, species diversity is limited. On the other hand, work at Bird Key Reef, Dry Tortugas, was intensive over a wide area and more than 50 species were identified (Jaap, in preparation). The same holds true for many other reef taxa. Small-scale studies report fewer species while large-scale (spatial and temporal) studies present long species lists. In some groups the species are so poorly known or so many species remain undescribed that it is truly impossible to evaluate total community species diversity.

7.5 SYMBIOSIS

Coral reefs exhibit a high level of species interaction; symbiosis contributes to the high diversity and productivity. There are many scales of symbiosis ranging from the microscopic (zooxanthellae-coral) (Figures 22 and 23) to macroscopic (cleaner shrimp-anemones-fish). It also includes commensalism, mutualism, and parasitism. Numerous organisms display some form of symbiotic relationship in coral reefs. One of the most dramatic forms of symbiosis is the fish-cleaning station. Several associations have developed to take advantage of this resource. One example is the cleaner shrimp, *Periclimenes pedersoni* (Chase). The shrimp lives in a host anemone; various anemones may serve as host, and the shrimp may move from one anemone species to another. *Condylactis gigantea* (Weinland) and *Bartholomea annulata* (LeSueur) are common hosts to *P. pedersoni*. The shrimp attract fish to clean by waving their antennae. The fish come to the anemone, and the shrimp swim to the fish and clean the mouth and gills. Another cleaning relationship involves the cleaning gobies *Elactinus oceanops* and *Gobiosoma genie*. These small gobies establish cleaning stations, usually around a specific coral, but sometimes a few fish form a collective station and cooperate in the cleaning. A fish requesting a cleaning approaches the station and displays a particular behavior to receive cleaning. Upon the displayed signal, the goby swims into the mouth, gill chamber, and around the fish body to remove parasites, fungi, algae, and necrotic tissue. Limbaugh (1961) reported that cleaning symbiosis was very important in coral reef communities. Bruce (1976) and Patton (1976) reported on associations of living corals and crustacean commensalism in coral reefs with most of the emphasis on Pacific reefs.

Organism interactions in a coral reef are also complex and highly developed. Some are obligate while others are mostly by chance. Patton (1976) wrote, "Corals exceed all other invertebrate groups in the diversity of forms and numbers of species to which they play host." Food and shelter are the major factors attractive to associates. The coral skeleton offers an especially good niche for smaller organisms to escape predation. Numerous sponges, polychaetes, bivalves, and sipunculids find habitat in the base of corals. Other

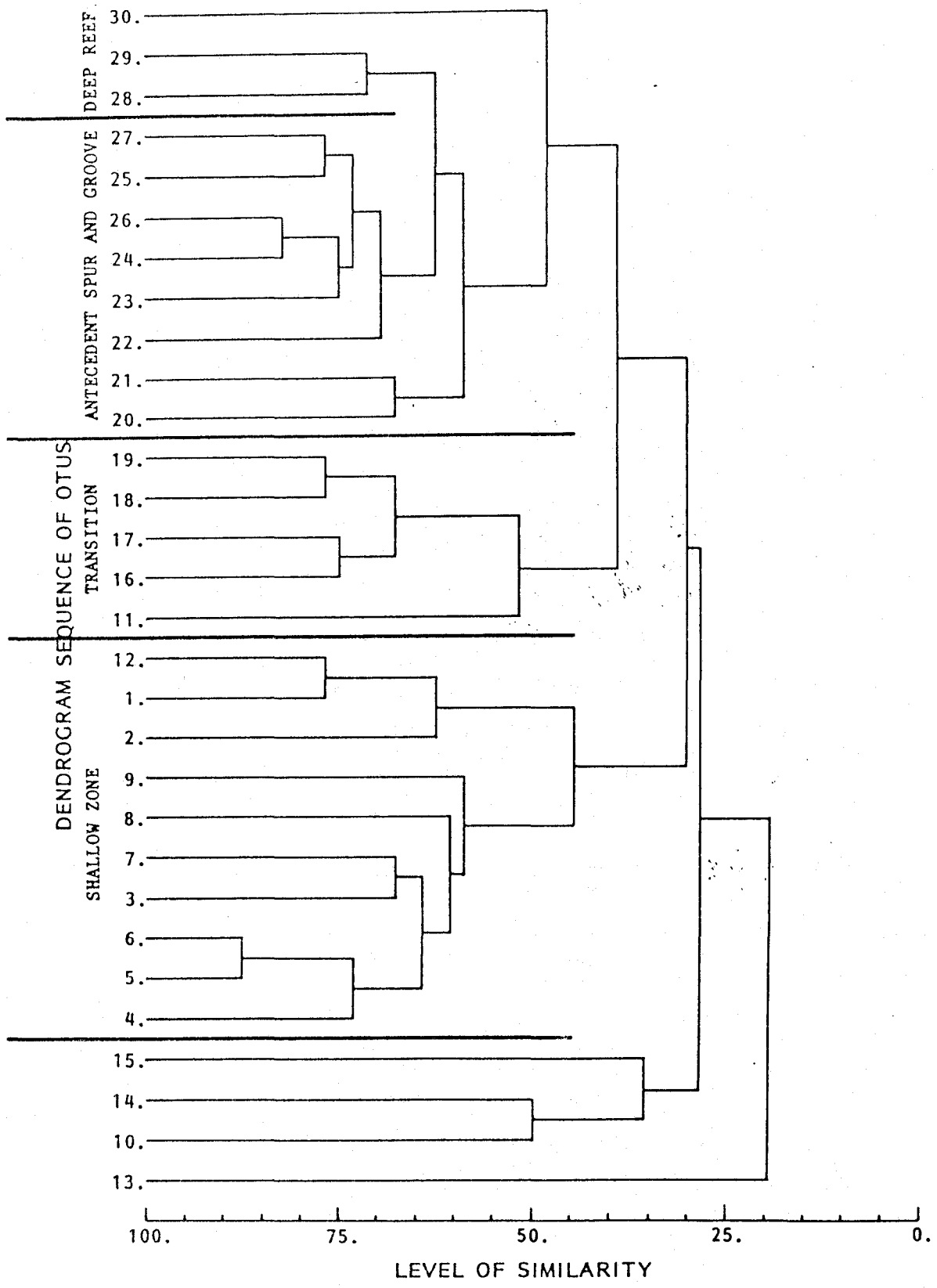


Figure 20. Classification of Bird Key Reef and Dry Tortugas based on abundance of stony corals using group average sorting and Czekanowski's coefficient.

BULLETIN OF MARINE SCIENCE, 69(3): 1149–1173, 2001

PARTIAL MORTALITY OF MASSIVE REEF-BUILDING CORALS: AN INDEX OF PATCH REEF CONDITION, FLORIDA REEF TRACT

Robert N. Ginsburg, Eberhard Gischler and William E. Kiene

ABSTRACT

Patch reefs are by far the most numerous reef type of the Florida Reef Tract. As they occur along the inner shelf, they are the nearest reefs to potential anthropogenic impacts from the islands of the Florida Keys by runoff of pollutants, fishing, boating and diving. Massive corals of four genera (*Montastraea* spp., *Diploria* spp., *Siderastrea siderea* and *Colpophyllia natans)* are the major reef builders of the patch reefs distributed discontinuously along some 200 km between the latitudes of Miami and Key West. To assess the condition of this coral community, we estimated and measured percent dead tissue of 3232 colonies by species and size on 22 shallow patch reef sites. Most colonies have diameters between 10–60 cm; those that are larger, to 300 cm, usually occur in clusters, which provide sheltered cavities for fishes and lobster. The size distributions of all but one of the nine species examined are skewed toward the smaller sizes. The smaller number of larger colonies is believed to be the result of the cumulative effects of disease, bioerosion, and removal by storm waves. For colonies <1 m in diameter, we made visual estimates of percent dead tissue by thirds (< 1/3, 1/3–2/3, >2/3) of each colony. Large variations are the rule at most sites and between sites. However, of all colonies combined 74% have less than 1/3 dead tissue, with only a small standard deviation, and cluster analysis revealed no major spatial variations. Overall, species of *Diploria* have less dead tissue than most other species and *M. annularis* generally has more than other species. The amount of dead tissue on clusters of colonies >1 m was measured by the line point intercept method of Loya (1978) along radial transect lines. It shows the same large variations within and between reefs as found for the smaller specimens. However, the amount of dead tissue on 60% of the 65 clusters measured is between 40–70%, much larger than on smaller colonies. The amount of dead tissue in the clusters in the Middle and Lower Keys is significantly higher than for clusters off the Upper Keys (Key Largo-Elliot Key) according to the Kruskal-Wallis analysis of variance. Given the overall marginal conditions for reef corals in the Florida Reef Tract—periodic low or high temperatures; periodic high turbidity, locally unfavorable water quality—we believe that the condition of massive corals does not show clear evidence of direct anthropogenic impacts. Our results do indicate the negative impacts of storms and of locally unfavorable water quality either in the nearshore zone or from the effluent of shallow, lagoonal Florida Bay.

Numerous reports of declines in the biota of coral reefs worldwide have prompted widespread concern about the future of these ecosystems (Brown, 1987; Grigg and Dollar, 1990; Glynn, 1991; Williams and Bunkley-Williams, 1990; Ginsburg, 1994; Hodgson, 1999). Of special concern to the United States and the State of Florida are the declines reported for Florida's reefs, as they are so valuable as a tourist attraction, an educational resource, and for recreational and commercial fishing. In addition to the direct impacts of users by divers, snorkelers, boaters, sport and commercial fishers, the wastes from the large and expanding population on the nearby Florida Keys and mainland are possible contributors to these declines (LaPointe and Clark, 1992; Porter and Meier, 1992; Hudson et al., 1994; Chiappone and Sullivan, 1997).

Most reports of declines in reef-building corals in Florida summarized below come from bank-barrier (shelf-margin) reefs. For the much more numerous patch reefs, which

dominant keystone species. *Siderastrea siderea, Diploria* spp., and *Colpophyllia natans* are also important. On the bank reefs, dominance and importance varies among reef zones with great variability between reefs. On reef flats *Porites astreoides* and *Diploria clivosa* are dominant; *Porites porites* and *Acropora cervicornis* are also important. Temporal stability in this zone is poor; hence, the existence of the arborescent species is often transitory. The shallow spur and groove zones are dominated by *Millepora complanata* and the zoanthid *Palythoa* sp. These species thrive in the turbulent conditions around this zone. In deeper spur and groove areas *Acropora palmata* is found to be the dominant and keystone species. Occasionally on some reefs the *A. palmata* zone extends onto the reef flat. This is especially true where the reef flat is deeper than 1-2 m.

On the flanks of the spurs a set of species that favor vertical orientation is conspicuous. This includes several species of *Mycetophyllia* and *Agaricia agaricites*. In the buttress-forereef zone the seaward portion of the spur and groove formation often continues as low relief features into deeper water. *Montastraea annularis* is of prime importance. Other important species include *Acropora cervicornis, Diploria* spp., *Colpophyllia natans, Agaricia agaricites*, and *Meandrina meandrites*. The diversity in this zone is often high. The physical extremes are moderated by depth, and biological interaction is much more significant in affecting community structure.

In the general sense the structure of the entire community can be envisioned, but in fact there is no field study that has quantitatively defined all the biota from a coral reef community. The autotrophic elements are represented by calcareous, crustose coralline, fleshy algae, and the other benthic organisms that contain producer organisms (zooxanthellae) within their tissues: corals, anemones, zoanthids, and sponges. The producers are also represented by a blue-green endolithic algae within the upper levels of living Scleractinia skeletons. All of the above have the function to fix carbon on the reef. The phytoplankton provide limited input; adjacent seagrass and benthic algae add to the carbon budget. Production is portioned into a number of categories. The carbon fixed within the zooxanthellae is conserved within the host or exported as a secretory product: mucus that is an energy source. The herbivore or primary consumer category is complex. Some of the better known herbivores include parrotfish (Scaridae), surgeonfish, tangs (Acanthuridae), and the sea urchins (*Diadema antillarum* and *Eucidaris tribuloides*). Various other organisms also are herbivores. Secondary consumers include those organisms that feed primarily on herbivore consumers. This includes a wide range of fish and invertebrates. There may not be great discrimination by the carnivore on prey selection; they may indiscriminately feed on carnivore, omnivore, and herbivore elements. Some known secondary consumers include the butterfly fish (Chaetodontidae) and fireworm (*Hermodice carunculata*; Plate 18b), which are obligate coral predators. Higher level consumers include larger predatory fishes: grouper (Plate 23b), jewfish, and barracuda. These fishes tend to range widely over numerous reef habitats and forage on prey as opportunity occurs. The omnivores include a number of crustaceans and echinoderms that scavenge plant and animal material. Planktivores include the corals, zoanthids, polychaetes (*Spirobranchus giganteus*; Plate 8b) and basket star (*Astrophyton muricatum*). The corals, as noted in Chapter 4, have a trophic structure that is species dependent. Other organisms are presumably more dependent upon a single resource, e.g., the basket starfish feeds exclusively on plankton.

Community structure of the corals appears to be physically controlled by depth, light, substrate, wave forces, sediment, and temperature. In a dendrogram (Figure 20) of Bird Key Reef (Figure 19), Dry Tortugas, the pattern is consistent with a change of species associations of a few opportunistic species that settle and exploit this region; but the physical extremes often make this area unsuitable for coral habitation. The dendrogram displays low similarity and weak linkage in this portion of the reef. In the moderate depths is a set of species that displays a wide range of distribution, but localized abundance patterns. This is presumably the result of microhabitat preferences, larval settlement, and competition among the other community elements. The similarity found in the dendrogram indicates that these species groups are bound together in a more organized manner than those species found in the shallower portions of the reef. The deepest portion of Bird Key Reef exhibited a unique set of species not found in any other portion of the reef; hence, the dendrogram set this coral association off by itself. The pattern displayed in patch reef communities is much less defined, and depth differences are moderate; hence, the random spatial dispersion usually makes the patch reef a community of greater similarity than that found in the bank reef.

7.4 DIVERSITY

Species diversity of the coral reef communities found off southeast Florida is a difficult parameter to estimate. Coral reefs in general have been described as the most diverse marine biological entities in the biosphere. They have been likened to the tropical rain forest with its multi-canopy of producers: high biomass, rapid turnover, and recycling of limiting nutrients. Physiography is often multilayered, e.g., in the *Acropora palmata* community (Plate 16a) the branches form layers, while smaller corals and other benthos live in the shadow of the elkhorn coral. Numerous other organisms live on, within, or under this coral association. Glynn (1964) reported that six species of crustaceans and echinoderms lived in or around the *A. palmata* community in Puerto Rico (*Gonodactylus oerstedii, Domecia acanthophora, Petrolisthes galathinus, Echinometra lucunter, Holothuria parvula*, and *Ophiothrix angulata*).

The diversity of a community is related to the complexity of the trophic relationships of the habitat (Hutchinson 1959; Paine 1966). Species diversity has developed into polarized theology. Pielou (1966) advo-

occur in the 5–10 km between the bank barrier and the islands of the Florida Keys for some 200 km. (Fig. 1), there are thorough descriptions of the benthos including coral cover and species diversity, but little or no published information on the condition of the coral communities. These patch reefs are widely used by commercial and sport fishers, by recreational divers and snorklers and by teachers and their students. As most patch reefs are closer to the populated islands of the Florida Keys, they should show more of any effects of land-based impacts than the bank barrier reefs. This combination of nearly no information on coral condition of patch reefs and the chance to assess the responses of the same reef type to variations in natural and anthropogenic impacts led to the research whose results are reported here.

The most reliable indications of declines in coral communities come from repeated assessments or revisits to reefs previously surveyed (Davis, 1982; Dustan and Hallas, 1987; Porter and Meier, 1992; Hughes, 1994). The lack of significant previous data on the condition of the corals of Florida Keys patch reefs led us to develop a method of instantaneous assessment (Ginsburg et al., 1996). This field-oriented approach uses visual estimates of the amounts of dead surfaces of massive corals by species and size. Our use of partial mortality followed earlier works by Endean et al. (1988), Gomez et al. (1994), and Diaz (1995). Another approach by Dustan (1994) assessed the incidence of damage to colonies. They reported that 60% of the nearly 10,000 colonies examined showed signs of physical or biological stress. Recently, Lewis (1997) used this same method of estimating partial mortality of *Siderastrea siderea* along a gradient of eutrophication in Barbados.

Previous Information on Coral Condition of Florida Reefs.—Most, but not all, of the well-documented examples of declines in corals come from bank-barrier reefs. Dustan and Hallas (1987) found a decline in *Acropora palmata* between depths of 10–21m at Carysfort Reef (Fig. 1) over a period of 8 yrs. From repeated photographs of quadrats 4.5 m^2, Porter and Meier (1992) reported significant declines in coral cover over a period of 7 yrs at Carysfort Reef (7–33%) and at Looe Key Reef (13–44%), while for the same period at Ball Buoy reef, cover increased some 30%. Jaap and Sargent (1994) summarized the repeated loss of *A. palmata* at the Dry Tortugas since 1881. Chiappone and Sullivan (1997) found generally low coral cover, <20%, of *A. palmata* in their assessment of 20 bank barrier reefs. Lirman and Fong (1995, 1997) documented the effects of storms on this same coral. Declines in *Acropora cervicornis* are more widespread than in *A. palmata* (Davis, 1982; Roberts et al., 1982; Jaap et al., 1988, pers. comm., 1998; Dustan 1994).

Of the several studies of massive corals, only a few provide information on condition of colonies, which is relevant to this study. The only well established example of a major decline in massive corals of patch reefs is the report of the nearly complete death of many of the giant colonies of *Montastraea annularis* at Hen and Chickens Reef off the Matecumbe Keys (Fig. 1), as a result of an episode of unusually cold water from Florida Bay in 1969–70 (Hudson et al., 1976; Walker et al., 1982; Roberts et al., 1982). Hudson (1981a) used the response of transplants of *M. annularis* to show that the absence of this species from nearshore areas is the result of natural aperiodic heating and chilling of the water.

Purposes of the Study.—The primary purpose of this research was to explore the use of partial mortality of massive corals by species and colony size as a measure of condition and provide data that could be used for comparison with other areas. Initially, we

Chickens Reef. Wells et al. (1973) reported that some corals were best classified as producers based on P/R (productivity/respiration) ratios being greater than one.

Temperature is related to solar radiation impinging on the water column and the influence of the Gulf Stream or Florida Current. While reef corals have been described as stenothermic (Wells 1957b), many species are very tolerant of temperature variation (Mayer 1914, 1916, 1918). Reef corals flourish (optimum physiological conditions) best between 25° and 29° C. Coral reef development is reported to be limited by low temperatures. This was proposed by Vaughan (1919) for Florida. He reported that corals did not build reefs where temperatures fell below the 18° C minimum for prolonged periods. The growth and demise of staghorn reefs at the Dry Tortugas are related to temperature control. During favorable periods these populations proliferate, but occasionally a cold winter reduces temperature below tolerance levels and mass mortality occurs (Porter et al. 1982). Within a decade, if mild conditions prevail, the populations recover. Temperature data in Figures 6-11 compared recent data with that from the early part of this century. The data imply no major change in climate.

It is apparent that temperature is one of the major controls of reef development off southeast Florida (Roberts et al. 1982). Another source of coldwater stress is from occasional upwelling from sources beneath the Florida Current. These stratified layers occasionally cause localized fish kills. Heat-related stresses in summer usually occur during midday when spring low tides coincide with calm wind conditions (Plate 24b). The shallow reef flats suffer from thermal stresses manifested in zooxanthellae expulsion. Ultraviolet light may also be involved with this phenomenon. As water depth is reduced, the UV light may have sufficient strength to be toxic and physically burn the tissues (Jokiel and York 1982).

Salinity is controlled by precipitation, evaporation, and runoff after major rainfall over adjacent land areas. Salinities are usually in the oceanic range. Table 9 reported ranges from 33.1 to 38.6 ppt. Jones (1963) reported some diurnal changes in a time series from Margot Fish Shoal off Elliott Key. Salinity does not normally pose a threat to the reefs. After hurricane rains, however, there is a potential for dilution due to runoff. The only reported possible salinity-related phenomenon was the 1878 Tortugas "blackwater," which was reported to have killed significant populations of corals. Mayer (1902) reported that a great number of the *Acropora* reefs were devastated by this event. It is suggested that this was a glut of freshwater runoff from the Everglades or a toxic phytoplankton bloom. There is no documented evidence to sustain either hypothesis. In other parts of the Caribbean, particularly the Greater Antilles and other high islands (e.g., Roatan) with mountain ranges, freshwater runoff is a significant threat to nearshore coral reefs. Goreau (1964) reported that freshwater runoff killed corals in Jamaica following a hurricane. Wells (1956, 1957a) reported that reef corals tolerated 27-40 ppt, and that optimal limits were 34-36 ppt.

Tidal conditions off the southeast coast of Florida were presented in Table 8. All ranges are less than 1 m. Tidal conditions only pose a threat to the shallower portions of the reef flat and spur and groove zones. Reef emergence rarely occurs except under synergistic meteorological influences. When spring low tides occur at or near midday during the summer, thermal heating can occur (Plate 24b).

Dissolved oxygen is dependent upon photosynthesis and respiration of benthic organisms. Temperature and salinity control the saturation level of oxygen in the water. Studies by Vaughan (1914d), Mayer (1918), Yonge and Nicholls (1931), Smith et al. (1950), and Jones (1963) reported that oxygen is not truly a limiting factor for corals under most circumstances. Oxygen remains in supersaturation during most of the day. Jones (1963) reported that the diurnal range was from 90% to 125% saturation during the summer.

Water column pH is influenced by organic metabolism. Studies by Jones (1963) and Jaap and Wheaton (1975) reported pH values of near 9. It is not a limiting factor under most circumstances.

7.3 COMMUNITY STRUCTURE

Coral reefs off southeast Florida have developed over the past 5,000-7,000 years. It is presumed that "survival stocks" living in what is now deeper water during the Wisconsin ice age were the seed populations for replenishment of the reefs as the sea level rose during the Holocene transgression. Some evidence for this is found in terraces seaward of some of the major reefs (Middle Sambo and Sand Key Reefs). These were probably active constructional reefs during a lower sea level stand which were drowned as sea level rose rapidly. The fossil barrier reef off Broward and Palm Beach Counties also provides credibility to this theory (Lighty 1977). Since the origin of the recent reefs, organisms have had sufficient time to develop into complex communities. They display all levels of complexity in their structure, diversity, interactions, competition, and trophic relationships.

In terms of abundance, dominance, and diversity, various elements display certain characteristic patterns. The sessile benthos is the most stable and best suited for time series studies. The mobile benthos, plankton, and nekton exhibit properties that make it difficult to make time series comparisons. The significance is that although some organisms are essential to the reef, others may be important, but have not been studied or have such radical seasonal variability that they are not a good indicator of reef vitality. Most of the primary framework coral species have a relatively long lifespan and, once established, are successful in competing for resources. These are keystone species in that they build the reef and create many niches for other biota. Table 29 details abundance measurements conducted at Elkhorn Reef. Additional information on the abundance and densities of stony corals at a number of coral reefs from the reef tract appears in Tables 11, 13-15, 17, and 19. In the patch reef it is apparent that *Montastraea annularis* is a

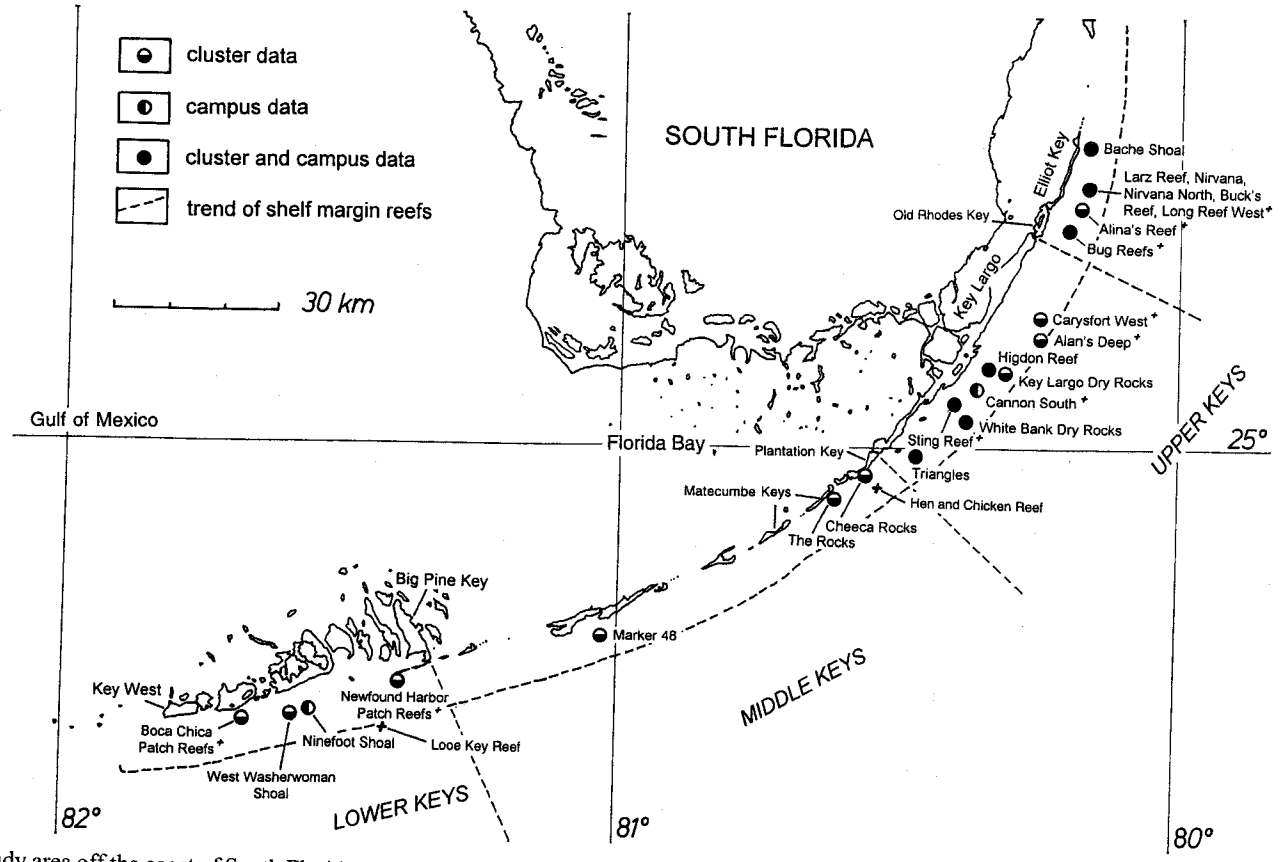


Figure 1. Study area off the coast of South Florida. The study area is divided into four zones based on variation in major natural impacts. Upper and lower Keys reefs are protected from unfavorable waters from Florida Bay and the Gulf of Mexico by a nearly continuous backstop of islands. Reefs of the middle Keys are not protected from these waters. Upper Keys are subdivided into two zones, the northern of which was passed by Hurricane Andrew (1992) and tropical storm Gordon (1994). Reefs, which were given names for this study, are indicated with asterisks.

CHAPTER 7

CORAL REEF ECOLOGY

7.1 INTRODUCTION

Wells (1957a) succinctly defined the nature of the coral reef as a "deterministic phenomenon of sedentary organisms with high metabolism living in warm marine waters within the zone of strong illumination. They are constructional physiographic features of tropical seas consisting fundamentally of a rigid calcareous framework made up mainly of interlocked and encrusted skeletons of reef-building (hermatypic) corals and calcareous algae. The framework controls the accumulation of sediments on, in, and around itself. These sediments are derived from organic and physical degradation of the frame and organisms associated with the reef constructors and have bulk ten or more times as great as the frame itself. The coral reef biotope is a facies of the marine tropical biochore, and its essential fauna and flora consists of corals and calcareous algae, which dominate in numbers and volume and provide the ecological niches essential to the existence of all other reef-dwelling animals and plants. In addition, there is an associated fauna and flora of other sedentary organisms which may be represented by relatively few species, and there is also the epifauna and epiflora of associated commensals, symbionts, and parasites living on and within the essential and associated organisms, and finally, the mobile fauna of benthic and nektonic species. Both physically and organically, reefs are complicated structures and are the result of a near balance of constructive and destructive forces. The constructional forces are largely organic, the accumulation of the calcareous skeletons of corals, calcareous algae, foraminifera, mollusks, etc., roughly in that order of importance. . . . Destructive and degradational forces tending to break down the stout framework of reefs are exemplified in the ceaseless breakdown of coral, algal, and molluscan skeletons and reef rock by the normal life activities of a wide variety of perforating, boring, and dissolving algae, sponges, mollusks, worms, and echinoids . . . . A more obvious, but no more important, destructive agency is wave action . . . [including] wind-driven waves, which during hurricanes strike prodigious hammer blows on reefs."

That which Wells (1957a) reported is still valid. Detailed investigations into various ecological functions have increased our understanding and appreciation of the coral reefs in general. Today, Florida's coral reefs are probably one of the most visited reef systems in the world, yet the life history of many species is still poorly understood. The recent increase in coastal development and sport diving has generated concern about the vitality of the coral reefs. Since very little early baseline ecological information is available for comparison, qualitative subjective statements are often offered in support that the reefs are deteriorating. The most significant impacts on the Florida coral reefs are, however, caused by natural events over which man has no control.

7.2 PHYSICAL-CHEMICAL ENVIRONMENT

The substratum for establishment of a coral reef must be rock or consolidated materials. Shinn et al. (1977) reported that the reefs they cored in Florida were established on a basement of Pleistocene reef facies, fossil mangrove, and lithified cross-beaded quartz (old sand dunes). The initial settlement of pioneering species is followed by successional stages during which the genesis for creation of the reef is established. Sheppard (1982) discussed the evolution of reefs based on data from the Red Sea and Hawaii and noted that about a 50-year period was required for a coral reef community to attain the fourth (final stage) or binding-of-sediment phase. Florida reefs are in various phases of development; some have reached considerable development while others are either juvenile or have suffered impacts denying them full development.

Most coral reefs off southeast Florida are found in depths of <43 m. Beyond these depths the substratum and physical environments are unfavorable to the existence of hermatypic reef-building Scleractinia. It should be noted that where the physical environment is favorable in other areas of the Caribbean (Bahamas, Belize, Jamaica), a set of deep reef Scleractinia are found colonizing the escarpment faces. These communities are found as deep as 70-80 m. Off southeast Florida this type of environment is, for the most part, nonexistent. A deep reef was recently found in 60- to 90-m depths west of the Dry Tortugas. Few details are available at this time. Sclerosponges are also a conspicuous element of deep reef communities; these are not reported from Florida reefs. Dustan et al. (1976) discussed the factors limiting sclerosponges from Florida.

Light is probably one of the most significant environmental considerations controlling coral reef development in general. Light is necessary for the symbiotic relationship between the coral and zooxanthellae. Any factor which reduces the amount of solar radiation impinging on the coral surface will affect growth and nutrition. Reef corals are almost universally phototropic. Wells (1957a) reported that species richness at Bikini Atoll was closely controlled by solar illumination and indirectly influenced by temperature and oxygen. General solar radiation characteristics in Florida were discussed in Chapter 2. The nature of light is significant. Jokiel and York (1982) reported that specialized pigments in coral tissues filter the potentially dangerous ultraviolet portions of the spectrum, thus allowing the corals to occupy the shallow waters without being harmed. The zooxanthellae are able to compensate for changes in radiation quality and quantity through changes in their pigments. Wethey and Porter (1967) reported that reef corals were able to compensate to a depth of 25 m without loss of autotrophic efficiency. Kanwisher and Wainwright (1967) reported on respiration and productivity in Florida reef corals from a study at Hens and

assumed that, by examining the massive corals on shallow patch reefs along some 200 km of the Florida Reef Tract, our results would reveal variations in partial mortality related to variations in natural and anthropogenic impacts. From our examination of the numerous patch reefs we found that there are two types and they are not represented equally along the study area. Accordingly, we had to limit the comparisons to the reef type most widely distributed.

Study Area and Setting

The Florida Reef Tract and Its Reef Types.—In this report, 'Florida Reef Tract' is used as proposed by Vaughan (1914) to include the entire assemblage of reefs and intervening environments extending from the Florida Keys to the seaward limit of reef growth. Others (Chiappone and Sullivan, 1997; B. Causey, pers. comm., 1997) would limit the use to the arc of bank barrier reefs (outer reefs, shelf-margin reefs).

The Reef Tract can be subdivided into three sections based on inferred water quality, continuity of the Keys and abundance of reefs. The Upper Keys section is characterized by an almost continuous backstop of islands of Pleistocene reef limestone (Elliot Key, Old Rhodes Key, Key Largo, and Plantation Key) and by the most numerous reefs, both patch reefs and the bank-barrier variety, of all three sections. In the Middle Keys, only about half of the backstop is composed of islands of Pleistocene limestone and Holocene sediments; the rest are shallow passes and channels that lead into Florida Bay and the Gulf of Mexico. Only a few patch reefs and no well developed bank-barrier reefs are present in this section, probably as result of the influence of poor water quality and frequent movement of the bottom sands (Ginsburg and Shinn, 1964, 1994; Smith, 1994). The Lower Keys, like the Upper, have a backstop of almost continuous islands of Pleistocene limestone with only extremely shallow channels separating them. Both bank-barrier and shallow patch reefs occur here, but they are less numerous than in the Upper Keys section.

The two major reef types are illustrated schematically in Figure 2. There are only some ten to twelve, near-surface bank-barrier reefs with abundant living coral in the entire Florida Reef Tract (Shinn et al., 1989). They are separated by much larger areas of relict reefs or limestone pavement (Chiappone, 1996), here termed bank margin shoals. Patch reefs are found in the crescent-shaped zone, usually some 5–10 km wide, between the bank-margin and the Florida Keys; a few occur along the bank margin (Fig. 1). Figure 3 shows the area of most abundant shallow patch reefs off Elliot Key, where nearly 4000 individual reefs can be identified on aerial photographs (Marszalek et al., 1977).

Patch Reefs.—In Florida the term 'patch reef' is used for localized, elevated accumulations of corals, octocorals, and associated benthos. Marszalek et al. (1977) mapped the distribution of all patch reefs from Miami to Key West using aerial photographs and diver observations. They found more than 6000 dome- and linear-shaped examples ranging in size from a few meters to several hundred meters and with relief over the surrounding sea floor of generally less than 5 m. An overview of patch reefs was given by Jaap (1984) who focused on patch reefs, which rise to near the level of low tides from depths of 2–9 m. These shallow patch reefs vary widely in size (30–700 m according to Jaap, 1984), in shape (sub-circular, linear, amoeboid), and in abundance and spacing. Shallow patches are most abundant and closely spaced off Elliot and Old Rhodes Keys (Fig. 3) where Marszalek et al. (1977) report almost 4000 in number. Off Key Largo these authors found

the protection and conservation of their resources.

The impetus to preserve coral reef resources stems largely from their recognized economic value through tourist attraction and recreational opportunities. But the negative impact of recreational use (i.e., snorkeling, diving, boating, and fishing) on coral reefs has not been extensively investigated. Interestingly, although the taking of tropical fish for aquarium purposes is prohibited in all coral reef preserves, spearfishing is permitted in at least one and hook-and-line fishing is permitted in all. Impacts to fish population through disturbance by boating and diving alone could become significant. On extremely popular reefs, such as Molasses Reef in the Key Largo National Marine Sanctuary, as many as 20-30 boats with divers are often anchored at one time within a 4-5 ha area (NOAA-OCZM 1979). Specific studies at locations with such an extremely high level of use are not available. However, within Biscayne National Park, a 5-year study of eight selected patch reefs revealed little disturbance to fish populations where maximum annual use per reef ranged from 3,400-3,600 persons diving or snorkeling (Tilmant et al., in preparation).

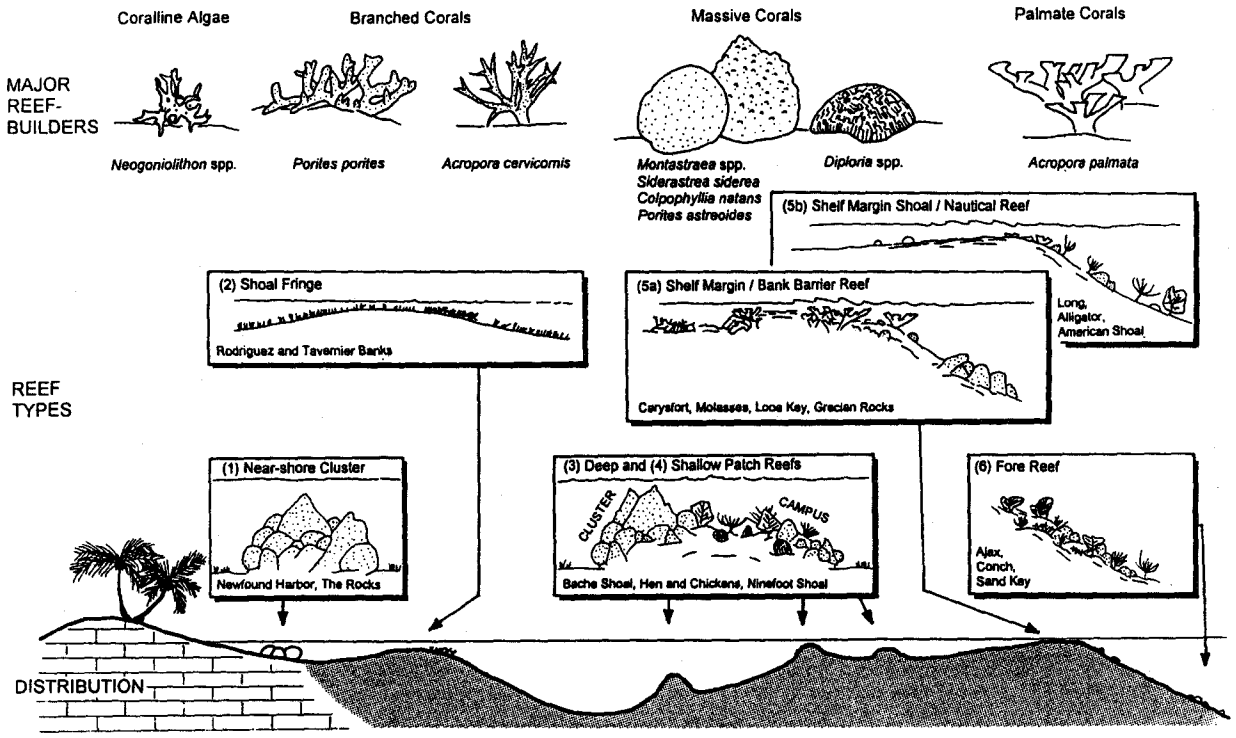
Past research on exploitation of reef fish stocks can best be described as gaining basic information on life histories, food habits, growth rates, and basic biology of important species, and on developing harvest techniques. Only recently have studies evaluating the ecological impacts of fishing activities begun to be reported (Campbell 1977; Davis 1977b; Tilmant 1981; Katnik, in press; Pauly and Ingles, in press; Bohnsack 1982).

The few studies available show that a limited number of reef fish are actually sought and comprise most of the sport and commercial harvest. Austin et al. (1977), after interviewing 4,275 recreational fishermen, reported that only four species groups (grunts, snappers, dolphin, and grouper) constituted almost the entire catch. Within the groups, gray snapper and yellowtail snapper accounted for 85% of the harvested snapper; white and bluestriped grunt, 97% of the grunts; and red and black grouper, 82% of the grouper. Thus, only six species made up about 80% of the total recreational catch. The National Park Service has recorded over 120 species of reef fish caught within Biscayne National Park (Dade County, Florida); however, 10 species accounted for more than 80% of the harvest.

The commercial harvest of fish from coral reef areas is almost entirely directed toward snappers (Lutjanidae) and groupers (Serranidae), although some tilefish (Branchiostegidae), jacks (Carangidae), and triggerfish (Balistidae) are harvested. A complete listing of commercially important reef species can be found in the U.S. Fishery Management Council's management plans for these fish in the Gulf of Mexico (Florida Sea Grant College 1979) and South Atlantic (South Atlantic Fishery Management Council 1982).

Within Biscayne National Park, a limited assessment of fishing impacts on reef fish populations was conducted by underwater visual surveys concurrently with fishermen's creel census (Tilmant 1981). During a 3-year period, fish catch rates varied inversely with the number of fishermen using park waters while reef fish populations remained relatively stable. Katnik (1981) found that of the reef flats surrounding the Pacific island of Guam, those with the highest fishing pressures showed a marked reduction in the large size classes of the most prized species. Also, some fishes of less economic importance were more abundant on heavily fished reefs than on reefs lightly fished (Katnik 1981). Bohnsack (1982) reported that he found significantly smaller piscivorous predator populations on Looe Key Reef (near Big Pine Key, Monroe County, Florida) than on either of the two similar reefs within the Key Largo National Marine Sanctuary. He attributed these differences to spearfishing on Looe Key and believed that the abundance of some remaining species on Looe Key Reef was affected by the larger predator loss.

In 1977 the United States passed the Fishery Conservation and Management Act, which extended jurisdiction over fisheries to 200 mi and called for establishing regional fishery management councils to develop specific long-range management plans for each coastal fishery resource within the Fishery Conservation Zone. In response to this legislation, the coral reef fishery resources within U.S. territorial waters are receiving much greater attention, and management plans for their conservation are being developed. The status of biological knowledge and application of fishery management principles to coral reef fish stocks was reviewed at a workshop on reef fishery management sponsored by the National Marine Fishery Service in October 1980 (Huntsman et al. 1982). The workshop proceedings succinctly summarized the requirements for such management. It is widely recognized that before coral reef ecosystems can be effectively managed, much basic data and many larger-scale multidisciplinary studies are required.



FLORIDA REEF TYPES: MAJOR COMPONENTS AND DISTRIBUTION

Figure 2. Major reef building elements, reef types, and reef type distribution in south Florida. Bank barrier reefs can be divided into well-zoned *Acropora palmata* reefs and low relief hard bottoms with scattered coral. Patch reefs consist predominately of massive corals either as cluster reefs of giant colonies of *Montastraea* spp. or as composite reefs composed of a campus of massive corals 0.2 to 0.5 m in diameter with localized clusters of giant *Montastraea* spp. The names of representative reefs for each reef type are given at bottom of each box and those that were examined in this study are listed in Table 1.

and Mojarras (Gerreidae) are among the most commonly observed species. Ballyhoo (*Hemiramphus brasiliensis*) can often be seen moving about just under the surface. In the quieter waters of the back reef, schools of small herring (*Harengula* spp.) are common.

Live Bottom

Live bottom communities are formed on broad areas of limestone outcrops occurring in relatively shallow water (2 m or less) within the protected reef zone. Coral growth may vary greatly in density over the area and often is mixed with seagrasses. The habitat generally has little relief or structure and is composed largely of octocorals, sponges, and small scleractinian corals. Only occasionally are large colonies of stony corals found and these often form an independent cluster.

Fish fauna of the live bottom is generally similar to that found on the top zone of patch reefs. A few notable differences include an increased tendency for tangs and surgeonfish to form large wide-ranging schools, an increased abundance of the large rainbow parrotfish, and frequently larger schools of white, Spanish, and Caesar grunts. An interesting species increase over live bottoms is that of the lantern bass. This small bottom-dwelling bass appears to prefer the broad rocky flats around turtlegrass beds and, occasionally, replaces the similar harlequin bass found more frequently on patch reefs.

Bank Reefs

Bank reefs (Figure 18) form elongated discontinuous structures along the seaward edge of the reef tract. They rise to within a meter or less of the surface and have extensive reef flats supporting only sparse encrusting corals over their shallow zones. Seaward, they slope rapidly to depths exceeding 20 m.

Redlip and saddled blennies, small gobies, and other small bottom-dwelling species dominate the reef flat. Within the shallow spur and groove zone branched and fan octocorals become much more prevalent. Among dense branches of staghorn or elkhorn coral (*Acropora* spp.) are dusky and threespot damselfish, many species of grunts (*Haemulon* spp.), black margates, gray and schoolmaster snapper, sergeant majors, and Bermuda chub. Within the water column over the reef, bar jack, barracuda, and yellowtail snapper are easily seen.

The fish fauna of the deep spur and groove zone can be highly varied depending on depth and the amount of reef structure. Below the *Acropora* coral zone (deep spur and groove zone), however, the following become more prevalent: yellowtail damselfish, the rock beauty, butterfly fish, small groupers (i.e., hamlets, hinds, and graysby), yellowtail and redtail parrotfish, large puddingwives, and large scrawled filefish. With increasing depth, there is a distinct increase in *Chromis* (*Chromis cyaneus* and *C. multilineatus*), the longsnout butterfly fish (*C. aculeatus*), triggerfish (*Balistes* spp. and *Canthidermis sufflamen*), filefish (*Aluterus* spp.), jackknife-fish, schools of creole wrasse, and the blue parrotfish. Along the outer base (mixed hardgrounds) of the bank reefs (usually at depths of 20-30 m), large mutton snapper, grouper, and porgies (Sparidae) become more abundant. The tobaccofish (*Serranus tabacarus*) and sand tilefish (*Malacanthus plumieri*) can easily be found resting openly on the flat calcareous silt bottom in the mixed hardground and sediment zone.

In the deep reef zone the bigeye (*Priacanthus arenatus*) tends to replace the glasseye snapper (*P. cruentatus*) commonly found on the shallower reefs. Similarly, the cubbyu is replaced by the jackknife-fish, and hinds and graysby (*Epinephelus adscensionis*, *E. guttatus*, and *E. cruentatus*) are replaced by the coney (*E. fulvus*). The snowy grouper (*E. niveatus*) becomes prevalent at depths greater than 30 m. Over these deep reefs, the number of species of jacks (Carangidae) and mackerels (Scombridae) greatly increases. Also commonly seen are the large bar jack (*C. ruber*), rainbow runner (*Elagatis bipinnulata*), amber jack (*Seriola dumerili*), black jack (*Caranx lugubris*), bonita (*Sarda sarda*), and cero mackerel (*Scomberomorus regalis*). Cloud-forming schools of small herrings (*Jenkinsia* and *Sardinella*) are seen over the reefs at depths greater than 20 m during the day. At depths greater than 30 m, a third species of *Serranus*, similar in appearance to the tobaccofish, becomes common. The chalk bass (*S. tortugarum*) is found around small rubble mounds, coral outcrops, and rocks near the base of the reef. At this depth, a short search over the sand plain next to or between reefs will usually reveal a colony of garden eels (*Nystactichtys halis*). They have long, slender bodies and are found in large colonies where, each protruding vertically from its burrow, they form "gardens" of waving heads while feeding on plankton carried by the current.

The number of species described above in no way approximates the total number found within the coral reef habitats of Florida.

6.7 REEF FISH MANAGEMENT

Fish resources on the coral reefs of Florida and elsewhere are highly prized economically and are extensively utilized. Reef-fishing activities commonly include commercial hook-and-line harvest, commercial trapping, sport angling, spearfishing, tropical fish collecting, and scientific collecting. The importance of reef fish resources and their economic potential have been described in a number of summary reports (Camber 1955; Strusaker 1969; Swingle et al. 1970; Stevenson and Marshall 1974; Bullis and Jones 1976; Klima 1976). In addition to descriptive reports of fishing activities, a number of exploratory studies and fishing development projects have been completed for reef fish resources (Brownwell and Rainey 1971; Munro et al. 1971; Kawaguchi 1974; Wolf and Rathjen 1974; Stevenson 1978). Little information, however, is available concerning the impact of commercial or recreational use on reef fish populations or on reef fish management. Fairly substantial sections of Florida's coral reefs are now designated as local, State, or National preserves and are being managed for

nearly 1600 examples, but only 50 off the Middle Keys. In the Lower Keys, they report 420 patch reefs of which fewer than 20 are as shallow as those in the Middle and Upper Keys.

Jaap (1984), Chiappone and Sullivan (1997), and Chiappone (1996) have reported quantitative inventories of the composition of nearly 20 patch reefs in south Florida. The reef-building corals are largely massive species varying widely in abundance, diversity and colony sizes. Coral cover is the highest of all Florida reefs, ranging from 8–61%, and half of the examples had 20% or more cover.

In this study we considered only shallow patch reefs whose surfaces are within a few meters or less of the level of low tides. Using size and relief of the massive corals, two main types of patch reefs can be identified (Fig. 2). 'Cluster reefs' consist almost entirely of giant colonies and coalesced colonies, 1–5 m in diameter, of *M. annularis* and/or *M. faveolata* with only occasionally other massive corals such as *S. siderea* and *Colpophyllia natans*. 'Composite reefs' usually have two or three subdivisions: (1) a campus of massive corals with abundant octocorals; which were it not on a elevated reef would be termed a hard ground community; (2) areas in which coral rubble and skeletal sands predominate; and (3) one or more localized clusters of giant colonies of *M. annularis or M. faveolata*. The corals of the campus are mostly less than 0.5 m in diameter and are distributed irregularly over the bottom in variable densities. They include most commonly *M. annularis*, *M. faveolata*, *M. cavernosa*, *Diploria strigosa*, *D. clivosa*, *D. labyrinthiformis*, *S. siderea*, *S. radians*, *Porites porites*, *P. astreoides*, *C. natans*, *Dichocoenia stokesii* and species of *Millepora*. Less common corals are *A. cervicornis*, *Stephanocoenia michelini*, *Solenastrea bournoni*, *Favia fragum*, *Manicina areolata*, *Meandrina meandrites* and species of *Mycetophyllia*. Among the most common octocorals are species of *Plexaura*, *Pseudoplexaura*, *Eunicea*, *Muricea*, *Pseudopterogorgia* and *Gorgonia* spp. The distinction between campus and cluster is comparable to the distinction between knob (cluster) and ledge (campus) for Bermuda patch reefs (Scoffin, 1972). Within each of the two types of patch reefs, there are further distinctions in size and depths (Table 1). We also assessed the massive corals of three bank-barrier reefs (Table 1). The shoal fringe build-ups built of the skeletons of *Porites furcata*, green and red algae (Fig. 2) were not examined.

To gain some idea of the relationships between campus and clusters, we made observations of belt transects for bottom types which could be identified from aerial photographs (1:1200) of the patch reefs of Bache Shoal (Fig. 4) and another area we named Nirvana (Fig. 1). For each bottom type, we made 10–12 belt transects, each 1×6 m, in which the massive corals and octocorals were counted independently by two persons. The abundance of areas of sea grass and of rubble was also estimated independently by two persons. The mean value of the two estimates was calculated to characterize the bottom types.

Table 30 (continued)

Species	Reef types and zones				
	Patch		Livebottom	Bank	
	Top	Outer Fringe		Shallow	Deep
Black grouper *Mycteroperca bonaci*		*			*
Harlequin bass *Serranus tigrinus*		*	*		*
Lantern bass *S. baldwini*			*		
Saucereye porgy *Calamus calamus*		*			
Jolthead porgy *C. bajonado*		*			
Great barracuda *Sphyraena barracuda*		*		*	
Sharpnose puffer *Canthigaster rostrata*		*			*

descriptions of some of the most common fish species follow.

Patch Reefs

On most patch reefs, fish occur in two distinct zones: top and outer. Species commonly seen over the coral rubble substrate of the reef top are bluehead and clown wrasses, the puddingwife, the slippery dick, and bicolor damselfish. The dusky and threespot damselfish staunchly defend small territories of algae-covered rocks. The cocoa damselfish is also abundant at some localities. Resting on coral rubble close to a crevice into which they can dart for cover are redlip blennies, the only species of combtooth blenny (Blenniidae) commonly found on Florida's coral reefs. Also near protective crevices are hamlets (*Hypoplectrus* spp.) of various colors. Scorpion fish (Scorpaenidae) can also be found frequently blending with coral rubble over the top of the patch reefs.

Wider ranging species typically seen moving among the oorals within the top zone are the surgeonfish (*Acanthurus* spp.); gray, French, and queen angelfish, white grunts, and striped, stoplight, and redband parrotfish. Frequently blue tang, ocean surgeons, and parrotfish (particularly the midnight parrot) will form large mixed or monospecific schools while ranging about the reef top. Common fish species typically found near coral heads, branching corals, or other outcrops on the top of patch reefs are the bluehead wrasse, sergeant major, tomtate, Caesar grunt, and Spanish grunt. The vertical standing trumpetfish and the slender filefish can usually be seen among the branches of the octocorals.

Around the outer edges of the patch reefs, the water depth is greater (8-10 m), and larger coral heads provide a varied and cavernous habitat. Along this outer zone larger predators such as grouper, particularly black grouper, red grouper, and Nassau grouper, mutton and gray snapper, and hogfish can be found. Close inspection of crevices and holes will commonly reveal sharpnose puffers, squirrelfish (*Holocentrus* spp.), small cardinal and flamefish (*Apogon* spp.), soapfish (*Rypticus* spp.), glassy sweepers, and, possibly, the green moray (*Gymnothorax funebris*). Clinging to coral heads are small neon and masked gobies. The neon goby is noted for its function as a parasite and mucus picker, or "cleaner," on large fish species. Gobies frequently establish "cleaning stations" into which larger fish will move, become quiescent, spread their opercula, and allow the cleaner fish to work freely through the gills and about the head. Juvenile angelfish and the juvenile Spanish hogfish have also been observed functioning as cleaners of larger fish on the reef (Thresher 1980).

Close to the bottom, among the corals along the outer edge of the patch reefs, the puddingwife and yellowhead wrasses become more abundant. Feeding more in the open along the reef edge are typically saucereye and jolthead porgies, spotted and yellow goatfish, redtail parrotfish, and angelfish. Close inspection along grassy areas will frequently reveal the small bucktooth parrotfish, blackear wrasse, and lizardfish (*Synodus* spp.). At the base of the corals on sandy substrate, nearly transparent bridled and goldspot gobies can be seen, as well as the harlequin bass. In open sandy areas immediately adjacent to the patch reef (but not on it), hovering gobies and yellowhead jawfish (*Opistognathus aurifrons*) can usually be seen protruding from their burrows.

The water column over the patch reefs usually does not support a large number of fish, but barracuda, bar jack (*Caranx ruber*), yellow jack (*C. bartholomaei*),

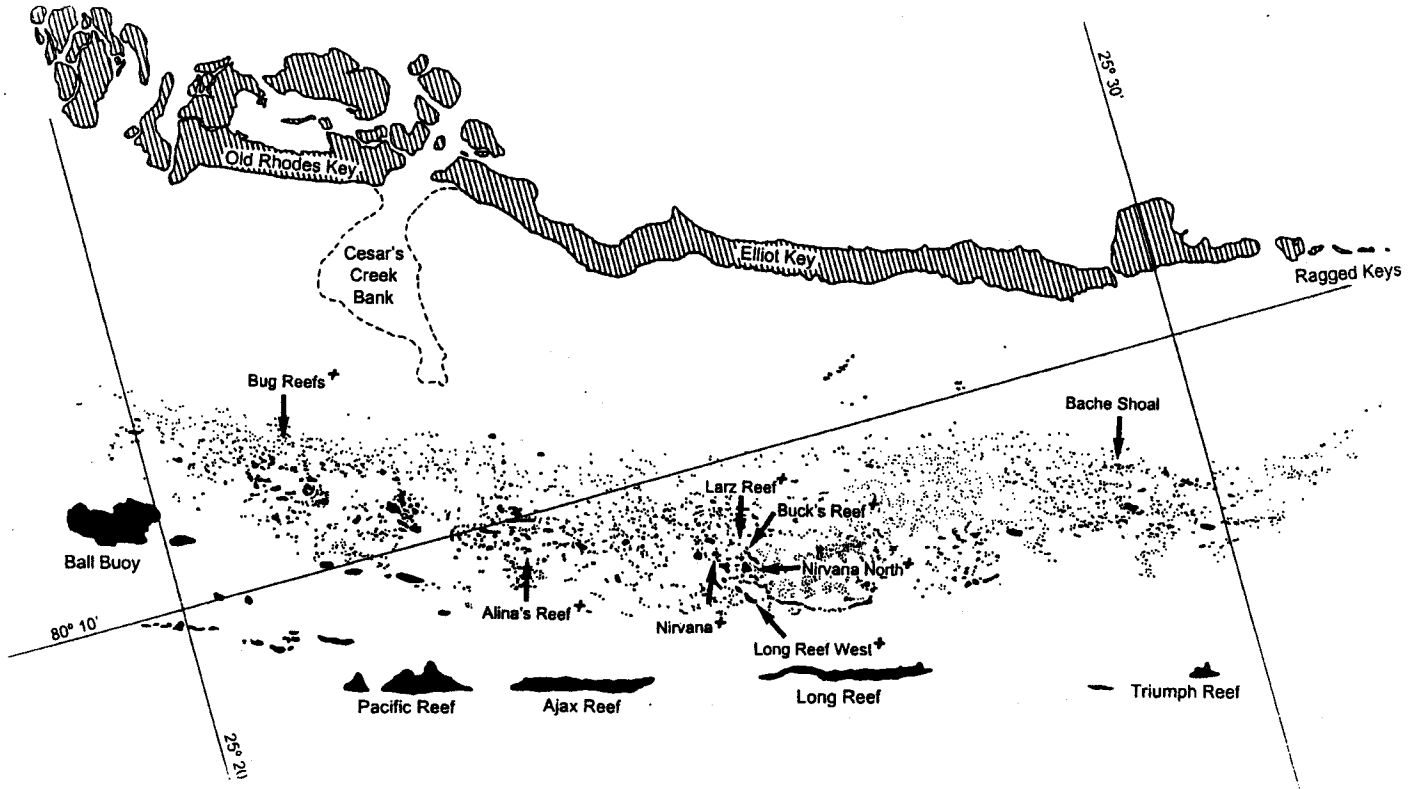


Figure 3. Patch reef belt off Elliot and Old Rhodes Keys traced from aerial photographs, scale 1: 48,000, National Geodetic Survey, NOAA. All the small black spots and dots indicate the locations of patch reefs, a total of nearly 4000. Triumph, Long, Ajax, and Pacific are bank-margin shoals composed predominantly of rubble and skeletal sands and or limestone pavements, with scattered corals (Burns, 1985). The only well-developed bank-barrier reef is Ball Buoy. Reefs, which were given names for this study, are indicated with asterisks.

Table 30 (continued)

Species	Reef types and zones				
	Patch		Livebottom	Bank	
	Top	Outer Fringe		Shallow	Deep
Smallmouth grunt *H. chrysargyreum*	*				*
French grunt *H. flavolineatum*	*	*	*	*	*
Spanish grunt *H. macrostomum*	*	*	*		*
White grunt *H. plumieri*	*	*	*	*	*
Bluestriped grunt *H. sciurus*	*	*	*	*	*
Bluelip parrotfish *Cryptotomus roseus*			*		
Midnight parrotfish *Scarus coelestinus*	*	*	*	*	*
Princess parrotfish *S. taeniopterus*					*
Blue parrotfish *S. coeruleus*		*			*
Striped parrotfish *S. croicensis*	*	*	*	*	*
Rainbow parrotfish *S. guacamaia*	*				
Queen parrotfish *S. vetula*	*				*
Redband parrotfish *Sparisoma aurofrenatum*	*	*	*	*	*
Redtail parrotfish *S. chrysopterum*	*	*	*		
Redfin parrotfish *S. rubripinne*	*	*			*
Bucktooth parrotfish *S. radians*		*	*		
Stoplight parrotfish *S. viride*	*	*	*	*	*
Jackknife-fish *Equetus lanceolatus*				*	
Cubbyu *E. umbrosus*		*		*	
Reef croaker *Odontoscion dentex*		*			*
Blue hamlet *Hypoplectrus gemma*			*		*
Barred hamlet *H. puella*		*	*		
Butter hamlet *H. unicolor*		*	*		*
Graysby *Epinephelus cruentatus*		*			*
Red grouper *E. morio*		*			
Nassau grouper *E. atriatus*		*			

(continued)

Table 1. Reef types and reef areas assessed in the Florida Keys (reefs that were named by the authors and cannot be found on nautical charts are marked with an asterisk). For exact location of the sites studied see the Appendix.

Reef type, reef area	distance to shore (km)	diameter (m)	depth surroundings (m)	depth top (m)	campus	cluster
(1) Marginal reefs						
Alan's Deep*	8.0	50	7	6	–	2
Key Largo D.R.	7.2	200	7	6	–	2
White Bank D.R.	8.4	150	7	2–6	2	3
(2a) Composite patch reefs						
Bache Shoal	2.8	30–60	4	1–2	4	6
Nirvana North*	5.2	20	3	1	–	2
Buck's Reef*	6.0	30	2	1.5	1	1
Cannon South*	4.4	50	7	1.5	1	–
Triangles	5.6	50	4	2	3	2
Nirvana*	5.2	150	7	1–2	2	6
Alina's Reef*	5.6	150	6	1–2	–	2
Long Reef West*	6.3	150	4	3–4	1	–
Higdon Reef	4.4	300	6	1.5	2	2
Sting Reef*	5.6	250	6	1.5	2	3
Marker 48	3.6	100	8	2	–	2
Ninefoot Shoal	4.5	50	7	5	1	–
West Washerwoman	4.6	150	9	0.5	–	4
(2b) Cluster patch reefs						
Carysfort West*	8.0	–10	2	<0.5	–	7
The Rocks	1.6	25	3	2	–	4
Cheeca Rocks	1.6	15	4	3-4	–	4
Newfound Harbor*	0.6	50–100	2	<0.5	–	5
Boca Chica*	0.8	20–50	3	1	–	4
Larz Reef*	5.2	30	4	1-2	–	1
Bug Reefs*	4.8	20	5	1	3	3

Methods: Assessing Coral Condition and Colony Size

The assessments were made between July 1995 and January 1996 by free diving from outboard-powered small boats 5–7 m long. In the Upper Keys (Fig. 1), reefs were selected to cover the geographic range of patch reefs and to include representatives of the major types. Off the Middle and Lower Keys where there are a limited number of patch reefs, all shallow examples were included. The location of each reef was determined with a GPS instrument whose uncertainty is approximately 60 m. At some reefs, more than one site was assessed either for corals of the campus or cluster, see Appendix.

The evaluation of corals in the campus areas was a census of massive corals only as listed above. We ignored the branched corals because they are not the major reef builders of these patch reefs, they are often transitory (Davis, 1982), and because estimates of their partial mortality is more

Table 30 (continued)

Species	Reef types and zones				
	Patch		Livebottom	Bank	
	Top	Outer Fringe		Shallow	Deep
Hogfish *Lachnolaimus maximus*		*			*
Clown wrasse *H. maculipinna*	*	*	*	*	*
Blackear wrasse *H. poeyi*			*		
Puddingwife *H. radiatus*	*	*	*		*
Bluehead wrasse *Thalassoma bifasciatum*	*	*	*	*	*
Schoolmaster snapper *Lutjanus apodus*	*	*			*
Mutton snapper *L. analis*		*			
Gray snapper *L. griseus*	*	*			*
Mahogany snapper *L. mahogoni*					*
Yellowtail snapper *Ocyurus chrysurus*	*	*	*	*	*
Yellow goatfish *Mulloidichthys martinicus*					*
Spotted goatfish *Pseudupeneus maculatus*		*	*		*
Glassy sweeper *Pempheris schomburoki*	*	*	*		*
Sergeant major *Abudefduf saxatilis*	*	*	*		*
Blue chromis *Chromis cyaneus*					*
Brown chromis *C. multilineatus*					*
Yellowtail damselfish *Microspathodon chrysurus*	*	*			*
Dusky damselfish *Pomacentrus fuscus*	*	*	*	*	
Beaugregory *P. leucostictus*		*	*		
Bicolor damselfish *P. partitus*	*	*	*	*	*
Threespot damselfish *P. planifrons*	*	*	*		*
Cocoa damselfish *P. variabilis*	*	*	*	*	*
Black margate *Anisotremus surinamensis*			*		*
Porkfish *A. virginicus*	*	*	*		*
Tomtate *Haemulon aurolineatum*	*	*	*	*	*
Caesar grunt *H. carbonarium*	*	*			*

(continued)

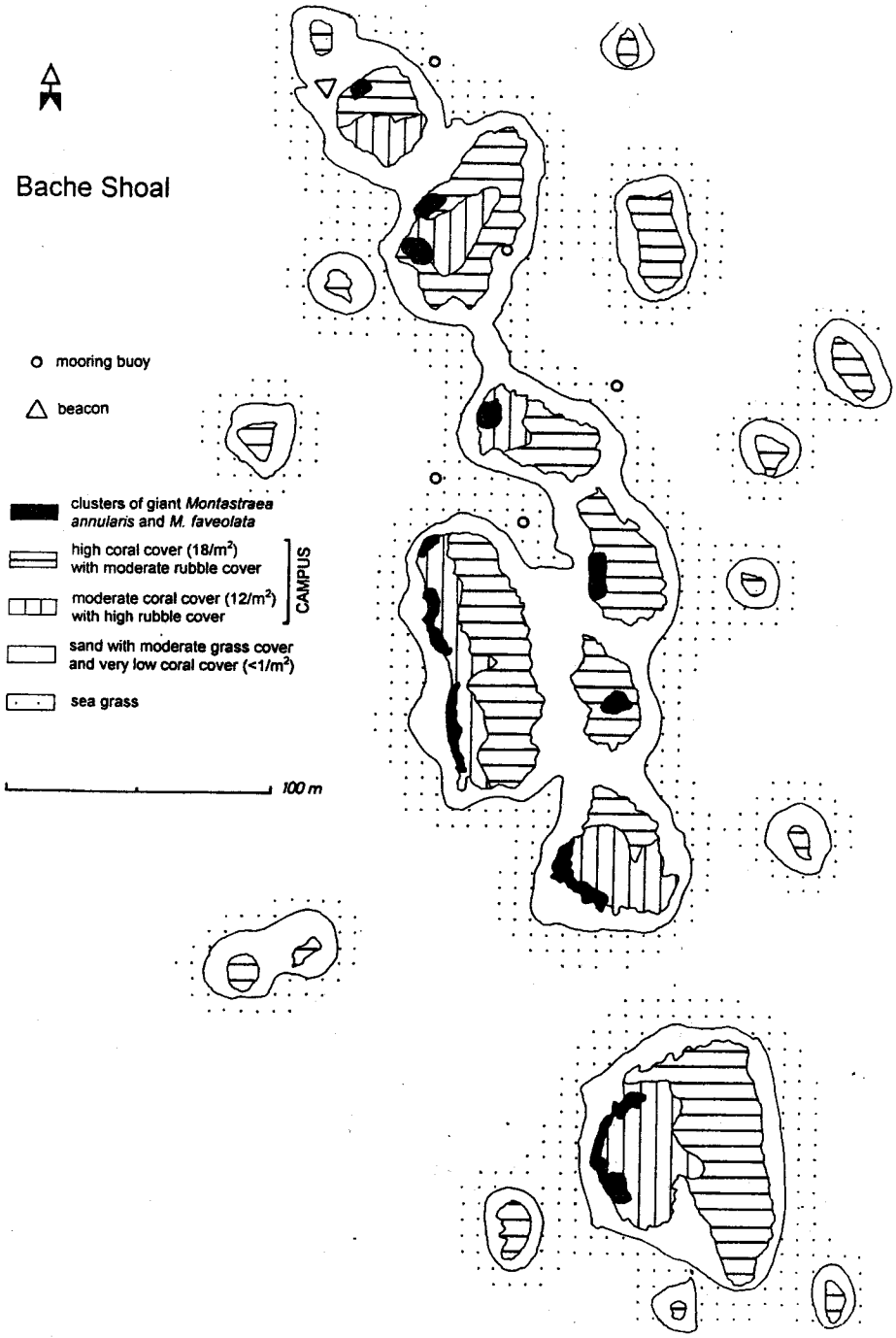


Figure 4. Map of Bache Shoal (Fig. 1) showing the distributions of campus, clusters, and other bottoms types. The distributions were based on transects within each of the areas identified on aerial photographs. Coral rubble in campus areas accumulated during Hurricane Andrew (pers. observations of the senior author).

Table 30 (continued)

Species	Reef types and zones				
	Patch		Livebottom	Bank	
	Top	Outer Fringe		Shallow	Deep
Orangespotted filefish *Cantherhines pullus*	*	*			
Scrawled filefish *Aluterus scriptus*					*
Slender filefish *Monacanthus tuckeri*	*				
Bar jack *Caranx ruber*	*	*		*	*
Queen angelfish *Holacanthus ciliaris*	*	*	*		*
Gray angelfish *Pomacanthus arcuatus*	*	*	*		*
French angelfish *P. paru*			*		*
Rock beauty. *Holacanthus tricolor*					*
Reef butterfly *Chaetodon sedentarius*			*		*
Foureye butterfly *C. capistratus*					*
Spotfin butterfly *C. ocellatus*					*
Saddled blenny *Malacoctenus triangulatus*			*		
Roughhead blenny *Acanthemblemaria aspera*	*	*			
Wrasse blenny *Hemiemblemaria simulus*	*	*			
Redlip blenny *Ophioblennius atlanticus*					
Neon goby *Gobiosoma oceanops*	*	*	*		*
Bridled goby *Coryphopterus glaucofraenum*		*	*		*
Masked goby *C. personatus*		*			*
Goldspot goby *Gnatholepis thompsoni*		*	*		*
Hovering goby *Ioglossus helenae*		*			*
Herrings *Clupeidae*		*			
Bermuda chub *Kyphosus sectatrix*	*	*			
Spanish hofish *Bodianus rufus*	*	*	*		*
Slippery dick *Halichoeres bivittatus*	*	*	*	*	*
Yellowhead wrasse *H. garnoti*		*	*		*
Creole wrasse *Clepticus parrai*					*

(continued)

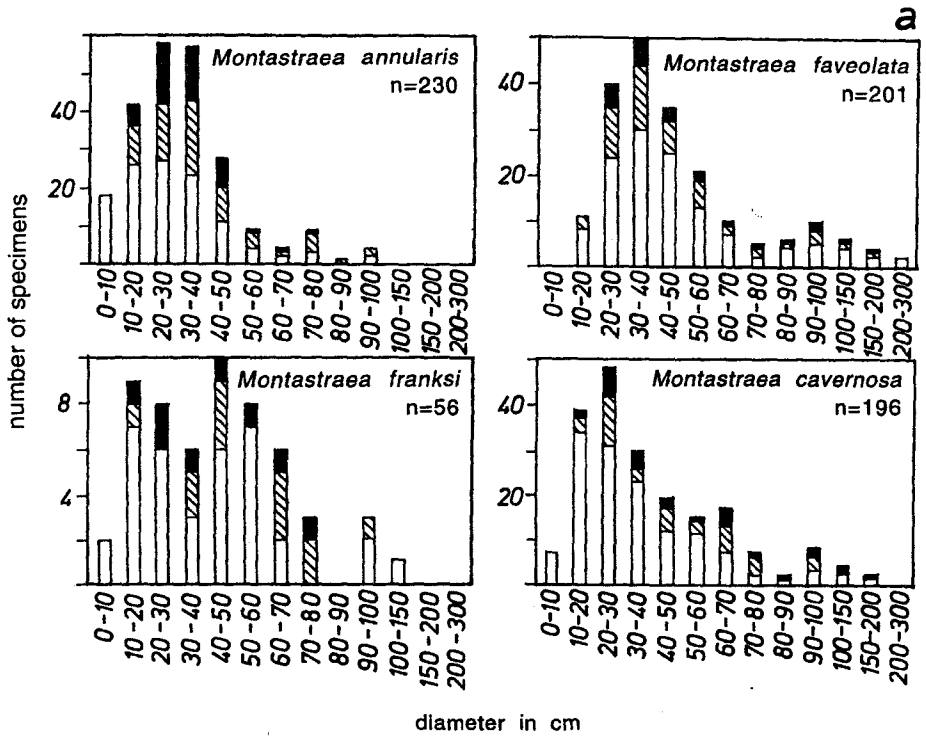


Figure 5A,B *(opposite page).* Size distribution of all coral species assessed in campuses. Giant colonies of *Montastraea* that form clusters are not included as they were assessed separately. Note that there is a change in the scale of colony diameters above 100 cm.

uncertain than for massive corals. At each reef selected, observers swam four radial transects of north, east, south and west from the approximate center of the reef, measuring and estimating partial mortality of the one to three species assigned to them that were in sight. The projection diameter of each colony was measured to 10 cm, with a section of small-diameter PVC tubing marked in 10-cm increments. The partial mortality of each colony was estimated visually as <1/3 dead, 1/3–2/3 dead and >2/3 dead surface (Endean et al., 1988; Ginsburg et al., 1996). For larger patch reefs such as Nirvana, Sting, and Higdon (Table 1), this census technique was applied at more than one location.

For the clusters of giant colonies of *M. annularis* and *M. faveolata,* we used the line point intercept transect sampling method (Loya, 1978) to determine partial mortality. Nylon lines 5 m long with marks at 25 cm and weights at each end were draped over the clusters diametrically or radially from the approximate center. Observers assigned what was under each mark to one of five categories: living, dead, rubble, corals other than *Montastraea,* substrate, i.e., neither coral nor coral rubble. At each cluster, a series of these transects were made by moving the line around the points of the compass. On some clusters, four transects 90° apart were made giving 100 points, at others 8 transects 45° apart were inspected to give 200 points, and at some, 16 transects some 20° degrees apart were examined to yield 400 points. A test of the variations in the results as a function of the number of points is shown in Table 2.

Table 29

Comparison of the most abundant reef fish families among three Florida coral reef areas as indicated by Jones and Thompson (1978) visual census methods.

Ranking	Pennekamp 1975[a]	Tortugas 1975[a]	Tortugas 1976[b]	Biscayne National Park 1979[c]
1	Haemulidae	Pomacentridae	Pomacentridae	Scaridae
2	Scaridae	Serranidae	Scaridae	Pomacentridae
3	Pomacentridae	Haemulidae	Haemulidae	Haemulidae
4	Labridae	Scaridae	Labridae	Labridae
5	Serranidae	Chaetodontidae	Serranidae	Chaetodontidae
6	Chaetodontidae	Labridae	Chaetodontidae	Serranidae

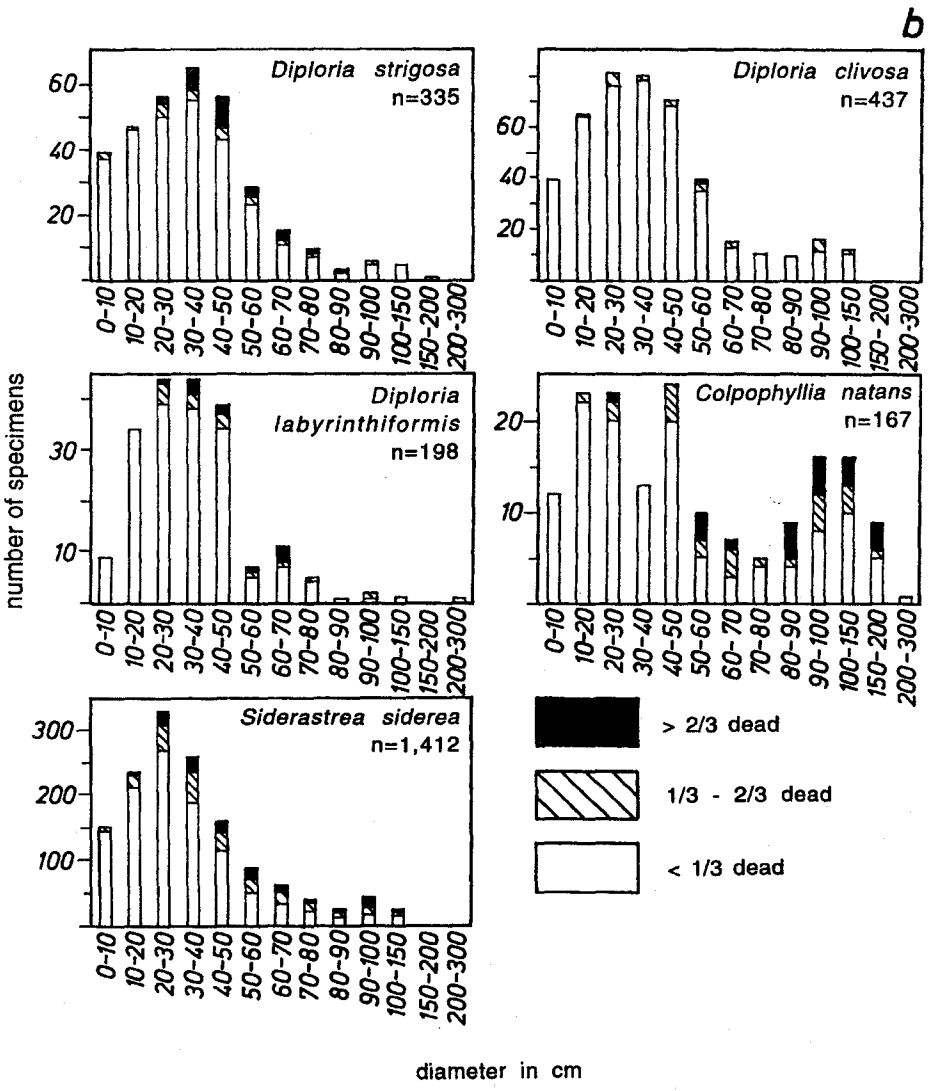
[a]Jones and Thompson 1978.
[b]Thompson and Schmidt 1977.
[c]Tilmant et al 1979.

Table 30

Coral reef fish most commonly observed by divers on reefs.
The list is based on summary ratings of the average length of time a diver must spend before observing the species.
Species averaging less than 30 minutes to observe are listed
(Thompson and Schmidt 1977; Jones and Thompson 1978; Tilmant et al. in press).

	Reef types and zones				
	Patch		Livebottom	Bank	
Species	Top	Outer Fringe		Shallow	Deep
Ocean surgeon *Acanthurus bahianus*	*	*	*	*	*
Doctorfish *Achirurgus*	*	*	*	*	*
Blue tang *A. coeruleus*	*	*	*	*	*
Barred cardinalfish *Apogon binotatus*		*			
Flamefish *A. maculatus*		*	*		
Belted cardinalfish *A. townsendi*		*			
Trumpetfish *Aulostomus maculatus*	*	*			

(continued)



Results

Size Distributions.—The size distributions of all corals by species, except those of the clusters, are shown on Figure 5. The distributions for *M. cavernosa, D. strigosa, D. clivosa, D. labryinthiformis, and S. siderea* are similar, they are skewed toward the smaller sizes and most colonies are between 20 and 50 cm in diameter. The irregular size distributions for *M. franksi* and *C. natans* are probably owing to the small number of colonies available.

Condition of Corals.—The results from the census of corals in the campus are shown in Figures 5 and 6. Seventy-four percent of the 3232 colonies examined have less than 1/3 dead surfaces with only a quite small standard deviation. Significant differences in the amounts of dead surfaces between species are revealed by the Kruskal-Wallis test (Table

group is not entirely clear. Two small tropical serranids have also been considered endemic to the continental United States. One of these, the blue hamlet (*Hypoplectrus gemma*), may only be one of many color morphs of a single species, *H. unicolor*, which is common throughout the Caribbean (Thresher 1978; Graves and Rosenblatt 1980). The other serranid is the wrasse bass (*Liopropoma eukrines*), which ranges northward along the continental shelf, but is not known to occur elsewhere in the Caribbean. The remaining possible endemic species is the cubbyu (*Equetus umbrosus*), but its distinction from *E. acuminatus*, found elsewhere in the Caribbean, is questionable (Robins et al. 1980).

The reason for high diversity of fish species on coral reefs is frequently debated and may be related to a number of factors (Sanders 1968; Goldman and Talbot 1976; Smith 1978; Talbot et al. 1978). All biological communities tend to diversify through colonization over time, and coral reefs exist in an environment generally without major perturbations or great temperature change. Most coral reefs have had long and relatively stable periods to develop. Within this overall long-range stability of the tropics, intermittent moderate disturbances from weather events occur. Although we are just beginning to understand the effects of disturbance events (Endean 1976; Bradbury and Young 1981; Pearson 1981; Woodley et al. 1981; Davis 1982; Porter et al. 1982; Roberts et al. 1982), they may help to maintain a higher diversity by preventing a resource-limited equilibrium and the competitive exclusion of some species (Connell 1978).

Coral reefs generally include a variety of microhabitats related to zones of coral growth, wave exposure, and reef structure (Wells 1957a; Maxwell 1968; Stoddart 1969). This diversity of habitat types allows for an increased diversity of fish species. Although habitat relationships have not been extensively studied on Florida reefs, few reef fish have been found to be cosmopolitan over all available habitats. At One Tree Island Reef, Australia, 49% of all species collected were restricted to one or another of five major habitats (Goldman and Talbot 1976). Similar faunal differences among habitats have been reported by Gosline (1965) for the Hawaiian Islands; Chave and Eckert (1974), Fanning Island, South Pacific; Jones and Chase (1975), Guam; Harmelin-Vivien (1977), Tulear Reef, Madagascar; and Williams (1982), the Great Barrier Reef.

The coexistence of a high number of fish species on coral reefs also implies either that these species are highly specialized (occupy finely partitioned niches) or that there is considerable overlap in resource utilization. Predators are generally food limited and tend to have more clearly separated niches (Hairston et al. 1960; Paine 1966). Reef herbivores such as parrotfishes, damselfishes, gobies, and angelfishes are generally believed to use many of the same food resources (Randall 1967; Smith and Tyler 1972; Hobson 1974). Both specialization and resource-sharing appear to occur among various reef fish groups and at various life stages within some species.

Recruitment of juvenile fish to coral reefs may also influence species diversity, although this is hotly contested (Sale 1976, 1980a; Sale and Dybdahl 1978; Smith 1978; Talbot et al. 1978; Brock et al. 1979; Ogden and Ebersole 1981; Sale and Williams 1982). The controversy centers around whether reef communities have an ordered structure with predictable species recruitment to vacant niches or an unpredictable chance species recruitment. An unpredictable larval recruitment would increase local variation in the species present and might well contribute to a higher overall diversity (Goldman and Talbot 1976). Recently some investigators have suggested that differences in recruitment and community structure may be a result of the size of the reef area considered (Ogden and Ebersole 1981) or of the time interval between which samples have been taken (Bohnsack, in preparation).

6.6 COMMUNITY DESCRIPTIONS

Although fish diversity is usually high on coral reefs, fewer number of species will appear abundant or highly obvious to the average reef diver at any one location. Reef fish, like most organisms, have depth and habitat preferences where they can typically be seen. Many are active only nocturnally or diurnally, and some species, such as yellowtail snapper and gag grouper (*Mycteroperca microlepis*), are abundant only seasonally.

A comparison of three Florida reef studies, all of which used the same 50-min visual census technique, shows significant differences in reef fish communities at each study location (Thompson and Schmidt 1977; Jones and Thompson 1978; Tilmant et al. 1979). Although the top six families comprising the fish community in terms of abundance were the same, their relative ranking and individual species members varied (Table 29). Damselfish (Pomacentridae) were the most common family at Tortugas while ranking third at John Pennekamp Coral Reef State Park (JPCRSP) and second at Biscayne National Park (BNP). Parrotfish (Scaridae) were the most common community member at BNP but were second at JPCRSP and the Dry Tortugas. Grunts (Haemulidae) were particularly abundant at JPCRSP (most common family) but were third at BNP and the Tortugas. Of the 165 species observed between JPCRSP and the Dry Tortugas, 115 were shared in common. Thirty-one species were seen only in JPCRSP and 19 were observed only in the Tortugas study areas (Jones and Thompson 1978). Overall, fish communities at John Pennekamp Coral Reef State Park were found to be more diverse and abundant than at the Dry Tortugas.

Seven of the top 10 reef fish species at Biscayne National Park were also within the 10 most common species in John Pennekamp Coral Reef State Park. However, only 10 of BNP's top 20 species were represented in the 20 most common species at JPCRSP.

Three major types of coral reefs are recognized along the Florida reef tracts: patch reefs, hardground live bottom, and bank reefs. Each general reef type supports a characteristic fish fauna (Table 30). General

Table 2. Variation of cluster data within two individual clusters at Bache Shoal and three individual clusters at Nirvana North. Percentages are calculated on the basis of numbers given under 'alive' and 'dead'. (For numbers of points counted at each of the 65 clusters see Appendix.)

Bache Shoal, cluster 1

line	alive	dead	rubble	substrate	other	total
1	31	41	0	0	2	74
	43 %	57 %				
2	44	21	5	3	0	73
	67 %	33 %				
3	33	33	3	0	0	69
	50 %	50 %				
4	42	24	2	2	1	71
	64 %	36 %				
Sum	150	119				287
Mean	56 %	44 %				
SD	11.4 %					

Bache Shoal, cluster 2

line	alive	dead	rubble	substrate	other	total
1	37	26	11	8	2	84
	59 %	41 %				
2	15	32	24	4	8	83
	32 %	68 %				
3	16	19	57	0	1	93
	46 %	54 %				
4	32	17	30	2	10	91
	65 %	35 %				
Sum	100	94	122	14	21	351
Mean	51 %	49 %				
SD	14.7 %					

Nirvana North, cluster 1

line	alive	dead	rubble	substrate	other	total
1	56	60	0	2	0	118
	48 %	52 %				
2	46	43	0	4	0	93
	52 %	48 %				
3	42	48	0	6	0	96
	47 %	53 %				
4	34	56	0	2	3	95
	38 %	62 %				
Sum	178	207	0	14	3	402
Mean	46 %	54 %				
SD	5.9 %					

edly related to the abundance and quality of food available within the seagrass bed and can be expected to vary considerably among locations.

6.4 SOCIAL ORGANIZATION

Literature on the social behavior and organization of reef fish assemblages is extensive (see Ehrlich 1975; Goldman and Talbot 1976; Sale 1977, 1980a; Thresher 1977; and Emery 1978 for reviews). It has been conclusively shown that individuals or groups of individuals are not scattered randomly about the reef. Rather, their distribution reflects topographic and biologic features of the environment as well as behavioral adaptations to disperse (Thresher 1977). The interaction of ecologically evolved behavior and the availability of existing resources largely determine the social organization within a given reef fish community.

Most smaller reef species are either herbivorous or planktivorous and are territorial to varying degrees. The size of territory and the extent to which it is defended is a function of resource availability for many species (Low 1971; Thresher 1977; Sale 1980a). Thresher (1976) found that the size of area defended by the threespot damselfish (*Pomacentrus planifrons* = *Eupomancentrus planifrons*) on Florida reefs varied with the type of resource secured and further that the size of the area defended against a given intruder was determined by the threatened severity of the intrusion. The size of territory defended against other families, for example, correlated with the amount of benthic algae in the diet of each species. Thresher (1977) reported that the threespot damselfish in the northern portions of its range generally defended larger territories than those in the southern portion, where thicker algal lawns developed within their territories.

Differences in social structure have been observed within a single species at different locations. Itzkowitz (1978) and Williams (1978), working at different sites in Jamaica, reported different social organizations for *Pomacentrus planifrons*. Itzkowitz found males and females occurring together as neighboring territory holders in the same habitat, while Williams reported the use of different habitats by the sexes. In other regions, Robertson (1972) at Heron Reef (Great Barrier Reef) and Potts (1973) at Aldabra Atoll reported *Labroides dimidiatus* occurring as males with harems and as mated pairs, respectively. Barlow (1974) found a correlation between the social structure exhibited by *Acanthurus triostegus* and the presence or absence of various other territorial acanthurid species. The extent to which the nature and distribution of food resources can predict the form of space and resulting social organization used by territorial species was demonstrated by Thresher (1977) for five species of pomacentrids common on Florida reefs. Invariably, the organization predicted closely matched that observed in the field.

The large reef fish species require a greater food supply and, therefore, tend to range over a larger area of the reef. These species, although often having distinct ranges, are less territorial and frequently form foraging groups (Buckman and Ogden 1973; Ogden and Buckman 1973; Alevizon 1976; Itzkowitz 1977).

6.5 ECOLOGICAL ASPECTS OF REEF FISH DIVERSITY

Only two studies have attempted to fully define the diversity of fish species on selected Florida reefs: Longley and Hildebrand (1941) and Starck (1968). Longley and Hildebrand provided a systematic account of all fishes they captured or observed during 25 years of investigations at the Dry Tortugas, and Starck listed fishes collected and observed during 9 years of study at Alligator Reef. Longley and Hildebrand listed 442 species, 300 of which are closely associated with coral reefs. Starck listed 517 species, 389 of which he considered reef species. The remaining species were either offshore pelagic forms, demersal species from deeper water, or strays from adjacent inshore areas. Both lists are from single reef areas and, therefore, probably underrepresent the actual diversity of fish species on Florida's reefs.

Bohlke and Chaplin (1968) identified 496 fish species within the Bahamas and adjacent waters. About 450 of these species are known to occur on coral reefs and probably approximate Florida's total diversity.

Several less extensive surveys of fish on Florida reefs involved visual census, filming, or limited collecting techniques. One of the earliest surveys was done by Jordan and Thompson (1904), who identified 218 species inhabiting the reefs at the Dry Tortugas by using baited lines and various nets.

The high diversity of fish on Florida's tropical coral reefs is exemplified by a few studies which reported the number of species observed within a given limited area. Bohnsack (1979) recorded a mean number of species ranging from 10 to 23 on isolated natural coral heads less than 330 x 210 x 150 cm in size off Big Pine Key, Florida, and 13 to 20 species on small artificial reefs (160 x 60 x 80 cm) that he established. Alevizon and Brooks (1975) observed an average of 14.7 fish species during 2.75-min samplings during which scuba divers took color movies. During the sample period the diver panned the camera to include most or all fishes sighted within 4-5 m (Alevizon and Brooks 1975).

At present, there appears to be only six or seven species of reef fish that might be considered endemic to the U.S. continental reefs. Two of these, *Lythrypnus phorellus* and *Gobiosoma oceanops*, are small gobies; the latter (neon goby) is common. The purple reef fish (*Chromis scotti*) is also known to occur only within U.S. waters, although the genus is well represented by at least three other species throughout the West Indies. *Ophidion selenops*, the mooneye cusk eel, is a species reported by Starck (1968) to occur occasionally within the area of Alligator Reef (near Matecumbe Key), but has not been reported elsewhere. Cusk eels are curious elongate fishes, highly nocturnal and burrowing into mud during the day. At least five species of cusk eels, representing two genera, are known to occur along the southeastern United States, but the taxonomy of this

Table 2. Continued.

Nirvana North, cluster 2

line	alive	dead	rubble	substrate	other	total
1	21	50	5	18	0	94
	30 %	70 %				
2	20	45	6	7	4	102
	31 %	69 %				
3	20	43	7	14	1	85
	32 %	68 %				
4	25	55	4	12	0	96
	31 %	69 %				
Sum	86	193				377
Mean	31 %	69 %				
SD	0.82 %					

Nirvana North, cluster 3

line	alive	dead	rubble	substrate	other	total
1	23	48	7	11	3	92
	32 %	68 %				
2	29	43	6	8	5	91
	40 %	60 %				
3	45	29	6	11	0	91
	61 %	39 %				
4	38	35	9	7	2	91
	52 %	48 %				
sum	135	155				365
mean	47 %	53 %				
SD	12.8 %					

3). Species of *Diploria* have less dead surface than most other species and *M. annularis* has more dead surface than other species. All species show to varying degrees an increase in the amount of dead surfaces with increasing size (Fig. 5).

Figure 6 shows the variations in condition at various spatial scales by species. On an individual reef we found specimens of *M. annularis* without any dead surface, yet nearby colonies could have 1/3–2/3 dead surfaces. A further indication of the variability on an individual patch reef is evident in the data for Bache Shoal in Figure 6. Similarly, for groups of reefs shown in Figure 6, the data for some species shows large variation in condition, but for others it is much less. Some of the large variations are probably owing to the small number of colonies we examined, i.e., *M. franksi* and *C. natans.* A cluster analysis indicates no major spatial variations in condition for the entire study area (Fig. 7). However, there are differences in the condition of four species between two zones (see Fig. 6). Off Elliot Key, *S. siderea* has a significantly larger percentage of colonies with less than l/3 dead surfaces than off Key Largo. (Kruskal-Wallis analysis of variance by ranks, $P = 0.05$). Off Key Largo, *M. cavernosa* ($P = 0.025$), *D. strigosa* ($P = 0.004$), and *D. labyrinthiformis* ($P = 0.005$) all have significantly fewer colonies with >2/3 dead surfaces than off Elliot Key (Kruskal-Wallis analysis of variance by ranks).

brates. Only a few blennies (none occurring in Florida) have been reported to be primary detritivores (Goldman and Talbot 1976). This number may increase as more food studies for the numerous smaller blennies and gobies become available. Also, much detrital material is ingested by those fish classified as herbivores, and determining actual material being foraged is often difficult (Randall 1967).

Many species utilize the reef only as a refuge. They use adjacent seagrass beds and sand flats as feeding grounds (Longley and Hildebrand 1941; Randall 1963; Starck and Davis 1966; Davis 1967; Ogden and Ehrlich 1977; Ogden and Zieman 1977). Randall (1963) reported that grunts and snappers were so abundant on patch reefs in the Florida Keys that it was obvious that the reefs could not provide food and possibly not even shelter for all of them. Both the abundance and diversity of haemulids and lutjanids have been reported to be reduced on reefs where adequate off-reef forage areas are unavailable (Starck and Davis 1966; Robins 1971; Alevizon and Brooks 1975; Gladfelter et al. 1980). Similarly, when reef shelter is lacking, what appears to be suitable grassbed forage areas may go unused (Starck and Davis 1966; Ogden and Zieman 1977).

In Tague Bay, St. Croix, Virgin Islands, 79.4% of the fishes actively feeding in the grassbeds at night were species that sought shelter on adjacent coral reefs during the day (Robblee and Zieman, in preparation). Starck and Davis (1966) listed species of the Holocentridae, Lutjanidae, and Haemulidae families as occurring diurnally on Alligator Reef and feeding nocturnally in adjacent seagrass beds. Typically both juvenile and adult haemulids and lutjanids form heterotypic resting schools over prominent coral heads (most commonly *Acropora palmata* and *Porites porites*) or in caves or crevices of the reef (Ehrlich and Ehrlich 1973; Ogden and Ehrlich 1977). At dusk these fishes move off the reef into adjacent seagrass beds and sand flats where they feed on available invertebrates (Randall 1967; Ogden and Ehrlich 1977; McFarland et al. 1979). At dawn they return to the reef.

Starck and Davis (1966) reported that 11 of 15 species of haemulids found in diurnal resting schools on Alligator Reef dispersed at night to feed. The lighter colored grunts (seven species) generally distributed themselves along sandy to thin-grass areas of the back reef zone. Snappers (Lutjanidae) followed a similar pattern with *L. griseus* and *L. synagris* in sparse grass to back reef habitat. At Tague Bay, St. Croix, the nocturnal distribution of grunts over the grass beds was quite similar to that reported in the Florida Keys. The French grunt was most abundant over thin grass or bare sand while white grunts were almost always observed by Robblee (in preparation), in thick grass. He also found the number of coral reef fishes feeding nocturnally over a particular area was positively correlated with a measure of habitat complexity, implying some form of organization of the fish assemblage while active over the feeding ground.

It has been hypothesized by Billings and Munro (1974) and Ogden and Zieman (1977) that migrating nocturnal feeders may contribute significantly to the energy budget of the coral reef through the import of organic matter in the form of feces. If so, their contribution to reef nutrient levels and maintenance of more sedentary fish abundance may also be important. Meyer et al. (1983) found what appeared to be higher nutrient levels and coral growth rates associated with diurnal resting schools of grunts. Verification of these links, however, requires further investigation.

Use of adjacent grass and sand flats by reef fish is not strictly a nocturnal phenomenon, but seems to be the dominant pattern. Only quite large herbivores, such as the rainbow parrotfish (*Scarus guacamaia*), venture far into the grass bed away from the shelter of the reef. Mid-sized herbivores are apparently excluded by predators and feed only near the reef (Ogden and Zieman 1977). Randall (1965) reported parrotfishes (*Scarus* and *Sparisoma*) and surgeonfishes (*Acanthurus*) feeding on seagrasses (*Thalassia* and *Syringodium*) closely adjacent to patch reefs in the Virgin Islands during the day. He attributed the formation of halos around patch reefs in St. John, Virgin Islands, to this grazing.

6.3 MOVEMENT

Most reef fish seldom change their residence once they have settled onto a reef and some become quite sedentary (Thresher 1977). Many smaller species, such as gobies (Gobiidae), blennies (Blenniidae), and damselfish (Pomacentridae), maintain relatively small territories which they vigorously defend (Salmon et al. 1968; Rasa 1969; Low 1971; Myrberg 1972; Vine 1974). Tagging studies have shown that even those larger, wider ranging species, such as serranids, lutjanids, haemulids, chaetodontids, and acanthurids, remain, at least diurnally, in a fairly circumscribed place on a reef (Bardach 1958; Randall 1961b, 1962; Springer and McErlean 1962a). Randall (1962) recaptured some serranids and lutjanids at their initial place of capture up to 3 years after their release. Tagged *Haemulon plumieri* were repeatedly captured on the same reef by Springer and McErlean (1962a). When the *H. plumieri* were transplanted, they exhibited a tendency to home (Springer and McErlean 1962a). Ogden and Ehrlich (1977) reported on the sucessful homing of *H. plumieri* and *H. flavolineatum* to original patch reefs over distances as great as 2.7 km in the U.S. Virgin Islands.

Only a small amount of information is available on the usual extent of nocturnal movements of reef fishes that feed on adjacent grass beds. As indicated above, these fishes potentially can range quite far from their diurnal resting sites. *Lutjanus griseus* and *Haemulon flavolineatum* ranged as far as 1.6 km from Alligator Reef (Starck and Davis 1966), while *H. plumieri* and *H. flavolineatum* typically migrated distances greater than 100 m over the grass beds in Tague Bay, St. Croix (Ogden and Ehrlich 1977; Ogden and Zieman 1977). The migrating schools follow a linear path for 20-40 m from the reef, and then begin to break up into smaller and smaller groups in a dendritic pattern (Ogden and Zieman 1977). The distance traveled to feed is undoubt-

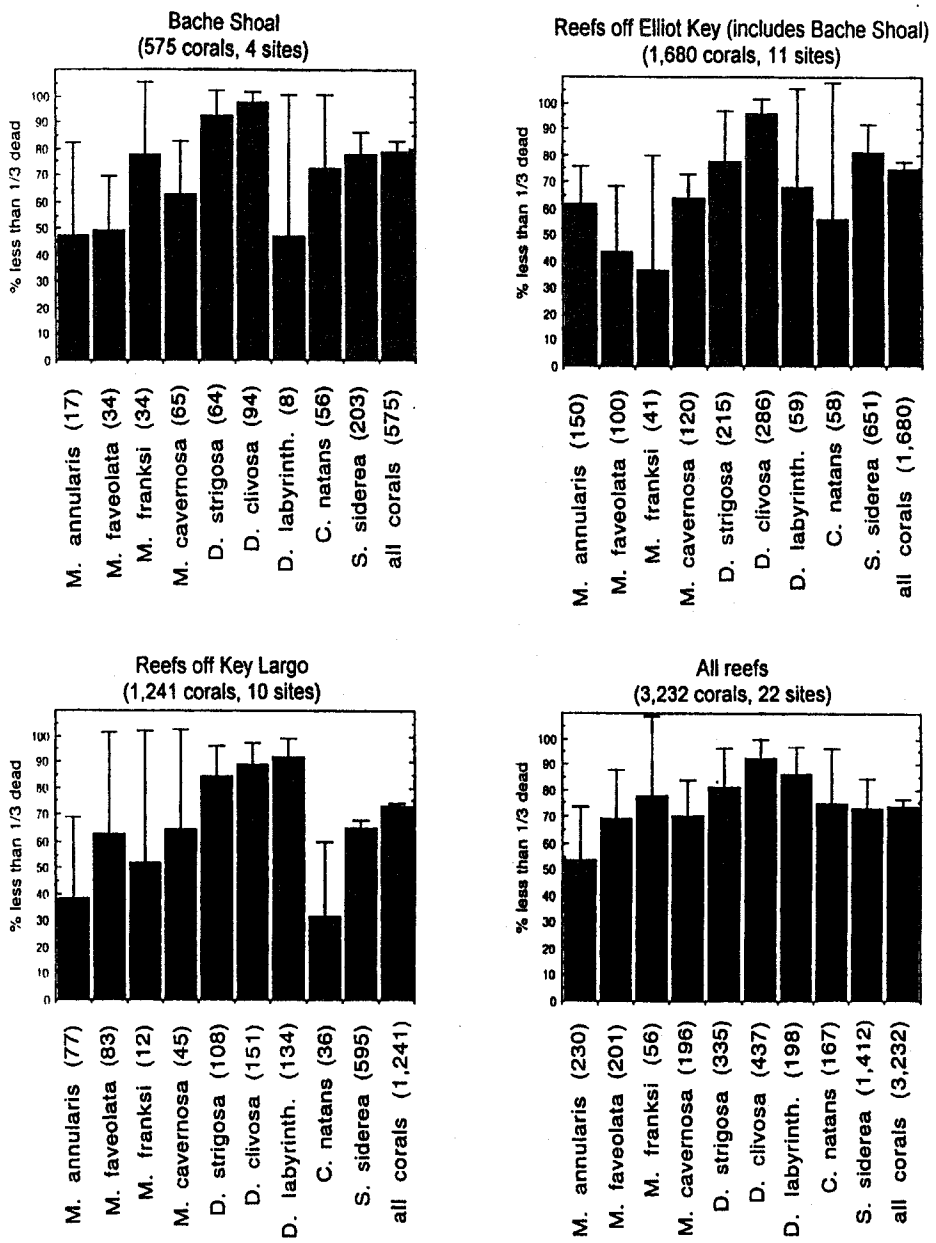


Figure 6. Results of the campus census. Black bars show mean percentages of colony surface that are less than 1/3 dead; arrows show standard deviation. The numbers of colonies are indicated for each entry. Note that there is both regional and local variation in the data.

For the clusters, the frequency distribution of dead colony surfaces is skewed and nearly 60% of those clusters measured have between 40–70% dead surface (Fig. 8). There are significant variations in the amount of dead surfaces on individual reefs, within reef areas and for all clusters (Fig. 9A). We did not find as might be expected, a significant decrease in dead tissue/colony on the few patch reefs examined that occur on the bank barrier (Fig.

species. Ogden and Zieman (1977) reported that at Tague Bay, St. Croix, juvenile spiny puffer (*Diodon*), squirrelfish (*Holocentrus*), yellowtail snapper (*Ocyurus chrysurus*), surgeonfishes (*Acanthurus*), and numerous wrasses (*Halichoeres*) were commonly present within the grassbed. The spotted goatfish (*Pseudupeneus maculatus*) and the yellow goatfish (*Mulloidicthys martinicus*) occur as juveniles in grassbeds off the Florida Keys (Springer and McErlean 1962a; Munro 1976). Springer and McErlean reported capturing eight species of juvenile scarids in *Thalassia* beds off Matecumbe Key; all but one, *Sparisoma radians*, are considered reef species as adults. These fish remain in the seagrass habitat until they become too large (> 20 cm) to hide among the blades (Ogden and Zieman 1977) and presumably migrate to the reef.

6.2 FOOD HABITS AND TROPHIC STRUCTURE

Fish constitute a major portion of the animal biomass on a coral reef, and they are an important component of the overall trophic structure. Most reef fish are carnivores and many studies have shown that carnivorous fishes normally represent three to four times the biomass of herbivorous fishes (Bakus 1969; Goldman and Talbot 1976; Parrish and Zimmerman 1977). This reversal of the "traditional" biomass pyramid results from many carnivorous fishes feeding on invertebrates that form the largest portion of lower trophic levels on reefs. Benthic invertebrates are of considerable importance to reef fish populations as energy assimilators at the planktivore, herbivore, and detrital levels (Vivien and Peyrot-Clausade 1974).

Herbivorous reef fish are sustained primarily by low algal turfs and low-growing filamentous algae and diatoms (Goldman and Talbot 1976). No phytoplankton feeders have been identified in any of the reported studies of reef fish food habits (Hiatt and Strasberg 1960; Randall 1967; Bakus 1969; Hobson 1974; Goldman and Talbot 1976; Parrish and Zimmerman 1977; Hobson and Chess 1978). This is in contrast to fish populations in temperate regions where up to 6% of the species may consume phytoplankton (Davies 1957). Benthic algal feeders include most parrot fish (Scaridae) and surgeonfishes (Acanthuridae) and some blennies (Blennidae), damselfish (Pomacentridae), butterfly fishes (Chaetodontidae), and filefish (Balistidae). A number of studies have shown that the herbivorous reef fish have a marked effect on the distribution and abundance of algae present on a reef. When protected from grazing by exclosures, algal communities will rapidly increase in standing crop (Stephenson and Searles 1960; Randall 1961a; Earle 1972a; Montgomery 1980; Montgomery et al. 1980; Hixon and Brostoff 1981).

The extent to which zooxanthellae is eaten by reef fish has been disputed (Randall 1974). Parrotfishes (Scaridae) have been reported to scrape coral in a feeding manner by Hiatt and Strasberg (1960) in the Marshall Islands; Motoda (1940) in the Palao Islands; Talbot (1965) off East Africa; Al-Hussaini (1947) in the Red Sea; and Bakus (1969) along the Pacific coast of Panama and Costa Rica. This habit was not observed by Randall (1967) during extensive studies in the Caribbean; Finckh (1904) in the Ellice Islands; Wood-Jones (1910) at Cross-Keeling Island; or Choat (1969, cited in Goldman and Talbot 1976) on the Great Barrier Reef. Randall (1974) did observe coral feeding by scarids in some areas of the Pacific, however, and discussed how this habit appears to vary among the same species of fish at different locations. Scraping of massive (head) corals by parrotfish does occur at least occasionally on Florida reefs (W.A. Starck II, personal comment in Randall 1974; J.T. Tilmant, personal observation). The amount of food taken in this way may be insignificant compared to algae ingested by grazing.

There are few true omnivores among most reef fishes. The majority of species tend to be substantially more carnivorous than herbivorous. Most herbivorous fishes have been found to take only a small amount of animal matter. Among the Caribbean species reported as omnivorous are the damselfish (beaugregory and the threespot damselfish); the grey angelfish and French angelfish; the scrawled filefish, orangespotted filefish, and fringed filefish; and the sharpnose puffer (Randall 1967).

Schools of small zooplankton-feeding fishes are common on coral reefs and zooplankton is an important energy source for larval stages of most reef species. Among adult zooplankton feeders commonly schooling on reefs are the herring genera *Harengula, Opisthonema, Sardinella,* and *Jenkinsia*; the anchovies (*Anchoa*); and silversides (*Atherinomorus* and *Allanetta*). Basslets (Grammidae), cardinalfish (Apogonidae), glassy sweepers (Pempheridae), and chromis (*Chromis* spp.) also typically occur in relatively large schools among reef crevices where they feed on plankton. In addition to these adult planktivores, dense schools of minute larval grunts (Haemulidae), snappers (Lutjanidae), and wrasses (Labridae) are often quite common hanging above coral heads or among branches of *Acropora* where plankton and coral mucus are the only available food.

Most of the carnivorous reef fish appear opportunistic, taking whatever is of the right size and is catchable within their habitat (Goldman and Talbot 1976). This conclusion is based primarily on the variety of food items observed within the same species at various locations. Only a few studies of reef fish species have evaluated food consumption in relation to what was actually available: Jones (1968); Vivien and Peyrot-Clausade (1974); and Hobson and Chess (1978).

Some carnivorous reef fish are highly specialized in their feeding habits. Among these are the parasite pickers or cleaners (*Labroides* spp.), juvenile bluehead wrasse, and neon gobies (*Gobiosoma* spp.), and several sponge feeders. Caribbean reef fish reported to feed on sponges include butterfly fish (Chaetodontidae), spadefish (Ephippidae), puffers (Tetraodontidae), and boxfishes (Ostraciidae) (Menzel 1959; Bakus 1964; Randall and Hartman 1968).

Few, if any, reef fish have been classified as detrital feeders and the utilization and turnover of detritus on coral reefs appear to be left primarily to inverte-

Table 3. Multiple comparison of coral condition at all (22) sites (% <1/3 dead colony surface). Kruskal-Wallis analysis of variance by ranks (* = significant difference at P < 0.05).

	1	2	3	4	5	6	7	8	9
M. ann. (1)	1								
M. fav. (2)		1							
M. fra. (3)			1						
M. cav. (4)	*			1					
D. stri. (5)	*	*		*	1				
D. cli. (6)	*	*		*	*	1			
D. lab. (7)	*	*					1		
C. nat. (8)	*					*		1	
S. sid. (9)	*				*	*	*		1

10). A statistical comparison of the condition of the corals for the four areas studied shows that those off the Lower Keys have more dead surfaces than those off Key Largo and Elliot Key (Table 4) The greater amount of coral rubble associated with clusters off Elliot Key (Fig. 9B) reflects the impact of Hurricane Andrew 1992 whose center passed over reefs off that island (Table 4), see also Lirman and Fong (1995, 1997).

Discussion

Data Limitations.—There are several inherent limitations in our data set. All but three of the 22 patch reefs examined are shallow, with their tops within a few meters or less of sea level (Table 1). This shallowness means the corals are more likely to be affected by sea surface waves and water quality, small boat groundings and possibly by fishermen and recreational divers. There are limited numbers of colonies of certain species on individual reefs and limited number of patch reefs in two of the sub areas of the Reef Tract. In Figure 6, it is evident that the relatively large variability in the percentages for *M. franksi* and *C. natans* are related to small numbers of colonies. Similarly, the limited number of patch reefs off the Middle Keys could be responsible for the large variability in the data on clusters (Fig. 6). In the Lower Keys, two of the three patch reefs examined are within less than a kilometer of the shoreline (Table 1).

Another limitation of our results is the inherent variability in the type of patch reef and their distribution. As shown in Figure 1 patch reefs are much more numerous in the Upper Keys than elsewhere. Moreover, seven of the twelve patch reefs, which we assessed

Table 4. Multiple comparison of *Montastraea* clusters off Elliot Key, Key Largo, and reefs south of Key Largo. Kruskal-Wallis analysis of variance by ranks. * = significant difference at P < 0.05.

	Elliot Key vs Key Largo	Elliot Key vs Middle Keys	Elliot Key vs Lower Keys
% dead	0.54	0.11	0.0012*
% rubble	0.007*	0.69	0.075

	Key Largo vs Middle Keys	Key Largo vs Lower Keys	Middle Keys vs Lower Keys
% dead	0.35	0.012*	0.402
% rubble	0.05*	0.468	0.515

CHAPTER 6

REEF FISH

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Tropical coral reefs are richer in fish species than any other habitat (Marshal 1965; Emery 1973). The fish fauna of the Florida reef tract is wholly tropical with only seven species that have not been recorded elsewhere in the West Indies. Thus, although the study of coral reef fishes in south Florida has not been extensive, considerable information concerning their biology and ecology has been developed through studies elsewhere in the Caribbean.

The most complete studies conducted in the Florida Keys are those by Longley and Hildebrand (1941) for the Dry Tortugas, and Starck (1968) for Alligator Reef. Field guides to Florida reef fish include Chaplin and Scott (1972); Greenberg (1977); Stokes and Stokes (1980); and Kaplan (1982).

Three major reviews concerning the general ecology of coral reef fish on a worldwide basis are Ehrlich (1975), Goldman and Talbot (1976), and Sale (1980b).

6.1 REPRODUCTION AND RECRUITMENT

Most coral reef fish spawn in the water column above the reef, and their eggs remain in the plankton during development. A few species either lay their eggs demersally and attend to them or they brood them by mouth (Smith 1982; Colin 1982). Breeding aggregations are common to most reef species. These serve to increase egg fertilization and release of egg and sperm in the lee of the reef, thereby increasing dispersion and reducing predation (Colin 1982). Coral reef fishes typically produce large numbers of offspring which are then dispersed by means of a pelagic larval stage (Breder and Rosen 1966; Ehrlich 1975; Johannes 1978; Sale 1980b). The timing of egg release (or hatching for those families with dermersal eggs) is often triggered by dusk, night, or the tides, increasing the ability of newly spawned or hatched eggs to elude predators (Myrberg 1972; Robertson and Choat 1974; Warner et al. 1975; Bell 1976; Colin 1976, 1978b, 1982; Moyer and Bell 1976; Johannes 1978; Lobel 1978; Moyer and Nakazono 1978).

Most species of reef fish spawn several times during their spawning season. Spawning may be daily, biweekly, or monthly (Robertson 1972; Holzberg 1973; Warner et al. 1975; Moyer and Nakazono 1978; Lobel 1978; Ross 1978). These multiple spawnings have been explained as a method of ensuring a wide dispersal of offspring (Sale 1978).

Sex reversal is also common in many reef species. Often the adult populations are largely females (with only a small but sufficient percentage of males). If the number of males in the population becomes reduced, new males are rapidly developed from female stock by some individuals undergoing a protogynous sex reversal. Egg production is maximized by this mechanism and a greater proportion of energy channeled into population maintenance (Goldman and Talbot 1976; Smith 1982). Florida reef species known to undergo sex reversal include most (if not all) parrotfish (Scaridae), many wrasses (Labridae), and some groupers (Serranidae).

A pelagic larval stage is almost universal among coral reef fish species. Little detailed information is known about the life of larval reef fish while in the pelagic phase, although they are frequently taken in offshore plankton tows. Studies in which the time of spawning and time of period of peak recruitment of juveniles from the plankton have been correlated indicate that the larval stage varies from a few weeks to months depending on the species (Randall 1961a; Moran and Sale 1977). Aging of larvae or newly transformed juveniles by counting daily growth increments on the otoliths has revealed that pomacentrids, gobiids, and blenniids have larval lives of about 21 days. The larval stage of siganids, acanthurids, chaetodontids, and labrids is 30 or more days (Sale 1980b). As is common among many marine invertebrates, many species can probably extend their larval life until suitable settlement habitat is found (Randall 1961a; Johannes 1978; Sale 1980b).

The methods by which larval fish are returned to a reef environment have been mostly hypothesized from circumstantial evidence. Generally, it is believed that current gyres that form in the lee of islands and reefs act as traps to prevent the loss of larvae downstream and, through their rotation, return the larvae to the reef (Munro et al. 1973; Leis and Miller 1976; Johannes 1978). Johannes (1978) reported that the spawning migrations, which bring some species to particular sites at precise times, release the gametes into a mass of water that is most likely to return them to the same reef at the end of their pelagic existence. He cited the variability in spawning peaks between various locations, often within the same region, as possible evidence that spawning patterns have arisen as responses to a variable pattern of water circulation. The season in which spawning occurs is not well known for many coral reef species, but it is known some species spawn on a regular basis all year (Colin 1982). For most species that have been studied, spawning peaks in the late afternoon and may last from a few minutes to an hour or more depending on the species (Colin 1982). Present knowledge concerning the reproductive behavior of coral reef fishes in the Caribbean has been summarized in papers by Smith (1982) and Colin (1982).

Seagrass beds are important to the reproduction of coral reef fishes in that they act as nurseries for some

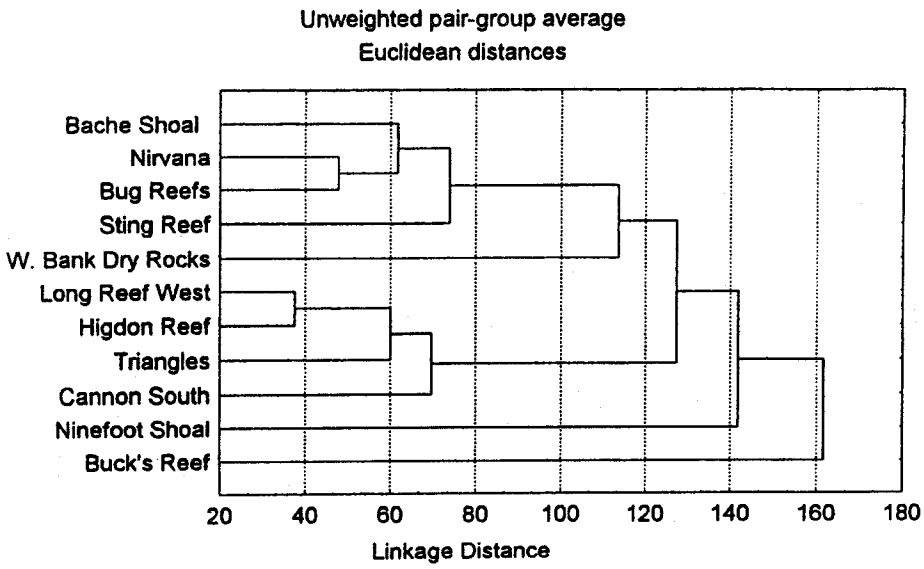


Figure 7. Tree diagrams of cluster analyses of 10 localities including the condition of 9 coral species and of all corals with less than 1/3 dead colony surface. Localities situated in the same areas do not group together, showing that there is no spatial pattern decipherable in the condition of corals in the campuses.

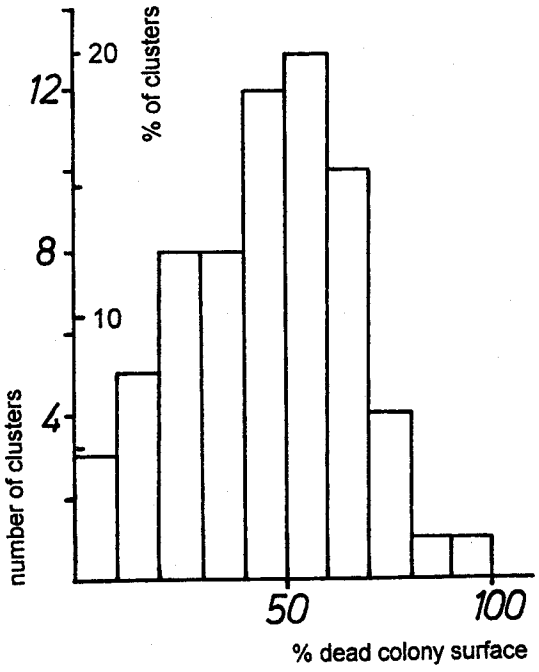


Figure 8. Histogram showing the condition of clusters of large *Montastraea* spp.

2. Most of the reef zooplankton belong to a resident community, which is able to maintain position on the reef.
3. The community consists partly of true planktonic forms living in dense aggregates and using the reef configuration and water currents to maintain position.
4. The major portion of the resident plankton community consists of epibenthic forms. This community generally migrates from the substrate to the water column at dark.
5. Phytoplankton communities found over the reefs appear to be little different from open ocean assemblages.

had both campus and cluster elements. In contrast only one of the seven reefs we studied in the Middle and Lower Keys had the campus element. These differences, which may well reflect succession (Jones, 1977), limit comparison of reefs to clusters.

A limitation of our data on dead surfaces for corals of the campus is that different observers collected it without inter calibration. However, the categories of dead surface are so broad, that we believe the estimates of different observers are comparable. For the clusters, the estimates from line point intercept counts of dead surface are not subject to operator error. The test of variability related to the number of points (Table 2) indicates that the standard deviation for individual transects is between 1 and 15%.

SIZE DISTRIBUTION.—For demographic studies in colonial organisms such as corals, it is legitimate to use colony size rather than age, even though processes like partial mortality, fission, or fusion can severely distort size-age relationships (Hughes and Jackson, 1980). Variation in genetic or environmental influence can cause significant differences in growth rates, which, e.g., in the case of *M. annularis* is about 200% in shallow reefs of the Florida Keys (Hudson, 1981b; Hudson et al., 1994). Size correlates better with probabilities of mortality and natality of colonial organisms and is therefore more useful (Hughes, 1984). For example, larger corals are generally more fecund than smaller ones and smaller colonies have higher rates of mortality. In several large massive corals, reproductive ability is dependent on size, not on age (Connell, 1973; Szmant, 1986). Studies including both size and age of corals are very rare, but have shown that size effects on population dynamics are stronger than age effects (Hughes and Connell, 1987; Babcock, 1991).

The size distributions of all species are skewed and have maxima between 0.2 and 0.5 m. Lewis (1997) found similarly skewed size distributions of *S. siderea* at Barbados. One obvious reason for the decreased abundance of larger colonies is the observed increase in percent dead colony surface with increasing size (Fig. 5). Evidently this relationship is a general one as it has been signaled by Hughes and Connell (1987) and by Lewis (1997). The longer a colony exists and the larger it grows, the higher the probability that diseases, bioerosion, and physical disturbance affect it. As a consequence, only few colonies reach large sizes. In *D. strigosa* and *D. labyrinthiformis* increasing mortality with increasing size is much less pronounced than in the other species investigated. This difference might be a result of the greater ability of *Diploria* to regenerate from damages with increasing colony size (Meesters, 1995).

The continued development of new clusters of giant colonies of *Montastraea* spp. is of special concern as these clusters provide essential habitats for fish and invertebrates through the large cavities within and beneath them. To determine if the condition of clusters in Florida is unusual and is owing to some combination of natural and or anthropogenic impacts, comparative studies are needed of clusters in areas outside the storm zone and in areas with minimal populations. As a first step in that direction, measurements of the dead surfaces of a few clusters in the Dry Tortugas National Park, some 100 km west of Key West were found to be similar to those in the Reef Tract reported here. If further measurements of dead surfaces in this remote Park confirm these initial results, they would indicate that clusters with half their surfaces dead in the Reef Tract are not the result of local direct anthropogenic impacts, but instead reflect a widespread condition.

CONDITION OF CORALS.—Our results for all massive corals we assessed (Fig. 6), indicate that 74% of the 3232 colonies examined have less than 1/3 dead surfaces. In evaluating this finding as well as in evaluating all our results, several special conditions of the study area need to be considered. The Florida Reef Tract and especially the north half of our

and *O. oculata*. He estimated that one swarm of *A. spinata* contained 110,000 copepods/m^3. Hamner and Carleton (1979) also reported extremely dense swarms of copepods (max. 3,320,000/m^3) on Australian reefs. Swarming species of copepods, in the Emery study, were most often found on the grass beds and reef tops. Monospecific schools of mysids, of one size class, were also found on the the reef tops often inside caves and along coral faces. Schooling implies a stronger social behavior than swarming since the individuals that belong to one size class are longitudinally aligned and move as a unit. Schooling behavior of mysids has also been reported by other investigators of Alligator Reef (Randall et al. 1964). On the deep reefs and the patch reefs of both Alligator and Looe Key Reefs, close aggregations of the plankton did not appear as important. Copepods and mysids were found individually or in looser aggregations. Emery also observed that the swarming and schooling behavior of these organisms was mostly a daytime phenomenon. They were often found individually at night. Hobson and Chess (1979), reporting on resident reef plankton of Hawaiian atolls, found a similar diurnal pattern for swarms of copepods, mysids, and larval fishes.

Swarming and schooling in dense aggregates are important examples of behavior adaptation by resident reef plankton, which differentiates them from pelagic forms. Hamner and Carleton (1979) stated that at least seven species of copepods, and probably more, engage in swarming behavior at coral reefs in three of the world's oceans. The same authors have suggested that swarming not only reduces predatory pressure, but also facilitates reproduction and permits the plankton to cluster in local eddies to maintain a favorable feeding position with minimum energy cost. In a subsequent paper, Hamner and Hauri (1981) related the resident reef zooplankton distribution to the reef configuration and the local water motion. They found swarms of copepods and chaetognaths directly upcurrent of the reef face in an entrained water mass, which was subject to less removal than downstream waters. This accumulation of biomass and increased primary productivity in areas upstream of reefs is one aspect of the well-known "island mass effect" phenomenon.

5.3 DIURNAL MIGRATIONS

Investigators of coral reef zooplankton who have taken care to sample the populations near the substrate and on a diurnal schedule have found the plankton community undergoes drastic daily changes. Emery (1968) found that nighttime collections contained four times greater volume than daytime collections. A suction device with a light close to its mouth to attract the plankton was used for these collections, and therefore, quantitative comparisons are not in order. Emery did, however, find a very different composition of the plankton at night. Many forms, such as polychaetes, cumaceans, and zoea, which he observed living in caves and crevices during the day, were swimming outside the reef in great abundance at night. Other forms which were most often captured at night included: fish larvae; large copepods; crab larvae; chaetognaths; ostracods; and shrimp larvae. Ohlhorst (1982) found that the zooplankton emerged from the substrate of Discovery Bay, Jamaica, at variable rates throughout the night. The peak activity was usually two hours after sunset. However, smaller species of copepods and juvenile members of large species migrated into the water column during the day and were least abundant in the water column during the night. She suggested that the reasons for diel vertical migration are many and varied. They include: feeding; reproduction; escape from predation; and dispersal. Porter et al. (1977) studied reefs in the Pacific Ocean and found that the volume of emerging plankton was greatest over branching coral and least over sand and rubble. Alldredge and King (1977) and McWilliams et al. (1981), sampling different reefs of the Great Barrier Reef, also found a positive relationship between the structural heterogeneity of the substrate and the amount of epibenthic plankton emerging at dark. The composition of the community Alldredge and King found was similar to the one described by Emery (1968), and they estimated that an average of 2,510 zooplankton emerged per m^2 of the reef substrate. McWilliams et al. (1981), conducting a more detailed study, found not only a greater volume of plankton emerging from the coral than from the sand but also that the composition of the rising communities were different. The reef bases were transitional zones with a mixture of "coral" and "sand" communities. These authors further found that more plankton emerged during the summer than during the winter. The annual range of the "coral" fauna was 5,030-2,350 animals/m^2 and the "sand" fauna 2,720-1,150 animals/m^2. Also, the plankton samples collected during the summer were generally more diverse in taxa than winter samples. Hobson and Chess (1979), collecting emerging plankton from the lagoon substrata of atolls in the Pacific Ocean, found a considerably less abundant plankton community in their traps than reported by Alldrege and King (1977) and McWilliams et al. (1981). Hobson and Chess (1979) suggested that the use of different types of traps may account for some of the variations reported between study areas. Youngbluth (1982) tested three types of emergence traps and found that both density and diversity of the zooplankton collected were affected by the trap design and sampling procedures. He concluded that different mesh size netting in the traps alone could probably account for much of the variability in plankton abundance and diversity between different study areas.

5.4 SUMMARY

The coral reef plankton community can be characterized as follows:

1. A highly abundant and diverse zooplankton community is found on the reefs. It is in striking contrast to the open water community nearby.

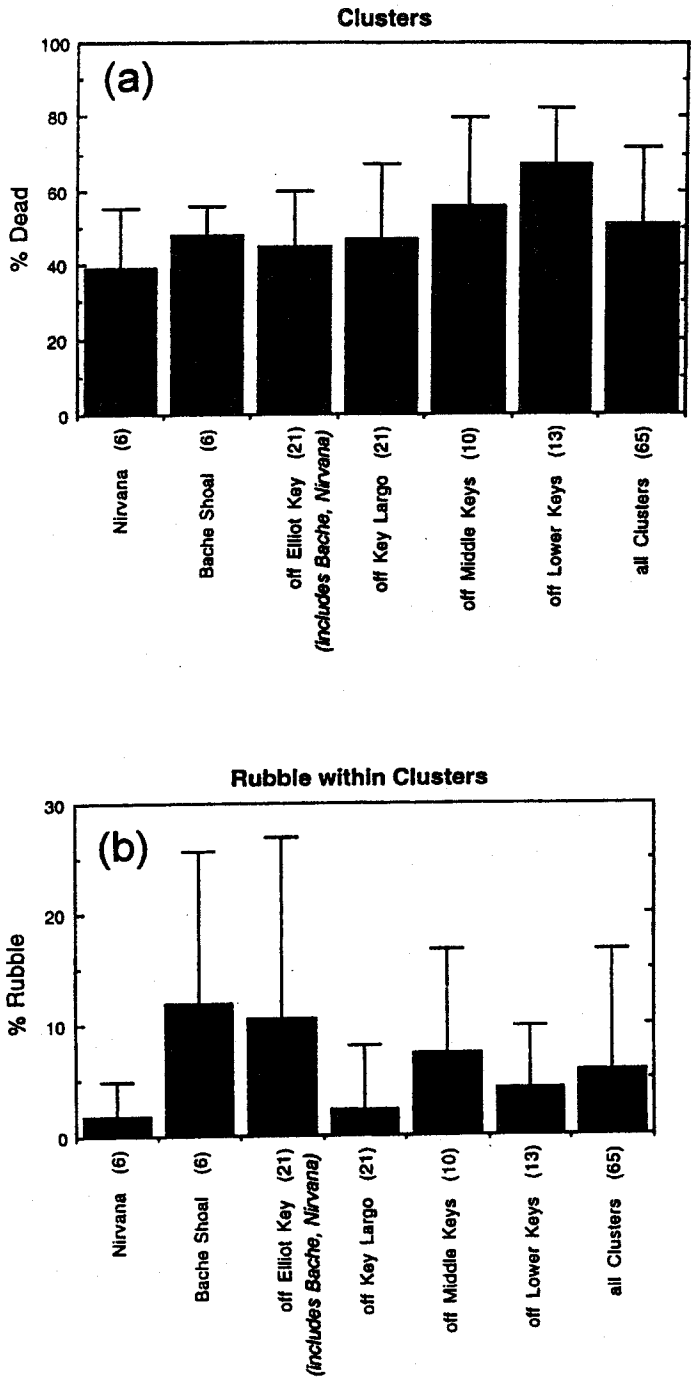


Figure 9. Results of observations on clusters. Black bars show mean percentages; arrows show standard deviations. (a) Percent dead colony surface. Note the local and regional variability of the data. (b) Percentage of rubble within clusters. Higher amounts of rubble off Elliot Key because of the effects of Hurricane Andrew and tropical storm Gordon.

CHAPTER 5

PLANKTON

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5.1 INTRODUCTION

Coral reefs are highly productive marine ecosystems with a great abundance and diversity of organisms. They are generally surrounded by waters with small plankton standing stocks. Most studies describing coral reef plankton communities have investigated the importance of zooplankton in coral nutrition. The results of these studies have been somewhat contradictory.

The early studies (Yonge 1930 and others) generally indicated that there was not a sufficient amount of zooplankton in the water column around the reef to support the corals. Recent studies of coral reef zooplankton (Emery 1968; Porter 1974; Sale et al. 1976; Alldredge and King 1977; Porter et al. 1977; Hobson and Chess 1978; Hamner and Carleton 1979; Hobson and Chess 1979; Rutzler et al. 1980; Hamner and Hauri 1981; McWilliams et al. 1981; and Ohlhorst 1982) have shown that methods used in the earlier studies for capturing the reef zooplankton were not adequate to describe the zooplankton community most nutritionally important to the corals. These plankton live in close association with the corals, sometimes within the reef itself.

The earlier collections used nets which were towed or drifted above and sometimes away from the reefs. The recent studies, using an array of different collection and observation methods such as stationary nets, diver-controlled nets, plankton pumps, diver-operated suction devices, emergence traps, light traps, and diver visual and photographic observations (see Porter et al. 1978; Hamner and Carleton 1979; and Youngbluth 1982 for discussion of sampling techniques), have found that coral reefs, worldwide, have an abundant and diverse resident near-reef zooplankton community different from the oceanic forms in the surrounding ocean. Porter et al. (1978), summarizing information from mostly Indo-Pacific reefs, estimated that 75% of the reef zooplankton standing stock was of benthic origin and that 85% of the biomass was of local origin. Parts of this community are, therefore, often not considered as truly planktonic, but rather as epibenthic or demersal. Many organisms in the resident community are only found in the water column at night and spend daylight hours on the sediment or within the reef itself (see Section 5.3).

It is still not clearly demonstrated, however, what importance zooplankton play in coral nutrition. Emery (1968) states that plankton represent a major source of food to the reef, while Muscatine and Porter (1977) suggest that zooplankton feeding does not contribute a majority of either calories or carbon required for reef corals. Hamner and Carleton (1979) summarize and critique studies of reef zooplankton and find that, due to often questionable methodologies used, no conclusive data on the relative importance of zooplankton to coral reef nutrition have yet been published.

Few studies have been conducted describing the free living phytoplankton community in the vicinity of coral reefs. Researchers generally agree that phytoplankton's contribution to the primary productivity of the coral reef ecosystem is small (e.g., Hargraves 1982). Further, Wood (1954) suggested that the waters of the Great Barrier Reef might have a distinctive reef phytoplankton community. Subsequent studies (Jeffrey 1968; Revelante et al. 1982), however, found a reef community similar to the nearby ocean phytoplankton community. The following discussion of coral reef plankton will, therefore, mainly be concerned with the zooplankton community.

5.2 TAXONOMIC COMPOSITION AND SPATIAL DISTRIBUTION

As discussed above, several researchers have described coral reef zooplankton communities in great detail. However, due to geographical considerations, the following discussion will generally be limited to observations of Alligator and Looe Key Reefs in Florida by Emery (1968). The information obtained in these studies is somewhat limited due to the lack of quantitative abundance measurements; however, the report gives a detailed account of the spatial and temporal distribution of the different zooplankton taxa found on the reefs. Emery used several different collection methods, including boat- and swimmer-towed nets, suction devices, light traps, and diver observations, in order to reduce sampling errors of zooplankton living near or within the reefs. Further, he made collections and observations during both day and night. He also subdivided the study areas into several habitats such as grass beds, lagoons, patch reef, reef tops, caves, and deep reefs. Visual observations by divers, swimmer-towed nets, and suction devices produced the most interesting information about the zooplankton on and in close vicinity of the reefs.

Close to the water surface of all areas of the reefs, Emery found a typical offshore zooplankton community, consisting mostly of free living copepods and larvaceans. Visual observations deeper in the water column and just above the bottom often found the reef plankton in close and dense aggregations or swarms. The swarms tended to hold together and move as a unit, and they also maintained their position against the current and the surge. Emery found four species of copepods in these swarms: *Acartia tonsa, A. spinata, Oithona nana,*

study area is near the northern limit of both well–developed patch and bank-barrier reefs. Reef-building corals extend farther north, but most of these communities do not produce significant sea-floor relief. A second aspect that bears on our results is the shallowness of all but three of the reefs we assessed as indicated above. Thirdly, the turbidity of the water is often high for prolonged periods during the winter when winds are often strong. The Middle Keys zone and perhaps part of the Lower Keys is under the influence of water issuing out of Florida Bay that is unfavorable for coral and reef development (see references cited above). Given these unfavorable conditions, the partial mortality we found could well be normal for part or the entire Florida Reef Tract. Confirmation of this inference must await data from comparable reefs in other areas of the Western Atlantic.

Species of *Diploria* have the least partial mortality, i.e., largest percentages of colonies with <1/3 dead surfaces. Comparable results were reported by Bythell et al. (1993) who compared chronic and storm-related, catastrophic mortality in *D. strigosa, M. annularis* and *P. astreoides.* They found that *D. strigosa* is generally unaffected by chronic factors such as grazing and tissue necrosis, but showed heavy damage by Hurricane Hugo. On the other hand, *M. annularis* showed only minor storm damage, but high chronic mortality from grazing and necrosis. *S. siderea is* known to withstand high turbidity as colonies thrive at distances less than 100 m from shore, e.g., in Florida (Hudson, 1981a) and in Belize (R.N . Ginsburg, E. Gischler, unpubl. data). This species alone can form patch reefs of giant colonies in the restricted lagoon of Turneffe Islands, Belize, where extreme fluctuations of temperature (up to 32°C) and of salinity (up to 70‰) have been reported (Smith, 1941; Gischler, unpubl. data) The fact that species of *Diploria* and *S. siderea* are tolerant forms can also be seen in the small variability of the data for these species (see Fig. 6).

Further and more detailed observations are needed to bolster our finding of the overall condition of massive corals. The category of <1/3 dead surface is too broad and distinctions must be made between recently dead with polyp surface still present (Diaz, 1995) and old dead. In addition, the nature of the dead surfaces need to be described and where possible the cause(s) identified (Dustan, 1994).

Natural and Anthropogenic Impacts.—On the basis of natural and human impact, the study area may be divided into four zones (Fig. 1). The northern zone includes the reefs off Elliot and Old Rhodes Keys, which are in the track of Hurricane Andrew of 1992, and the unusually severe tropical storm Gordon of 1994. As a consequence, reefs in this zone have large amounts of coral rubble (Fig. 9B), (see also Lirman and Fong, 1995, 1997). The next zone south, the area off Key Largo, probably has large human impacts because of the relatively large population and the focus of fishing and diving. There is however, no clear increase in dead tissue/colony for those off Key Largo as compared with the same species off uninhabited Elliot Key.

The Middle Keys Zone has a perennial influence of unfavorable water quality resulting from outflows from Florida Bay and the Gulf of Mexico which is reflected in the limited number of reefs and in the condition of the corals (Ginsburg and Shinn, 1964, 1994; Smith, 1994). Episodes of cold water outflow from Florida Bay in the winters of 1969 and 1977 killed large amounts of coral including the near demise, in 1969–70, of those massive corals on one of the largest patch reefs of the area, Hen and Chickens Reef (Roberts et al., 1982). The fact that *Montastraea* clusters in this zone have more dead surface than those off Elliot Key and Key Largo (Fig. 9A) is believed to be a combination of those known episodes of cold water and other episodes of unfavorable water quality

are often a limiting factor. Rapid growth among the Acroporid species can shade out other slower growing species (Shinn 1975). Some species have potent external digestive mechanisms whereby the mesenterial filaments are extended and kill the tissues of adjacent corals. Lang (1971, 1973) documented this digestive mechanism as hierarchical among the species of Atlantic Scleractinia. Some species compete with this agressive territorial behavior through sweeper tentacles which keep the mesenterial filaments away from the lower hierarchy species. It is also probable that alleochemicals are important in protecting space. Biological interactions are probably more significant in deeper reef environments where physical events are less frequent and of an intermediate magnitude.

Coral pathology and disease is an infant research area. Phenomena were reported by Preston (1950) and Squires (1965). Laboratory experiments demonstrate that bacteria cause morbidity and mortality in corals (Mitchell and Chet 1975; Ducklow and Mitchell 1979a, 1979b). Antonius (1974b) reported that a blue-green alga, *Oscillatoria,* was capable of killing corals under certain (laboratory and field) conditions (Plate 19a). The alga grew over the coral, killing it in a short period. Gladfelter (1982) reported on an undetermined pathogen that caused epidemic mortality in *A. palmata* on a reef off St. Croix, U.S. Virgin Islands. A similar condition is often seen on Florida reefs; Grecian Rocks appears to be currently infested with this pathogen (Plate 25a). Pathology and band diseases in corals were reviewed by Antonius (1981a, 1981b).

4.5 OTHER BENTHIC GROUPS

The level of insight into many other coral reef benthic groups is poor. Detailed examination will not be attempted here. There are numerous diverse habitats within a coral reef that provide niches to a multitude of species belonging to nearly every phylum (Plate 8b). Sedimentary deposits provide habitat for infaunal organisms. Many mobile forms find refuge under the sedimentary surface and forage for food at night. The reef rock itself is a habitat for both epifauna and boring and cryptic fauna. A single coral head weighing 4.7 kg at Heron Island contained 1,441 polychaete individuals (Grassle 1973); 67% of all organisms from the coral's interior were polychaetes. Vittor and Johnson (1977) studied polychaetes from Grand Bahama Island and reported that 84 species were present. Robertson (1963), Ebbs (1966), Hein and Risk (1975), and Hudson (1977) reported on the boring fauna of Florida corals. Specific references that deal with the other benthos include the proceedings volumes from the past International Coral Reef Symposia, the two volumes from the *Biology and Geology of Coral Reefs*, Volumes 23 (1, 2) of *Bulletin of Marine Science*, Frost et al. (1977), Colin (1978a), and Rutzler and MacIntyre (1982b). Voss et al. (1969) provided a qualitative account of the biota found within BNP prior to its becoming a national monument. The study of most other benthic organisms, save certain commercial species (e.g., spiny lobster), is for taxonomic purposes. Decapod crustaceans were reported on by Gore (1981). Lyons and Kennedy (1981) and Lyons et al. (1981) reported on biological aspects of the spiny lobster *Panulirus argus.* Work (1969) studied West Indian mollusk communities. Kier and Grant (1965) and Kissling and Taylor (1977) discussed echinoderms from Florida reef communities.

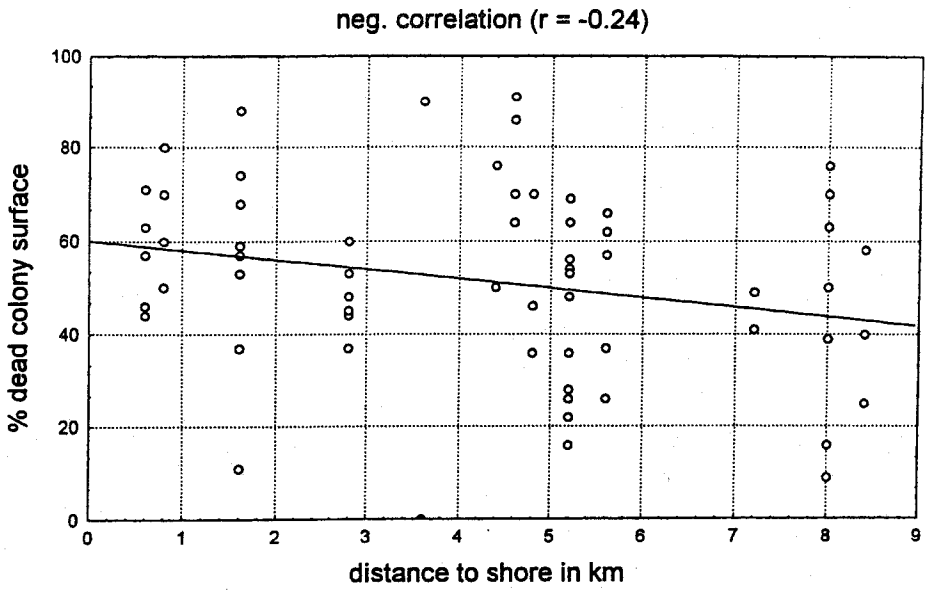


Figure 10. Graph showing the distance from shore of 65 *Montastraea* clusters plotted against percentage of dead surfaces.

from Florida Bay, i.e., warmer, more saline, or unusually turbid (see references cited above).

In the Lower Keys, the clusters of *Montastraea* have more dead surfaces than in any of the other zones (Fig. 9A). However, the limited number of cluster reefs (4) is an inadequate sample; moreover the fact that there are so few patch reefs suggests that conditions for their occurrence are relatively unfavorable. Given the limited data base and the less favorable setting for patch reef development, there is no clear evidence to determine whether or not localized human impacts from divers, fishers, and runoff have contributed to the declines we observed.

Lewis (1997) used the same methods as we did to determine if variations in partial mortality of *S. siderea* are related to variations in eutrophication on fringing reefs of the West Coast of Barbados. He found no clear relationship, but he did find the same positive correlation between size and percent dead tissue reported above.

Conclusions

- Shallow patch reefs of the Florida Reef Tract consist of combinations of two size populations of nine species of massive corals: a campus composed of colonies generally < 1m in diameter and/or clusters of larger colonies 1–5 m in diameter.
- The more numerous colonies of the campus have diameters between 10–60 cm. The size distributions of all but one of the nine species examined are skewed toward the smaller sizes. The smaller number of larger colonies is believed to be the result of the cumulative effects of disease, bioerosion, and removal by storm waves.
- Visual estimates of partial mortality of 3232 massive corals at 23 patch reefs off the Florida Keys found that 74% had <1/3 dead surfaces. Of 65 clusters of giant colonies of *M. annularis* and *M. faveolata*, 2–5 m in diameter, the line point intercept transect

Table 28

Time series for abundance, density, and dispersion of stony corals at Elkhorn Reef (one 4-m^2 plot) (Jaap, unpublished).

Species	B. I.[a] (ranking)	Abundance (total no. of colonies)	Percent of total colonies	Density ($\bar{x}\pm s$)	D.I.[b]
1978					
Acropora cervicornis	7	7	24.14	1.75±0.50	R
Acropora palmata	6	6	20.69	1.50±1.29	R
Porites porites	5	5	17.24	1.25±1.26	R
Porites astreoides	4	4	13.79	1.00±0.00	R
Siderastrea siderea	3	3	10.34	0.75±0.96	R
Millepora alcicornis	2	2	6.90	0.50±1.00	R
Favia fragum	1	1	3.45	0.25±0.50	R
Diploria clivosa	1	1	3.45	0.25±0.50	R
Yearly total		29			
1979					
Acropora cervicornis	7	9	36.00	1.75±0.96	R
Acropora palmata	6	6	24.00	1.50±1.29	R
Siderastrea siderea	4	4	16.00	1.00±1.15	R
Porites astreoides	4	4	16.00	1.00±0.82	R
Diploria clivosa	1	1	4.00	0.25±0.50	R
Millepora alcicornis	1	1	4.00	0.25±0.50	R
Yearly total		25			
1980[c]					
Acropora palmata	9	26	74.29	6.50±3.70	R
Acropora cervicornis	4	4	11.43	1.00±1.15	R
Siderastrea siderea	3	3	8.57	0.75±0.96	R
Porites astreoides	2	2	5.71	0.50±0.58	R
Yearly total		35			
1981					
Acropora palmata	10	23	62.16	5.75±1.71	R
Siderastrea siderea	3	3	8.11	0.75±0.96	R
Porites astreoides	3	4	10.81	1.00±0.82	R
Porites porites	3	3	8.11	0.75±1.50	R
Acropora cervicornis	1	1	2.70	0.25±0.50	R
Diploria clivosa	1	2	5.41	0.50±1.00	R
Millepora complanata	1	1	2.70	0.25±0.50	R
Yearly total		37			

[a] B.I. = Biological Index, McCloskey (1970).

[b] D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

[c] Note that a storm during the winter of 1979-80 fragmented a large *A. palmata* colony. Survivors established a new set of colonies, thus changing dominance and density.

sampling method (Loya, 1978) showed that some 60% had between 40 to 70% dead surfaces. The amount of dead surfaces on massive corals of shallow patch reefs increases with size of colony.

- In terms of relative amounts of dead surfaces, colonies of the three species of *Diploria* have the least, next are the two species of *Siderastrea*, *C. natans*, *M. cavernosa*, *M. franksi*, *and M. faveolata*, and those of *M. annularis* have the most dead surfaces.
- As the conditions of the Florida Reef Tract are less than optimum for reef-building corals, we do not believe that the amount of dead tissue indicates a regional, anthropogenic impact, nor do the results reflect a significant effect of the large population or heavy use off Key Largo. The increased amount of dead tissue in clusters of the Middle Keys and Lower Keys is believed to be the result of unfavorable water quality. For the Middle Keys Section, it is likely that outflows from lagoonal Florida Bay are responsible; for the Lower Keys, both natural and anthropogenic impacts in the nearshore zone are the probable cause of increased colony mortality.

Epilogue

The results of this study were the foundation for the development of an expanded method to assess the condition of key reef elements. The new method includes a more precise estimate of partial mortality subdivided into recent and old mortality and the relative abundance of major algal communities. For reef fish the expanded method combines a roving diver census of fish species with belt transects to estimate sizes and abundance of target species. This new method has been applied throughout the Wider Caribbean and Gulf of Mexico under the Atlantic Gulf Rapid Reef Assessment Program (AGRRA). A full description of the method and preliminary results of assessments can be found at http://coral.aoml.noaa.gov/agra/.

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Table 27

Growth rates of scleractinian species from Florida and the Bahamas[a].

Species	Growth rate[b] (mm/yr)	Location	Source
Acropora cervicornis	40.0 H	Dry Tortugas	Vaughan and Shaw 1916[c]
	109.0 H	Key Largo Dry Rocks	Shinn 1966
	115.0 H	Eastern Sambo	Jaap 1974
Acropora palmata	39.5 H	Goulding Cay, Bahamas	Vaughan and Shaw 1916
	105.0 B	Eastern Sambo	Jaap 1974
Acropora prolifera	37.2 H	Goulding Cay, Bahamas	Vaughan and Shaw 1916
Agaricia agaricites	3.5 H	Dry Tortugas	Vaughan and Shaw 1916
Porites porites	17.9 H	Dry Tortugas	Vaughan and Shaw 1916
Porites astreoides	17.6 D	Dry Tortugas	Vaughan and Shaw 1916
Siderastrea radians	4.3 D	Dry Tortugas	Vaughan and Shaw 1916
Siderastrea siderea	6.3 D	Dry Tortugas	Vaughan and Shaw 1916
Favia fragum	4.9 D	Dry Tortugas	Vaughan and Shaw 1916
Diploria labyrinthiformis	7.8 D	Dry Tortugas	Vaughan and Shaw 1916
Diploria clivosa	17.3 D	Dry Tortugas	Vaughan and Shaw 1916
Diploria strigosa	6.9 H	Dry Tortugas	Vaughan and Shaw 1916
	5.0 H	Carysfort	Shinn 1975
Manicina areolata	8.2 D	Dry Tortugas	Vaughan and Shaw 1916
Manicina areolata mayori	14.0 D	Dry Tortugas	Vaughan and Shaw 1916
Montastraea cavernosa	4.4 H	Dry Tortugas	Vaughan and Shaw 1916
Montastraea annularis	9.0 H	Key West	Agassiz 1890
	5.0-6.8 H	Dry Tortugas	Vaughan and Shaw 1916
	10.7 H	Carysfort	Hoffmeister and Multer 1964
	8.4 H	Carysfort	Shinn 1975
	8.0-9.7 H	Key Largo area	Hudson 1981
Oculina diffusa	14.3 H	Dry Tortugas	Vaughan and Shaw 1916
Dichocoenia stokesii	6.7 D	Dry Tortugas	Vaughan and Shaw 1916
Dendrogyra cylindrus	10.4 H	Dry Tortugas	Vaughan and Shaw 1916
Isophyllia sinuosa	5.1 D	Goulding Cay, Bahamas	Vaughan and Shaw 1916
Eusmilia fastigiata	5.8 H	Dry Tortugas	Vaughan and Shaw 1916

[a]Goulding Cay, Bahamas, data were only used when Tortugas information was unavailable.
[b]B = increase in branch length, D = increase in diameter, H = increase in height.
[c]Vaughan and Shaw's multiple values were averaged.

high turbulence *P. astreoides* is dominant with *D. clivosa*. In the spur and grooves, *Acropora palmata* (Plate 5a) is dominant (Table 18). In the buttress zone *M. annularis* is most significant in the reef-building processes. Tables 17, 19, and 20 present the species ranks, abundance, densities, and dispersion patterns for a number of reefs; note the high degree of variability within and between reefs. In deep reef communities ($>$ 30 m) the species that dominate are *Agaricia lamarcki, Madracis mirabilis, Stephanocoenia michelinii, A. fragilis*, and *M. formosa*.

Dynamic population changes affect the nature of coral associations in shallower reef habitats. Colonies are frequently relocated following storms. In many cases, they do not die, but reestablish themselves in the new habitat (Plate 10a). This makes it very difficult to evaluate mortality in a time series within a sampling site. Fragmentation also complicates the issue. During the 4-year BNP study, branching species *(A. palmata, A. cervicornis,* and *P. porites)* were frequently fragmented and scattered throughout the site causing major change in abundance and dominance. What was originally a single colony in some cases was broken into 10 or more living fragments. The great variability over the period of this study points out that shallow patch reefs are dynamic and that physical controls are significant. Table 28 presents a time series of a representative 4-m^2 plot at Elkhorn Reef.

Biological interactions among the Scleractinia are documented by Lang (1971, 1973, 1980); Jackson and Buss (1975); Richardson et al. (1979); Wellington (1980), and Sheppard (1981, 1982). These interactions are mostly involved with maintaining and/or expanding space, "lebensraum" in the reef where spatial resources

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captured by the small tentacles and ingested. Some observations of external digestion via mesenterial filaments have also been reported (Yonge 1973). Plankton can also be caught in mucus nets that are on the coral surface or in the water column. The prey is brought to the mouth for ingestion. Lewis and Price (1975) reviewed coral feeding.

Digestion of animal material occurs in the region of the mesenterial filaments; partially digested material is translocated to the cells for final digestion. Translocation of food and wastes is by diffusion or wandering cells (Yonge 1973). Cellular oxygen and carbon dioxide exchange also occurs via diffusion. Muscatine and Porter (1977) reported that most reef corals cannot receive sufficient energy from planktivory to support their energy requirements; they extrapolated that approximately 20% of energy needs could be met from zooplankton. The role of zooplankton in the diet is suspected to be one of providing critical minerals and nutrients not gained via the autotrophic pathway. Other sources of energy include bacteria, detritus, organics dissolved in seawater, and external mesenterial feeding of animal tissues adjacent to the colony. Wastes are removed through the mouth.

The life history and autecology for many stony coral species are incomplete or totally unknown and are based on hypothesis and conjecture rather than fact. Sexual reproduction includes gametogenesis (Plate 8a) within the polyps near the base of the mesenteries. Some species have separate sexes and some are hermaphroditic. Fertilization occurs internally or externally. Some species such as *Acropora cervicornis* and *A. palmata* appear to be synchronous in development of gametes. Embryology terminates with the development of planktonic larvae, the planula. If there is larval brooding by the species, the planula is released through the mouth and has limited powers of locomotion by cilia. Kojis and Quinn (1981) reported that several species of Pacific Scleractinia had benthic swarming larvae. Lewis (1974) noted that *Favia fragum* in the laboratory were bottom swarming. Fadlallah (1983) reviewed scleractinian reproductive - larval biology. Upon proper stimulation, the larvae settle on appropriate substrates. Negative phototropism is partially responsible for settling. Initial calcification ensues with the forming of the basal plate and the initial protosepta, followed by the theca or wall and axial skeletal members. Buds formed on the initial corallite develop into daughter corallites.

Connell (1973) reviewed the population ecology of reef-building corals. Two generalized contrasting life history strategies are suggested; many species probably fall between the extremes. Opportunistic or R strategists attain small adult size, exhibit determinant growth, reach sexual maturity at an early age, place a great deal of available energies into reproduction, and produce small eggs and sperm that are released into the water column for fertilization. The lifespan of this type of species is short; success is insured by the vast numbers of progeny produced. These species may also be the more eurytopic in environmental tolerances. They are able to invade harsher reef habitats. *Porites astreoides* and *F. fragum* are examples of this form of strategy. Jaap (in progress) studied populations of stony corals at 24 sites (96 m^2) at BNP (1978-81). He found that *P. astreoides* was one of the most commonly recruited species in the patch reef environments. The K strategist exhibits slow growth and a long period before reaching sexual maturity. Most energy is expended toward growth and maintenance. Growth may be indeterminate. Apparently little energy is diverted toward reproduction. These species may live for hundreds or even thousands of years and sexual reproduction may be a very rare event. *Montastraea annularis* is the best example of this type of life history. Some colonies are hundreds of years old. Dustan (1977a) and Bak and Engel (1979) both reported very low or no recruitment for *M. annularis*.

Growth in scleractinian corals involved asexual tissue division and skeletogenesis (skeleton construction) (Barnes 1973). The two processes are highly interdependent; imbalance of either causes change which results in skeletal abnormalities. Growth in branching species such as *A. cervicornis* and *A. palmata* is quite rapid, while growth for the more massive star and brain corals is relatively slow. Table 27 presents growth data for several scleractinian species; many others have not been studied. Hudson (1981) noted that certain cyclic patterns appear over the 75-year growth period of the corals he cored, slabbed, and x-rayed for growth-rate skeletal density patterns. Buddemeir and Kinzie (1976) reviewed coral growth.

Recruitment is critical to perpetuation of the species and ultimately to the vitality of the coral reef communities. Dustan (1977a) reported on stony coral recruitment and mortality at Carysfort Reef (Figure 17) off Key Largo. Because the duration of his study was less than one year, the conclusions are qualified. The study showed that *Agaricia agaricites* was the most commonly recruited species. Bak and Engel (1979) studied recruitment off Bonaire and Curacao, Netherlands Antilles. They also reported that *A. agaricites* was the most commonly recruited species. Again, the one-year time frame of this study is subject to some qualifications. The overall net recruitment comparison of Dustan and Bak and Engel is difficult, since Dustan only considered corals less than 15 cm to be juvenile recruits and Bak and Engel considered colonies in the 2-40 cm range as juveniles. Both of the studies were limited to depths greater than 6.5 m. This is beyond the spur and groove zone, hence it is most representative of the fore reef or buttress zones.

As reported earlier, each reef has its own particular species composition of scleractinian corals. However, certain key framework species are fundamental to the reef-building processes. In patch reefs *M. annularis* (Plate 5b) is usually the most important species. *Diploria strigosa* (Plate 6a), *D. labyrinthiformis, Colpophyllia natans,* and *Siderastrea siderea* are also significant. The remaining species are either in low abundances or frequencies, or their biomass and framework building capacity is low.

In the bank reef communities, different zones manifest different species dominance. On reef flats with

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Table 26 (continued)

SUBORDER FAVIINA (Vaughan and Wells 1943)

Superfamily Faviidae (Gregory)

Family Faviidae (Gregory)

Favia fragum (Esper)
F. gravida (Verrill)
Diploria labyrinthiformis (Linne')
D. clivosa (Ellis and Solander)
D. strigosa (Dana) (Plate 6a)
Manicina areolata (Linne')
M. areolata mayori (Wells)
Colpophyllia natans (Houttyn)
C. amaranthus (Muller)
C. breviseralis (Milne, Edwards, and Haime)
Cladocora arbuscula (LeSueur)
Montastraea cavernosa (Linne') (Plate 6b)
M. annularis (Ellis and Solander) (Plate 5b)
Solenastrea hyades (Dana)
S. bournoni (Milne, Edwards, and Haime)

Family Rhizangiidae (d'Orbigny)

Astrangia astreiformis (Milne, Edwards, and Haime)
A. solitaria (LeSueur)
Phyllangia americana (Milne, Edwards, and Haime)

Family Oculinidae (Gray)

Oculina diffusa (Lamarck)
O. varicosa (LeSueur)
O. robusta (Pourtales)

Family Meandrinidae (Gray)

Meandrina meandrites (Linne')
M. meandrites braziliensis (Milne, Edwards, and Haime)
Dichocoenia stellaris (Milne, Edwards, and Haime)
D. stokesii (Milne, Edwards, and Haime)
Dendrogyra cylindrus (Ehrenberg) (Plate 7a)

Family Mussidae (Ortmann)

Mussa angulosa (Pallas)
Scolymia lacera (Pallas)
S. cubensis (Milne, Edwards, and Haime)
Isophyllia sinuosa (Ellis and Solander)
I. multiflora (Verrill)
Isophyllastraea rigida (Dana)
Mycetophyllia lamarckiana (Milne, Edwards, and Haime)
M. danaana (Milne, Edwards, and Haime)
M. ferox (Wells)
M. aliciae (Wells) (continued)

Table 26 (continued)

SUBORDER CARYOPHYLLIINA (Vaughan and Wells 1943)

Superfamily Caryophylliidae (Gray)

Family Caryophylliidae (Gray)

Eusmilia fastigiata (Pallas)
Paracyathus pulchellus (Philippi)

SUBORDER DENDROPHYLLIINA (Vaughan and Wells 1943)

Family Dendrophylliidae (Gray)

Balanophyllia floridana (Pourtales)

corals have developed other methods to conserve and recycle limiting resources such that high productivity is maintained. Muscatine and Porter (1977) reported that reef corals are primary producers, primary consumers, secondary and tertiary consumers, deposit feeders, and saprotrophs; different species have perfected different strategies.

The most unusual and probably the most important trophic strategy that is almost universal among the reef-dwelling corals is the primary producer activity. The autotroph or phototroph is carried within the coral tissue as an endosymbiont. Hermatypic scleractinia possess the dinoflagellate *Zooxanthella microadriaticum* (Loeblich and Shirley 1979) (also reported as *Symbiodinium* or *Gymnodinium)* within their endodermic tissues. The zooxanthellae complement the corals by recycling nitrogen and phosphorus, fixing carbon (lipids, amino acids, nonamino organic acids, glycerol, organic phosphates, and glucose), producing oxygen, enhancing calcification, and removing animal metabolic products (CO_2, nitrogenous wastes). Muscatine (1973), Taylor (1973), and Muscatine and Porter (1977) reviewed the coral host zooxanthellae symbiont relationship. Muscatine and Porter (1977) reported that 30% of the carbon fixed by the zooxanthellae on a clear day would satisfy all of the coral's carbon needs.

Corals are suspension feeders. Several techniques are used singularly or in combination to capture zooplankton. The most common technique is to capture drifting zooplankton by stunning the zooplanktors with the nematocysts, a special poison organelle found in the tentacles. (Although most polyp expansion for feeding occurs nocturnally and the tentacles of most species are retracted during the day, *Dendrogyra cylindrus* is an exception (Plate 7a). Porter (1974) reported on polyp expansion.) The captured zooplanktors are delivered to the mouth by the tentacles or by reverse beating of the cilia. In family Agariciidae small polyps generate water currents with the cilia. Food caught in the current is

Vaughan, T. W. 1914. Investigations of the geology and geologic processes of the reef tracts and adjacent areas in the Bahamas and Florida. Carnegie Inst. Wash. Year Book. 12: 183.

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5. Numerous fish have been observed feeding; however, they do not appear to be obligate octocoralivores (Randall 1967).

Octocorals are increasingly harvested for human purposes. Many octocorals contain pharmacologically active compounds within their tissues. Medical-pharmacological research requires harvest of prodigious quantities of octocorals to isolate active compounds. Bayer and Weinheimer (1974) reported on the prostaglandin compounds extracted from *Plexaura homomalla*. Concern has been registered that this might eliminate a species population over a wide area if harvest restrictions were not instituted. Another exploitation of octocorals within the area is for live aquaria. Information provided to the Gulf of Mexico Fishery Management Council reported 5,845 colonies of octocorals belonging to nine species are harvested annually and sold as aquarium specimens; several are nonreef species. Current State and proposed Federal statutes only protect the sea fan, genus *Gorgonia*.

Scleractinia

The Scleractinia (stony corals) are a specialized order of Zoantharia, distinguished by an aragonite calcareous exoskeleton. The skeleton (Plate 9a) is composed of a basal plate, external wall, and specialized internal structures--the septa, pali, and columellae. The group in general expresses radial symmetry set in a hexamerous mode. Yonge (1940, 1973) and Wells (1957b) reviewed scleractinian biology, and Vaughan and Wells (1943) and Wells (1956) provided a glossary of terms and definitions.

The order Scleractinia is divided into five suborders (Table 26)—Astrocoeniina, Fungiina, Faviina, Caryophylliina, and Dendrophylliina. Most shallow-water, reef-building corals are found in the first three suborders, with the greatest number in the Faviina. With few exceptions taxonomic characters are based on the skeleton, especially the septa.

The fundamental unit of the coral colony is the polyp (Plate 7b), a tiny mass of tissue with a set of tentacles and a central mouth. The tentacles and adjacent connecting tissues are covered with cilia and nematocysts. There are three tissue layers: ectoderm, mesoglea, and endoderm or gastroderm. The endoderm of reef Scleractinia is usually filled with dense concentrations of zooxanthellae. The color of coral tissue, a complex of plant and animal tissue, is mostly the result of the plant pigments within the chloroplasts of these zooxanthellae. Coral tissue covers only the very surface of the limestone skeletal mass. McCloskey (in Muscatine and Porter 1977) reported that this tissue complex was 45% plant and 55% animal by weight. Because coral tissues contain the producer, and fixed carbon can be passed directly to the coral animal tissues for utilization without a herbivorous intermediary, the association of coral and zooxanthellae is successful in nutrient-impoverished tropical waters. To augment this ability,

Table 26

Southeast Florida reef Scleractinia.

ORDER SCLERACTINIA

SUBORDER ASTROCOENIINA (Vaughan and Wells 1943)

Family Astrocoeniidae (Koby)

Stephanocoenia michelini (Milne, Edwards, and Haime)

Family Pocilloporidae (Gray)

Madracis decactis (Lyman)
M. formosa (Wells)
M. mirabilis (sensu Wells)

Family Acroporidae (Verrill)

Acropora palmata (Lamarck) (Plate 5a)
A. cervicornis (Lamarck) (Plate 4b)
A. prolifera (Lamarck) (Plate 5a)

SUBORDER FUNGIINA (Verrill)

Family Agariciidae (Gray)

Agaricia agaricites (Linne')
A. agaricites agaricites (Linne')
A. agaricites danai (Milne, Edwards, and Haime)
A. agaricites carinata (Wells)
A. agaricites purpurea (LeSueur)
A. lamarcki (Milne, Edwards, and Haime)
A. undata (Ellis and Solander)
A. fragilis (Dana)
Helioseris cucullata (Ellis and Solander)

Family Siderastreidae (Vaughan and Wells 1943)

Siderastrea radians (Pallas)
S. siderea (Ellis and Solander)

Superfamily Poritidae (Gray)

Family Poritidae (Gray)

Porites astreoides (Lamarck)
P. porites (Pallas)
P. porites divaricata (LeSueur)
P. porites furcata (Lamarck)
P. porites clavaria (Lamarck)
P. branneri (Rathbun)

(continued)

APPENDIX

Locations of the reefs studied. For some localities less coordinates than sites are given because the distance between sites is below the resolution of the Magellan GPS-instrument. Localities that were given names by the authors and cannot be found on nautical charts are marked by an asterisk.

Reef	campus sites	cluster sites (points assessed)	Latitude (N)	Longitude (W)
Upper Keys				
Carysfort West*	-	7 (80–181)	25°13.752	80°14.050
			25°13.756	80°13.823
			25°13.892	80°14.041
			25°11.673	80°15.967
			25°11.376	80°15.522
			25°11.776	80°15.850
Bache Shoal	4	6 (100–351)	25°29.074	80°08.917
			25°29.161	80°08.892
			25°29.126	80°08.892
			25°28.970	80°08.981
			25°29.126	80°08.966
Larz Reef*	–	1 (81)	25°25.171	80°09.259
Nirvana North*	–	2 (357, 402)	25°25.327	80°08.838
Buck's Reef*	1	1 (101)	25°25.334	80°08.843
Bug Reefs*	3	3 (102–204)	25°21.329	80°11.402
Cannon South*	1	–	25°06.150	80°21.400
Triangles	3	2 (80, 100)	25°01.121	80°26.374
			25°01.182	80°26.418
Nirvana*	2	6 (78–365)	25°24.973	80°09.094
			25°25.120	80°09.033
Alina's Reef*	–	2 (180, 204)	25°23.201	80°09.768
Long Reef West*	1	–	25°25.272	80°08.625
Higdon Reef	2	2 (106, 107)	25°08.144	80°18.981
			25°08.450	80°18.873
Sting Reef*	2	3 (60–100)	25°04.170	80°22.243
			25°04.165	80°22.284
Alan's Deep*	–	2 (80, 106)	25°10.050	80°15.600
Key Largo D. R.	–	2 (84, 90)	25°07.357	80°17.915
White Bank D. R.	2	3 (100–102)	25°02.430	80°22.272
			25°02.605	80°22.120
Middle Keys				
The Rocks	–	4 (79–173)	24°56.645	80°33.387
			24°56.670	80°33.180
Cheeca Rocks	–	4 (80–142)	24°54.130	80°36.920
Marker 48	–	2 (195, 200)	24°41.330	81°02.320
Lower Keys				
Newfound Harbor*	–	5 (172–194)	24°36.987	81°23.629
			24°36.946	81°23.515
West Washerwoman	–	4 (180–201)	24°37.929	81°35.396
Boca Chica*	–	4 (96–104)	24°33.116	81°42.012
			24°33.043	81°42.191
			24°33.097	81°42.096
Ninefoot Shoal	1	–	24°34.177	81°33.127

Table 25

Octocoral fauna in shallow (<30 m) southeast Florida reef communities (Bayer 1961; Opresko 1973; Wheaton 1981, in preparation b).

Species	Patch reef	Bank reef
Briareum asbestinum	x	x
Iciligorgia schrammi	x	x
Erythropodium caribaeorum	x	x
Plexaura homomalla	x	x
P. flexuosa	x	x
Pseudoplexaura porosa	x	x
P. flagellosa	x	x
P. wagenaari	x	x
P. crucis	x	x
Eunicea palmeri	x	x
E. pinta	x	x
E. mammosa	x	x
E. succinea	x	x
E. fusca	x	x
E. laciniata	x	x
E. tourneforti	x	x
E. asperula	x	x
E. clavigera	x	x
E. knighti	x	x
E. calyculata	x	x
Muriceopsts flavida	x	x
Plexaurella dichotoma	x	x
P. nutans	x	x
P. grisea	x	x
P. fusifera	x	x
Muricea muricata	x	x
M. atlantica	x	x
M. laxa		x
M. elongata	x	x
Lophogorgia hebes	x	
Pseudopterogorgia bipinnata	x	x
P. kallos	x	x
P. rigida	x	x
P. acerosa	x	x
P. americana	x	x
P. elisabethae	x	x
P. navia		x
Gorgonia ventalina	x	x
Pterogorgia citrina	x	x
P. anceps	x	x
P. guadalupensis	x	
Nicella schmitti		x

release sperm into the water column; however, fertilization and embryological development are internal. Planula larvae are released through the polyp mouth. Those species studied spawn during the spring, summer, and fall. Recruitment of new colonies results from larval settlement following a brief planktonic period. Metamorphosis occurs after the larvae settle on appropriate (solid) substrate. Juvenile (sexually immature) characteristics are not significantly different from the adult's. Greatest mortality occurs during larval and juvenile stages. Growth proceeds by asexual budding of polyps and is determinant. Octocoral growth rates have not been intensely studied. Kinzie (1974) reported that the black sea rod *(Plexaura homomalla)* exhibited colony growth of 10-40 mm annually. The study also noted that sexually mature colonies were 25-35 mm in height. Kinzie's study was in the Cayman Islands but would generally apply to Florida populations.

Octocorals suffer high mortality from storms when wave surge is too great for the holdfast or the substrate itself becomes dislodged. The colony is often carried off the reef proper and recovery after dislodgement is frequently unsuccessful.

Density of octocorals ranges from very dense to sparse, dependent upon the habitat; variability is quite high. Work at Biscayne National Park, for example, documented a range of 10-50 colonies within a square meter. Both Wheaton (in preparation a) and Opresko (1973) conducted studies in patch reef habitats. Dominant species at Biscayne National Park were *Plexaura flexuosa, P. homomalla, Gorgonia ventalina, Eunicea succinea,* and *Pseudopterogorgia americana*. Opresko reported mean densities of 6.9, 11.3, and 27.1 colonies/m^2 at three reefs.

The octocoral fauna from about Stuart-Palm Beach to Dry Tortugas in depths to near 30 m is typical Caribbean or Tropical Atlantic in species composition. Local environmental conditions (depth, light, substrate, and current) control community structure.

The octocoral fauna is an important component of coral reef communities, principally as shelter and refuge for numerous commensal and epibiotic species important in the trophic structure of the reef community ranging from bacteria to fish. Copepod, decapod, amphipod crustaceans, barnacles, ophiuroids, gastropod and pelecypod molluscs, and often small stony corals attach to the central axis stem or holdfast. The fisheries management plan for coral and coral reefs reported the following predators and parasites of western Atlantic octocorals:

1. Algae in *Pseudoplexaura, Pseudopterogorgia, Plexaurella, Plexaura,* and *Muriceopsis* are manifested in abnormal growth (tumors) in the branches.

2. *Millepora* (fire coral) overgrows the octocoral.

3. The fireworm *Hermodice carunculata* (Plate 18b) preys on many corals including a number of reef octocorals.

4. *Cyphoma* spp. gastropod molluscs feed, sometimes in groups, on octocorals. *Gorgonia ventalina* is a favored prey.

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capsules (nematocysts) on the tentacles narcotize prey before they are drawn into the mouth, and sometimes can inflict powerful stings on humans.

The two classes of Cnidaria in which major colonial reef forms are found are the Hydrozoa and Anthozoa. Within the Hydrozoa class is the order Milleporina, containing the fire corals. The Anthozoa class has two subclasses: (1) Octocorallia or soft corals, including those in the order Gorgonacea (gorgonians), and (2) Zoantharia, containing the order Scleractinia or true stony corals. The following will describe the fire corals; the soft corals, especially the gorgonians; and the stony corals.

Milleporina

On Florida reefs, the Milleporina are represented by a single genus, *Millepora*. These fire corals are quite common throughout the western Atlantic tropical coral reefs. A colony consists of a calcareous skeleton with an internal meshwork and external pores through which the polyps retract and expand. The two kinds of polyps are the dactylozooid and the gastrozooid. The dactylozooid, the defensive and food-collecting polyp, has potent stinging apparatus, the nematocyst. The nematocyst contains a small hypodermiclike structure. This is a capsule with a coiled barb, flagella trigger, and a strong neurotoxin. Upon stimulation the trigger releases the barb that is shot into the prey or predator by hydraulic pressure, and the poison is released. The gastrozooid contains a mouth and digestive enzymes. Dactylozooids and gastrozooids are distributed in cyclosystems of five to seven dactylozooids around each gastrozooid.

Two species of *Millepora* are found in Florida. *M. alcicornis* is a digitate branching form, and *M. complanata* (Plate 3b) is a truncated bladed form. In many cases, it is impossible to render a specific determination. Thin encrusting veneers of reef rubble, the skeletons of other organisms, and jetsam prevent recognition of the specific characters. The western Atlantic species, *M. squarrosa*, is a nominal species. Stearn and Riding (1973) and DeWeerdt (1981) showed that *M. squarrosa* was an ecomorph of *M. complanata*. Boschma (1948, 1956) discussed the systematics and taxonomy of *Millepora*.

Millepora's life history reflects hydroid metagenesis or alternation of polyp and medusa generations. The polyp represents the benthic stage. It asexually produces planktonic medusae, which develop gametes that, when fertilized, produce planktonic larvae. The larvae settle and metamorphose into a juvenile *Millepora* colony. Recruitment can also come from fragment propagules. Following storms or physical impact, the broken pieces have regenerative powers to grow into new daughter colonies.

Millepora is a functional autotroph and heterotroph. It has very dense concentrations of zooxanthellae (microscopic, symbiotic dinoflagellate algae) in its endodermic tissues, discussed in detail in Chapter 7. The zooxanthellae are autotrophic and provide the host animal tissue with carbohydrates and some proteins. Polyp nitrogenous wastes and CO_2 are used by the zooxanthellae in protein synthesis. The calcification rate and colony growth are greatly enhanced by this symbiotic relationship. Plankton, captured by the dactylozooids and digested by the gastrozooids, probably provide the micronutrients to the polyps.

Growth rate data for *Millepora* are limited or nonexistent. After settlement the growth seems to be very rapid, probably upward growth approaches 10 cm annually (author's subjective estimate). Encrusting forms are transitory, instability of substratum usually leads to early mortality for the colony.

Wahle (1980) reported that *Millepora* colonies detect octocoral colonies from stimuli present in surrounding seawater and redirect growth to reach the octocoral colony. *Millepora* then grow over the surface of the octocoral, thus gaining new space.

Millepora complanata has a limited bathymetric distribution. It is generally restricted to the reef flat and shallow spur and groove zones (0-5 m). On Looe Key Reef (Table 23) it was second in abundance and frequency, with a mean density of slightly greater than three colonies per square meter. Mergner (1977) reported that *M. complanata* was an indicator species of photophilic and rheophilic environments; its ecological niche is apparently limited to the shallow, well-illuminated and turbulent waters found in shallow windward reef communities.

Octocorallia (Soft Corals)

The Octocorallia, commonly called soft corals or octocorals, are conspicuous in coral reef communities off southeast Florida (Table 25). They have various shapes ranging from inconspicuous encrusting mats to large sea fans. Nearly all types possess calcareous spicules embedded in an organic matrix. Specific species characteristics include colonial morphology, branching patterns, and morphology and configuration of the spicules. The fundamental morphological character is the polyp, which has eight pinnate tentacles.

The Gorgonacea (gorgonians) are the commonest octocoral in southeast Florida reefs in depths less than 30 m. They include the sea fans, sea plumes, sea feathers, sea whips, and sea rods (Plate 4a), which are all very flexible and attached by a holdfast or base to the reef platform. Branches of gorgonians possess a horny, solid center, while other groups have a solid or calcareous axis.

The taxonomy of the major categories is currently being revised. Bayer (1961) is the most complete single source for identification of the shallow water octocorals found off southeast Florida, and Cairns (1977) is a useful field guide. Deichmann (1936) reported on the deep-water octocorals.

Octocoral autecology, including environmental tolerances summarized by Bayer (1956), is similar to that of the stony corals (see next section, Scleractinia). Octocorals exhibit polytrophism, obtaining energy from multiple sources; planktivory and autotrophism are the two major sources.

Reproduction is generally dioecious. Colonies

tons. They weaken the substrate, causing the collapse and dislodgement of some corals and creating cryptic habitats in the interior of coral skeletons. In a study of *Cliona lampa* in Bermuda, Neumann (1966) found that as much as 6-7 kg of carbonate detritus could be generated from 1 m^2 of sponge-infected substrate in 100 days. Hudson (1977) reported six species of boring sponges that were principal in the bioerosion of *Montastraea annularis* (star coral) at Hens and Chickens Reef in Florida.

In contrast to the erosional effects of the boring species, many other species contribute to the structural integrity of coral reefs by binding unconsolidated reef frame material together and thereby increasing rates of carbonate accretion (Wulff and Buss 1979).

Sponges play a major role in the ecology of Florida coral reefs, but have been greatly neglected in ecological studies. As William Beebe (1928) wrote: ". . .when, in the *Iliad*, Homer described a sponge as 'full of holes,' he expressed about all the knowledge which mankind has possessed until comparatively recent times." Although there have been some advances in knowledge of sponge biology since 1928, there is still much to be learned about the physiology, ecology, and evolution of sponges.

4.4 CNIDARIA

The phylum Cnidaria (Table 24) includes jellyfish, sea anemones, corals, and hydrozoans. Although extremely variable in appearance, all members have a radially symmetrical body plan. The saclike body has a central stomach cavity with a single opening that is usually surrounded by food-capturing tentacles. Stinging

Table 24

Classification of major reef benthic Cnidaria.

PHYLUM CNIDARIA (COELENTERATA)

CLASS HYDROZOA

ORDER MILLEPORINA: fire corals

ORDER STYLASTERINA: hydrocorals

CLASS ANTHOZOA

SUBCLASS OCTOCORALLIA (ALCYONARIA) *sensu* Bayer 1961

ORDER STOLONIFERA

ORDER TELESTACEA

ORDER ALCYONACEA: fleshy soft corals

ORDER GORGONACEA: sea whips, sea feathers, sea fans, sea plumes, other gorgonian corals

ORDER PENNATULACEA: sea pens

SUBCLASS ZOANTHARIA (HEXACORALLIA)

ORDER ACTINIARIA: anemones

ORDER CORALLIMORPHARIA: false coral anemones

ORDER ZOANTHIDEA: carpet anemones

ORDER CERIANTHARIA: tube anemones, often parasitic in other organisms

ORDER SCLERACTINIA (MADREPORARIA): true stony corals

ORDER ANTIPATHARIA: black or thorny corals

Alcolado 1979), presumably because of the scouring action of waves and the increased sediment load caused by turbulence. Many species cannot tolerate high sediment loads. In *Verongia lacunosa* pumping rate is reduced under increased sediment conditions (Gerrodette and Flechsig 1979). Species with high sediment tolerance, such as *Tethya crypta*, can be common on the reef flat as are encrusting species such as *Spirastrella cunctatrix* and *Thalysias juniperina*. Species of the genus *Cliona* are also common, infesting dead coral skeletons and other suitable substrate. In deeper areas ($>$ 7 m), where conditions are more predictable and favorable, massive sponges increase in abundance. Common species found on the outer reefs of the upper Florida Keys include *Amphimedon compressa, Iotrochota birotulata, Ulosa ruetzleri, Ircinia strobilina, Ectypoplasia ferox, Callyspongia vaginalis, Niphates erecta, N. digitalis, N. amorpha, Cliona deletrix,* and *Xestospongia muta* (name designations after van Soest 1978 and 1980, and Wiedenmayer 1977).

Synecology

Sponges are major competitors with other epibenthic organisms for space and other resources in reef habitats. Sponges have the greatest overgrowth capability of the major groups of organisms encrusting undersurfaces of foliaceous corals (cheilostome ectoprocts, crustose algae, and other algae). Results varied with depth, but sponges were the superior overgrowth competitors in 77% of the interactions monitored (Jackson and Winston 1982). Overgrowth of Caribbean corals by sponges has been observed for *Chondrilla nucula* (Glynn 1973), *Ectyoplasia* sp., and *Plakortis* sp. (Lang 1982), and has been demonstrated for *Anthosigmella* var. f. *incrustans* (Vicente 1978), which was found to have a high level of competitive superiority compared with corals and other sponges. Some sponge species have been shown to exhibit toxicity to corals which they overgrow, causing necrosis of the coral tissue along the line of contact (Bryan 1973). Such a mechanism of competitive interaction presumably concerns the production of species-specific allelochemicals (Jackson and Buss 1975; Buss 1976), which can lead to intricate competitive networks and act to allow high diversity in areas of low disturbance. Sponges have also been shown to enter into complex epizoic relationships (living on one another) with one another (Rutzler 1970) which may be in response to competitive pressures.

Sponges are involved in symbiotic relationships with other reef organisms. Many sponges exist in symbiosis with bluegreen algae (or Cyanobacteria), which are mostly free living within the mesophyll and may constitute up to 52% of the cellular material of the sponge (Rutzler 1981). Nutrient translocation of algal products to coral reef sponges has been demonstrated by Wilkinson (1979). Sponges can, therefore, supplement their energy requirements through this relationship. Goreau and Hartman (1966) noted that the Caribbean sponge *Mycale laevis* has a symbiotic relationship with some stony corals. The sponge benefits from a protected and enlarging coral base to grow on, while the coral is aided by protection from boring organisms that usually gain access through the coral's undersurface. The coral possibly benefits also from greater access to heterotrophic energy sources carried in the sponge-created water currents. An obvious symbiotic relationship in Caribbean sponges involves species of Zoanthidea (Anthozoa) which grow on the surface of some sponges. Taxonomy of the sponge-associated zoanthids has been given by West (1979). Aspects of the ecology of sponge-zoanthid associations have been investigated by Crocker and Reiswig (1981), who found a high specificity between species of host sponges and their associated zoanthids. Lewis (1982) studied some functional aspects of this relationship and suggested that the zoanthid presence may have a deleterious effect by decreasing the host sponge's pumping capabilities.

Another important role of sponges in coral reef ecosystems is that of providing shelter for other reef organisms. Tyler and Bohlke (1972) listed 39 species of fish that associate with sponges, at least 5 of which are obligate sponge dwellers. The interior cavities of certain sponges are inhabited by numerous invertebrates (Pearse 1932; Westinga and Hoetjes 1981), mostly crustaceans, of which the alpheid shrimps are the most prominent. The residents also include polychaete and annelid worms. Reiswig (1973) reported that the sponge *Verongia gigantea* supported large populations of *Haplosyllis spongicola* in the canal system; densities of 50-100 polychaete individuals per ml of sponge were found. *Haplosyllis spongicola* is also a frequent inhabitant of the sponge *Neofibularia nolitangere*.

Sponges serve as a food source for other organisms, predominantly coral reef fish and some marine turtles. In general, however, predation is not intense. Only in 11 of 212 fish species (5%) studied by Randall and Hartman (1968) did sponge remains comprise over 6% of stomach contents. Angelfish of the genera *Holocanthus* and *Pomacanthus* and the whitespotted filefish (*Cantherhines macrocerus*) were the major sponge predators. Abundance of mineralized sclerites, noxious chemical substances, and tough fibrous components have been identified as reasons for low predation pressure on most coral reef sponges. The toxicity to fishes of many common exposed (noncryptic) Caribbean sponges has been shown by Green (1977) through forced feeding experiments. He also noted that, in general, as latitude decreases, the incidence of toxicity in sponges increases, presumably in response to the high diversity and density of associated fishes in the tropics. Predation, therefore, is not usually considered a direct force limiting the distribution of coral reef sponges. This is not true for all sponge ecosystems, as was illustrated by Dayton et al. (1974) in an Antarctic community.

Sponges have been regarded as a major force in the bioerosional process on coral reefs (Goreau and Hartman 1963; Rutzler 1975). The boring sponges are classed mostly in the family Clionidae (genus *Cliona*), but species of the Adocidae *(Siphonodictyon)* and the Spirastrellidae (*Spheciospongia, Anthosigmella*) have also been shown to excavate coral limestone skele-

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SOUND PRODUCTION BY A CORAL REEF FISH (*POMACENTRUS PARTITUS*): EVIDENCE FOR A VOCAL, TERRITORIAL "KEEP-OUT" SIGNAL

Arthur A. Myrberg, Jr.

ABSTRACT

The Chirp-sound, produced by males of the bicolor damselfish *Pomacentrus partitus,* plays an important role in influencing the behavior of conspecific females during the pre-spawning period. Evidence is provided here that the same sound possesses another function, i.e., it is a vocal, territorial "keep-out" signal. A field-study, conducted on a reef off southern Florida, showed that such sounds, when transmitted by an underwater loudspeaker from unguarded territories (residents removed), can inhibit territorial intrusion by neighboring male conspecifics for a significantly longer time than when such sounds are not transmitted from a territory. Evidence was also obtained that the visual presence of the resident was a more effective deterrent to intrusion, however, than sound-transmission. Finally, a significant relationship was found between the size of a given territory and the time of territory-intrusion by a neighboring conspecific male, suggesting that neighbors are aware of the resource-holding potential of territorial residents. A brief laboratory study also indicated that the Chirp-sounds of a resident were a more effective deterrent to territorial intrusion than Chirp-sounds of non-residents. Transmission of other sounds from unguarded territories, including random noise and feeding stridulations by residents and non-residents, showed no deterrent effect on territorial intrusion.

Sound production is a characteristic often shared by territorial fishes (see reviews by Tavolga, 1971; Fine et al., 1977; Myrberg, 1981; Hawkins and Myrberg, 1983). Generally, reports relate that sounds occur simultaneously with aggressive actions either during pair-encounters or by territorial residents as they encounter intruders (Winn et al., 1964; Myrberg et al, 1965; Caldwell and Caldwell, 1967; Lanzing, 1974; Ladich, 1989, Ladich et al., 1992). That vocalizations play an important role in territorial defense has been experimentally demonstrated in both avian and piscine species. Peek (1972) showed that while intact red-winged blackbirds *Agelaius phoeniceus* can maintain their territories, muted individuals lose them. Valinski and Rigley (1981) carried out a similar study with the cobitid fish *Botia horae* and their results were no different. So long as territorial individuals could produce sounds (intact or sham-operated individuals), they maintained their territorial boundaries; however, muted individuals were unable to deter intruders from entering their shelter sites, despite appropriate visual displays. Although such experiments signify the importance of sound as a component in territorial maintenance, they have also led workers to suggest that such sounds may act as advertisement signals, informing nearby conspecifics about the location of a defended resource (Horch and Salmon, 1973; Myrberg, 1981; Crawford et al., 1986).

Demonstrating such a function requires controlled testing whereby sounds are transmitted in the absence of their natural sources, i.e., residents, and cause hesitancy in entering the region of transmission by non-residents. Such testing has proven that the song of at least one bird species, i.e., the Great Tit, *Parus major,* is indeed a territorial "keep out" signal (Krebs, 1976, Krebs et al, 1978).

The bicolor damselfish *Pomacentrus partitus* is a soniferous resident of the coral reefs off southern Florida. Among its six different sounds (for structural details, see Myrberg, 1972a), the Chirp-sound is produced solely by territorial males not only during courtship and during the early morning spawning period,

groves, and inshore pilings. Those sponges that dominate in reef areas are a more or less distinct group and, with some overlap, are substantially different from those which are abundant in lagoonal areas (Wiedenmayer 1977). An extensive study of the patch reefs of Biscayne National Park (upper Florida Keys) reported the occurrence of 98 species associated only with inshore reefs in less than 10 m of water (Schmahl and Tilmant 1980). Additional species have been collected from deeper water on the outer bank reefs. From the evidence so far, a conservative estimate of the sponge species occurring on or around Florida reefs must be at least 120.

Autecology

Sponges exhibit both asexual and sexual reproduction. Asexually sponges may be regenerated from fragments, gemmules, and reduction bodies. Sexually, the group has both dioecious and hermaphroditic species. Fertilization is usually internal and both oviparous and viviparous species are common. This fact forms the basis of the division of the Demospongiae into its two main subclasses: Tetractinomorpha (oviparous) and Ceractinomorpha (viviparous), although exceptions are known. Viviparous species usually incubate parenchymula (solid) larvae, while development in oviparous forms is usually external.

Amphiblastula (hollow) larvae are exhibited by a third subclass of Demospongiae, the Homoscleromorpha, and some calcareous forms. A promising method that may be used to access the extent of asexual reproduction in an area is the ability of sponges to recognize tissue of like genetic composition ("self"). Experiments may be carried out whereby strains can be recognized through differential acceptance of tissue from other individuals in an area (Kaye and Ortiz 1981). Reproduction in sponges was reviewed by Fell (1974), but there is much yet that is unknown about that process in most species. A recent review by Simpson (1980) pointed out the many areas open to research.

Larval ecology and behavior is fundamental to the distribution of adult forms. Most sponges have sexually produced larvae that are free-swimming, at least for a short period, although some species have been shown to produce larvae that do not swim but creep over the substrate (Bergquist 1978). Three physical attributes influence the swimming and settlement of sponge larvae: light, gravity, and water turbulence. The comparitive morphology and behavior of some Demosponge larvae have been reviewed by Bergquist et al. (1979).

Sponges are filter feeders and must take in great quantities of water from which they remove plankton, bacteria, organics, and other nutrients from the water column. It has been estimated that the abundance and pumping activity of sponges on the fore reef slope of Discovery Bay, Jamaica, are such that a volume equivalent to the entire water column passes through the population every 24 hours (Reiswig 1974). Sponges are capable of removing extremely small organic particles. In a study by Reiswig (1971b), 80% of the organic carbon removed by three species of sponges could not be seen under an ordinary light microscope and was thus postulated to be of colloidal (quasi-particulate) nature. Many sponges depend on ambient currents to aid in water transport through their tissues and to decrease the amount of energy expended on pumping activities (Vogel 1977). Thus, hydrodynamic regimes are important in shaping sponge distributions. In tropical areas, where reef boundary layers are typically low in nutrients and organic particulate matter, increased water flow by currents can be essential for the survival of many large species.

Light intensity can be important in shaping sponge communities for various reasons. In one respect, reduced light intensity increases sponge abundance due to decreased competition from reef corals that depend on light for survival of symbiotic zooxanthellae. Sponges typically proliferate in deep fore reef areas below the zone of maximum coral growth. Some sponges, however, have been shown to contain species of symbiotic blue-green algae (or Cyanobacteria) which have been implicated in the distribution of those species, restricting them to shallow areas where light is abundant (Wilkinson 1978).

For a good general review of sponge biology, consult Bergquist (1978). Several recent collected works have been compiled as the result of symposia on the biology of sponges or in response to the need for cohesiveness in sponge research. These include Fry (1970), Harrison and Cowden (1976), Levi and Boury-Esnault (1979), and Hartman et al. (1980).

Quantitative ecological studies of sponges on Caribbean reefs are few. The most complete series of studies of Caribbean demosponges to date were those carried out by Reiswig (1971a, 1971b, 1973, 1974) on three common species found on Jamaican reefs. These studies set the standard for ecological methodology of sponges and their information is generally compatible with Florida populations. His findings emphasized the variability displayed by the different species in regard to pumping activities, feeding, life history characteristics, population dynamics, and respiration. Ecological studies on entire sponge communities are rarer still. Alcolado (1979) investigated the ecological structure of sponges on a Cuban reef, and data were given in Wiedenmayer (1977) stressing synecological relationships of sponges in his Bahama sites. The difficulty of carrying out such studies is reviewed by Rutzler (1978) who also gave some methods for quantitative assessment of sponges on coral reefs.

From these studies and from qualitative and incidental observations, sponge communities are known to be partitioned along habitat and depth gradients on coral reefs. Habitat preference, reproductive strategies, growth form, and competitive ability are important biological agents that influence sponge distribution. Abiotic factors, some linked directly or indirectly with depth (e.g., light intensity, temperature, intensity of wave and surge action, and sedimentation) are also major controlling forces in shaping sponge assemblages.

Massive sponges are rare on reef flats where small or low encrusting forms are predominant (Reiswig 1973;

but also during the day when females are not in the vicinity of vocalizing males. The latter situation suggested that the sound may have a function unrelated to the reproductive function *per se,* i.e., advertising the presence of a defended area. I report here the results of a series of experiments which suggest that fishes do posses an acoustical, territorial signal, i.e., a keep-out signal. A brief extension of time at the field-site also permitted several tests regarding the visual effect of a resident in deterring territorial intrusion. Results from these tests are also reported.

Materials and Methods

Field.—The subjects of the field phase of the study were males of a large colony of bicolor damselfish, located in the immediate vicinity of Carysfort Light, a lighthouse within the Florida Keys National Marine Sanctury. The territorial boundaries, surrounding the natural shelters of 27 males, were established by determining the maximum distance from its residence that a resident consistently attacked a male conspecific, housed in a large, glass model-bottle (Myrberg and Thresher, 1974). Only adult males, longer than 55 mm, standard length (= SL: measured from the tip of the snout to the crease of the skin at the base of the caudal fin) were housed in such bottles. Territorial borders were marked by small tire-weights. Chirp-sounds were, then, recorded approximately 1m from 17 males of the colony by a hydrophone (Clevite, CH-17), suspended off the substrate, and cable-connected via a preamplifier (Ithaco, 144 L) to a tape-recorder (Uher, 4000 Report L), set at a speed of 19 $cm \cdot s^{-1}$. Sound-analysis was carried out with the same recorder, a band-pass filter (Kron-Hite, 3100) and a memory-oscilloscope (Tectronics, 5103 N). Ten resident males, whose territories were located in different sections of the large colony and whose sounds included at least four that showed a good signal to noise ratio, were chosen as test-subjects. Ten tape-loops were constructed, each containing three different chirps from one of the test-subjects. Each tape was adjusted so that the sound repetition rate was 25 $chirps \cdot min^{-1}$, a typical rate that has been monitored in the field.

The playback-system consisted of an underwater speaker (University, UW-30), cable-connected via a power amplifier (Schober, TR-2) to the tape recorder that was used during the recording periods. All electronic equipment, used during recording and transmission periods, was operated from within the lighthouse. Playback-level, reflecting that of naturally produced chirps, was established by matching record- and transmission-levels by an oscilloscope as well as by experienced field-observers, listening at the "face" of the speaker. The shallow depths (1.5–3.0 m) allowed observers to use snorkels.

The experimental design included the following: 1) each sound-test, involving a given territory, was paired on that same territory with a control (silent) test, the latter conducted either two days before or within three days after the sound-test (to minimize possible behavioral effects of one test confounding the results of another); 2) the resident of that territory was removed from its territory during both the sound- and control tests; 3) sounds were continuously transmitted during a sound-test until its termination; 4) tests were terminated when either an intruding male conspecific entered the residence of the absent resident and remained at least 30 s in the territory or after 1 h had expired without an intruder reaching the residence. The 1-h time-limit was based on preliminary observations of intruders normally entering the residences of unguarded territories and remaining in such territories within 20 min (often within a few minutes).

Just prior to initiating a test, the territorial resident was captured and caged away from the colony. As that was being done, another observer placed the underwater speaker adjacent to that individual's residence. Testing began almost immediately thereafter. Timed records included test-onset and when a male conspecific: 1) initially intruded across the territorial boundary, 2) reached the midpoint between the boundary and the shelter, and 3) entered the residence. Final analyses used only 1) and 3). Timed records were also maintained on other species of intruders; however, the scarcity of such intrusions precluded analysis. The resident was released on its territory at the conclusion of every experiment. If an intruder was present, the resident was invariably in control of its territory within 2 min. Statistical analyses included Spearman rank correlations, Wilcoxon matched-pairs signed rank tests, and simple regression analysis.

The visual effect of a resident in deterring territorial intrusion was examined during the last 3 days in the field. Tests involved placing a model bottle, holding the resident of a test-territory, adjacent to the territorial residence. Males did not produce sounds while confined in such bottles. Control tests, involving the same unguarded territories, used empty bottles, placed adjacent to the residence after the resident had been captured and caged away from the colony. Several such tests were run simultaneously, although a given "vision"-test and its comparable control test were run on different days.

icantly to the dissolving of limestone, adding calcium and bicarbonate to the mineral pool in the reef environment.

4.3 SPONGES

(by G.P. Schmahl, South Florida Research Center, U.S. National Park Service, Homestead).

Sponges (Porifera) are an important component of the benthic fauna of Florida reef. Although not usually dominant, sponges are common in most reef zones and can be especially abundant in certain situations. Substrate analysis of the benthic fauna on selected upper Florida Keys patch reefs indicated a sponge component ranging from 1.2% to 9.2% of the surface area sampled (Jaap and Wheaton 1977).

Taxonomy

Sponges are grouped into four classes. The largest is the Demospongiae, which account for 95% of all recent species. Virtually all common shallow water reef sponges are demosponges with most of the remainder belonging to the class Calcarea. The Demospongiae are characterized by skeletal components consisting of siliceous spicules that are supplemented or replaced by organic spongin, which forms fibers or acts as a cementing element. The skeleton of the Calcarea, as the name implies, is made up of calcareous, usually triradiate spicules. A third class of sponges, the Sclerospongiae, secrete a compound skeleton of siliceous spicules, spongin fibers, and calcium carbonate. Sclerosponges can be an important structural component of some deep fore reef environments (Lang et al. 1975) but have not been reported from Florida reefs (Dustan et al. 1976). The fourth class of sponges, the Hexactinellida, are mainly deep water species and are characterized by hexactinal (six-rayed) megascleres (type of spicule).

Classification of the sponges is based primarily on the size and shape of the spicules (megascleres and microscleres) and the organization of the skeletal matrix of spicules and organic fibers found within the various species. Gross morphology, surface texture, color, and arrangement of the incurrent and excurrent ostia are also considered important. Recently, studies in the areas of comparative biochemistry (Bergquist and Hartman 1969), reproductive life history characteristics (Levi 1957), structure and function of sponge cells (Simpson 1968), and ecology have contributed much to clarify taxonomic organization. In spite of this, classification of the Porifera is still in a state of change and confusion. However, the widespread use of scuba, *in situ* color photography, and standardized collecting techniques have all helped in the field identification of major sponge species. Field guides are now available (Voss 1976; Colin 1978a; Kaplan 1982) which offer to the nonspecialist some information on Caribbean reef sponges. Of these, the identifications given in Kaplan (1982) are the most up-to-date. Inconsistencies in nomenclature found in these publications reflect the confusion that surrounds sponge systematics. Most common sponge species have characteristic shapes, colors, and habitat preferences which allow them to be identified confidently in the field, at least within a specified geographic area (e.g., Florida).

Of the more technical taxonomic literature on Caribbean sponges, only a few were based on collections primarily from Florida. An early work that described some Florida reef sponges was that of Carter (1885). Later Florida studies on the sponges of the Gulf of Mexico by de Laubenfels (1953) and Little (1963) also included some reef species. The most complete work of sponge taxonomy for Florida reef sponges was made by de Laubenfels (1936) in the Dry Tortugas. Although now somewhat out of date in terms of the present interpretation of sponge classification, this is an important work in that all known Caribbean sponge families were listed and their taxonomic characteristics described. Since the sponge fauna found on Florida reefs is decidedly West Indian, taxonomic works from other areas of the Caribbean are sufficient for most Florida species. Recent studies of this type include those from the Bahamas (de Laubenfels 1949; Wiedenmayer 1977), Bermuda (de Laubenfels 1950), Jamaica (Hechtel 1965), and Curaçao (van Soest 1978, 1980). The studies by Wiedenmayer (1977) and van Soest (1980) introduced new classificatory interpretations. Taxonomic works on burrowing sponges likely to be found in Florida include Pang (1973a, 1973b) and Rutzler (1974).

A definitive list of Florida sponge species does not exist. de Laubenfels (1936) described 76 species from the Dry Tortugas, but 5 were dredged from 1,047 m and 9 others were collected from sites ranging from 70 to 90 m, which is out of the range of most typical Florida coral reef growth. Wiedenmayer (1977) described 87 shallow water species from the western Bahamas in a work that reevaluates the validity of scientific names applied to many common reef species. Careful reference to synonymy must be taken into consideration when comparing Wiedenmayer's (1977) lists with those of previous workers. Given the proximity of his study site, it is reasonable to assume that most of the 87 species Wiedenmayer (1977) described can also be found in Florida. Fifty-seven species of sponges have been recorded from Bermuda (de Laubenfels 1950) and Jamaica (Hechtel 1965). Of the species treated by Wiedenmayer (1977), 39 listed are from the Dry Tortugas and 22 from the Florida Keys. These lists were the result of a literature review and not based on field studies, so the actual number of species in these localities is open to question.

A brief survey of sponges of the Dry Tortugas by National Park Service investigators revealed 85 species, only 43 of which were recorded by de Laubenfels (1936), and 57 of which were among the 87 species described by Wiedenmayer (1977). The low overlap of species lists indicates a species pool much larger than reported by any one study; the number of species present is seemingly correlated with the amount of time spent looking. It is important to note that the above studies deal with all sponge species encountered in the area, including those common in lagoonal areas, man-

Any test was terminated when an intruding conspecific entered the residence and remained in the territory for longer than 30 s or if that did not occur, after 1 h.

Laboratory.—A brief series of experiments examined whether other sounds, when transmitted from within a territory, might also prevent intrusion. Five adult male bicolor damselfish, all of similar size, were housed in two 800-liter aquaria after being captured on Fowey Rock Reef, a reef located several kilometers southeast of Miami, Florida. Coral was arranged such that three males became territorial in one aquarium (Colony A) and the remaining two males became territorial in the other (Colony B). All tests were conducted in these two aquaria. Females were placed into both aquaria to reinforce territoriality by the males and to assure frequent sound-production. Chirps and stridulation (=strid)-sounds were recorded from each male, using the same equipment as used in the field. The experimental design of the laboratory phase included four test-situations in addition to the two that had been used in the field. The former included playing back: 1) a brief (200ms) sequence of white-noise (produced by a random-noise generator), 2) a resident's strids and 3) chirps and 4) strids from a non-resident. Each tape-loop possessed three sounds of a given sound-type recorded from one resident. Loops of the chirps and the white-noise sequence had a repetition rate of $25 \cdot min^{-1}$. Strids, involving four or five pulses, 1.5 to 2 s in duration, had an arbitrary repetition rate of $12 \cdot s^{-1}$.

Playback-tests were initiated in the two aquaria 30 days after the males had been brought in from the field. All five were captured in the same colony and so it is likely that each individual had interactions with its companion(s) prior to entering the laboratory. Playback equipment was the same as used in the field. Each of the experimental series comprised one or more tests separated by at least one day. One series was separated from another by at least 7 days. Any test, involving playing back non-resident chirps or strids, used sounds recorded from one of the males housed in the aquarium not involved in that particular test.

Due to the disturbance that occured when fishes had to be captured in the large aquaria during the day, we deviated from the procedure followed prior to initiating a field-test. Selecting the specific territory for a test occurred on the day prior to testing. The resident of that territory was then quietly removed from its resting area (using a dark red light) the following morning, at least 1 h before the lights came on in the laboratory. It was placed into a large, glass jar with netting over the opening and the jar, with a line and a small float attached, was then set adjacent to the coral within its territory. The speaker was also placed into the same territory immediately thereafter. The other fish in the aquarium reached their normal morning activity about 15 min after the tank-lights had come on. Shortly after tank-residents had reached such activity, the jar, holding the resident, was removed from the aquarium by the attached line. Such actions resulted in only a momentary change in normal activity by the remaining individuals. Testing began immediately thereafter. Timed records included test-onset and when an intruder: 1) initially crossed a territorial boundary, 2) reached the midpoint between that boundary and the residence, and 3) entered the residence. A test was terminated either when an intruder entered the residence or after 1 h, if the latter had not been entered. As with the field data, final analyses used only 1) and 3).

RESULTS

Field: Sound-tests.—Data from the field-phase are provided in Table 1 (sound-transmission) and Table 2 (silent controls). Conspecific intruders took a significantly longer time to cross the border into an unguarded territory from which resident chirp-sounds were transmitted than when the unguarded territory had no such sound-transmissions (Wilcoxon signed-rank test: $p = 0.008$; $n = 10$ paired tests). However, once the border had been crossed, no significant difference was shown between the time it took for intruders to reach the residences of unguarded territories during the sound-tests and the control tests (Wilcoxon matched pair signed-rank test: $p = 0.084$; $n = 10$ paired tests). This signified that the major factor involving intrusion was the "decision" to cross the border. Some intruders, under both test-conditions, held back for several minutes after crossing the border before moving to the residence, while others darted rapidly to the residence.

There also existed no correlation between the size (= length) of a resident and the time to intrusion (Spearman rank corr. = 0.321 [sound tests]; $n = 10$; S.r.c. = 0.806 [control tests]; $n = 12$) nor between the size of a resident and the size of its territory (Spearman rank corr. = 0.392; $n = 10$). Since males of bicolor damselfish-colonies have demonstrated a social hierarchy that can include territorial intrusion (Myrberg, 1972b), a regression analysis examined how the interval

Crustose corallines form small, scattered colonies or large, distinct patches. On Florida reefs, there may be some degree of development of incipient algal ridges, a formation found extensively on coral reefs in the eastern Caribbean Sea (Adey 1978). Coralline algae are common on the underside of corals such as *Acropora* spp. and colonize dead coral fragments that break off and fall to the seafloor. Large patches are found on the reef platform limestone, the living surface layer covering formerly living veneers of the same species. Minute species that form small, thin crusts are often epiphytic upon larger, fleshy algae, seagrass leaves, octocoral skeletons, mollusk shells, and hydroid colony bases. Crustose corallines are best developed in shallow, turbulent areas where light intensity is high and fish grazers are partially deterred by wave forces.

Colonization, succession, and growth rate of the tropical crustose coralline algae were unknown until the study of Adey and Vassar (1975) in St. Croix. Their results probably apply in Florida, which has fewer species, for April through November. Adey and Vassar (1975) reported that the margins of a crust grow 1-2 mm/month and that accretion rates are 1-5 mm/year, depending on herbivore grazing, especially parrotfish.

Filamentous and Fleshy Algae

Filamentous and fleshy algae are uncalcified coral-reef macroalgae that colonize coral rubble and reef limestones. This group is most adversely affected by grazing. Two subdivisions are recognized: the dense and sparse vegetation. They comprise the same species, although the dense community, if not spatially limited to crevices or small patches, exhibits greater species diversity. The sparse community occurs in areas receiving the heaviest grazing pressure, resulting in cropped forms often 1-2 mm high. There is a transition of sparse community on or near the reef to the dense community located away from the reef, resulting from a gradient in grazing pressure.

Unconsolidated Sediment Algae

Few algae have the functional ability to anchor in unconsolidated sediment. For this reason, the seagrasses, rooted forms that evolved on land and radiated into the marine environment, dominate shallow sedimentary habitats, especially in tropical regions. There are, however, a few specialized algae on loose sedimentary environments; these are especially well represented in coral reef habitats.

There are two major groups capable of colonizing sandy or muddy bottom areas. The bluegreen algae (Cyanobacteria) form mats and penetrate the sediment to some extent. Green algae, belonging to the order Siphonales, erect coenocytic plants (lacking cell walls) having a dense cluster of root-like rhizoids at the base that provides a firm anchorage in unconsolidated sediments. Mathieson et al. (1975) included an underwater photograph of this community.

The mat-forming bluegreen algae community is composed primarily of filamentous species (sensu Drouet 1968), e.g., *Microcoleus lyngbyaceus* and *Schizothrix calcicola*. Other filamentous species, including *Porphyrosiphon notarisii* and *Schizothrix arenaria*, and several coccoid (spherical) species are usually associated with these mats. Ginsburg (1972b) reported that the filaments of mat-forming bluegreens grow upward during the day and selectively trap sediment particles at night; horizontal growth of another species results in binding of trapped sediments.

Erect-growing anchored green algae in sediments are found within the genera *Halimeda, Penicillus, Udotea, Rhizocephalus, Avrainvillea,* and *Caulerpa*. They are usually scattered and scarce immediately around the reefs, but become progressively more abundant away from the reef proper as grazing pressure is reduced. The dense cluster of rhizoids that anchor these plants stabilizes the sediments and absorbs nutrients. Since these algae are coenocytic, transport of nutrients to the tops and of photosynthetic products to the rhizoids is carried on rapidly in conjunction with cytoplasmic streaming. They are a unique group of highly evolved green algae, as advanced among the algae as the flowering plants on land.

Members of this group also contribute significantly to calcium carbonate production and sediment on and around the reef. This is especially notable among the species of *Halimeda*.

Excavating or Boring Algae

Among the least conspicuous and most often overlooked algae are those possessing the ability to bore into limestone by dissolving it as they grow. To the unaided eye they are visible as a greenish tinge or discoloration at the surface of dead coral, mollusk shells, dead coralline algae, and other limestone material. Boring algae belong to three taxonomic groups. Most are bluegreen (Cyanobacteria), some are green (Chlorophyta), and the remaining one (Xanthophyta) has no common name.

Representatives of three families of bluegreen algae are known from Florida coral reefs: *Entophysalis deusta,* family Chamaesiphonaceae; *Schizothrix calcicola,* family Oscillatoriaceae; *Mastigocoleus testarum,* family Stigonemataceae. The green algae *Gomontia ployrhiza* and the xanthophyte *Ostreobium quekettii* are known from Florida.

These algae are collected by dissolving a small sample of greenish limestone in dilute hydrochloric acid and examining isolated filaments. Keys to the species are found in Humm and Wicks (1980). A comprehensive experimental study of limestone-boring algae is found in Perkins and Tsentas (1976); the study was from St. Croix. They reported five bluegreen and three green algae species. One of their bluegreens, *Calothrix* sp. (*Calothrix crustacea*; sensu Drouet 1968), has not been reported as a boring alga in Florida; however, it is abundant on Florida reefs and must be presumed to be a borer. Algae that bore into limestone contribute signif-

Table 1. Differential responsiveness (territorial intrusion) by males of the field colony to unguarded territories during sound playback (Individuals and intruders indentified by relative location or visual field markers). Significance levels: Table 1 (A) vs. Table 2 (A): $P = 0.008$ [Wilcoxon matched paired test]; Table 1 (B) vs. Table 2 (B): no significant difference.

Territorial resident	Circumference of territory (m)	Length of resident (SL, mm)	Intruder	Length of intruder (SL, mm)	(A) Time between start of test and initial border-crossing* (min)	(B) Time to reach residence after initial border-crossing† (min)
Mid	23.1	62	Pillar	?	5	11
Weak	16.8	61	Rock	61	16	21
Rock	17.1	61	Compressor	?	44	16‡
Outside	20.9	60	Compressor	?	23	37‡
Dock	18.6	61	Corner	60	29	6
Corner	15.2	60	South-Center	66	13	10
Center	20.0	60	West	65	41	<1
Far East	30.5	73	North-North	?	16	3
North	14.8	58	Battery	63	44	13
East	13.9	63	West	65	39	5

* Mean = 27.0, SD = 14.4, median = 26.0, SE = 4.6 and N = 10.
† Mean = 12.3, SD = 10.6, median = 10.5, SE = 3.4 and N = 10.
‡ Test terminated after 1 h.

(in min) between the initial crossing of a territorial border by an intruder related to the size (= circumference) of that territory (Fig. 1). The analysis included only intrusions during the control-tests to eliminate the confounding variable of sound-transmission. A significant relationship was found ($r = 0.61$; $p < 0.05$; $n = 12$), indicating that the greater the territory-size, the less inclined an neighboring male was to intrude.

Field: Vision-tests.—The deterrent effects of the visual presence of silent residents in their territories were examined in six cases involving different males of the colony (Table 3). No intrusion occurred across the territorial border during the

Table 2. Differential responsiveness (territorial intrusion) by males of the field colony to unguarded territories in the absence of sound playback (Individuals and intruders indentified by location or visual field markers). Significance levels: Table 1 (A) vs. Table 2 (A): $P = 0.008$ [Wilcoxon matched paired test]; Table 1 (B) vs. Table 2 (B): no significant difference.

Territorial resident	Circumference of territory (m)	Length of resident (SL, mm)	Intruder	Length of intruder (SL, mm)	(A) Time between start of test and initial border-crossing during test* (min)	(B) Time to reach residence after initial border-crossing during test† (min)
Mid	23.1	62	Pillar	?	16	7
Weak	16.8	61	Rock	61	3	11
Rock	17.1	61	Battery	63	7	12
Outside	20.9	60	Compressor	?	15	14
Dock	18.6	61	Corner	60	4	10
Corner	15.2	60	South-Center	66	8	<1
Center	20.0	60	West	65	7	13
Far East	30.5	73	North-North	?	11	2
North	14.8	58	Martin	?	8	<1
East	13.9	63	Center	60	3	6
Dock‡	18.6	61	Tiny	49	2	3
Far East‡	30.5	73	North-North	?	13	<1

* Mean = 8.2, SD = 5.0, median = 8.0, SE = 1.5 and N = 12.
† Mean = 6.8, SD = 5.0, median = 6.5, SE = 1.5 and N = 12.
‡ Unpaired test.

demonstrated experimentally in many reef studies, although apparently not in Florida, by placing a barrier over a selected site and observing the response of the algae that are protected from most grazing. Randall (1961b), working in Hawaii, found a significant difference between the algal cover inside an enclosure and that of areas outside it after 2 months. Inside the enclosure the algae grew to normal height and breadth (to 30 mm); outside the enclosure, the algae averaged 1 mm in height. In Lameshure Bay, St. John, Virgin Islands, Randall excluded fish, but allowed herbivorous sea urchins *(Diadema antillarum)* in the closed area. Results showed that the fish were the major grazers. While the urchins also fed on algae, their action did not affect the algae as severely as did the fish. Randall also showed that parrotfish and surgeonfish graze on seagrass adjacent to the reef, thereby causing the sand halos around patch reefs. Research conducted during the submersible habitat study known as Tektite II at Lameshur Bay, St. John, Virgin Islands, confirmed and expanded Randall's observations on grazing. Fish grazing was found to be a major factor influencing biomass and species diversity of benthic algae on coral reefs. In addition to cage experiments, algae was transplanted from elsewhere to the reef; the algae was rapidly eaten. Grazing pressure was intense to a distance of 30 m; beyond that distance it gradually tapered off (Earle 1972a; Mathieson et al. 1975).

Ogden (1976) reported on algae-grazer relationships on coral reefs and reported those algae that grazers tend to avoid. Prolific algal growth occurred only in areas inaccessible to grazing herbivores, such as wave-washed surfaces and beachrock benches. Ogden and Lobel (1978) summarized the role of herbivorous fish and urchins in coral reef communities with special reference to reefs around St. Croix, Virgin Islands.

A comprehensive study of the effects of elimination or reduction of grazing by means of cages was reported by Wanders (1977), who worked at Curacao. His results are applicable to Florida reefs. He found that crustose coralline algae depend upon grazing for protection from competition by erect fleshy algae. Under a cage that covered a patch of coralline algae, the fleshy algae soon colonized the surface of crustose species, resulting in the death of the crustose species. The crustose forms were penetrated by microscopic species that bored into the limestone. When clean artificial substrates were placed under cages on the reef, a succession was observed as the fleshy algae colonized it. During the first 6-8 weeks the colonizers were principally filamentous brown and green algae of the genera *Griffordia, Cladophora,* and *Enteromorpha.* After 10-15 weeks these were replaced by larger filamentous and parenchymatous species, in particular, the filamentous red algae *Centroceras clavulatum* and *Wrangelia argus;* a small, erect-growing coralline red, *Jania capillacea;* the larger red algae *Spyridia filamentosa, Pterocladia americana,* and *Laurencia microcladia;* and the flat, dichotomous brown algae *Dictyota dichotoma.* All of these are common species on Florida coral reefs and can be found where succession on new substrates would be similar to the experiment at Curacao. Wanders concluded that grazing does not reduce the primary productivity per unit area in Curacao, but only affects species composition.

Brawley and Adey (1981) observed the effects of another category of grazers on coral reefs (other than fish and macroinvertebrates such as urchins) that might be referred to as micrograzers, crustaceans of the Order Amphipoda. In a coral reef microcosm in the Smithsonian Institution, Washington, D.C., they observed that a tube-building amphipod of the genus *Amphithoe* grazed selectively on filamentous algae. They suggested that this micrograzer may help reduce competition for the encrusting coralline algae.

While grazing by fish is a major factor in the paucity of fleshy algae in coral reef habitats, there are a few coral reef fish whose activity has the opposite effect. One of these is the three-spot damselfish, *Pomacentrus planifrons.* It establishes a territory, especially in the proximity of *Acropora cervicornis, A. palmata,* and *Montastraea annularis,* and then bites segments, strips, or patches of the coral, killing the polyps. These dead coral areas are colonized in a few days by a variety of erect-growing fleshy algae. The damselfish, by its unusual aggressive habit of defending its territory, keeps out algal grazers and thus maintains extensive patches of fleshy algae on the reef where normally they would not exist. Detailed observations on the damselfish and their algal lawns were reported in Jamaica by Brawley and Adey (1977) and in other Caribbean localities including Jamaica by Kaufman (1977). The three-spot damselfish occurs on Florida's coral reefs as do all the algae species recorded and listed by Brawley and Adey from Discovery Bay, Jamaica. The exception is *Halimeda goreauii.*

Algal Groups

Benthic algae of tropical coral reefs can be categorized into four major groups, all occupying areas of the reef itself or areas under the influence of grazers inhabiting the reef. They are crustose coralline algae that encrust corals, reef rock, and other limestone skeletal material; filamentous and fleshy algae, which occur as sparse vegetation and dense vegetation; algae on unconsolidated sediments, which are erect macroalgae of the order Siphonales and mats of bluegreen algae; and excavating or boring algae.

Crustose Coralline Algae

The most distinctive and characteristic algal group of the coral reef is the crust-forming coralline red algae Rhodophyceae, order Cryptonemiales, family Corallinaceae, subfamily Melobesieae. These algae form a thin or massive crust with or without erect branches and are calcified throughout. When living, they are usually a shade of red in low light, but may be yellow-brown in surface light. They are chalk-white when dead, but soon become greenish as a result of the establishment of the green and bluegreen algae that bore into limestone and lend color to the upper few to 5 mm of the skeleton.

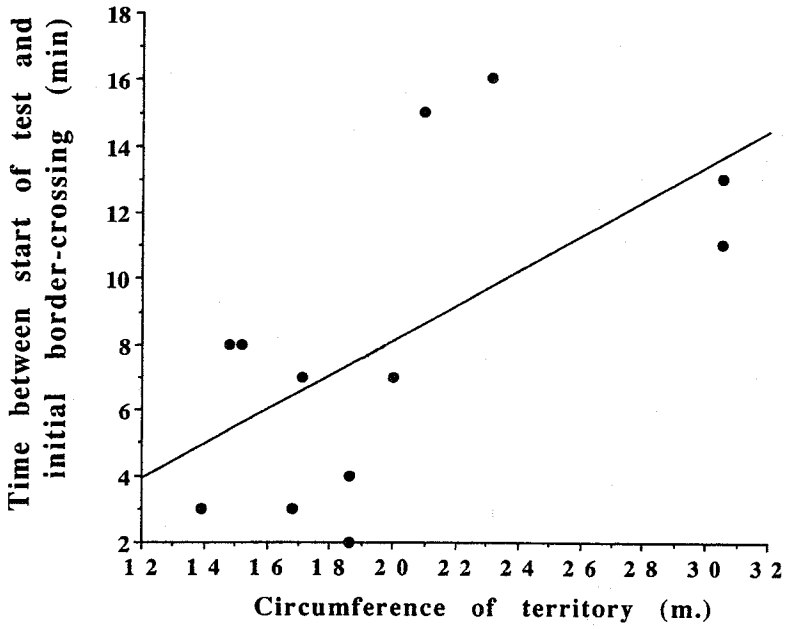


Figure 1. The relationship of the circumference of an unguarded territory (without sound-transmission) to the time taken by an intruder to make the initial border-crossing of that territory after the onset of a test ($y = -2.38 + 0.52x$; $r = 0.61$; $p < 0.05$).

1-h-test-period in three cases and among the remaining cases in which the border was crossed, only one intruder reached the territorial residence within the test-period and that was within 1 min of termination. All model bottles remained in the respective territories for an additional 0.5 h after test-termination and even after that time, five of the six territories had not been taken over by intruders. In the sixth case, the intruder that had reached the residence shortly before the test had been terminated, was aggressively confronting the confined resident. All six control-tests, involving the same territories, had intruders reaching the residences of the unguarded territories within 8 min. This experimental series demonstrated

Table 3. Differential responsiveness (territorial intrusion) by males of the field colony to unguarded territories, whose resident males, housed in model-bottles, were located adjacent to their residences (Individuals and intruders indentified by location or visual field markers)

Territorial resident	Circumference of territory (m)	Length of resident (SL, mm)	Intruder	Length of intruder (SL, mm)	(A) Time between start of test and initial border-crossing during test (min)	(B) Time to reach residence after initial border-crossing during test (min)
Mid	23.1	62	Black	?	12	test terminated at 1 h
Rock	17.1	61	none	—	—	—
Dock	18.6	61	none	—	—	—
Center	20.0	60	West	65	19	test terminated at 1 h
North	14.8	58	none	—	—	—
East	13.9	63	Center	60	11	48

CHAPTER 4

CORAL REEF BENTHOS

4.1 INTRODUCTION

The benthos (bottom-dwelling organisms) within a coral reef is complex, diverse, and for many taxa, poorly known. Benthos in a coral reef constitutes the critical biota or foundation species. In particular, the corals and crustose coralline algae are most significant in niche creation for the other multitudes of species. Complexity is shown by the infaunal boring biota; reports of species within a single coral head ranged from 30 to 220 and the number of individuals ranged from 797 to 8,267 (McCloskey 1970; Gibbs 1971). Most organisms were polychaetes, a group that is poorly understood. Because it would be literally impossible at this time to compile a total benthic community profile, this chapter will cover those groups which are critical to the community: algae, sponges, and Cnidarians (e.g., corals). Since corals are major elements of the reef, emphasis will be on the Milleporina, Octocorallia, and Scleractinia.

Volumes 2 and 3 of *Biology and Geology of Coral Reefs* (Jones and Endean 1973, 1976) contain information on many benthic groups, but the major emphasis is on Indo-Pacific reefs. Although the information can be extrapolated in many cases to Florida, the species are for the most part different. Recently, Rutzler and Macintyre (1982b) published a fine volume on the biota from the barrier reef at Carrie Bow Cay off Stann Creek Town, Belize.

4.2 ALGAE

(by Harold Humm, Department of Marine Science, University of South Florida, St. Petersburg)

Historical

Knowledge of the benthic algae found on coral reefs of southeast Florida is based largely on inference from work done on coral reefs in the West Indies, especially in the Virgin Islands, Puerto Rico, Jamaica, Curacao, Barbados, Guadalupe, and Martinique. There are many seaside research facilities open to visiting scientists in the Caribbean area but only one in southeast Florida, and that with limited facilities for visitors. Thus, for these and other reasons, studies of the benthic algal flora of Florida coral reefs are sparse.

William Randolph Taylor of the University of Michigan was the first to make a significant contribution to the knowledge about the species of benthic algae found on Florida coral reefs, after he spent the summers of 1924-1926 at the Carnegie Laboratory, Dry Tortugas. Taylor's work at Tortugas was a general floristic survey; his field data provided information on species associated with reef environments. These data are included in Taylor (1928) and Taylor (1960), *Marine Algae of the Tropical and Subtropical Coasts of the Americas*, still available from the University of Michigan Press.

Earlier references for the study of benthic algae found on Florida reefs and the western Atlantic in general include Harvey (1852, 1853, 1858); Vicker (1908); Collins (1909); Borgesen (1913-1920); Collins and Harvey (1917); and Howe (1918, 1920).

Contemporary studies of great value include Earle (1969, 1972b), which list virtually all algae known to occur on Florida's coral reefs.

Grazing on algae of coral reefs is discussed by Randall (1961a), Mathieson et al. (1975), Wanders (1977), and Brawley and Adey (1981).

Productivity of algal components within coral reef communities, including those that bore into limestone and the coral symbionts, is treated by Marsh (1970), Littler (1973), and Vooren (1981).

Colonization and succession of reef algae were reported by Adey and Vasser (1975), Wanders (1977), and Brawley and Adey (1981). Algal zonation at Curacao was described by van den Hoek et al. (1975).

Algae that bore into coral and limestone were studied experimentally by Perkins and Tsentas (1976). Coralline algal ridges (Note: these are not found in Florida) are reported by Adey (1975, 1978). The coralline algae were recently treated by Johansen (1981).

The only recent reef algae study from Florida reefs is Eiseman (1981), who made diving observations and collections during the KLNMS deep reef survey using a submersible. The study began at a 30-m depth and reported 60 species from reef and lithothamnion cobble habitats. The algal species from these two habitats were virtually exclusive.

Algae in Coral Reefs

One of the characteristics of coral reefs the world over is the apparent paucity of benthic macroalgae on and around the reefs, at least to the casual observer. "Where are the plants?" might be an immediate question of a biologist who is familiar with temperate or boreal seas and views a coral reef for the first time because rocky substrata in clear, shallow water would normally support a dense stand of large benthic algae.

A significant biological control of algae on coral reefs is the competition for space with other epibenthic sessile organisms. The diversity of organisms on a coral reef probably exceeds that of all other marine ecosystems. The sessile animals occupy space that would otherwise be colonized by benthic algae. On recently exposed limestone substrates, especially following physical impact, benthic algae may be the first colonizers, but they are usually replaced by sponges, tunicates, corals, and bryozoans after a short period. Another major biological control on benthic macroalgae is grazing by the herbivorous invertebrates and fish. Of all shallow-water marine ecosystems, none are more profoundly affected by grazing than coral reefs.

The effects of grazing on coral reefs have been

Table 4. Differential responsiveness (territorial intrusion) to various sounds by males in the laboratory colonies. Couplet = interval (in min) between start of test and initial border-crossing by intruder: interval (in min) between initial border-crossing and reaching the residence of an unguarded territory by intruder (M, R, L indicate individuals labeled by relative positions in tanks). Sample sizes of the various conditions precluded statistical comparisons.

	Resident male	Intruder male	No sounds	Random noise	Non-resident		Resident	
					Strids	Chirps	Strids	Chirps
Colony A								
1.	M	R	2:1					
	2 days later							
	M	R						10:7
2.	L	R	2:1					
	3 days later							
	L	R					7:1	
	3 days later							
	L	R			2:1			
3.	L	R				4:3		
	2 days later							
	L	R						14:1
	2 days later							
	L	R				5:1		
4.	L	R	2:1					
	4 days later							
	L	R						8:1
Colony B								
5.	R	L	3:1					
	2 days later							
	R	L		4:1				
	2 days later							
	R	L						17:9
	3 days later							
	R	L					4:1	
6.	L	R				4:2		
	3 days later							
	L	R						11:5
	3 days later							
	L	R				7:9		
	Mean =		2.3:1.0			5.0:3.8		12.0:4.6
	SD =		0.5:0.0			1.4:3.6		3.5:3.6
	Median =		2.0:0.0			4.5:1.8		11.0:1.6
	SE =		0.3:1.0			0.7:2.5		1.6:5.0

that the visual presence of the resident inhibited intrusion far more effectively than by sound-transmission alone.

Laboratory.—Testing was unexpectedly terminated when one male of Colony A died and territorial instability occurred in Tank B due to increased aggression by one of the males.

Six experimental series were completed, but the small sample-size precluded statistical comparisons (Table 4). Nevertheless, several findings were noteworthy. Chirp-sounds from residents inhibited intrusion into their unguarded territories for more than twice as long as when Chirp-sounds of non-residents were transmitted from the same territories (means: 12.0 min; n = 5 vs. 5.0 min; n = 4). The other test-sounds (i.e., random noise and [feeding] stridulations), were no more effective in inhibiting intrusion than when sounds were not transmitted from territories. Also, based on the short distance between territorial residences in the laboratory,

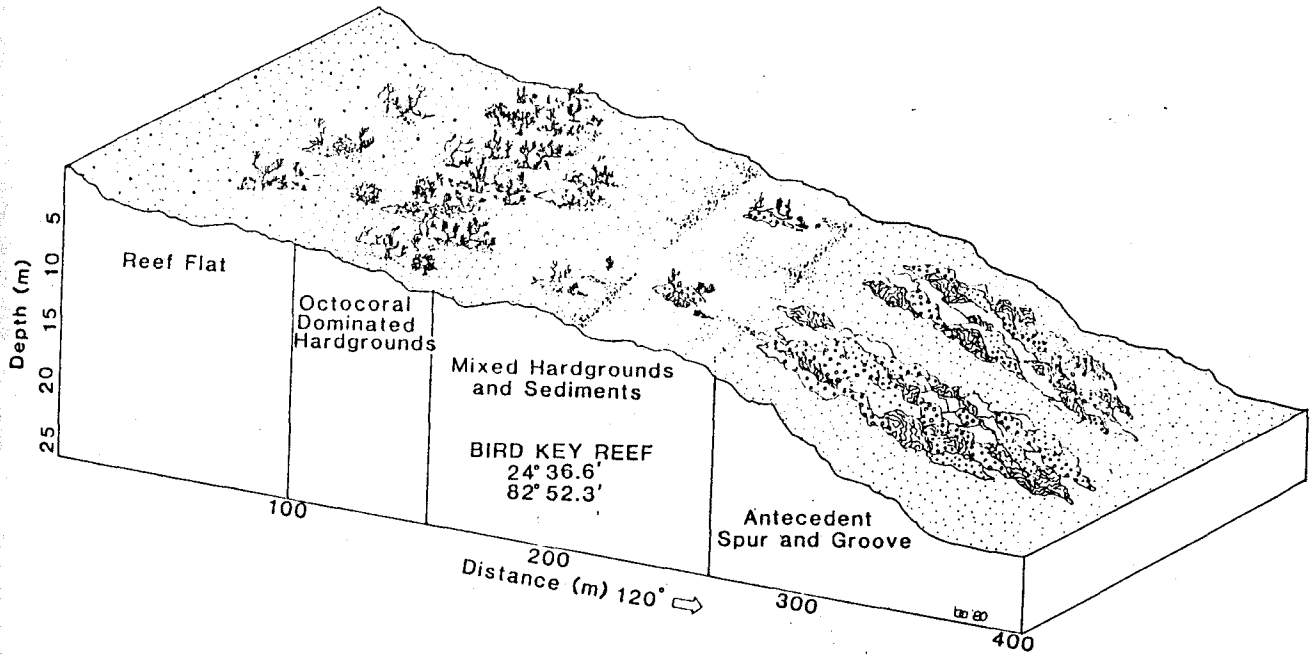


Figure 19. Cross-sectional diagram of Bird Key Reef.

solidated sediments overlying a Pleistocene basement. The shallowness of the reef and severe winter temperatures probably prevent *A. palmata* from occurring on the shallow reef at Bird Key.

Summary

No universal pattern exists; each reef has different features. Major controls include geographic configuration of the Florida Keys archipelago (Ginsburg and Shinn 1964); winter cold fronts chilling Florida Keys water masses (Hudson et al. 1976, Walker et al. 1982); reef age or stage of development (Shinn et al. 1977; 1981); and relationships with sedimentary environments (Ginsburg 1956; Shinn et al. 1981). Community structure patterns reflect the stage of reef development. For example, spur and groove construction requires long term dense aggregations of *Acropora palmata* (Shinn 1963; Shinn et al. 1981). Development of the spur and groove habitat in turn creates microhabitats (niches) that are necessary for the existence of other reef organisms. For example, the *Millepora complanata* association is found in the turbulent shallower portions of the spur and groove habitat (Mergner 1977).

once the "decision" was made to cross a border, intruders generally reached residences within 1 min (11 out of 17 tests).

DISCUSSION

Previous studies have shown that the Chirp-sound of males plays an important role in the activities of bicolor damselfish on the coral reef (Spanier, 1979; Myrberg and Riggio, 1985; Myrberg et al, 1986; Mohler, 1984; Kenyon, 1994). The present study adds another functional aspect to the sound; it can act as a keep-out signal in territorial maintenance. The deterrent effect of the sound was short-term, however, when transmitted in the absence of the resident. The visual stimulus of a silent resident, confined in a model-bottle, was a more effective deterrent since it inhibited intrusion by neighboring males for a longer time than when only the sound-stimulus was present. It is unlikely that the short-term effectiveness of sound-production was due, solely, to using a loudspeaker during experiments. Oscillographs showed essentially no differences between sounds produced by the loudspeakers and those produced by individuals of the colony. Rather, it appears that although Chirp-sounds can be considered a component of territorial advertisement, they are less important than the actual visual presence of the resident on its territory. Also, the significant, inverse correlation between the speed of intrusion during silent control-tests and territory-size (based on circumference) suggests that the decision to intrude a given territory by neighbors also involves some factor related to that specific territory within the colony. Since the size of territory had no relationship to the size of the resident, the factor involved may be that neighbors have learned the resource holding potential (Parker, 1974) of the resident as reflected, by the level of defensive aggression. This is speculative since levels of such aggression by colony-residents were not examined during the study.

An empty damselfish-territory on the reef is often taken over in a few minutes by a neighbor which incorporates it into its present holdings (Robertson et al., 1976: p. 1210; pers. observ.). Success in maintaining the new holding depends, in turn, on that neighbor's ability to defend the larger area from its own neighbors. The deterrent effect of sound-playback on territorial intrusion, though reflecting the importance of sound production during periods when the resident may not be seen due to nearby barriers, is relatively short-term due to potential intruders likely habituating to a repetitive stimulus in the absence of the visual presence of the resident. The latter stimulus, though clearly a longer term-deterrent to intrusion, can eventually lose its effect as well, however, when the resident, confined in a model-bottle, is unable to deter invasion by defensive aggression despite its presence. Such invasions have been repeatedly observed on the reefs off southern Florida whenever territorial individuals of many species (not only those of the genus *Pomacentrus*) were confined in model-bottles on their territories for various reasons (not related to this study). When returning to such territories after several hours, observers usually saw a conspecific aggressively confronting the confined resident as was noted in one of the tests involving a confined resident in this field study.

Many questions remained unanswered following the field study. One of the most important of these was whether Chirp-sounds were invariably keep-out signals for a territory regardless of whether the source was the resident or a non-resident-conspecific. Another was whether other sounds, transmitted from a territory, might also serve as keep-out signals simply because they emanated from a territory. The laboratory phase of study was, therefore, designed to suggest

Table 23

Looe Key Reef stony coral fauna at 1 - 27 m (fifteen 1-m^2 plots; Jaap, unpublished).

Species	B.I.[a] (ranking)	Abundance	Percent of total colonies	Density Mean	Density Std.dev.	D.I.[b]
Porites astreoides	23	52	26.94	3.51	3.72	C
Millepora complanata	19	47	24.35	3.13	4.61	C
Agaricia agaricites	16	35	18.13	2.32	3.33	C
Porites porites	7	8	4.15	0.51	1.34	R
Favia fragum	6	7	3.63	0.50	0.62	R
Siderastrea siderea	6	8	4.15	0.51	1.13	R
Acropora cervicornis	6	7	3.63	0.50	1.10	C
Madracis decactis	5	9	4.66	0.61	1.63	C
Stephanocoenia michelinii	4	5	2.59	0.32	0.70	R
Siderastrea radians	3	4	2.09	0.30	0.82	C
Montastraea cavernosa	3	3	1.55	0.23	0.83	C
Mycetophyllia lamarckiana	2	2	1.04	0.12	0.42	R
Millepora alcicornis	2	2	1.04	0.12	0.50	C
Acropora palmata	1	1	0.52	0.10	0.30	R
Montastraea annularis	1	2	1.04	0.12	0.42	R
Meandrina meandrites	1	1	0.52	0.10	0.32	R
Total species		16				
Total colonies		193				
Density, square meter	Mean	Std. dev.	Range			
Species:	4.06	2.19	1 - 8			
Colonies:	12.19	9.29	3 - 34			

[a]B.I. = Biological Index, McCloskey (1970).
[b]D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

press) reported that net sediment transport was to the southwest and that sediment was slowly covering the reef's deeper areas.

Eastern and Middle Sambo, Eastern Dry Rocks, Rock Key, and Sand Key Reefs

These reefs follow the general bank reef pattern. They have well-developed seaward platforms that are separated from the main reef structure and that have significant relief. Again, these platforms are separated from the main reef body by sediments.

Bird Key Reef

Bird Key Reef, Dry Tortugas National Monument (Figure 19), is unusual in that it does not have a spur and groove zone in shallow water, and *A. palmata* is not found at all in this reef community. The major coral accretion is in waters deeper than 10 m on an antecedent spur and groove formation that apparently developed during a lower Holocene sea level stand. Shinn et al. (1977) reported that cores bored on the shallow areas of Bird Key Reef revealed that the reef was not founded on a solidified platform but rather on considerable uncon-

answers to such questions, although its results could not be considered definitive without direct evidence from the field. Unfortunately, the laboratory study was not completed. I have added its relatively few results because they provide an indication of the answers to the two questions, posed above, and point to future experiments.

Laboratory transmissions of Chirp-sounds from a resident of a territory resulted in periods of a longer inhibition from intrusion than Chirps produced by non-residents. This suggested that individuals, within a given laboratory aquarium, can discern individualistic or "signature" differences in such sounds. Such an ability has been already demonstrated by males in a field colony of bicolor damselfish (Myrberg and Riggio, 1985). Thus, acoustical keep-out signals appear linked to the specific resident of a territory. Other sounds, such as the feeding sounds produced by residents and non-residents alike, appear to possess no more "keep-out" signal-qualities than random-noise or those stimuli present in a "silent" territory without its resident.

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Since the hurricane, staghorn corals (*A. cervicornis*) have overgrown a great deal of Key Largo Dry Rocks previously unoccupied by reef corals. The slower growing star corals in the reef proper are also being overgrown by the more rapid growing staghorn corals. Shinn (1975) reported on this phenomenon and has followed up the situation with annual inspections of a particular set of colonies that are being encroached upon by *A. cervicornis*.

Molasses Reef

Molasses Reef, KLNMS (Figure 17), is the southernmost of the offshore bank reefs in the park system. It is the most popular reef with scuba diving tourists and has a large lighthouse that makes it very easy to find. This reef fits most of the patterns defined in Table 18; however, its reef flat is located a relatively long distance from the spur and groove zone. The buttress zone is quite narrow, but has large colonies of *M. annularis* just seaward of the deep spur and groove zone. Table 22 provides information on the densities and abundances of stony corals in the spur and groove zone at Molasses Reef. The investigation of seaward zones with a submersible revealed rocky outcrops and sedimentary environments similar to those described for Carysfort and French Reefs (Jaap 1981).

Looe Key Reef

The zonation and morphology of Looe Key Reef, Looe Key National Marine Sanctuary (Plates 2a and b) are presented in Figure 18. Table 23 lists the density and abundance of stony coral fauna on Looe Key Reef. The major significant difference in this reef from others is the wide area between the buttress zone and the deep reef. In the northeastern part of the reef, the deep reef does not exist; however, in the southwestern end, the deep reef community is evident in patches between sedimentary deposits. Shinn et al. (in

Table 22

Molasses Reef stony coral fauna at 5 - 6 m (twenty-five 1-m^2 plots; Jaap, unpublished).

Species	B.I.[a] (ranking)	Abundance	Percent of total colonies	Density Mean	Density Std.dev.	D.I.[b]
Acropora palmata	43	108	33.23	4.33	3.43	C
Acropora cervicornis	39	125	38.46	5.00	6.31	C
Montastraea annularis	19	38	11.69	1.53	4.11	C
Millepora alcicornis	17	20	6.15	0.82	1.00	R
Siderastrea siderea	6	6	1.85	0.22	0.73	C
Millepora complanata	4	5	1.54	0.21	0.50	R
Agaricia agaricites	4	4	1.23	0.20	0.51	R
Montastraea cavernosa	3	3	0.92	0.10	0.43	R
Porites astreoides	2	2	0.62	0.10	0.32	R
Favia fragum	2	2	0.62	0.10	0.43	R
Diploria labyrinthiformis	2	2	0.62	0.10	0.32	R
Madracis mirabilis	2	3	0.92	0.11	0.60	C
Mycetophyllia lamarckiana	2	2	0.62	0.10	0.30	R
Colophyllia natans	2	2	0.62	0.10	0.41	R
Dichocoenia stokesii	1	1	0.31	0.04	0.21	R
Meandrina meandrites	1	1	0.31	0.04	0.21	R
Mycetophyllia aliciae	1	1	0.31	0.04	0.21	R
Total species		17				
Total colonies		325				
Density, square meter	Mean	Std. dev.	Range			
Species:	3.36	1.55	1 - 7			
Colonies:	13.00	6.71	4 - 29			

[a]B.I. = Biological Index, McCloskey (1970).
[b]D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

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Table 20

French Reef stony coral fauna at 6 m (twenty-seven 1-m^2 plots; Jaap, unpublished).

Species	B.I.[a] (ranking)	Abundance	Percent of total colonies	Density Mean	Density Std.dev.	D.I.[b]
Acropora cervicornis	40	172	51.05	6.40	9.10	C
Millepora alcicornis	32	50	14.84	1.90	1.90	R
Acropora palmata	20	42	12.46	1.60	1.60	R
Agaricia agaricites	17	18	5.34	0.74	1.23	C
Montastraea annularis	16	19	5.64	0.72	1.00	R
Siderastrea siderea	13	14	4.15	0.50	0.83	R
Porites astreoides	12	14	4.15	0.50	0.93	R
Dichocoenia stellaris	2	2	0.59	0.11	0.32	R
Mycetophyllia sp.	1	1	0.30	0.03	0.21	R
Colpophyllia natans	1	1	0.30	0.03	0.21	R
Porites porites	1	1	0.30	0.03	0.21	R
Montastraea cavernosa	1	1	0.30	0.03	0.21	R
Favia fragum	1	1	0.30	0.03	0.21	R
Diploria clivosa	1	1	0.30	0.03	0.21	R
Total species		14				
Total colonies		337				
Density, square meter	Mean	Std. dev.	Range			
Species:	3.37	1.71	1 - 6			
Colonies:	12.48	8.74	1 - 36			

[a]B.I. = Biological Index, McCloskey (1970).
[b]D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

Table 21

Grecian Rocks zonation pattern (Shinn 1963, 1980).

Zone	Depth (m)	Conspicuous organisms and remarks
Back reef	0 - 0.9	Nonoriented *Acropora palmata*, *A. cervicornis*
Reef flat	0 - 0.9	*A. palmata*
Acropora palmata	0 - 1.2	Oriented *A. palmata*
Weak spur and groove	1.2 - 1.8	*Montastraea annularis, M. complanata*
Seaward rubble	1.8 - 2.4	Mostly coral rubble, few *Siderastrea siderea* and *M. annularis*

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Table 19

Carysfort Reef stony coral fauna at 14 - 15 m (ten 1-m^2 plots; Jaap, unpublished).

Species	B.I.[a] (ranking)	Abundance	Percent of total colonies	Density Mean	Density Std.dev.	D.I.[b]
Montastraea annularis	18	45	36.00	4.50	3.70	C
Acropora cervicornis	11	26	20.80	2.60	4.60	C
Agaricia agaricites	8	15	12.00	1.50	3.10	C
Siderastrea siderea	6	6	4.80	0.60	0.80	R
Porites porites	5	12	9.60	1.20	3.50	C
Stephanocoenia michelinii	5	7	5.60	0.70	1.90	C
Porites astreoides	5	7	5.60	0.70	1.90	C
Colpophyllia natans	2	2	1.60	0.20	0.40	R
Mycetophyllia aliciae	2	2	1.60	0.20	0.40	R
Mycetophyllia lamarckiana	2	2	1.60	0.20	0.40	R
Millepora alcicornis	2	2	1.60	0.20	0.60	C
Helioseris cucullata	1	1	0.80	0.10	0.30	R
Total species		12				
Total colonies		125				
Density, square meter	Mean	Std. dev.	Range			
Species:	3.70	1.06	2 - 5			
Colonies:	12.50	8.44	4 - 31			

[a]B.I. = Biological Index, McCloskey (1970).
[b]D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

French Reef

French Reef, KLNMS (Figure 17; Plate 1b) is farther south and is a popular reef for dive tours. It has a widely separated reef flat and poorly developed shallow spur and groove zones. The deep spur and groove zone is well developed and has cavernous tunnels through many of the spurs. *Acropora palmata* and *M. annularis* are the dominant stony corals on the spur formations. The spurs are usually 5-6 m deep on their tops; this limits the firecoral *Millepora complanata* and the yellow mat zooanthid *Palythoa* sp. from this reef zone. Table 20 presents information on the abundances and densities of stony corals from the deep spur and groove zone at French Reef. The deep spur and groove zone merges with a well-developed fore-reef buttress zone. Seaward outcrops similar to those at Carysfort Reef are also present seaward of French Reef. A deep-reef survey seaward of about 40 m characterized the bottom as sedimentary with occasional sponges, tilefish burrows, and occasional outcrops of limestone with epibenthic reef biota (Jameson 1981). A few solitary corals (*Paracyathus puchellus*) were collected. Algal nodules were found between 33 and 45 m (Shinn 1981).

Grecian Rocks

Grecian Rocks, KLNMS (Plate 3a), described in detail by Shinn (1963, 1980), is located somewhat inshore of the main reef line of Carysfort, Elbow, French, and Molasses Reefs. Unlike most bank reefs, Grecian Rocks has no fore reef or buttress zone. The zonational pattern includes five zones based on Shinn's (1963) terminology (Table 21). It is about 600 m long and 200 m wide with the long axis in a northeast/southwest trend. The reef is surrounded by sediments and has a narrow bathymetric range of 1.5-7.6 m.

Key Largo Dry Rocks

Key Largo Dry Rocks is near and similar to Grecian Rocks, but has greater depth and more defined spur and groove development. Orientation of *A. palmata* branches are toward the prevailing seas, east to east/southeast.

Key Largo Dry Rocks received much study following Hurricane Donna in 1960 (Ball et al. 1967; Shinn 1975). At that time the charts referred to Grecian Rocks as Key Largo Dry Rocks and vice versa.

Table 18

Bank reef zonation patterns.

Zone	Depth (m)	Conspicuous organisms
Back reef/rubble area	0.6 - 1.8	*Porites astreoides, Favia fragum*
Reef flat (Plate 14a)	0.6 - 1.2	*Diploria clivosa, Porites astreoides,* Crustose coralline algae
Shallow spur and groove (Plates 14b and 15a)	1.2 - 2.4	*Millepora complanata, Palythoa* sp.
Deep spur and groove (Plates 15b and 16a)	2.4 - 4.6	*Gorgonia ventalina, Acropora palmata*
Buttress or fore-reef (Plates 16b and 17a)	4.6 - 30.0	*Montastraea annularis, Diploria strigosa, Colpophyllia natans*
Deep reef (Plate 17b)	41.1	*Helioseris cucullata, Agaricia fragilis, Madracis mirabilis*

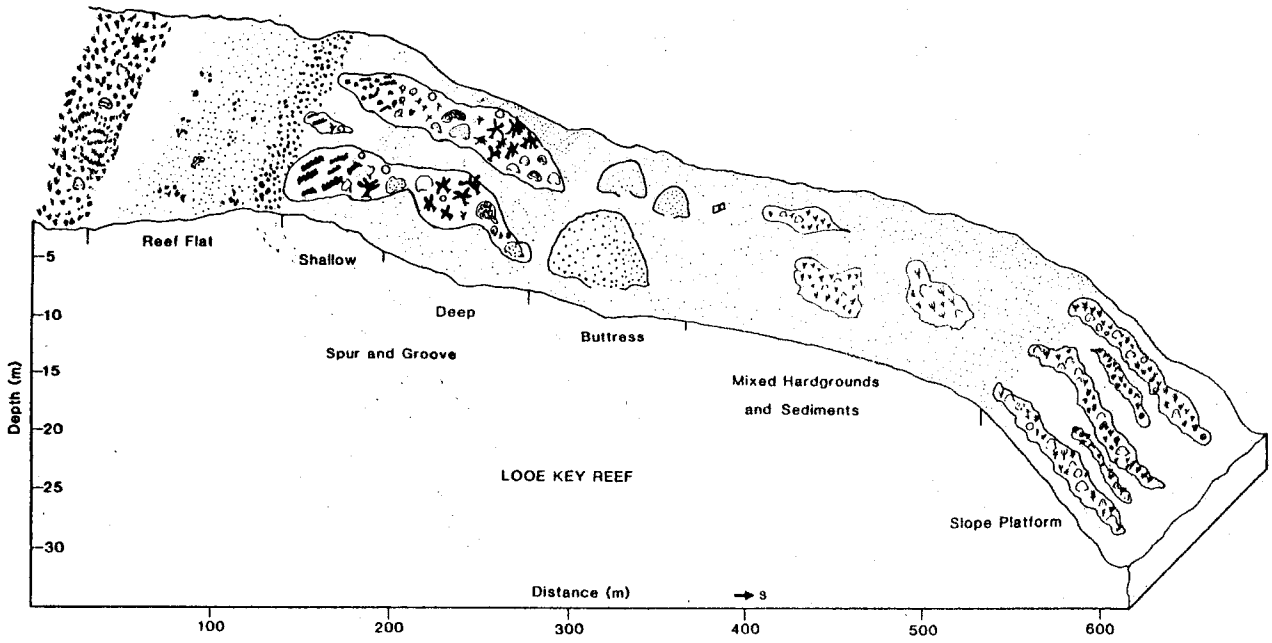


Figure 18. Cross-sectional diagram of Looe Key Reef.

Table 17
Ajax Reef stony coral fauna at 17 m (fifteen 1-m^2 plots; Jaap, unpublished).

Species	B.I.[a] (ranking)	Abundance	Percent of total colonies	Density Mean	Density Std.dev.	D.I.[b]
Montastraea annularis	32	52	24.19	3.47	2.92	C
Siderastrea siderea	32	50	23.26	4.17	2.86	C
Millepora alcicornis	25	32	14.88	2.13	1.96	R
Montastraea cavernosa	18	21	9.77	1.40	1.55	R
Stephanocoenia michelinii	10	14	6.51	0.93	1.75	C
Madracis decactis	9	9	4.19	0.60	0.74	R
Porites astreoides	8	8	3.72	0.53	0.64	R
Agaricia agaricites	5	5	2.33	0.40	0.51	R
Dichocoenia stellaris	3	3	1.40	0.20	0.56	R
Porites porites	3	3	1.40	0.20	0.77	C
Eusmilia fastigiata	3	3	1.40	0.20	0.41	R
Agaricia lamarcki	2	2	0.93	0.13	0.52	C
Siderastrea radians	2	2	0.93	0.13	0.35	R
Diploria labyrinthiformis	2	2	0.93	0.13	0.52	C
Meandrina meandrites	2	2	0.93	0.13	0.35	R
Acropora cervicornis	2	2	0.93	0.13	0.35	R
Mycetophyllia aliciae	1	1	0.47	0.07	0.26	R
Madracis mirabilis	1	1	0.47	0.07	0.26	R
Mycetophyllia lamarckiana	1	1	0.47	0.07	0.26	R
Helioseris cucullata	1	1	0.47	0.07	0.26	R
Colpophyllia natans	1	1	0.47	0.07	0.26	R
Total species		21				
Total colonies		215				
Density, square meter	Mean	Std. dev.	Range			
Species:	6.13	2.36	1 - 9			
Colonies:	14.33	6.59	1 - 27			

[a]B.I. = Biological Index, McCloskey (1970).
[b]D.I. = Dispersion Index, Elliott (1971): C = Contagious (clustered), R = Random, U = Uniform.

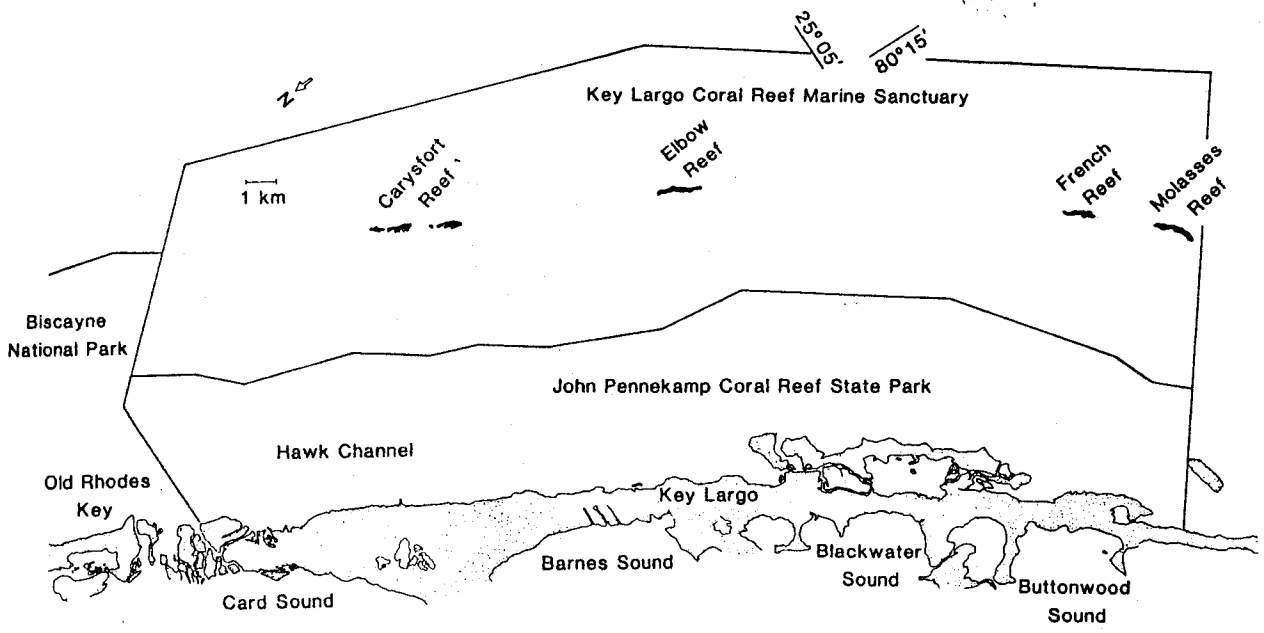


Figure 17. John Pennekamp Coral Reef State Park and Key Largo National Marine Sanctuary.

III.

THE FLORIDA REEFS.

FLORIDA projects between the Gulf of Mexico and the Atlantic as a broad, low peninsula, not strictly limited to the land which rises above the level of the sea. Extensive shoals on its southern extremity reach between the mainland and the line of keys, and stretch nearly as far west as the Tortugas. Taken in connection with the immense bank to the westward of the peninsula, they form the continuation of the mainland, below the surface, to about the hundred-fathom line, — the mass of the Florida plateau proper. To this must be added the narrower coast-shelf of the eastern face of the peninsula. This shelf has, however, a very different character; for on the eastern side of the peninsula, the calcareous or coral sand gives way to the siliceous sand characteristic of the eastern Atlantic coast south of Cape Hatteras.

The shore line of the southern extremity of the peninsula is ill-defined, and, with the exception of the short stretch between Cape Sable and Cape Florida, marked by bluffs of coral limestone, is similar to that of the Everglades. It consists mainly of innumerable low islands separated by narrow channels from the mainland, to which it becomes united by flats, often bare at low water. Similar flats, but far more extensive, stretch westward from the mainland, back of the keys as far as to the northward of Key West and the Marquesas. (Fig. 34.)

Portions of these flats are dry at low tide, and are separated by occasional patches, more or less extensive, of deep water. The water which covers these flats gradually deepens as one passes westward from the mainland. The flats, as well as the whole of the tract of surface between the mainland and the Tortugas, dip slightly to the westward. These shoals are liter-

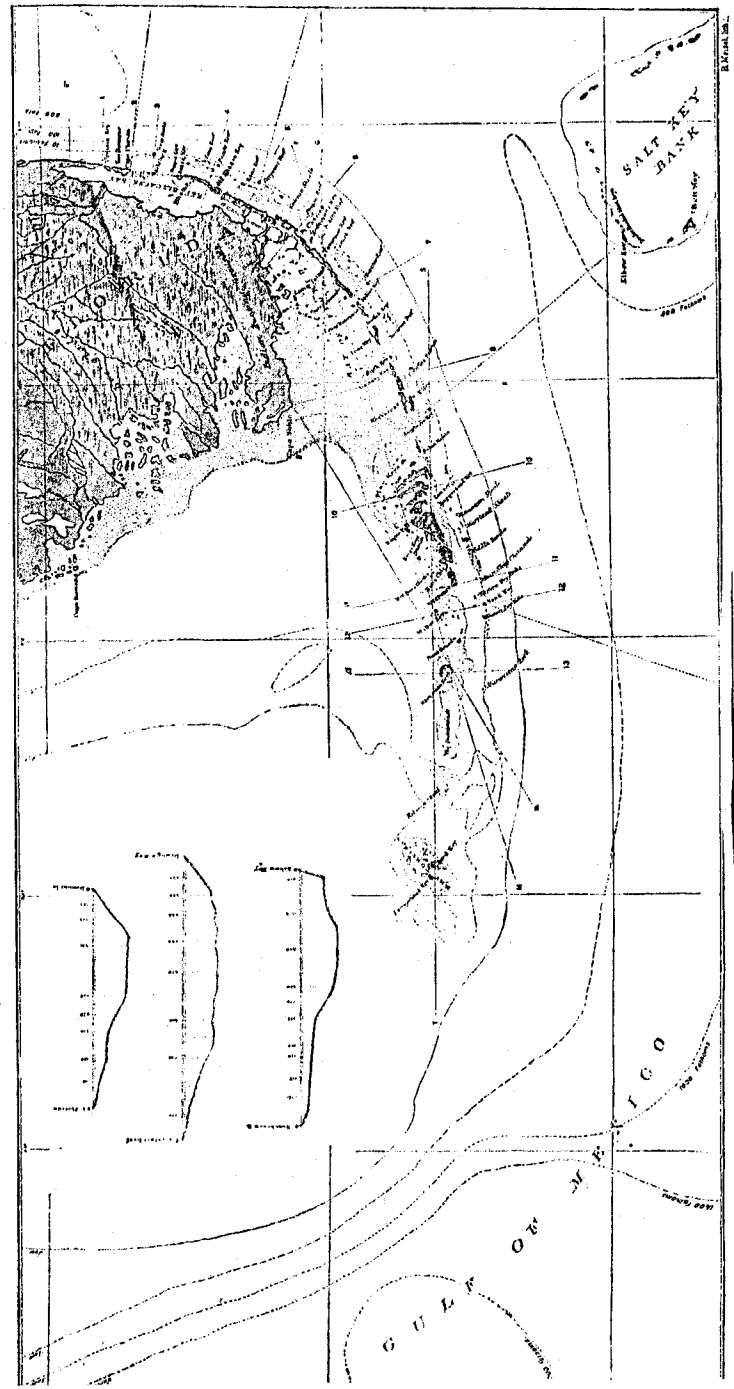


FIG. 34.—STRAITS OF FLORIDA, FROM COAST SURVEY CHARTS.

Table 16a

Elkhorn Reef octocoral fauna (three 20-m transects, 1977; Wheaton, in preparation b).

Species	B.I.[a]	Frequency	No. of colonies	Percent of total colonies
Gorgonia ventalina	59	3	46	22.01
Eunicea succinea	56	3	31	14.83
Plexaura flexuosa	55	3	28	13.40
Pseudopterogorgia americana	54	3	35	16.75
Plexaura homomalla	48	3	13	6.22
Muricea atlantica	46	3	9	4.31
Pseudoplexaura porosa	45	3	7	3.35
Pseudoplexaura flagellosa	42	3	3	1.44
Eunicea tourneforti	34	2	17	8.13
Plexaurella fusifera	29	2	5	2.39
Pseudopterogorgia acerosa	27	2	3	1.44
Eunicea laciniata	27	2	3	1.44
Pseudopterogorgia kallos	16	1	6	2.87
Muriceopsis flavida	13	1	1	0.48
Eunicea calyculata	13	1	1	0.48
Plexaurella dichotoma	13	1	1	0.48
Total			209	

[a]B.I. = Biological Index, McCloskey (1970).

Table 16b

Elkhorn Control Reef octocoral fauna (three 20-m transects, 1977; Wheaton, in preparation b).

Species	B.I.[a]	Frequency	No. of colonies	Percent of total colonies
Pseudopterogorgia americana	54	3	39	13.27
Eunicea succinea	55	3	50	17.01
Gorgonia ventalina	54	3	49	16.67
Plexaura homomalla	52	3	29	9.86
Pseudoplexaura crucis	52	3	32	10.88
Plexaura flexuosa	51	3	31	10.54
Eunicea tourneforti	43	3	15	5.10
Muricea atlantica	40	3	11	3.74
Pseudoplexaura porosa	39	3	10	3.40
Pterogorgia citrina	37	3	8	2.72
Muriceopsis flavida	35	3	4	1.36
Pseudoplexaura flagellosa	28	2	7	2.38
Plexaurella dichotoma	24	2	3	1.02
Plexaurella fusifera	22	2	3	1.02
Eunicea fusca	13	1	1	0.34
Briareum asbestinum	13	1	1	0.34
Eunicea calyculata	10	1	1	0.34
Total			294	

[a]B.I. = Biological Index, McCloskey (1970).

ally studded with mangrove islands, often arranged without any apparent regularity, either forming continuous ranges or small archipelagos, broken by narrow and shallow channels. The vegetation of these low islands is most luxuriant, and consists mainly of mangroves.

Upon the flats which have reached the surface of the sea the young mangrove plants drift in immense quantities. They are fusiform bodies of about six inches in length, resembling a cigar; they float vertically, and when once stranded soon work their way into the soft mud of the flats, and take root, sending out shoots in all directions. The new stem rises rapidly, sending down new shoots to the ground from higher points, forming thus an arch of roots from which spread the branches of the mangrove trees. Around such a nucleus additional sand and mud soon collect, and gradually build up extensive islands, covered with a thick tangle of mangroves and other plants. The mangrove islands on the flats to the north of Key West are specially noteworthy. (Fig. 35.) The keys proper are all similar in structure, and form an extensive chain of low islands, rising nowhere more than about twelve feet above the level of the sea. Starting from north of Cape Florida, they form an immense crescent extending as far west as the Tortugas. The keys usually consist of the accumulation of dead corals, or of coral rock or coral sand cemented into a greater or less degree of compactness. The principal ones are long, narrow islands, varying in width from a mile to less than a quarter of a mile, and in length from mere patches to such islands as Key Largo, Indian Key, or Key West, the longest of which extends about fifteen miles. The keys are separated by shallow channels; they all slope very gradually to the north into the mud flats, and present their steepest face to the south on the shores which skirt the ship channel that separates them from the reef proper.

The reef proper forms a curve similar to that of the keys, never receding from them more than from three to fifteen miles. The channel thus formed, which separates the reef from the keys, is navigable for small vessels the whole length of the reef as far as Cape Florida. The reef reaches the surface of the sea at only a few points, as at Carysfort, Alligator Reef, and Ten-

Table 15a

Elkhorn Reef stony coral fauna (four 4-m^2 plots sampled per reef, 1978; Jaap, unpublished).

Species	B.I.[a] (ranking)	Frequency	No. of colonies	Percent of total colonies	Mean no. colonies/m^2	
Porites astreoides	315	16	60	54.05	3.7500	Density
Acropora cervicornis	210	11	15	13.51	0.9375	
Diploria clivosa	132	7	11	9.91	0.6875	Mean colonies/m^2 = 6.94
Porites porites	95	5	7	6.31	0.4375	Standard deviation = 2.35
Acropora palmata	59	3	6	5.41	0.3750	Range = 3-12
Siderastrea siderea	57	3	4	3.60	0.2500	
Millepora alcicornis	38	2	3	2.70	0.1875	Diversity indices
Palythoa sp.	19	1	1	0.90	0.6250	
Millepora complanata	19	1	1	0.90	0.6250	Mean species/m^2 = 3.31
Favia fragum	18	1	1	0.90	0.6250	Standard deviation = 1.54
Diploria strigosa	18	1	1	0.90	0.6250	Range = 1-6
Dichocoenia stellaris	18	1	1	0.90	0.6250	
Total			111			H' = 2.99
						H' max. = 3.59
						J' = 0.64

[a]B.I. = Biological Index, McCloskey (1970).

Table 15b

Elkhorn Control Reef stony coral fauna (four 4-m^2 plots sampled per reef, 1978; Jaap, unpublished).

Species	B.I.[a] (ranking)	Frequency	No. of colonies	Percent of total colonies	Mean no. colonies/m^2	
Porites astreoides	260	14	68	59.65	4.2500	Density
Millepora alcicornis	146	8	9	7.89	0.5625	
Diploria clivosa	115	6	7	6.14	0.4375	Mean colonies/m^2 = 7.13
Acropora cervicornis	96	5	6	5.26	0.3750	Standard deviation = 2.35
Porites porites	94	5	7	6.14	0.4375	Range = 3-9
Agaricia agaricites	76	4	6	5.26	0.3750	
Siderastrea siderea	56	3	5	4.39	0.3125	Mean species/m^2 = 3.19
Palythoa sp.	38	2	2	1.75	0.1250	Standard deviation = 1.22
Dichocoenia stellaris	20	1	1	0.88	0.6250	Range = 1-5
Millepora complanata	19	1	1	0.88	0.6250	
Porites branneri	19	1	1	0.88	0.6250	Diversity indices
Favia fragum	19	1	1	0.88	0.6250	
Total			114			H' = 2.22
						H' max. = 3.58
						J' = 0.62

[a]B.I. = Biological Index, McCloskey (1970).

nessee Reef. At other points it forms extensive shoals, which are covered with a few feet of water. In other localities again, the pounding of the breakers on the edges of the reefs has accumulated dead corals which form small keys along the line of the main reef, as at Sand Key, Sombrero, and the Samboes. There are passages of greater or less depth across several parts of the reef, giving access from the Gulf Stream to the interior ship channel. The main entrances to Key West Harbor are formed by such channels. The depth of water on the reef, like that of the mud flats, increases as one passes from Cape Florida towards Sand Key and the Marquesas.

The small keys of the reef proper are built of accumulations of larger coral boulders forming the foundation pieces of corals, and fragments of shell and coral sand arranged according to their size in the interstices, and heaped up by the action of the waves, the tides, and the winds. Similar agencies must have formed the keys proper, for they consist of the same coral rock and sand, acted upon for a much greater length of time by the storms.

A walk along the sea-face of any one of the keys will show its coast line to be in incessant movement. In exposed places

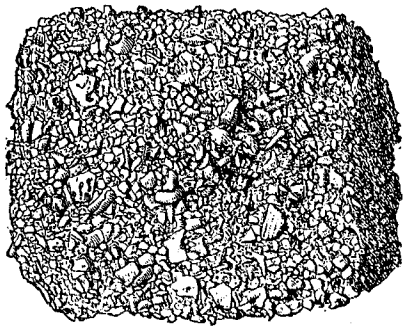


Fig. 36. — Coral Breccia.

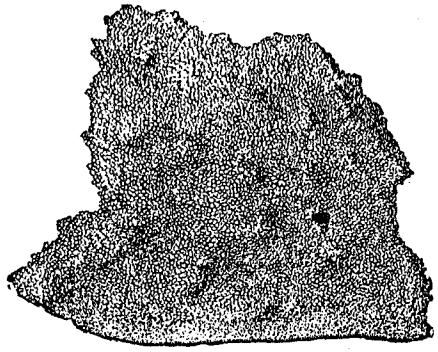


Fig. 37. — Coral Oölite.

the larger fragments broken off by the breakers from the coral rock of the shores are split into smaller fragments, which in their turn are changed to pebbles, and then finally become cemented into coarser or finer sand or impalpable powder. The cementation of these fragments at different stages gives us the

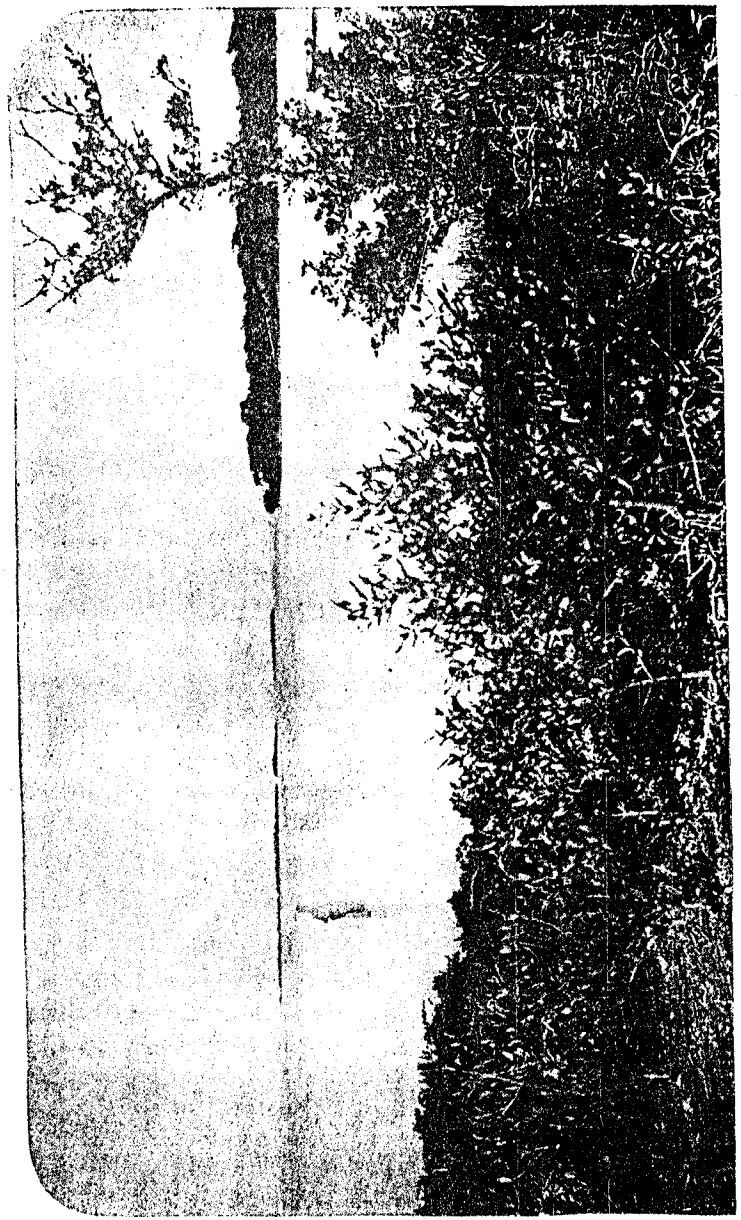


Fig. 35. — DISTANT MANGROVE ISLANDS SEEN FROM MANGROVE BEACH NORTH OF SLAUGHTER HOUSE, KEY WEST.

Section 3.5) but are not as fully developed. They can be thought of as embryonic bank reefs, or a series of coalesced patch reefs, or well-developed hardgrounds with relief. The marginal bank reefs found inshore of Pacific Reef and continuing south to Pennekamp Park boundary in BNP are examples of the embryonic bank reefs. They possess a well-developed reef flat with some trend of spur development by *Acropora palmata* on the seaward fringe. The reef at number 1 buoy (Elkhorn Reef) at BNP (Plate 18a) exemplifies these reefs. Elkhorn Reef is about 500 m long in its north/south axis and some 200 m long in its east/west axis. The reef flat is a rocky platform with undercut solution holes and ledges and sedimentary environments seaward and landward. Off the northeast reef flat there are several large haystack colonies of *Montastraea annularis* (Plate 5b), which are extensively excavated on the undersurface. Their upper surfaces are dead, in some cases supporting the sea fan, *Gorgonia ventalina*. The area seaward of the reef flat platform is visually dominated by octocorals and occasional large clusters of *Porites porites*. There is a slight slope to the reef flat that in some places has dense clusters of *Acropora palmata*, elkhorn coral. A summary of coral species, abundance, and density is presented in Tables 15a, 15b, 16a, and 16b.

Acropora palmata colonies on the reef flat interface are situated with major branches oriented into prevailing seas, east/southeast. On the reef flat small, more uniformly oriented colonies in less dense aggregations are common. They are associated with colonies of *Millepora complanata, Gorgonia ventalina,* and *Diploria clivosa*. This coral often propagates or spreads by vegetative "fragments" (Plate 10b). Broken fragments settle in the nearby bottom and in a short time are solidly attached. They grow upward forming new colonies. The clustered distribution of this species is probably related to the fact that fragments are not transported great distances from parent colonies. Mergner (1977) reported that *M. complanata* (Plate 3b) is an indicator of heavy wave surge. It is common in the reef flats and spur and groove tract areas where wave surge is greatest. *Acropora cervicornis* (Plate 4b), the other common stony coral, occurs in small patches. It is not firmly attached to the bottom and is moved about a good deal during storms. *Porites astreoides* and *P. porites* are also very common on the reef flat. The former is firmly attached, while the latter is not.

On occasion, dislodged *A. cervicornis* colonies come in contact with *A. palmata* colonies; a gall or fuse is formed by a rejection reaction where the tissues of the two colonies meet. The tapering cylindrical branches of *A. cervicornis* grow upward entwined with the flat frondose branches of *A. palmata*. *A. palmata* overgrows *A. cervicornis* when they are in contact (J. C. Lang, University of Texas, Austin; personal observation).

Another type of transitional reef develops on the artificial substrates found throughout the reef tract. They attract reef biota and in time become very reeflike. They include shipwrecks and other materials. A good example is the *Benwood* wreck in KLNMS. This large steel ship sank during WWII and has numerous corals and other sessile growth. The fish fauna is similar to those of nearby natural reefs. The "French wreck" is a similar phenomenon off Loggerhead Key, Dry Tortugas. Artificial reef substrate is also provided by ballast stone or large blocks of igneous rock that were lost in shipwrecks. These are also colonized by reef organisms, notably *Millepora* sp. A number of large barges and ships have been purposely scuttled in waters of 30 m and greater as fish havens; these also develop natural reef growth.

3.5 MAJOR BANK REEF COMMUNITIES

Bank reefs are typically elongated and form a narrow, linear, discontinuous arc from Miami south and west along the Keys to the Dry Tortugas. They are located near the abrupt change in bottom slope, which marks the seaward edge of the Floridan Plateau and they occur mostly between the 5- and 10-m depth contours.

The distinctive features of these reefs are the occurence of *Acropora palmata*, the coral zonation by depth (Table 18 and Figure 18), and the seaward spur and groove formation.

Major bank reefs vary in morphology and species composition. Some, such as Long and Ajax Reefs (Figure 16 and Table 17), off Elliott Key, are sparsely developed in their shallow zones, but below 12 m there is growth on antecedent reef platforms. Better developed bank reefs exhibit a zonation which varies from reef to reef. Reef age, relative position, hydrodynamics, and underlying topography are the major influences on differences in reef morphology and zonation. The general pattern is presented in Table 18. Specific details for individual reefs are given below.

Carysfort Reef

Carysfort Reef (Figure 17) is the northernmost reef in the KLNMS system. A large lighthouse is near the north end of the reef flat. The reef flat has an extensive concentration of *Acropora palmata* on its seaward flank. The spur and groove formations are in an early stage of development. Seaward portions of the reef flat grade into a nearly barren area that separates the *A. palmata* colonies from the buttress zone. The buttress zone has extensive areas of low relief residual spurs and grooves that have coral development. Haystack size colonies of *Montastraea annularis* and fields of *A. cervicornis* are common. The reef platform terminates at about 27 m. Table 19 presents density and abundance information for the stony corals in the 14- to 15-m depth range. A broad expanse of rock separates the reef platform proper from hard-substrate deep reef communities. These deeper communities were described by Jaap (1981) and Wheaton (1981). Outlying communities continue to a depth of about 41 m. The stony coral composition is similar to that of the deep reef; *Agaricia lamarcki, A. fragilis,* and *Helioseris cucullata* are the dominant species on vertical faces, while *Siderastrea siderea, M. cavernosa,* and *Madracis mirabilis* are common on the horizontal surfaces.

so-called coral breccia (Fig. 36), and the different grades of oölitic (Fig. 37) or compact limestone characteristic of the recent reef formation.

The coral boulders are the remnants of huge masses of astreans and mæandrinas, and similar species of corals. The broken fragments of corals come from the different species of branching madrepores and porites or the smaller masses, such as Manicina, Agaricia, and the like; while the fragments of shells, etc., are derived from the limestone carcasses of the hosts of invertebrates which once lived on the active coral reef. The boring mollusks, annelids, and sponges have little by little riddled masses of corals with their burrows, weakening them to such an extent that the breakers pounding upon the exposed sea-faces of the reef break off larger or smaller masses; these are then heaped up and ground together to form either the top of the reef proper or the inner keys, as just described.

Of course it can hardly be expected that, with all this pounding and grinding and constant rehandling of the material which goes to make the limestone rock of the keys, many animal remains should be preserved intact. In fact, with the exception of fragments of the stouter shells of some of the mollusks or tubes of annelids and the like, there are but few organic remains to be found.

Corallines, or limestone algæ, also play a most important part in the formation of keys. They grow in great abundance upon flats and upon the dead fields of corals which have reached the surface of the sea; their joints are easily recognized in the components of the coral sand of many a Florida key. Nowhere else along the reef or the line of the keys do we find indications that the highest elevation of the land is due to any causes except those now acting in the formation of the keys. There is not a single point so high that it cannot be reached by the waves in severe storms, or the elevation of which cannot be traced to the action of the tides and winds upon the material of the shore lines.

All naturalists who have visited the Florida reefs have felt the difficulty of applying Darwin's theory of reef formation to the peculiar conditions existing along the Straits of Florida. Agassiz, Le Conte, and E. B. Hunt have each in succession attempted

Table 14

Attributes of stony coral associations, Biscayne National Park, based on several line transects at each reef (8 reefs, 18 transects) (Jaap, unpublished).

Attributes	Stony coral associations		
	Transitional bank reefs	Patch reefs	Livebottom
Transects[a] (1977)	E 2, 3; EC 1, 2, 3: 5 transects	St 1, 2; StC 1; D 1, 2; DC 1: 6 transects	E 1; Sc 1, 2; ScC 1, 2; StC 2; DC 2: 7 transects
Dominant species	*Acropora cervicornis* *Acropora palmata* *Porites astreoides*	*Montastraea annularis*	*Porites porites* *Millepora alcicornis*
% of colonies	67.2	44.2	48.2
Unique species	*Millepora complanata* *Siderastrea radians*	*Stephanocoenia michelinii*, *Colpophyllia natans*, *Mycetophyllia ferox*, *Mycetophyllia lamarckiana*	*Diploria labyrinthiformis*
No. of species	12	16	14
No. of colonies	186	124	140
Diversity indices[b]			
H'n	2.79	2.89	2.84
H'c	2.57	2.14	2.91
H' max.	3.58	4.00	3.81
J'n	0.78	0.72	0.75
J'c	0.72	0.54	0.76
% cover ($\bar{x} \pm$ SD)			
Algae	0.3 ± 0.3	1.7 ± 2.7	2.0 ± 2.5
Sponge	0.7 ± 0.8	1.1 ± 1.4	2.7 ± 3.3
Octocoral	25.2 ± 12.8	23.2 ± 11.4	38.3 ± 15.3
Stony coral	28.9 ± 15.1	25.7 ± 10.6	14.3 ± 9.7
Abiotic substrate (sand, + rubble + rock)	46.7 ± 9.3	48.4 ± 12.1	42 ± 19.0

[a] E: Elkhorn Reef
D: Dome Reef
Sc: Schooner Reef
St: Star Reef
C: Control Reef, e.g., StC: Star Control Reef.

[b] H'n, J'n computed by abundance.
H'c, J'c computed by cover.

to explain, from a different standpoint, the mode of formation of the Florida reefs. Agassiz stated, and his statement was afterward confirmed by Le Conte, that the Florida reefs had a distinctive character, and could not be explained by subsidence, to which cause Darwin had ascribed the formation of barrier reefs in general. In his report[1] on this subject, Agassiz has shown, not only that the southern extremity of Florida is of comparatively recent growth, but that the causes by which it has for the greater part been built up are still going on, and that we have a specimen, as it were, of the past action in the mode of growth of the present reef, keys, and mud flats. He shows that the whole southern portion of Florida is built of concentric barrier reefs, which have been gradually cemented into a continuous sheet of land by the accumulation and consolidation of mud flats between them, — a process which is now going on between the Florida keys and reefs from Cape Florida to the Tortugas, and must end in transforming them, in like manner, into a continuous tract, to be connected eventually with the mainland.

In Agassiz's report no attempt is made to explain the substructure of the peninsula upon which the reef-corals grow. Le Conte, however, attributed this substratum to the mass of material brought along by the Gulf Stream. He believed that the Gulf Stream once ran parallel with the line of the present peninsula, and that the substratum was formed by the heaping up of these loose materials along that line. All the later investigations show, however, that the Gulf Stream never followed this course. Then, as now, it swept across, and not parallel with, the line of the peninsula, and though it undoubtedly assisted in the building up of Florida, it simply brought then, as it does to-day, the food, or the greater part of the food, consumed by the animals living on the Bank of Florida. These animals supply, by their growth and decay, the building material for the great Florida Bank. No doubt, the floating animals brought by the Gulf Stream add something besides to the mass of the bank itself; but they are chiefly consumed by the animals living upon it.

[1] Mem. Mus. Comp. Zoöl. VII. No. I. 1880.

The curve of the Florida Reef (Fig. 34) along the Gulf Stream is due in great measure, as Hunt shows, to a counter current along the reef, running westward. This current is known to all navigators, and though ill-defined at Cape Florida, becomes stronger and wider as it goes west. It has a width of at least ten miles at Key West, and of twenty miles at the Tortugas. This is clearly shown by the mass of surface animals driven along upon this westerly counter current by the south-easterly winds.

The tides set strongly across the reefs, and through the channels between the keys, the flood running north and the ebb south. When storms occur, the fine silt of the bank, made up of coral sand from the reefs, is taken into the bay back of the keys and deposited there. The counter current then carries this to the westward, and thus material has gradually been added to the flats. As Hunt has already noticed, tides and currents have undoubtedly been the principal agents here. That this material has not been brought by the Gulf Stream from the mouth of the Mississippi, is shown by the fact that no trace of Mississippi mud has ever been found in any of the innumerable soundings taken to the eastward of the Mississippi, or more than a hundred miles from its mouth. It is also probable that the action of the waves from the southeast, in forming a talus of coarser material, does not penetrate below one hundred fathoms, and everything once fixed below that depth has its final character. The line of keys seems to be formed by the waste of the exterior present reef, rather than by the remains of an older anterior reef. At the Tortugas, the contrary seems to be the case; but this perhaps is due to the fact that the strong currents which sweep over the reefs, and have excavated the Southwest Channel, have also established conditions favorable to the growth of corals on both sides of this channel, and that the two lines of keys are due to this cause. Had the currents run only from the southeast through the Northwest Passage, larger keys, separated by channels running north and south, would then have been formed.

I shall first show by an examination of the Tortugas[1] how

[1] A. Agassiz, The Florida Reefs; Mem. Am. Acad. xi. 1883.

Table 13a
Stony corals at Dome Reef (two 25-m transects, 1977; Jaap, unpublished).

Species	B.I.[a] (ranking)	Frequency	No. of colonies	Percent of total colonies	Cover (cm)	Percent of total cover	
Montastraea annularis	40	2	21	53.85	880	0.6592	Density
Millepora alcicornis	38	2	8	20.51	140	0.1049	
Siderastrea siderea	36	2	2	5.13	30	0.0225	Mean colonies/trans. = 19.50
Porites porites	36	2	2	5.13	15	0.0112	Standard deviation = 2.12
Colpophyllia natans	19	1	1	2.56	170	0.1273	
Dichocoenia stellaris	19	1	1	2.56	10	0.0075	Diversity indices[b]
Mycetophyllia ferox	19	1	1	2.56	65	0.0487	
Porites astreoides	19	1	1	2.56	5	0.0037	H' = 2.20
Favia fragum	19	1	1	2.56	5	0.0037	H' max. = 2.20
Diploria clivosa	19	1	1	2.56	15	0.0112	J' = 0.66
Total			39		1,335		

[a]B.I. = Biological Index, McCloskey (1970). [b]Diversity computed with $\log_2$.

Table 13b
Stony corals at Dome Control Reef[a] (two 25-m transects, 1977; Jaap, unpublished).

Species	B.I.[b] (ranking)	Frequency	No. of colonies	Percent of total colonies	Cover (cm)	Percent of total cover	
Siderastrea siderea	39	2	10	33.33	290	31.69	Density
Dichocoenia stellaris	38	2	4	13.33	105	11.48	
Agaricia agaricites	36	2	2	6.67	20	2.19	Mean colonies/tran. = 15.00
Millepora alcicornis	20	1	3	10.00	75	8.20	Standard deviation = 11.31
Montastraea annularis	19	1	1	3.33	280	30.60	
Porites astreoides	18	1	2	6.67	25	2.73	Diversity indices[c]
Porites porites	18	1	2	6.67	25	2.73	
Diploria labyrinthiformis	18	1	2	6.67	40	4.73	H' = 2.88
Montastraea cavernosa	18	1	2	6.67	45	4.92	H' max. = 3.32
Favia fragum	17	1	1	3.33	5	0.55	J' = 0.87
Eusmilia fastigiata	17	1	1	3.33	5	0.55	
Total			30		915		

[a]Reef similarity = affinity between Dome experimental and control reefs: Jaccard's coefficient = 0.3333; Morisita's coefficient = 0.5295.
[b]B.I. = Biological Index, McCloskey (1970).
[c]Diversity computed with $\log_2$.

far the explanations given by Agassiz, Le Conte, and Hunt are satisfactory as regards the formation of the group of islands making the extremity of the reef, and shall then attempt, by the help of the dredging operations of the "Blake" along the Florida Bank, to reconstruct the past history of the peninsula in its southern portion. Beginning with an account of the formation of the present reef, based upon the knowledge obtained by a careful survey of the Tortugas, I shall then proceed to the elucidation of the structure of the peninsula itself.

The Tortugas (Fig. 38) are situated at the very extremity of

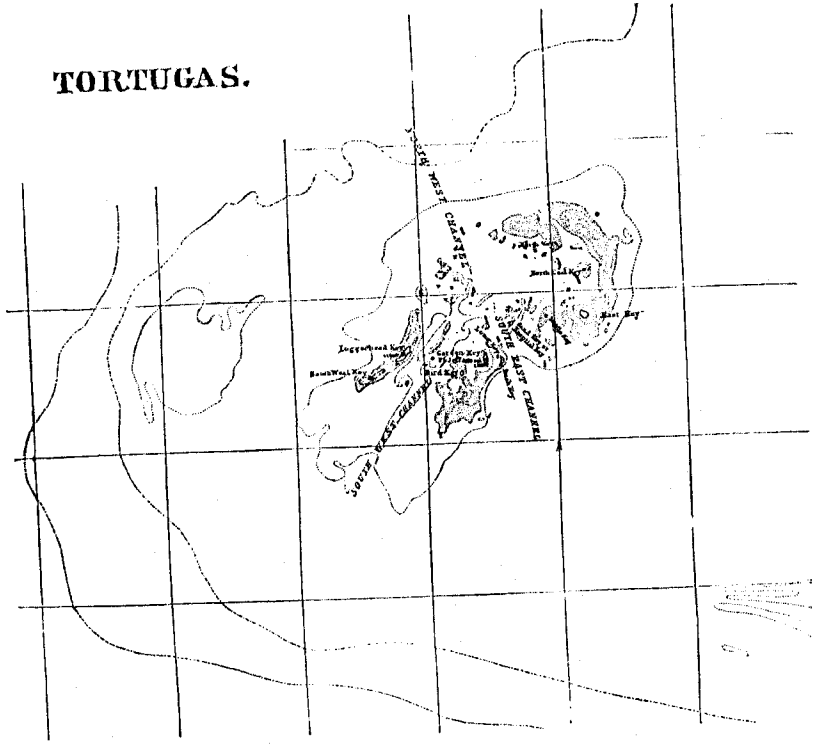


Fig. 38. — The Tortugas from Coast Survey Charts.

the slope upon which the line of the Florida reefs has been built up. They form the most recent of the cluster of Florida reefs, and have not as yet been transformed into the normal coral reef characteristic of the whole line extending from the Rebecca Shoal and Marquesas to Cape Florida. There is as yet nothing at the Tortugas corresponding to the extensive mud flat stretching uninterruptedly, a few feet below the surface of the water, to the northward of the line of keys. (Fig. 34.) The northern part of this flat, from Cape Sable to Key Biscayne, is fringed on the southeast face by the line of narrow keys reaching from Cape Florida to Bahia Honda. (Fig. 34.) In the oldest part of the reef, the bay to the north of the keys, the waters of which once undoubtedly covered the whole space between Pine Keys and Cape Sable, has little by little been filled up and transformed for the greater part into the wide, shallow mud flats now extending over that area. Next comes, from the Pine Keys to Rebecca Shoal, a comparatively more recent portion of the reef, in which the northern extremities of the keys rise somewhat higher above the general level of the mud flats.

These two adjoining regions of flats and keys run parallel to the main reef, at a distance of from one to nine miles from the outer line of reefs, — the reef, that is, *par excellence*, over the whole surface of which the living corals still prosper. Farther yet to the westward, at a distance of fifteen miles from the western extremity of the outer parts of the reef, rise the Tortugas. In this group a condition of things prevails at the present day which must have been repeated over and over again, from the time when the Florida Reef formed but an insignificant point south of the line extending from Cape Sable to Key Biscayne, until it reached the extremity of the present continuous mud flat, about ten miles to the west of the Marquesas. As is well shown on the Coast Survey maps, the mud flats, keys, and reef, dip as a whole to the southwest, as does also the Florida plateau which extends to the westward of the Marquesas. It is only upon such parts of this plateau as from some cause or other have attained a sufficient elevation to allow corals to flourish that the reef may be expected to extend. Such an area is the knoll rising above the general level upon which the Tortugas have little by little been built up; and such also is the patch to the westward of the Tortugas, upon which, as I shall show hereafter, an incipient coral reef is already forming, at a depth of a little less than twenty fathoms. (Fig. 38.)

It is not difficult to go back to a time when the great mud flats of Florida did not exist. In their place was a steep slope,

Table 12a

Octocorals at Dome Reef (two 20-m transects, 1977; Wheaton, in preparation a).

Species	B.I.[a] (ranking)	Frequency	No. of colonies	Percent of total colonies
Plexaura flexuosa	39	2	41	19.33
Plexaura homomalla	36	2	29	13.67
Pseudoplexaura porosa	36	2	28	13.20
Pseudopterogorgia acerosa	34	2	29	13.67
Pseudoplexaura flagellosa	31	2	12	5.66
Gorgonia ventalina	31	2	12	5.66
Pseudopterogorgia americana	30	2	17	8.01
Briareum asbestinum	29	2	10	4.71
Plexaurella fusifera	26	2	7	3.30
Eunicea tourneforti	25	2	6	2.83
Plexaurella nutans	22	2	2	0.94
Eunicea fusca	15	1	4	1.88
Eunicea succinea	14	1	3	1.41
Muricea atlantica	12	1	4	1.88
Eunicea laciniata	12	1	4	1.88
Eunicea calyculata	10	1	1	0.47
Plexaurella grisea	10	1	1	0.47
Muricea elongata	10	1	1	0.47
Eunicea mammosa	10	1	1	0.47
Total			212	

[a]B.I. = Biological Index, McCloskey (1970).

Table 12b

Octocorals at Dome Control Reef (two 20-m transects, 1977; Wheaton, in preparation a).

Species	B.I.[a] (ranking)	Frequency	No. of colonies	Percent of total colonies
Plexaura homomalla	40	2	49	19.76
Pseudoplexaura porosa	36	2	30	12.10
Plexaura flexuosa	35	2	32	12.90
Pseudopterogorgia americana	35	2	26	10.48
Pseudopterogorgia acerosa	34	2	25	10.08
Gorgonia ventalina	27	2	10	4.03
Briareum asbestinum	26	2	12	4.84
Eunicea tourneforti	26	2	9	3.63
Pseudoplexaura flagellosa	26	2	12	4.84
Eunicea calyculata	26	2	12	4.84
Eunicea succinea	22	2	4	1.61
Plexaurella fusifera	22	2	4	1.61
Plexaurella grisea	22	2	4	1.61
Muricea elongata	22	2	4	1.61
Eunicea fusca	21	2	3	1.21
Muricea atlantica	21	2	3	1.21
Muriceopsis flavida	14	1	5	2.02
Eunicea laciniata	11	1	2	0.81
Plexaurella nutans	10	1	1	0.40
Eunicea clavigera	10	1	1	0.40
Total			248	

[a]B.I. = Biological Index, McCloskey (1970).

such as we now find to the west of the Tortugas. Continuing the parallel, it is easy to imagine how, little by little, since easterly winds and currents prevailed, materials coming from the small outside reefs and held in suspension were gradually driven to the westward, and accumulated finally upon what was then the extremity of the great Florida Bank. There they gave rise to knolls similar to those upon which the Tortugas have been built. From the moment these knolls attained a sufficiently favorable elevation for the growth of corals, a western reef was formed, holding to the small Florida Reef then existing very much the same relations as the Tortugas at the present day hold to the great Florida Reef. Again, by the same agencies, the channels which once undoubtedly ran back into the mud flats to the north of the oldest keys were gradually closed, since such channels as are still open, in part or wholly, in the more recent and westerly portions of the reef, as, for instance, the entrance to Key West Harbor, run from the south to the north across from the reef to the mud flats. In like manner these channels, and those which form an extensive strait in the most recent part of the reef between Rebecca Shoal and the Tortugas, will in time disappear, and become, in consequence of the extension of the mud flats beyond Rebecca Shoal, narrow channels, like those of Key West, of the Pine Keys, and of the Marquesas. By this time there will also have been formed an extension of the outer reefs along the twenty-fathom line, connecting the Tortugas with the present reef, and only broken here and there by passages similar to those already existing along the reef, by which vessels find free access to the middle passage between the reef and keys. These channels are kept open by the same tidal agencies as are now more powerfully at work at the Tortugas, but which have gradually diminished in force from the Pine Key Channel to the northward. The depth of the passage between the Tortugas and Rebecca Shoal allows a larger and stronger body of water to pass through that channel than through any other.

It has been clearly proved by Hunt that the extensive flats to the northward of the keys have been formed by the agency of the tides, the whole triangular space between the Rebecca Shoal

and Cape Sable being filled up with silt. Since the flood runs in a northerly and the ebb in a southerly direction, the tides in their alternation hold in suspension the silt which they wear away from the reef or from the shores of the keys. During storms this floating silt is driven either on to the flats to the north of the keys, or on to the slope of the reef toward the Gulf Stream. An examination of the present condition of the Tortugas, and of the mud flats beyond the Marquesas, gives us a very simple explanation of the formation, and gradual extension westward to its present limits, of the small reef originally existing only as a diminutive spit, but gradually spreading to the southwest from Cape Florida until it has reached its present gigantic proportions.

The Tortugas show us, as will be seen, how the reef was actually formed, while the extension of the mud flats beyond the Marquesas explains how the bottom is prepared and gradually raised to a level at which corals will flourish. One other condition was, however, essential to the development of the coral reef, — that of the existence of a powerful current, such as the Gulf Stream, bringing an immense quantity of pelagic animals to serve as food for the corals found along its path. There is practically no evidence that the Florida Reef, or any part of the southern peninsula of Florida which has been formed by corals, owes its existence to the effect of elevation; or that the atolls of this district, such as those of the Marquesas or of the great Alacran Reef, owe their peculiar structure to subsidence.

It cannot be denied that the backbone of the Florida peninsula was first produced by a fold of the earth crust in an earlier geological period. Smith and Hilgard have also shown that such a fold or folds formed the axis which has raised a part of the northern base of the peninsula to a height of something less than two hundred feet; and that this axis, which has still, at the latitude of Lake Okeechobee, an elevation of about forty feet, but sinks gradually as we go south, was formed before the Vicksburg limestone age, while on either side of it are deposited the more recent limestones which have given Florida its present width. They have pointed out, moreover, as a secondary result

(1) Initial pioneering settlement of coral larvae on appropriate substrates. These species might include *Porites porites, Manicina areolata,* and *Favia fragum.* They would be preparatory colonizers which would eventually die and their skeletons would become the hard substrate that the major framework corals would settle on. If the bottom were rocky, this stage might be unnecessary.

(2) The settlement and growth, both upward and outward, of the primary framework builders. While other coral species are common in the patch reef community, *Siderastrea siderea, Montastraea annularis, Diploria strigosa, D. labyrinthiformis,* and *Colpophyllia natans* build the massive frame or three-dimensional structure of most reefs. Shortly after the framework element has settled, the boring and rasping fauna starts the production of reef sediment. Sediments fill interstitial space and are incorporated into the reef frame. In time, some coral deaths occur providing space for settlement of coral larvae, an essential element for growth of the reef. The newly developing reef is a focal point for attracting the diverse flora and fauna common to the coral reefs. Some of this occurs because of larval settlement, especially for the sessile species. Mobile invertebrates and vertebrates (some residents, some temporary refugees) move to the reef as niches favorable to their requirements become available (Plates 13a and b).

(3) The maturing stage. During this stage the reef grows upward and outward, providing surface area for secondary colonizers. The major framework builders attain 2 m in diameter and greater. The boring and rasping fauna excavate considerable material from the basal surfaces of the corals, creating a labyrinth of caves that become occupied by a cryptic biota. In time, these caves and tunnels are enlarged, and larger fish and invertebrates take refuge in them. The new niches within the interior of the reef are colonized by a wide taxonomic spectrum of shade-loving organisms.

(4) The fully mature stage. Because the primary framework-building corals have approached sea level, upward growth is limited. The undersurface of these corals is cavernous, and in time the framework becomes so weakened that the upper surface may collapse inward forming a rubble or boulderlike surface. This is usually irregularly flat and, in many cases, is dominated by octocorals. Haystacklike colonies of *M. annularis* appear to have large dead areas that are colonized by other species (*Millepora alcicornis* and *Gorgonia ventalina*). If the reef completely collapses from a major storm or vessel grounding, the former major relief patch reef becomes a low-relief pile of rubble that is usually dominated by octocorals and nonframework building stony corals. In this growth and decay of the patch reef community into the live bottom community, geochemical processes play an important role in cementing and binding sediments.

The association of coral found on any particular patch reef is most probably governed by random chance. Some patch reefs have very diverse stony coral faunas while other reefs, only a few meters or kilometers away, have a less diverse, nearly monospecific fauna. Patch reefs exhibit extreme variability in coral abundance, density, and diversity (Table 14). Macrobenthic algae constituted from 0% to 7% of the linear biomass, sponge 0% to 3.6%. Octocorals constituted a numerically dominant element; however, their linear biomass and macrohabitat potential are less than many of the stony corals, especially the massive framework builders. Octocorals do occupy much of the space on the mature older patch reefs. There appears to be a competitive exclusion by octocorals in the interior of older patch reefs. A representative patch reef is the reef at buoy number 4 (Dome Reef) in BNP 16. It is about 250 m in diameter. The greatest relief is about 2 m and is found on the northwest side. Tables 12a and b and 13a and b present the octocoral and stony corals found in this reef based on several transects. Reef organic linear biomass based on line transect surveys from four patch reefs in Biscayne National Park shows that mean stony coral cover was 25.7±10.6% in the stony coral-dominated zones (Table 14). In the interior octocoral-dominated zones the organic linear biomass for stony corals was 14.3% ±9.7% (Table 14). There is usually a halo of barren sand and reef talus (rubble) with sparse grasses and algae surrounding the periphery of most patch reefs (Plates 11a and b). The rubble, composed mostly of dead coral colonies that have been swept away from the reef by storms, is potential substrate for colonization. Outward reef expansion is presumably dependent on the reef talus in sedimentary environments for substrate creation. Halos around some patch reefs resulted from the black sea urchin (*Diadema antillarum*) feeding nocturnally on algae and seagrasses surrounding the reef, according to Sammarco (1972), Ogden et al. (1973), and Sammarco et al. (1974). Randall (1965), however, reported that herbivorous reef fish were responsible for patch reef halos. In either case, the herbivorous consumers graze away the flora adjacent to the reef, creating a barren zone or halo.

Patch reefs are important habitats for many reef fish, permanent and transient (Plate 13a). They provide shelter, food, and breeding ground for mobile fauna. The spiny lobster (*Panulirus argus*) (Plate 19b) utilizes patch reef habitats during part of its life history.

Like most reefs, patch reefs show a temporal change when storms or temperature extremes disturb the communities. Smaller coral colonies are dislodged and transported from their growth positions. If the new position is favorable, they may continue to grow; if not, they may die. This is especially true for octocorals and encrusting colonies of *Millepora* that are on unstable substrates, principally octocoral axes. These colonies may be swept completely off the reef by heavy wave surge. There appears to be high mortality due to this stress; if so, intense recruitment usually prevents large open areas.

3.4 TRANSITIONAL REEF COMMUNITY

The term transitional reef is used to describe those reefs that have the rudiments of bank reefs (see

of this folding, the formation of an immense submarine plateau, directly in the track of the Gulf Stream, by the accretions of the solid parts of mollusks, echinoderms, corals, halcyonoids, annelids, crustacea, and the like, which have lived and died upon it; these solid parts have furnished the limestone for the gradual completion of the peninsula. No one who has not dredged near the hundred-fathom line on the west coast of the great Florida plateau can form any idea of the amount of animal life which can be sustained upon a small area under suitable conditions of existence. It was no uncommon thing for us to bring up in the trawl or dredge large fragments of the modern limestone now in process of formation, consisting of the dead carcasses of the very species now living on the top of this recent limestone. To the westward of the western shore line, Florida now stretches out as an immense submarine plateau, forming, as the sections show, a huge tongue coated or veneered only by coral limestone over its very top. The whole of the peninsula of Florida south of St. Augustine, as far as Tampa Bay, has probably in this way been built up from north to south, of limestone somewhat older than the reef limestone. The plateau, judging from the inclination of the axis, has but a slight southward dip until one reaches the southern extremity of the peninsula, where the fall is more rapid toward the outer reef.

The whole of the eastern and western edges of Florida consist of recent limestones, the immediate predecessors of that which is now forming on the western and southern slopes of the great Florida plateau. The early dredgings of Mr. Pourtalès, in 1867 and 1868, developed on the Gulf Stream slope off the Florida reefs an extensive rocky plateau (Pourtalès Plateau) from a depth of about ninety fathoms to about two hundred and fifty fathoms. The rock of which this plateau is built (see Fig. 192) consists of the same species of corals and shells as those now living upon it, to which it owes its formation.[1] A similar sea-bottom is found on the north side of Cuba,

[1] Mr. S. P. Sharples, who examined specimens of rock from the Pourtalès Plateau, found the corals made up of about ninety-five per cent. of carbonate of lime, the balance being organic matter and phosphate of lime.

The recent limestone found on the Pourtalès Plateau contained from thirty-six to forty-seven per cent. of carbonate of lime and from thirty to thirty-five per cent. of phosphate of lime, with ten to twelve per cent. of carbonate of magnesia, and from ten to twelve per cent. of oxide of iron. This large amount of iron is probably brought down by the rivers, and, coming in contact with the decomposing organic matter, is deposited as a carbonate, and then slowly changed to a sesquioxide.

The most recent limestone contains, like the corals of which it is almost entirely made up, ninety-six per cent. of carbonate of lime and a little silica. In the ooze the amount of carbonate of lime was eighty-five per cent., there being also over four per cent. of carbonate of magnesia, and eight per cent. of organic matter, with about one and one half per cent. of silica, and only a trace of phosphoric acid, which distinguishes this ooze from Atlantic ooze.

but with a much steeper slope. These fringing limestones also formed the southern extremity of Florida at a time when the northern part of the Everglades had perhaps been built up to a level favorable for the growth of coral reefs.

In the northern portion of the Everglades alone can we confidently speak of the first concentric reefs, which have little by little built up Florida toward the south. It seems highly probable that on the remainder of the peninsula north of the Everglades, both the newer and older limestones were built up by the same agencies now at work on the Florida Bank. There are to-day other submarine banks which undoubtedly owe their origin to similar agencies. The great bank to the east of the Mosquito coast, which practically extends to Jamaica, has probably been formed in the same way as the Yucatan and Florida banks; that is, by the gradual decay of the animals subsisting in great abundance upon its slope, and fed by the pelagic materials which the currents and the prevailing winds bring to the bank, and which have been pouring upon the top of the plateau for ages past. All the reefs on the south coast of Cuba between the Isle of Pines and the shore of the east and west may have had a similar origin. Among the West India Islands the barrier reefs of the windward side are built upon plateaux of a similar structure. The Grande Terre of Guadeloupe is a fine example of such a plateau, which has been elevated slightly above the level of the sea. At Barbados the whole shell of the island consists of a series of terraces, which have been successively lifted by the trachytic centre that forms the nucleus of the island. These terraces are entirely composed of limestone formed of the species of mollusks and radiates now living in the West India seas.

Table 11

Live bottom corals from Schooner Reef, Biscayne National Park (four 1-m^2 quadrants; Jaap and Wheaton 1977 MS.).

Species	Type[a]	B.I.[b] (ranking)	Frequency	No. of colonies	Percent of total colonies	Mean no. of colonies/m^2
Plexaura homomalla	O	73	4	18	9.63	4.50
Porites porites	S	73	4	18	9.63	4.50
Gorgonia ventalina	O	70	4	14	7.49	3.50
Pseudopterogorgia americana	O	70	4	14	7.49	3.50
Briareum asbestinum	O	67	4	10	5.35	2.50
Eunicea tourneforti	O	65	4	8	4.28	2.00
Muricea atlantica	O	65	4	8	4.28	2.00
Pseudoplexaura porosa	O	63	4	6	3.21	1.50
Plexaurella fusifera	O	62	4	5	2.67	1.25
Eunicea succinea	O	58	3	25	13.37	6.25
Plexaura flexuosa	O	51	3	11	5.88	2.75
Muriceopsis flavida	O	51	3	10	5.35	2.50
Porites astreoides	S	47	3	6	3.21	1.50
Plexaurella dichotoma	O	47	3	3	1.60	0.75
Millepora alcicornis	S	34	2	7	3.74	1.75
Pseudoplexaura flagellosa	O	32	2	4	2.14	1.00
Eunicea laciniata	O	32	2	2	1.07	0.50
Agaricia agaricites	S	32	2	2	1.07	0.50
Plexaurella grisea	O	31	2	2	1.07	0.50
Eunicea mammosa	O	30	2	2	1.07	0.50
Pseudoplexaura wagenaari	O	29	2	2	1.07	0.50
Dichocoenia stellaris	S	16	1	2	1.07	0.50
Pseudopterogorgia acerosa	O	15	1	1	0.53	0.25
Eunicea calyculata	O	15	1	1	0.53	0.25
Eunicea fusca	O	15	1	1	0.53	0.25
Favia fragum	S	15	1	1	0.53	0.25
Pseudopterogorgia kallos	O	14	1	1	0.53	0.25
Pseudopterogorgia bipinnata	O	14	1	1	0.53	0.25
Siderastrea siderea	S	14	1	1	0.53	0.25
Montastraea cavernosa	S	14	1	1	0.53	0.25
Total				187		

Density

Mean colonies/m^2 = 46.75
Standard deviation = 15.46
Range = 25-61

Mean species/m^2 = 18.50
Standard deviation = 4.53
Range = 13-21

Diversity indices[c]

H' = 4.27
H' max. = 4.91
J' = 0.87

[a]O = octocoral, S = stony coral.
[b]B. I. = Biological Index, McCloskey (1970).
[c]Diversity computed with $\log_2$.

While there is thus undoubted evidence that a great part of the shore line of the northeast extremity of South America has been washed away, there is also evidence that the lines of the bank connecting the lesser West India Islands have been built up by agencies similar to those which have formed the Yucatan and Florida banks, except that these latter have been formed around the volcanic islands or folds which extend along the eastern edge of the Caribbean Sea. In some cases these banks have been elevated since the existing condition of things came about; in others their elevation dates back to the period when the separation of the Caribbean from the Pacific took place, at the time of the closing of the Isthmus of Panama. Evidence of this action is found in the elevated coral reefs and the raised earlier tertiary and later cretaceous deposits of the West Indies and Central America.

Nowhere do we find better examples than in the West India Islands of the formation of submarine banks in connection with volcanic peaks. A great number of peaks of volcanic origin have risen nearly to the surface of the sea, or above it, and serve as the foundation of great submarine or littoral banks. It is well known, also, that the "Challenger" and "Tuscarora" soundings have developed a number of submarine elevations, covered by deposits of pteropod and globigerina ooze, and these deposits form extensive banks which serve as foundations for barrier reefs and atolls, while the volcanic substratum has been completely hidden. In the West Indies, as at Martinique, there are volcanic peaks rising to a height of over four thousand feet; on their windward side are extensive submarine plateaux, formed, I imagine, by agencies similar to those to which we ascribe the formation of the Yucatan and Florida plateaux. Whenever such plateaux have reached on their windward side the level at which corals prosper, there coral reefs spring up and flourish. Side by side with such conditions we find plateaux at lower levels, under a greater depth of water, covered only by the invertebrates living upon their surface, — as is the case, for instance, in the northern extremity of the plateau of the Grenadines. These plateaux have probably never risen to the surface. We have also the still older phenomenon of such

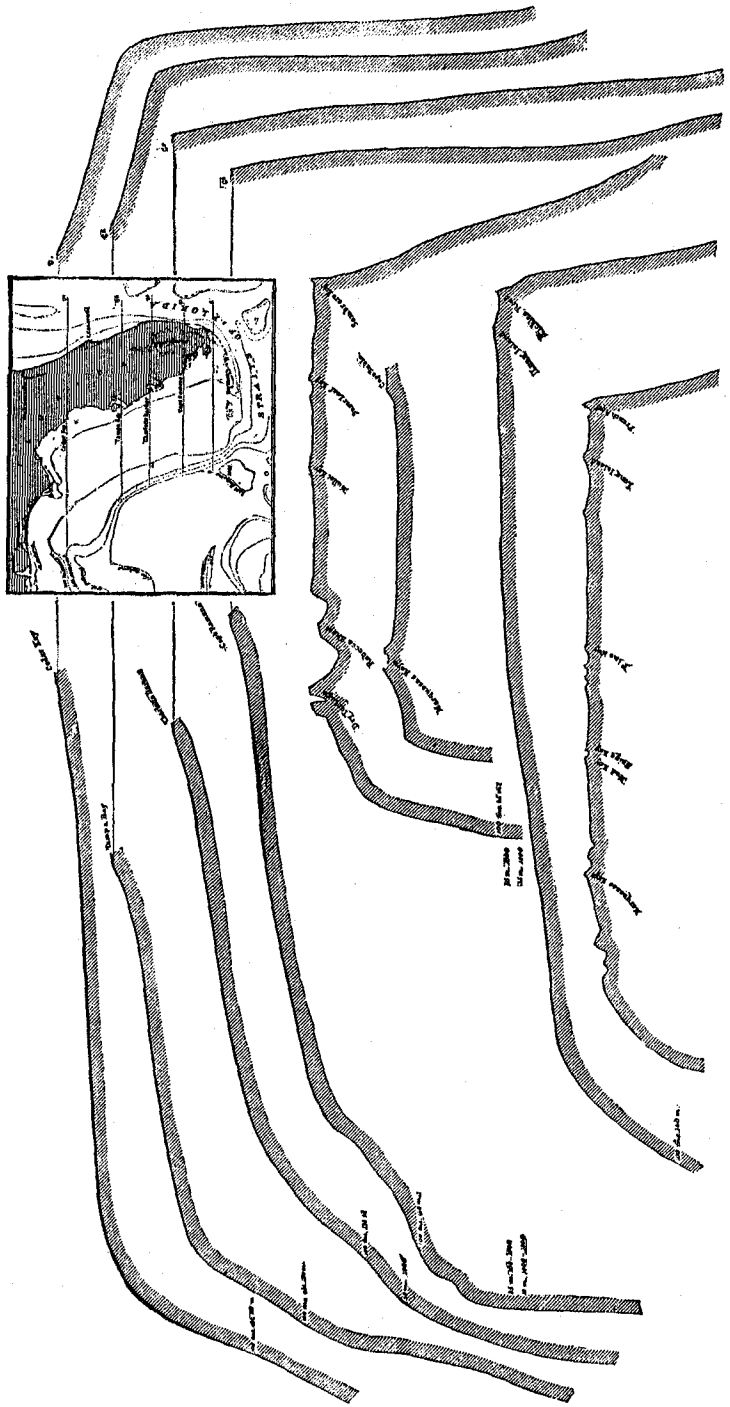


FIG. 40. — SECTIONS ACROSS THE PENINSULA OF FLORIDA.

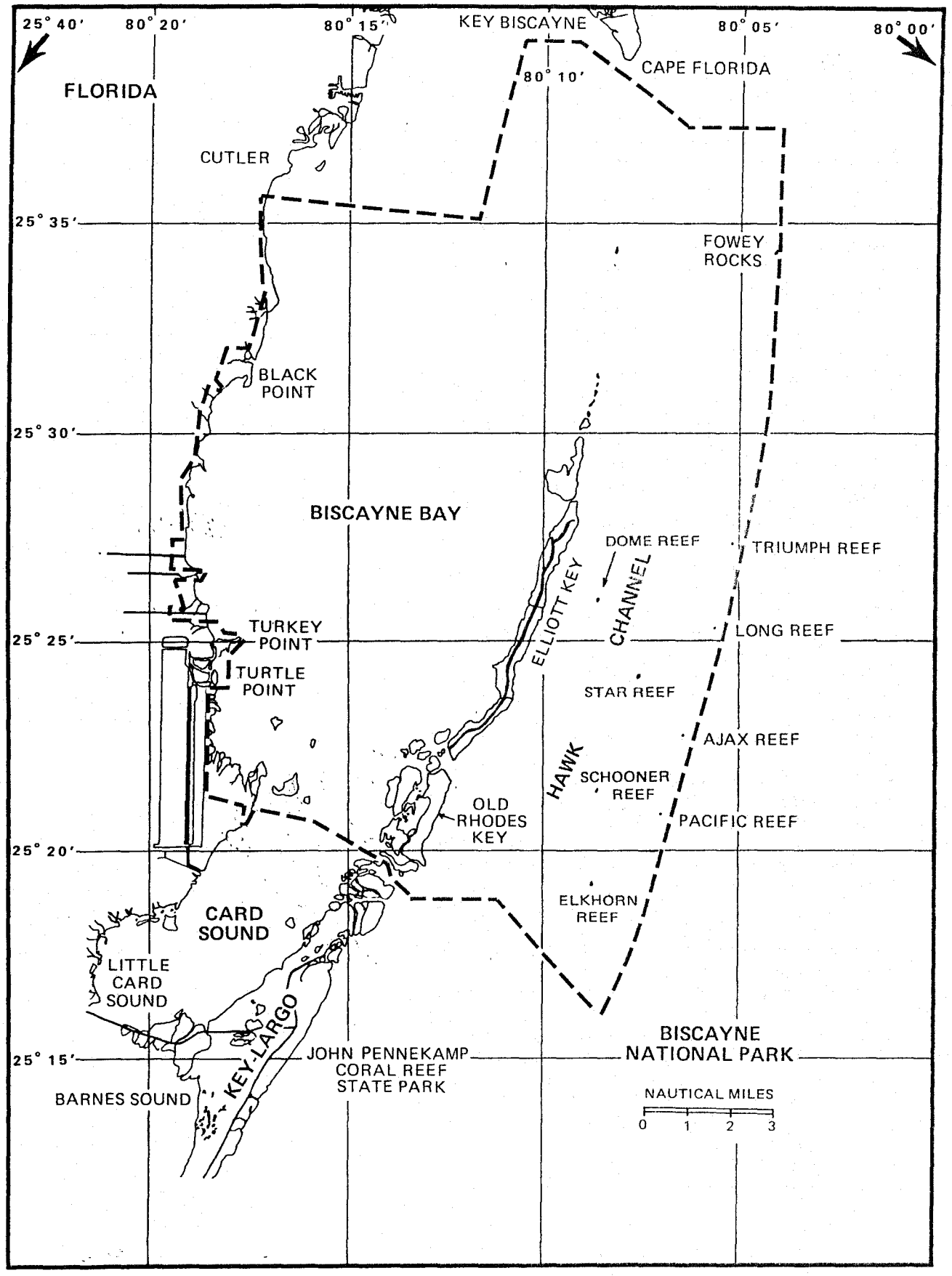


Figure 16. Coral reefs in Biscayne National Park.

islands as Barbados (Fig. 39), where the terraces formed by the raised coral reefs mark the successive elevation of the volcanic cone; or we may have still another combination, like that of Guadeloupe, where a high volcanic peak forms the main island, and an elevated plateau forms the Grande Terre with a growing coral reef to the windward.

The fact that these great submarine banks of modern limestone lie in the very track of the great oceanic currents sufficiently shows that these currents hold the immense quantity of carbonate of lime needed in the growth of the bank. Its amount has, besides, been actually measured by Murray. He

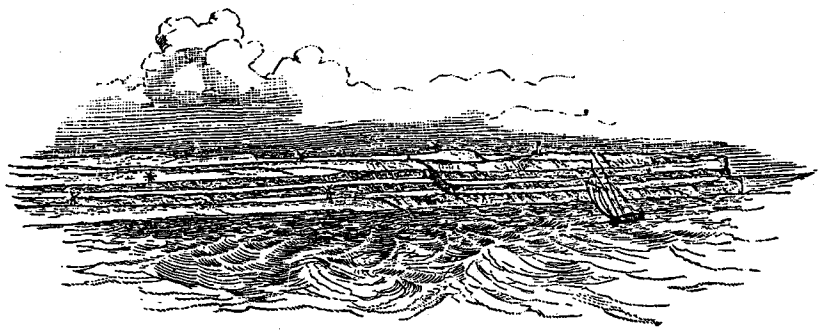


Fig. 39. — Barbados Terraces.

has shown that, if the pelagic fauna and flora extend, as the experiments carried on by the "Challenger" and the "Blake" seem conclusively to prove, to a depth of one hundred fathoms, we should have sixteen tons of carbonate of lime for every square mile one hundred fathoms deep. But the greater the depth at which these plateaux begin to form, the less rapid must be their formation. The fact that the deeper part of the ocean, below three thousand fathoms, does not contain any of the larger shells of pelagic type can be readily explained on the supposition that these, being very thin, like pteropod shells, present a large surface to the action of the carbonic acid, which is most abundant in deep water. Attacked as soon as they reach deep water by this action, these shells of thinnest surface are reduced to a bicarbonate, and are carried off in solution. They do not, therefore, appear at these greater depths, and are

CHAPTER 3

CORAL REEF COMMUNITY TYPES

3.1 INTRODUCTION

A biotic community as defined by E.P. Odum (1971) is any assemblage of populations living in a prescribed area of physical habitat. Four discernible coral community types occur off southeast Florida.[1] Generally in a seaward progression are found live bottoms, patch reefs, transitional reefs, and bank reefs. The relief (height above bottom) of these communities and the dominance of stony corals as a structural element increase in a similar progression. All of these communities can be physically characterized as shallow water, wave-resistant, three-dimensional carbonate accretions constructed by limestone-secreting organisms (principally corals, algae, and bryozoans) on a pre-existing hard substrate. This basic structural component is augmented by other community members, sedentary and mobile, permanent and transient.

3.2 LIVE BOTTOM COMMUNITY

The live bottom community, also known as hardground, is generally found closest to shore, e.g., in tidal passes, under bridges, and short distances seaward of the intertidal zone. It usually occupies exposed fossil reef formations, limestone, and other rocky substrates. The faunal and floral elements are not consistent, and the assemblage is usually visually dominated by octocorals, algae, sponges, and smaller hardy stony coral species.

These communities do not actively accrete or build massive structures. They support diverse invertebrate and vertebrate communities and provide an important nursery area for commercial and sport harvested species. Live bottom habitats are scattered from St. Lucie Inlet southward to Dry Tortugas in depths ranging from less than 1 m to beyond 30 m. While these descriptions may imply a single community type, the nearshore and offshore types differ greatly in species composition. In either case the octocorals (soft corals) often dominate in terms of numerical abundance and density. An example of an offshore live bottom community is the reef (Schooner Reef) at number 2 buoy in Biscayne National Park (BNP, Figure 16) off Elliott Key. It exhibits little relief with the exception of a small ballast pile from an old shipwreck on the north side off the reef. The platform is limestone with small ledges, solution holes, and pockets of sediments. It is heavily colonized by octocorals and a sparse number of stony (hard) corals (Table 11). The live bottom community may vary in size from a small area of tens of square meters to one of several hundred square meters. The stony corals most commonly found in the nearshore associations include *Siderastrea radians, Porites porites, P. astreoides, Manicina areolata, Solenastrea hyades,* and *S. bournoni.* Along with these species, *Diploria clivosa, Millepora alcicornis,* and *Dichocoenia stellaris* are commonly found in deeper communities. The region surrounding the live bottom communities is sedimentary, seagrass, rock, or sponge. The seagrass community is treated in detail in Zieman (1982).

Stony coral species are commonly found in the seagrass and sedimentary environments adjacent to the reef communities. These are *Manicina areolata, Porites porites, Cladocora arbuscula,* and *Siderastrea radians,* hardy tolerant species that do not attain great size.

3.3 PATCH REEF COMMUNITY

Patch reefs (Plates 11a, 11b, and 12a) are the second major type of coral community, and they are a most conspicuous element in this region. Their distribution is mostly seaward of Key Largo and Elliott Key; however, they also occur off Big Pine Key, Key West, and Dry Tortugas. They are usually found seaward of Hawk Channel, but a few very nearshore patch reefs exist. Two examples of nearshore patch reefs are (1) an assemblage of patch reefs just to the north of Caesar's Creek (BNP) and (2) a small reef just off Cow Key Channel, Boca Chica Key. Both of these reefs present the general impression of survival under marginal conditions.

A patch reef characteristically has upward of 3 m of relief and is dome-shaped. The surrounding bottom may be sedimentary, seagrass (Plate 12b), or rock. Most patch reefs off southeast Florida are found in 2- to 9-m depths; their upper surface may be nearly emergent at low tide, exemplified by Basin Hill Shoals off Key Largo. Patch reefs are roughly circular in outline and vary in size from about 30-700 m in diameter. Because of different ages of the numerous patch reefs and their local environmental conditions, generalizations fail to adequately characterize them. Jones (1963, 1977) presented information about their physical and chemical environment near Margot Fish Shoal off Elliott Key and the dynamics of developmental stages. Smith and Tyler (1975) and Jones (1977) presented the view that the patch reef community is similar to a super organism, in that it goes through several life stages. The nature of the community reflects the reef's age. While the coral community goes through its cycle of development, the fish assemblages change according to niche availability. An assumed developmental sketch of a patch reef would include the following:

[1] Darwin (1842), based on his experiences in the Pacific and Indian Oceans, defined three types of coral reefs: fringing, barrier, and atoll. Although many attempts have been made to extrapolate these forms to Atlantic coral reefs, Darwinian-defined reefs do not presently occur in Florida.

indeed rarely to be found below two thousand fathoms. The thicker-shelled foraminifera reach a greater depth, not because they are of different chemical composition, but because their greater amount of substance yields less easily to the solvent action of the acid or sea-water. At shallower depths the solvent action of carbonic acid must be far less efficient, since there is a rapid accumulation of dead siliceous and calcareous shells of foraminifera, sponges, hydroids, corals, halcyonoids, mollusks, polyzoa, echinoderms, etc., which must have lived upon the bank long before they had by their accumulation brought it to a level at which coral reefs could begin to grow.

The bathymetrical sections (Figs. 40, 41) of the peninsula of Florida to the eastward into the trough of the Gulf Stream are very different from those taken on the western side of the peninsula. Proceeding northward from Cape Florida, we pass out of the action of the current from the Straits of Bemini, where the velocity of the Gulf Stream is the greatest. As soon as we reach a latitude at which the trade winds do not blow, we come gradually upon the usual comparatively gentle slope off shore, which shows little trace of disturbance either from currents or from the action of the prevailing winds. Judging from what I have seen of the east coast of the peninsula of Florida, the shore line deposits, such as the coquina of St. Augustine and the shelly beaches of Indian River, indicate the presence in deep water of a limestone deposit formed of the detritus of mollusks, annelids, starfishes, and sea-urchins. There are a few corals only, and occasional patches of reef-builders, but no extensive reefs; but this is a difficult point to decide even at Key West. Indeed, all along the line of the reefs it would be hard to determine to-day whether the reefs have been formed, like the Marquesas Keys, merely by the accumulation of detrital matter driven to the westward and northward, or whether the Mangrove Keys and the reefs really indicate the old lines of a reef similar to the one now in full activity on the northern edge of the Gulf Stream, parallel to the main line of keys. The absence of the more delicate shells from limestone, in the formation of which they must nevertheless have shared, may be explained by the solvent action of carbonic acid upon them, and by the deposition

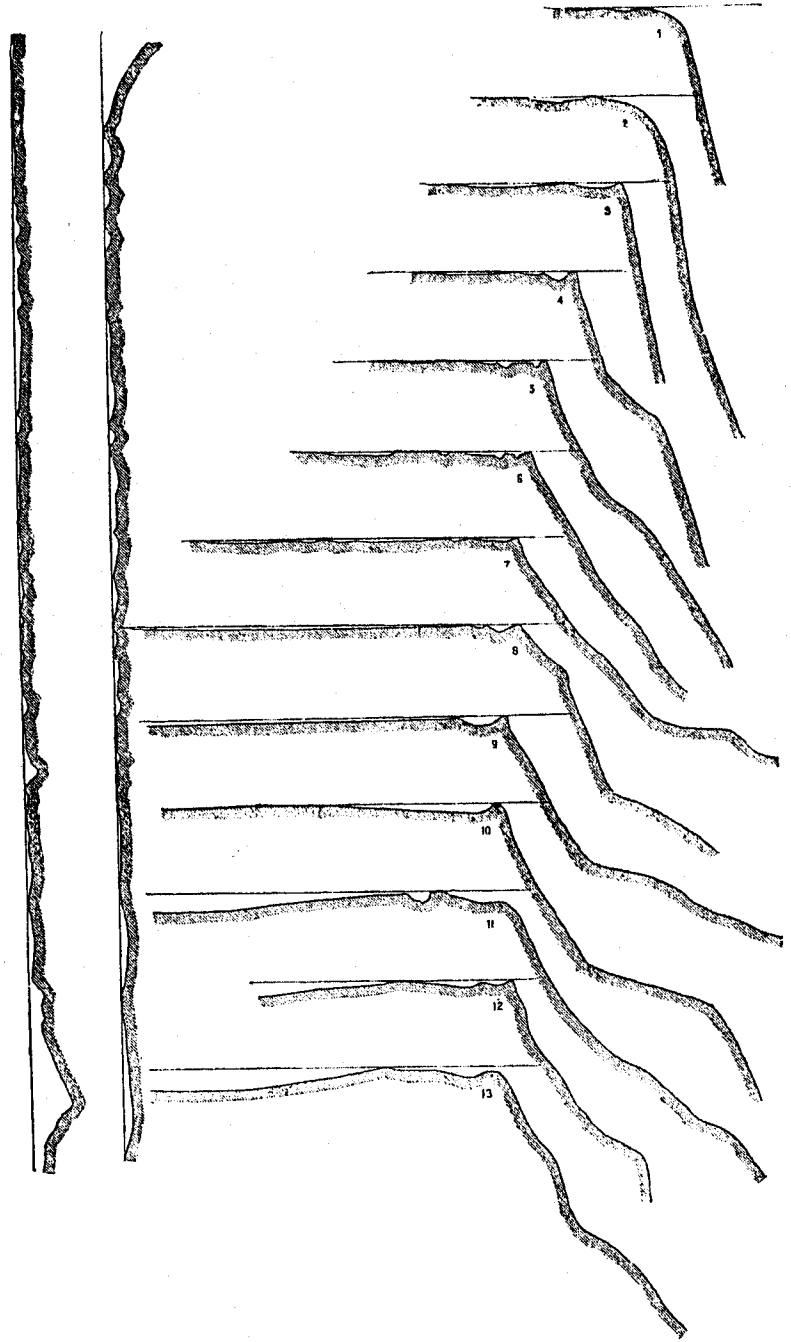


FIG. 41. — SECTIONS ACROSS THE FLORIDA REEF. SEE FIG. 34.

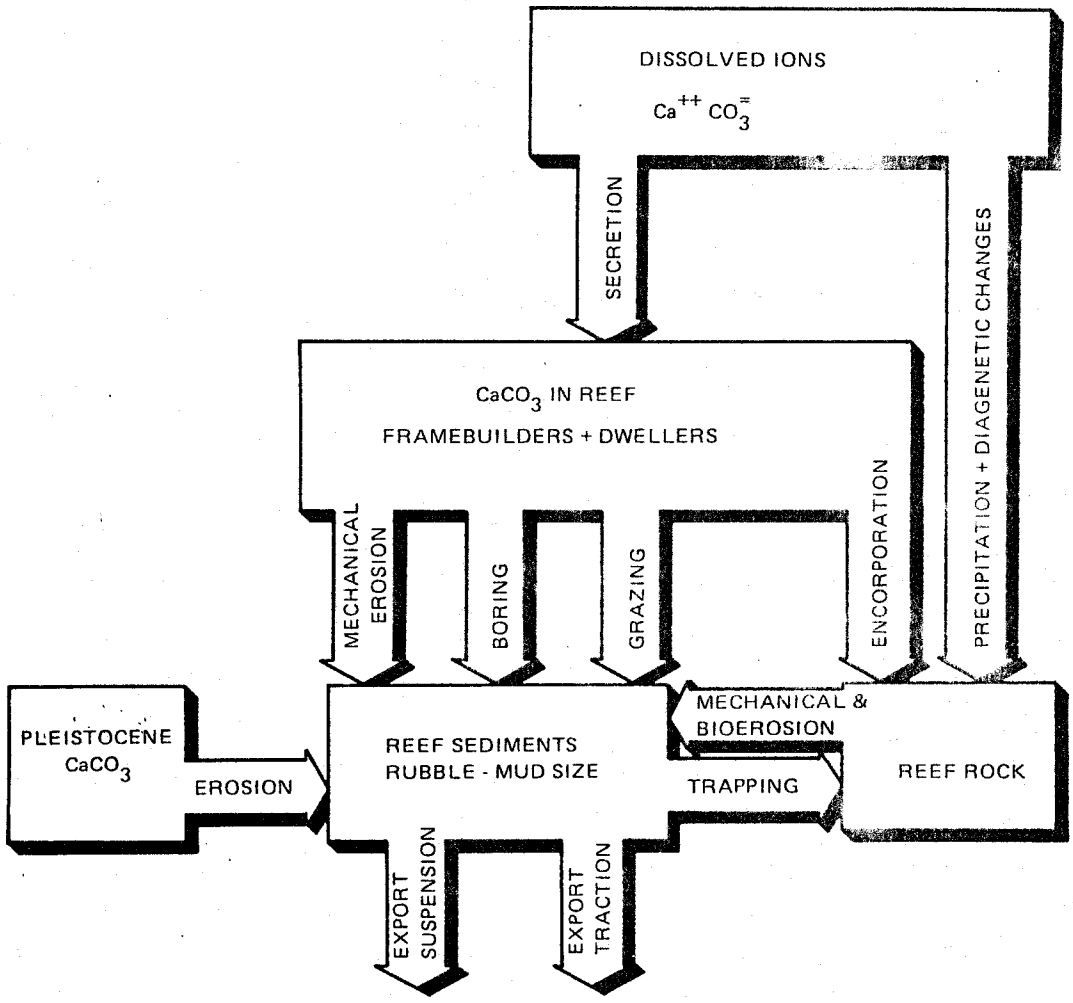


Figure 15. Calcium carbonate flow model based on a Barbados fringing reef (Stearn et al. 1977).

near Key West (Kissling 1977). *Montastraea annularis* has demonstrated annual $CaCO_3$ production of 20 kg $CaCO_3/m^2$/year in Barbados (Stearn et al. 1977).

Ghiold and Enos (1982) extrapolated production values to vertical reef accretion rates of 2.2 m/1,000 years, which is within the magnitude of Holocene reef growth in Florida (Shinn et al. 1977).

Frost et al. (1977) and Taylor (1977) contain many papers about coral reef geology.

of carbonate of lime as a cement. A comparison of the structure of Loggerhead Key at the Tortugas with that of the Mangrove Islands and the main keys shows us the difficulty of deciding these points. At Loggerhead Key we have a shore line made up of brecciated and oölitic coral limestone, fully as characteristic as any similar shore line on the older keys like Key West (Fig. 42.) Yet we still find on the southern, eastern, and northern sides of Loggerhead an active growth of reef-building coral, while other parts of the island and some of the flats, if covered by mangroves, cannot be distinguished by their structure from the genuine mangrove islands on the flats to the north of the inner line of keys along the main reef. (Fig. 43.)

We must be careful to distinguish the line of islands running from the mouth of the St. John's to Cape Florida, and parallel with the coast of Florida, from the line of islands forming the Florida Keys. The latter seem at first glance to be the continuation of the former; but this is not the case, their mode of formation, as well as their geological structure, being radically different. As was long since pointed out by H. D. Rogers, the line of narrow islands to the eastward of Florida belongs to the series of coast islands lying parallel to the coast from Long Island to Florida, and extending around the whole Gulf of Mexico. They all seem to have been formed by the same cause; the action of currents along the continental shores has formed lines of deposit of but little width, and separated from the mainland by a shallow channel. Some of these islands have been slightly elevated at a comparatively recent period. This is especially the case with the islands along the east coast of Florida, Anastasia Island, and those running south to Cape Florida, separating Indian River from the Atlantic Ocean. In all these we find the so-called coquina of St. Augustine raised from ten to twenty feet above the level of the sea at such points as Anastasia, Merritt's, and Worth Islands, showing all along the east shore of Florida a very recent formation of shell *débris* or breccia, very similar to the formation now going on in the lagoons near Venice. This bed of shell breccia was probably deposited after the low backbone of the peninsula, extending perhaps from

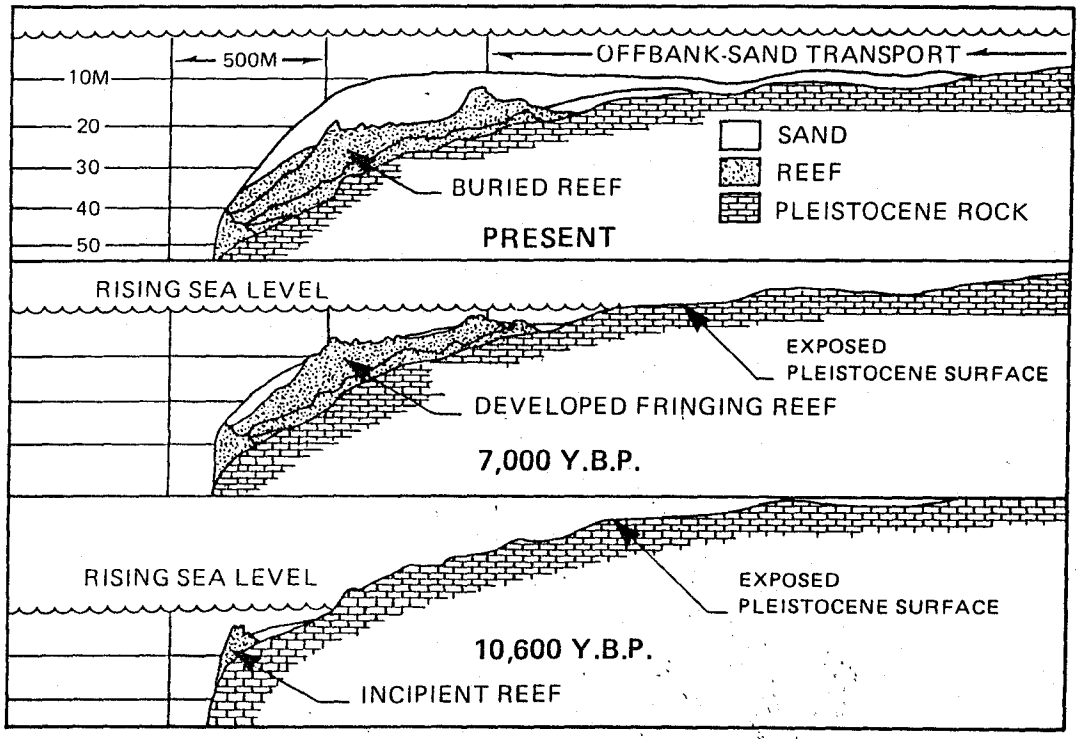


Figure 14. Sea-level change in a Bahamian shelf reef system during the last 10,600 years (Hine and Neuman 1977).

Table 10

Age and growth rate of Recent Florida reefs (Shinn et al. 1977; Shinn 1980).

Reef	Base age (YBP) (with confidence limits)	Accretion (m)	Growth rate (m/1,000 yr)
Long Key	5,630±120	5.0	0.65
Carysfort	5,250±85	7.3	0.86-4.85
Grecian Rocks	5,950±100	9.5	6-8
Bahia Honda	7,160±85	4.6-8.2	1.14
Looe Key	6,580±90	7.3	1.12
Bird Key	6,017±90	13.7	1.36-4.85

(Ginsburg 1956). *Halimeda* and other codiacean algal plates are the most common algal skeletal material. The sedimentary material becomes incorporated into the reef framework through the process of being bound to the platform by crustose coralline algae and through the geochemical processes of *in situ* cementation by high magnesium calcite cements. Ginsburg and Schroeder (1973), among others, detailed the processes of marine cements in coral reefs.

Stearn et al. (1977) presented the most recent quantitative budget of calcium carbonate ($CaCO_3$) within a coral reef ecosystem (Figure 15). This was based on the study of a Barbados fringing reef. While the magnitude of individual components may differ, the concepts are valid and applicable to Florida reefs. Stearn et al. concluded that crustose coralline algae and stony corals (nine species) annually fixed 163 metric tons of $CaCO_3$ on a reef platform with a surface area of 10,800 m^2 (9 kg $CaCO_3/m^2$/year). For comparison, nonreef depositional marine environments in southeastern Florida are reported to produce 0.25-1 kg $CaCO_3/m^2$/year (Stockman et al. 1967; Moore 1972).

Ghiold and Enos (1982) studied $CaCO_3$ production in the brain coral *Diploria labyrinthiformis* from several patch reefs in John Pennekamp Coral Reef State Park (JPCRSP)-Key Largo National Marine Sanctuary (KLNMS). Production ($CaCO_3$) was 11.8±0.3 kg $CaCO_3/m^2$/year of area occupied by the colony. *Porites astreoides* annual $CaCO_3$ production ranged from 13.6±3.5 to 14.0±3.1 kg/m^2/year at Middle Sambo Reef

southern Georgia and Alabama to the northern part of Lake Okeechobee and the Everglades, had been raised, and when the peninsula of Florida from the St. John's to the eastward was below the level of the sea at a shallow depth. At any rate, it seems plain from recent evidence that no trace of reef-building corals exists on the east coast north of Cape Florida. Mr. Dietz is inclined to look upon the formation of these islands as due to the action of the waves. But there seems to be nowhere, as is well stated by Rogers, any deposit of the kind going on now; and when such masses of shells are thrown up on beaches, the tendency is strong to consolidate from fragments to the concrete form known as coquina.[1] The mode of formation does not, however, seem adequately accounted for by the action of currents moving along the coasts. These currents must have flowed over a wide plateau, and have supplied the large amount of food needed for the development of a thriving bank of mollusks and other invertebrates. As soon as these growing colonies had risen high enough to form banks parallel to the shores, they were in their turn cut off and isolated from the shore by the action of the tides and currents, which must then have begun to deepen the channels intervening between the bars and the mainland. They must also have forced their way across the banks to form the shifting inlets, such as Mosquito Inlet, etc., so characteristic of the channels leading into the inland waters along our whole Southern Atlantic coast. The dip of the coquina bed to the westward is well shown by the borings of artesian wells at Palatka. I was informed by the contractor that he met the coquina beds at a depth of about forty feet, when he reached a mass of clay, which in its turn was underlaid by pebbles resembling the small pebbles found on flats off a rocky shore. Possibly this mass of clay was formed by the silt of the Gulf Stream at a time when it flowed over the low ridge of central Florida, before that ridge had risen to form a dividing line between the two plateaux, one of which must have extended to the westward much as at present, while the other undoubtedly extended in some localities north of Cape Cañaveral somewhat to the eastward of the present shore line of Florida.

[1] Fourth Report British Association, for 1834–1838, p. 11.

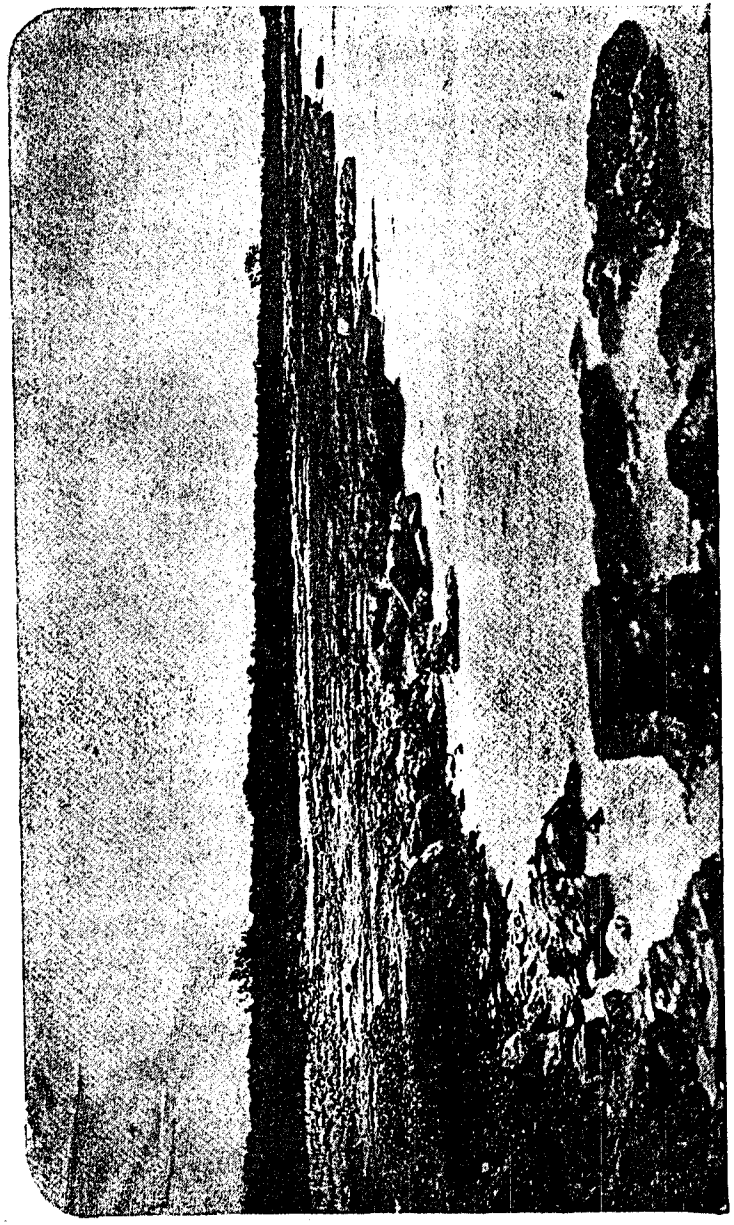


FIG. 42.—CORAL ROCK BEACH, NORTH OF FORT TAYLOR, EXPOSED TO ACTION OF WAVES OF CHANNEL BETWEEN OUTER REEF AND KEY WEST.

cated, the formation was found to rest atop calcareous-quartz sands. From near Miami to Big Pine Key the Key Largo formation is found near the surface, but from Big Pine Key to Key West it is overlain by the Miami Oolite formation, which may be upwards of 12 m thick (Hoffmeister and Multer 1968). Hoffmeister and Multer (1968) and Hoffmeister (1974) reported that the exposed portion of the Key Largo formation in the Florida Keys is representative of a low-wave-energy patch-reef community. The main evidence for this is that certain scleractinian corals, in particular *Acropora palmata* (elkhorn coral), are absent in the fossil record. Presumably a series of events occurred such that the seaward part of the Key Largo formation did, at one time, possess high wave-energy communities similar to today's reefs; however, as sea level rose during the Holocene transgression, these fossil communities were apparently eroded away by wave action. Hoffmeister (1974) reported that a core made near Looe Key Reef recovered fragments of *A. palmata* from 18 m below the surface.

The Holocene transgression of sea level (Figures 13 and 14) indicates that 10,000 years ago the sea level was about 30 m lower than today (Lighty et al. 1982). Shinn et al. (1977) cored several recent reefs from Miami Beach to Dry Tortugas and dated initial growth from 5,250 to 7,160 YBP. Reef growth or accretion rates ranged from 0.65 to 4.85 m/1,000 years (Table 10; Shinn et al. 1977). For comparison, Adey (1977) reported reef growth off St. Croix, U. S. Virgin Islands, was 15 m/1,000 years (this is the upper limit for Caribbean reef growth). Shinn et al. (1977) reported that the base of recent reefs was Pleistocene Key Largo Reef, fossil mangrove peat, and cross-bedded quartz fossil sand dunes.

More recently, an extensive barrier reef existed off the Ft. Lauderdale area, but it was extirpated about 7,000 YBP (Lighty 1977; Lighty et al. 1978). This reef was a shallow-water *Acropora palmata* community. The demise of this reef was attributed to environmental change caused by increasing sea level (Lighty et al. 1978). Recent coral reef growth off the Florida Keys started from 5,000 to 7,000 years ago.

Development of a coral reef integrates biological, geological, chemical, and physical processes. Soon after the first coral colonies settle and start to grow, the breakdown of organism skeletons by biological and physical agents occurs. Sediments created by these activities become a part of the reef.

Finer sediments filter into voids and borings, and the coarser fractions fill the interstitial space between the reef framework. Reef tract sediments are carbonate and are dominated by algal and coral skeletal material

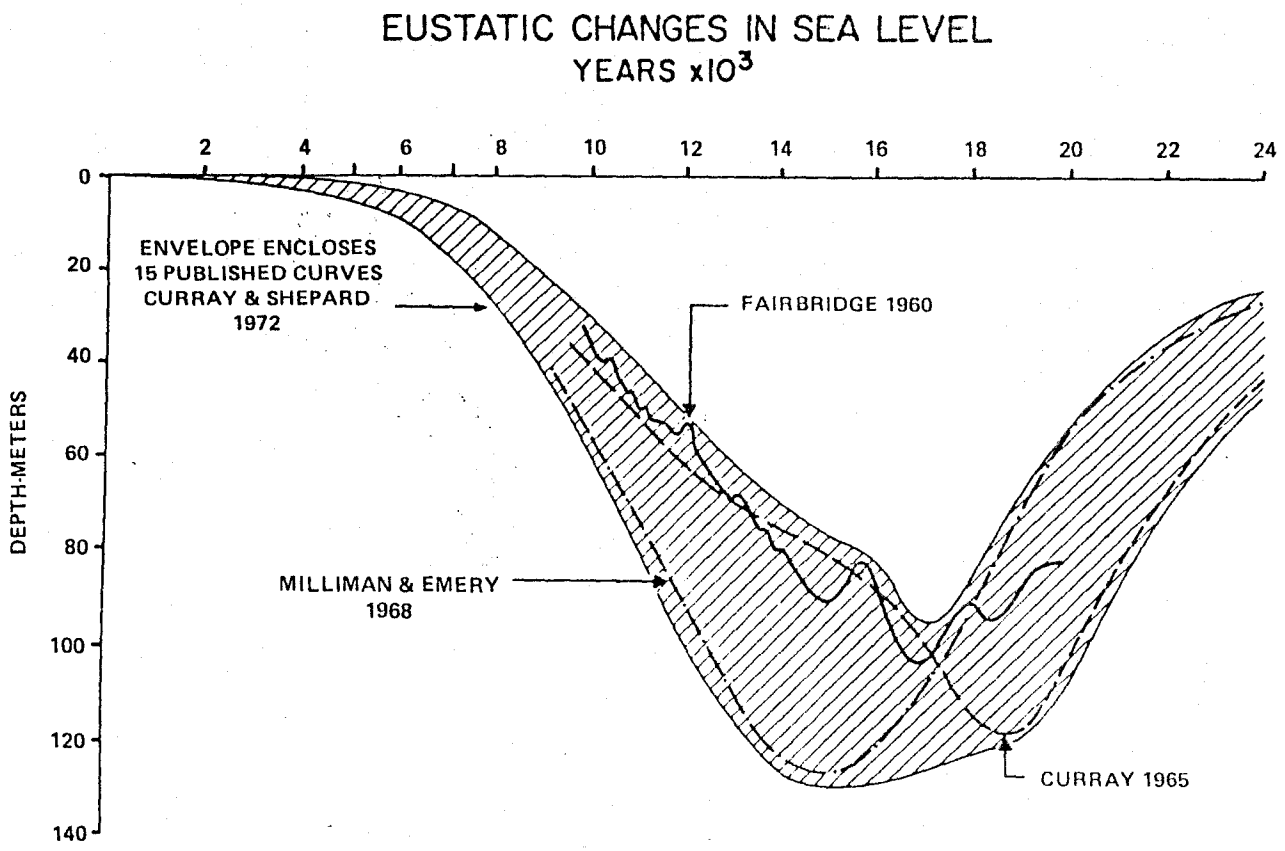


Figure 13. Sea-level change during the Holocene Period (Ginsberg, Comparative Sedimentology Laboratory, University of Miami, Florida).

All this evidence tends to show that the coral reefs had little, if anything, to do with the building up of the peninsula of Florida north of Cape Florida. The existing line of reef is indeed probably the only one which has played any important part in the formation of land south of the line of the present southern extremity of the peninsula of Florida. There seems, however, some reason to believe that a line of reefs, or perhaps two lines not very distant from each other, once stretched along the southeastern end of the Everglades before the present reef began to extend westward. Judging from the sections shown by the maps, the growth of the present reef, as fast as the mud flats were formed to the south of it, has been altogether in that direction. (Figs. 40, 41.)

The Bahamas, the San Pedro, and Yucatan banks have probably all been formed by a similar process, — by the accumulation of limestone either upon an early fold of the earth's crust, or upon a volcanic plateau, or upon a foundation of slower growth from great depths. In Yucatan we can actually descend into the bank itself through any one of the aguadas, or caverns, found everywhere in the northern part of that country. Many of these caverns extend to a considerable depth; one of them, that of Bolonchen, has a depth of seventy fathoms, the whole formation consisting of recent limestone entirely composed of species of invertebrates now living on the Yucatan Bank. In Yucatan, as in Florida, we find a low ridge of limestone, somewhat older than that of the coast, extending across the peninsula. The uplifting of this ridge has caused the slight undulations of the surface traceable throughout Yucatan, at a distance of from twenty to thirty miles from the coast, and running nearly at right angles to it. Judging from its fossils and lithological characters, the limestone of which this ridge is formed is identical with the so-called Vicksburg limestone of the central backbone of Florida. The fauna of the Yucatan Bank is identical with that of the Florida Bank, being characterized by the same species of echinoderms, mollusks, crustaceans, corals, and fishes, so well known already from shallow water on the Florida side.

While on the Yucatan Bank I had the opportunity of exam-

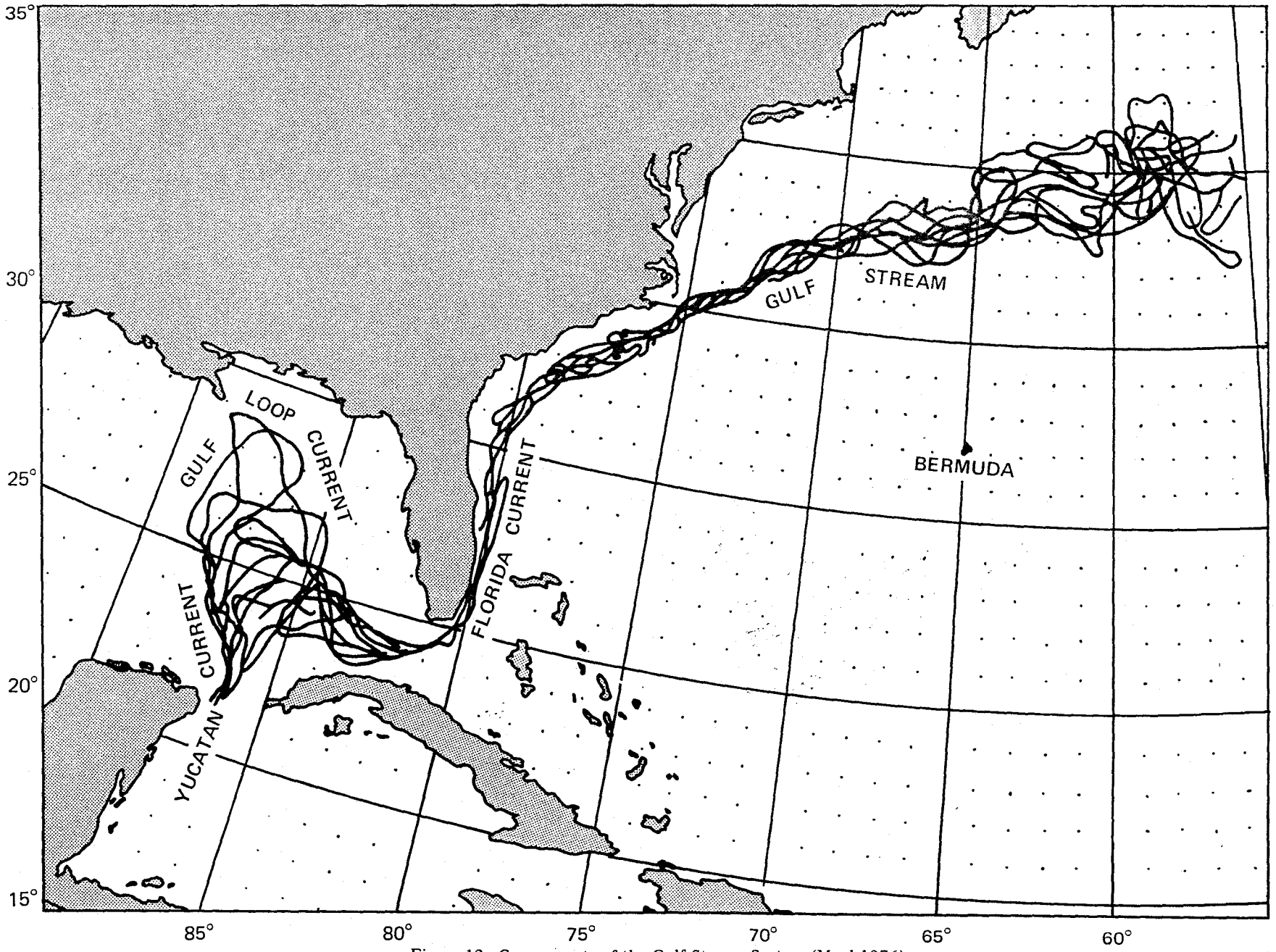


Figure 12. Components of the Gulf Stream System (Maul 1976).

ining the great Alacran Reef,[1] an excellent plan (Fig. 44) of which is given on one of the British Hydrographic maps of the Gulf of Mexico, from the surveys of Commander Barrett, R. N. It is one of the circular reefs resembling atolls, and I was the more desirous to get an idea of its mode of formation because, according to Darwin's theory of coral reefs, such atolls should not occur in areas of elevation like those in which the Florida reefs, the coast reefs of Cuba, the Bahamas, and the Central American reefs are found.

The examination of Alacran Reef showed it to be in full activity. The greatest length of the reef is about fourteen miles; its width, eight miles. It consists of a steep semicircular wall rising abruptly on the eastern side, which is also that of the prevailing winds, from a depth of thirty fathoms to ten fathoms, where the corals begin to grow, and the slope becomes much more gradual. The eastern edge of the reef presents a singularly regular section, where the huge masses of heads of *Madrepora palmata* form a nearly compact level wall, with its top flush with the level of the sea. This wall is constantly beaten by the sea, and the breakers, pounding upon the coral heads exposed to their action, detach large pieces or break off the dead masses, which are again triturated into smaller fragments until they form a fine sand swept by the wind in a westerly direction; this sand little by little fills up the channels left between the masses of coral which form the outer wall and extend towards the centre of the reef. The detritus from the outer reef diminishes gradually in quantity, and leaves a channel varying from three to nine fathoms in depth on the eastern edge of the low islands to which the reef dwindles at its western extremity. This channel describes deep indentations in the western edge of that section of the plateau which extends from the eastern edge of the reef. On the eastern edge of the islands the reef is completely choked with sand, while on the gentle western sea-slope of their outer side the corals are thriving, but creep out very gradually seaward instead of building a steep, abrupt wall like that of the outer edge of the reef.

It is probable that, in the case of an atoll of this sort formed

[1] Letter No. 1, Bull. M. C. Z., V. No. 1, April, 1878.



FIG. 43.—LAGOON FORMED BY PROMONTORIES AND LOW ISLANDS COVERED WITH MANGROVES, NORTHEAST SHORE OF KEY WEST ISLAND.

Table 9

Salinities in the Florida reef tract and vicinity.

Location	Dates	Salinity range (ppt)	Source
Dry Tortugas	1913	35.2 - 36.1	Dole 1914
Fowey Rocks	1914-1916	34.2 - 38.6	Dole and Chambers 1918
Soldier Key	1945-1946	33.1 - 37.1	Smith et al. 1950
Key West area	1953-1954	33.3 - 37.0	Chew 1954
Margot Fish Shoal	1961-1963	36.8 - 37.3	Jones 1963

from 0.5 to 3.7 mg/l at a nearshore patch reef. Suspension concentration within the dredge plume ranged from 18 to 212 mg/l. These levels are probably comparable to the upper limits on the reef tract following a hurricane or major storm.

2.9 CURRENTS

A warm water current (the Florida Current) flows through the Straits of Florida. Wust (1924) calculated that 26 m^3/sec pass through the constricted area between Florida and Cuba. The current's velocity is in the magnitude of 150 cm/sec. It is composed of two water masses in its surface layers. The eastern core is composed of Caribbean water that flows into the Gulf of Mexico through the Straits of Yucatan; the western or nearshore portion of the current is composed of water that flows from the Gulf of Mexico (Wennekens 1959). The Florida Current comes closest to Florida off Palm Beach, where the central axis is about 15 km off the coast. Off Dry Tortugas the current is 124 km south of the islands. The current is very dynamic and meanders a good deal. Generation of eddies off the main body of the current brings current waters onto the shelf and to the reef environments. As noted earlier, the current moderates winter temperature and brings plankton of Caribbean origin into the reefs. Maul (1976) presented the variability of various components of the Gulf Stream system (Figure 12). Schomer and Drew (1982) recently reviewed the physical and chemical environment of southern Florida.

2.10 GEOLOGICAL SETTING

The following information is paraphrased from a field guide to south Florida sediments (Ginsburg 1972a). The Florida-Bahamas region is a carbonate platform part of the Atlantic and Gulf coastal province. The platform is dissected by deep-water channels. The most important consideration here is the Straits of Florida, which is nearly 550 m deep. Marine portions of this platform are generally shallow, less than 16 m deep in most places. Deep test drilling in the area indicates the platform has had a history of continuous subsidence and deposition of shallow-water carbonates and evaporites. Maximum depths of drill penetration (5,486 m at Cay Sal Bank) imply that no near-surface formations older than upper Miocene are extant. The Florida pennisula south of Lake Okeechobee has been a carbonate depositional region during portions of the Mesozoic and throughout the Cenozoic. Recent carbonate sediments are grossly similar to older material. Two major strata dominate the southern Florida coastal areas from Miami southward along the keys. The Key Largo formation is a reef facies formed during the Pleistocene and will be discussed in more detail later. The Miami formation is also a Pleistocene stratum that is composed of oolite and bryozoan skeletons.

2.11 GEOLOGIC HISTORY AND PROCESSES

During the past 20 million years, major change has occurred in western Atlantic coral reefs. Previously, a cosmopolitan reef biota was found throughout the tropics. Twenty million YBP, a land barrier emerged terminating water movement between the Indian Ocean and the Mediterranean Sea. Approximately 7 million YBP, the Central American Isthmus developed, separating the Caribbean Sea and Atlantic Ocean from the Pacific Ocean. What was previously a circum-equatorial tropical zone had thus been isolated into separate biogeographic provinces. During the late Oligocene and early Miocene, 20-30 million YBP, the western Atlantic area experienced its greatest proliferation of reef building. During the Pleistocene (at least 1 million YBP), major environmental change extirpated the Pan Atlantic-Pacific biota. Glacial periods occurred during this time; during each period, sea level was drastically reduced and the marine climate was cooler. Pacific genera of Scleractinia that were eliminated from the western Atlantic include *Stylophora, Pocillopora, Goniastrea, Goniopora, Pavona,* and *Seriatopora* (Newell 1971).

In Florida, a major coral reef community developed during the last major interglacial period, Sangamon, 100,000-112,000 YBP; it was killed during the last glacial advance (Wisconsin) because of the reduction in sea level and the cooler climate. This Pleistocene reef, known as the Key Largo formation, extends from Miami Beach to at least Dry Tortugas and seaward to the Straits of Florida. It varies in thickness from 23 to 61 m or more; the basement has not been reached in several cores. Wherever its base has been lo-

on a flat plateau, the low islands now constituting the western edge of the reef were at one time exposed to the full action of the sea. As their sea-slope became little by little surrounded by the wall now encircling the outer edge of the reef, the growth of the corals was checked, the interstices and spaces between the coral masses were gradually choked by sand and coral fragments, until the low islands now known as Perez, Chica Pajaros, and the great sand-bars of the western edge of the reef were slowly built up a few feet above the level of the sea, — mere strips of sand gradually cemented together by the accumulation of the loose materials held in suspension by the water.

The outer eastern edge of the reef or wall is from one to two hundred yards in width, and inside of this extends for a maximum distance of seven to eight miles an extensive section which is more or less filled with masses of astreans, of mæandrinas, of gorgonians, and madrepores in more or less irregular patches, with a general westerly trend. They reach nearly to the water's edge, where it is quiet, and are separated by deep gullies of clear water varying from one to seven fathoms in depth. Through these gullies a regular current sets to the westward, and has deposited on its path the coral sand held in suspension, thus keeping these gullies clear of coral and gorgonian growth. These heads are gradually but steadily approaching the western strip of islands, and will in time completely fill the whole space in the interior of the reef, or will leave only a narrow channel of various depth between the outer broad bank to the east and the narrow islands to the west.

The whole structure of this reef shows its identity of formation with that of the main Florida Reef, and with that of the reefs on the northern coast of Cuba, where the line of distinct and powerful elevation can still be plainly traced by old coral slopes and by the ancient coral reefs in the hills surrounding Havana and extending to Matanzas. These hills attain a height of over 1,200 feet, and are entirely composed of species of corals identical with those now found on the living reefs. Alacran Reef thus gives us an easy explanation of atolls, apparently formed in areas of elevation; I look upon the structure of this

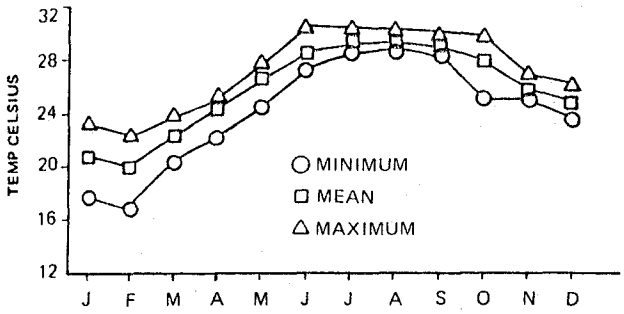


Figure 11. Monthly minimum, mean, and maximum seawater temperature (3m) at Elkhorn Control Reef, Biscayne National Park, 1978 (from thermograph data, Biscayne National Park).

air masses (Roberts et al. 1982). Offshore (into the Atlantic) transport is the effect of tidal pumping, northerly winds, and density gradients. Communities adjacent to tidal channels suffer the greatest impact from this thermal stress. Conversely, during the summer, the Florida Bay water may become hyperthermal ($> 31^{\circ}$ C) because of solar heating, and communities near tidal passes are more affected.

Seawater temperature reflects the annual climatic cycle: seawater temperatures are lowest from December through March. Temperature peaks in August or early September and cools throughout the fall and winter. A comparison of seawater temperature with air temperature (Tables 2, 6, and 7) for Miami with the recent Biscayne National Park data shows that mean seawater temperature is warmer than mean air temperature throughout the year.

2.5 TIDES

The Atlantic coast from Miami to Key West exhibits a semidiurnal tidal pattern. The area close to Key West is influenced by the Gulf of Mexico, which experiences semidaily or daily tides. Table 8 presents mean and spring tide ranges for several reefs. The major effect of tides on reef communities is the reduction of water depth during spring low tides when shallow reef flats may be near emergent. During the summer, if wind speed is low, heating of the water column may cause hyperthermic conditions such that zooxanthellae (symbiotic algae within the coral tissue) may be expelled (Jaap 1979; Hudson, in press). During the winter the reef flat water may be hypothermic, again causing thermal stress (Hudson et al. 1976; Hudson, in press).

A trend of decreasing mean levels and ranges is noted as one approaches the Gulf of Mexico. Tidal currents for the reef area are not presented in the Tide Current Tables prepared by the National Oceanic and Atmospheric Administration. There are significant tidal currents between Florida Bay and the Atlantic.

Table 8

Tidal ranges for several southeast Florida reefs (NOAA 1981).

Location	Mean tide level (m)	Mean tide (m)	Spring range (m)
Fowey Rocks	0.4	0.7	0.7
Molasses Reef	0.3	0.7	0.8
Alligator Reef	0.4	0.6	0.7
Sand Key Reef	0.2	0.4	0.5
Garden Key, Dry Tortugas	0.2	0.3	Not given

2.6 SALINITY

The reef tract area experiences oceanic salinities as summarized in Table 9. The region adjacent to Biscayne Bay is an area where heavy rainfall can reduce salinities for short periods. Dole and Chambers (1918) reported that heavy precipitation in Miami almost always was followed by temporary reduction in chlorinity and salinity at Fowey Rocks 24 hr later. Flat low land, porous soils, and distance offshore minimize the effect of rainfall on salinity in the reef tract areas. Rarely, entrained Mississippi River spring runoff is carried along the inshore side of the Florida Current. This water mass has salinities of 32-34 ppt, which is within the tolerance limits of reef corals.

Diurnal salinity fluctuations at Margot Fish Shoal ranged from 37.8 to 37.3 ppt because of evaporation and precipitation (Jones 1963).

During hot summer periods, density sinking on shallow reef areas is common. Evaporation creates dense hypersaline surface layers which sink and mix poorly with subsurface cooler waters. Swimmers can feel and see this phenomenon.

2.7 DISSOLVED OXYGEN

Jones (1963) and Jaap and Wheaton (1975) provide limited information on dissolved oxygen. The water column ranges diurnally from 90% to 125% oxygen saturation. Daily maximum values are attained between 1400 and 1600 hr (Jones 1963).

2.8 TURBIDITY

Transparency (equivalent Secchi disc depth) for several stations off the Florida Keys was reported by Williams et al. (1960). They reported that the equivalent Secchi distances ranged from 4.5 to 35 m in this area. Variability of water clarity is considerable. Following storms the water may be nearly opaque. Plankton and suspended matter also affect water clarity.

Water clarity and sedimentation rates for a dredge operation near Basin Hills, Key Largo, were reported by Griffin (1974). Ambient or background suspension concentration in the water column ranged

interesting reef as a sort of epitome of the mode of formation of the great Florida Reef and of the Bahamas Bank. Taken in connection with its position on the Yucatan Bank, it will perhaps explain the mode of formation of the greater part of the Florida peninsula as connected with the bank lying to the westward of the mainland and to the northward of the Florida reefs.

The specimens thus far obtained from the rock composing the Yucatan plateau consist of the same limestone as those of the great Florida Bank; and there are forming upon it, though to a much more limited extent, patches of reefs near the thirty and twenty fathom curve, such as the Shoals, the Triangles, Cay Arenas, the Arcas, the Madagascar, English, Alacran, and the fringing reefs of the eastern edge of Yucatan, that extend along the Mosquito coast to the central part of Central America.

It is evident from the above that we need not refer the atoll-shaped form of this reef (Fig. 44) to the subsidence of the Yucatan Bank as a whole, since the action of the prevailing winds and currents would account for all the existing phenomena. The decay of the animals living upon the great plateau, added to the deposition of all the animal life brought to it by the currents, would explain a gradually increasing elevation of the surface till the level was reached at which reef-building corals could flourish, and at which a reef would naturally be formed. Darwin has noted the close resemblance between encircling barrier reefs and atolls. It seems to me that the structure of the Marquesas (Fig. 44) and of Alacran proves conclusively that not one point of difference exists between a barrier reef and an atoll. Darwin has also called attention to the fact that in shallow seas, such as the Persian Gulf and parts of the East Indian Archipelago, the reefs lose their fringing character and appear as irregularly scattered patches, often covering a considerable area; and he also observes that many reefs of the West Indies have been formed in like manner upon large and level banks lying a little beneath the surface, — banks which he believes to have been caused by the accumulation of sediment. Such patches of reef-building corals would seem, from their analogy with the Tortugas, to be the beginning of more extensive reefs.

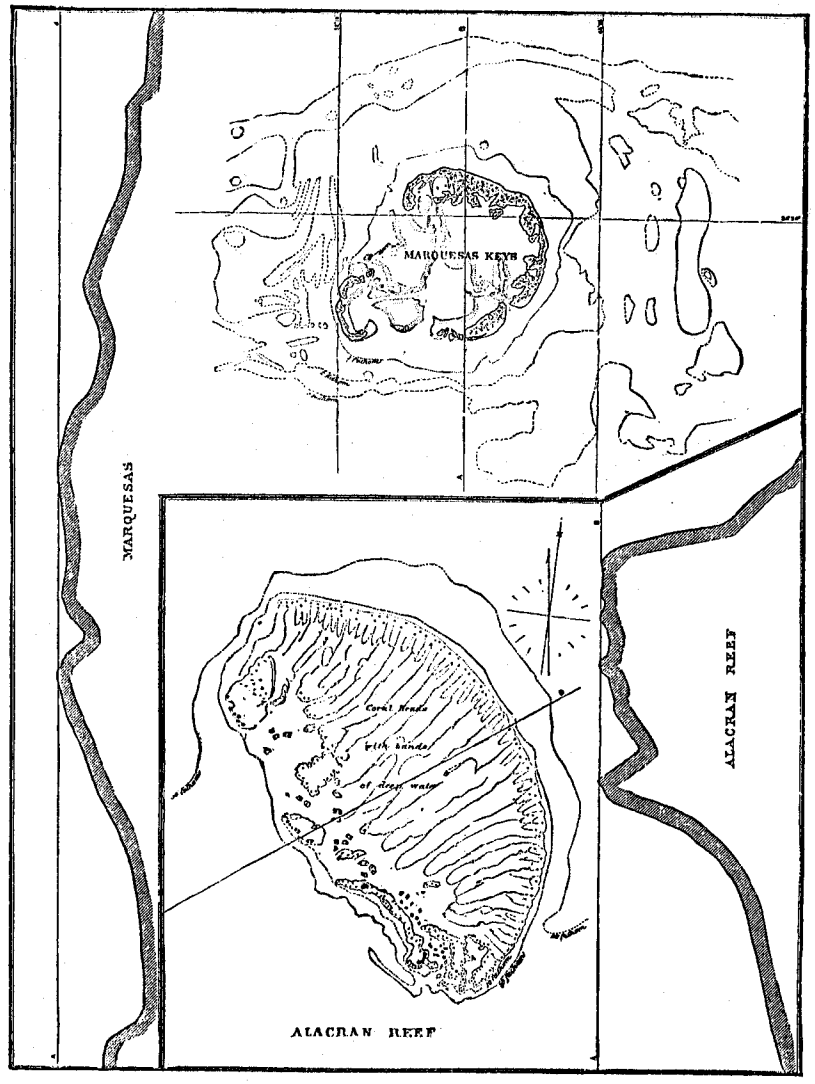


Fig. 44. — SKETCH MAP OF ALACRAN REEF AND OF THE MARQUESAS KEYS.

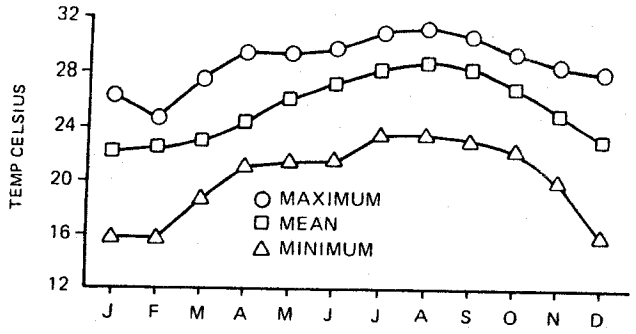


Figure 6. Monthly minimum, mean, and maximum seawater temperature at Fowey Rocks, 1879-1912 (Vaughan 1918).

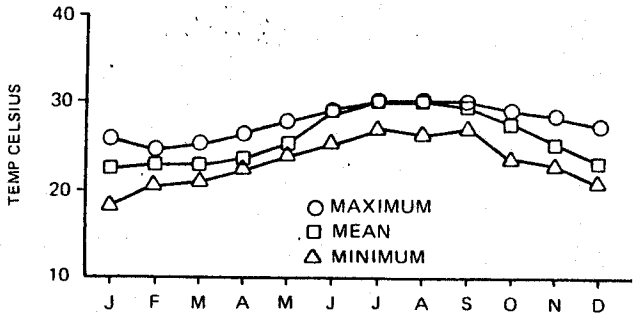


Figure 7. Monthly minimum, mean, and maximum seawater temperature at Carysfort Reef, 1878-1899 (Vaughan 1918).

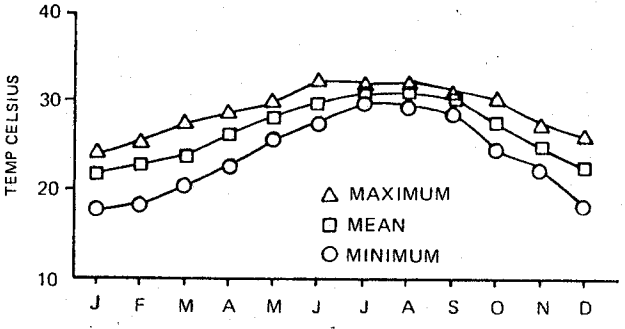


Figure 8. Monthly minimum, mean, and maximum seawater temperature at Sand Key, 1878-1890 (Vaughan 1918).

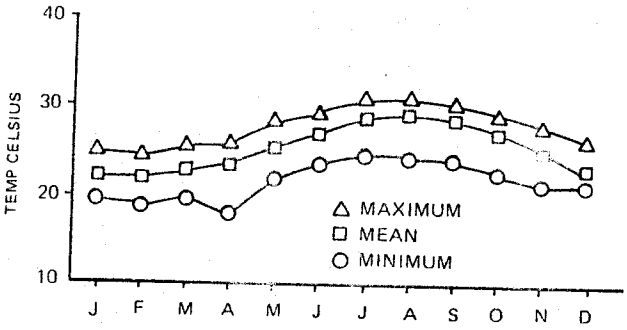


Figure 9. Monthly minimum, mean, and maximum seawater temperature at Dry Tortugas, 1879-1907 (Vaughan 1918).

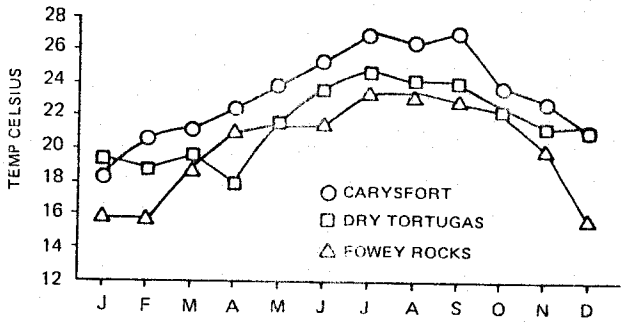


Figure 10. Minimum monthly seawater temperature at Carysfort Reef, Dry Tortugas, and Fowey Rocks.

Table 7

Bottom (3 m) seawater temperature (°C) at Elkhorn Control Reef, Biscayne National Park, 1978 (from daily thermograph data, Biscayne National Park).

Month	Range	Mean	Standard deviation
January	17.5-23.1	20.8	1.3
February	16.7-22.4	20.0	1.4
March	20.4-23.8	22.3	0.9
April	22.3-25.1	24.2	0.7
May	24.5-27.8	26.6	0.7
June	27.2-30.3	28.6	0.8
July	28.5-30.3	29.3	0.4
August	28.7-30.3	29.4	0.4
September	28.4-29.9	29.0	0.4
October	25.2-29.6	28.0	1.3
November	25.1-27.0	25.9	0.4
December	23.8-26.1	24.9	0.8

While on the way from Key West to the Tortugas we stopped at the Marquesas,[1] which are grouped as a circular ring of islands. Their formation has undoubtedly been identical with that of the great Alacran Reef; and from the fact that no corals are now found living on their weather side, these islands must have assumed their present shape at the time when their weather side made a part of the outer reef in connection with the islands of Key West and the other keys, previous to the formation of the present growing reef, or while the latter existed only in the shape of a submerged reef several fathoms below the surface. The plan and section of the Marquesas Keys (Fig. 44) show the formation of the keys on a knoll rising from the general platform of the surrounding reef plateau. This knoll has undoubtedly been built up, as were the Tortugas, from the remains of the corals which once lived upon its face and surface until the formation of the outer reef shut out the prevailing easterly winds, and the corals were killed through the accumulation of silt upon them.

The filling of a lagoon like that of the Marquesas must be a slow process, for we find the water of the inner lagoon deeper than that of any part of the reef immediately surrounding the outer slope. We can imagine that when the outer ring of the reef surrounding the inside lagoon is once completed, or nearly so, the enclosed calm area is so placed as to be subject to but few disturbing agencies, and is practically excluded from receiving any appreciable amount of sediment from the water of the outer reef, since the lagoon connects with the surrounding waters only by the narrow passages which form the channels between the lagoon and the main channel. Whether the removal of the dead coral rock from the interior of the lagoon of an atoll, by the action of the current through the narrow connecting channels, and by the solvent action of the carbonic acid, will sufficiently explain the great depth of the interior lagoon seems somewhat doubtful. The mud of the interior of the Marquesas atoll was found to be calcareous, as is practically all the mud which forms the extensive mud flats to the northward of the keys. This mud is, however, generally covered by a thin dark-

[1] See Bull. M. C. Z., V. No. 6. Letter No. 2, July, 1878.

Table 5

Major hurricanes crossing the coral reefs from 1873 to 1966 (Sugg et al. 1970).

Hurricane name	Date		Wind speed (km/hr)	Tide height (m)
	Day	Year		
	18-30 September	1894	167 (est.)	–
		1896	161 (est.)	–
	27 August	1900	–	–
	11-22 October	1906	–	–
	6-13 October	1909	–	–
	9-23 October	1910	177-201 (est.)	5
	2-15 September	1919	177 (est.)	–
	11-22 September	1926	222	2-4
	22 September-4 October	1929	–	–
	31 August-7 September	1933	201-225	–
	29 August-10 September	1935	322	5-6
	30 October-8 November	1935	121	–
	3-14 October	1941	121-198	–
	12-23 October	1944	193	2-4
	11-20 September	1945	175-315	2-4
	5-14 October	1946	129	5
	9-16 October	1947	–	–
	18-25 September	1948	196	2-6
	3-15 October	1948	161	2
Easy	1-9 September	1950	117	–
King	13-19 October	1950	196-241	2
Donna	29 August-13 September	1960	225-322	4
Cleo	20 August-3 September	1964	177-217	2 (est.)
Betsy	27 August-12 September	1965	266 (gusts)	2-3
Alma	4-14 June	1966	201	–
Inez	21 September-11 October	1966	21-150	2

Table 6

Reef seawater temperatures (°C) (Vaughan 1918).

Month	Reef							
	Tortugas (1879-1907)		Sand Key (1878-1890)		Carysfort (1878-1899)		Fowey Rocks (1879-1912)	
	Range	Mean	Range	Mean	Range	Mean	Range	Mean
January	19.4-24.8	22.1	17.9-24.1	21.8	18.2-25.9	22.5	15.8-26.2	22.2
February	18.7-24.4	22.1	18.3-25.3	22.8	20.6-24.8	23.0	15.6-24.5	22.5
March	19.6-25.4	22.8	20.4-27.3	23.8	21.1-25.6	23.1	18.7-27.4	22.9
April	17.9-25.8	23.6	22.5-28.5	26.1	22.4-26.4	23.9	21.0-29.4	24.4
May	21.9-28.3	25.6	25.8-29.9	28.2	24.0-27.9	25.5	21.4-29.2	26.2
June	23.6-29.3	27.2	27.7-32.2	29.8	25.4-29.4	28.8	21.5-29.6	27.2
July	24.7-31.1	28.8	29.9-31.9	31.1	27.1-30.2	30.0	23.4-30.9	28.3
August	24.2-30.9	29.3	29.2-32.2	30.7	26.5-30.3	30.0	23.5-31.2	28.7
September	24.1-30.5	28.8	28.7-31.2	30.3	27.2-30.1	29.6	22.9-30.7	28.3
October	22.5-29.4	27.3	24.5-30.1	27.6	23.8-29.1	27.6	22.3-29.4	27.0
November	21.4-28.0	25.3	22.3-27.1	25.1	23.0-28.7	25.5	20.0-28.4	25.0
December	21.3-26.4	23.2	18.4-26.0	22.5	21.0-27.3	23.3	15.8-27.9	23.1

colored layer of decomposed vegetable and animal matter. The Marquesas are covered by a thick growth of mangroves.

Judging from my examination of the Tortugas reefs, it would seem that corals do not thrive below a depth of from six to seven fathoms. It is, of course, impossible to determine whether that is their bathymetrical limit, or whether they are killed by the accumulation of ooze in the channels and adjacent slopes. We find them confined, however, to the same shallow depths, along the whole of the main reef to the northward (Agassiz). Captain Moresby also has shown that at a depth of ten fathoms in the Maldive and Chagos archipelagoes the masses of living coral are scattered at greater distances with intervening patches of smooth white sand, and that at a slightly lower depth even these patches merge into a smooth steep slope wholly bare of coral. All the evidence accumulated by Dana, Darwin, Ehrenberg, Quoy, and Gaimard tends to show that the limit of reef-building corals is found at about twenty fathoms. On the Yucatan, as on the Florida Bank, the conditions favorable for coral-reef growth have been produced, not by the uplifting of the continent, but by the gradual rising of the bank itself in consequence of the accumulation of animal *débris* upon it. The requisite level once attained, reef-building corals (Fig. 45) would first establish themselves on such spots as were most favorably situated with reference to currents and prevailing winds, both of which are essential to their healthy growth, and thus the reef would be begun.

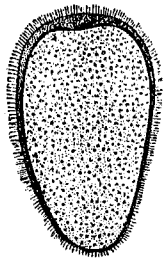


Fig. 45. — Pelagic Porites Embryo, magnified.

How far the growth of corals is affected by such local conditions is perhaps nowhere better seen than in the smaller West Indian Islands. On the eastern side exposed to the prevailing trade winds and washed by the great equatorial currents, the corals flourish, while on the lee side they do not exist at all. The whole eastern coast of Honduras, of Yucatan, and of Venezuela, exposed to the same action and washed beside by the Gulf Stream, is studded with coral reefs. To the action of the Gulf Stream on the south coast of Jamaica and of Cuba we must ascribe the presence of extensive coral reefs, and to the same cause is undoubtedly due the great San Pedro Bank. The

fringing reef which skirts nearly the whole northern coast of Cuba is in a less flourishing condition than the Florida Reef on the opposite shore, which is reached not only by the main current of the Gulf Stream, but also by the prevailing winds. The circular outline of the main reef is readily explained by the action of the Gulf Stream, which sweeping along the steep edge of the southern extremity of the great Florida plateau carries with it a superabundance of animal life, and gives the general direction along which the conditions most favorable to the luxuriant growth of corals exist when once the proper depth has been reached.

For a similar reason, corals are found alive only on the edges of the Great Bahama Bank, where they are subjected to the beneficent action either of currents or of winds, that drive the silt clear of the growing corals, and bring an abundant supply of food. The same causes which have formed the great mud banks to the northward and westward of the Florida Reef have, in the case of the Bahama Banks, formed the immense sand flats and shallows which are fringed by living corals on the east and west. They owe their existence, on the one side, to the wash of the northerly trend of the great equatorial current, and to the action of the trades; on the other, to the clearing action of the Gulf Stream. It must also be remembered that the Bahama plateau was originally joined to Florida, as part of the great fold which built up the framework of that peninsula, and that it was also connected at one time with the island of Cuba. It was also united with the reefs, now elevated to eleven hundred feet, which joined the eastern and western islands in more recent geological times, and formed, before the tertiary, the two extremities of Cuba. On the southern side the reefs are still in full activity, while on parts of the northern coast, in the vicinity of Havana, they have been elevated to a height of no less than one thousand or eleven hundred feet, while the present barrier reef of the north shore of Cuba forms an immense reef, extending with scarcely a break from Cape San Antonio to the eastern edge of the old Bahama Channel.

The Bahama plateau we may also fairly assume to have been built up, little by little, from its original level, by the accumulation of limestone formed in great part from the bodies of the

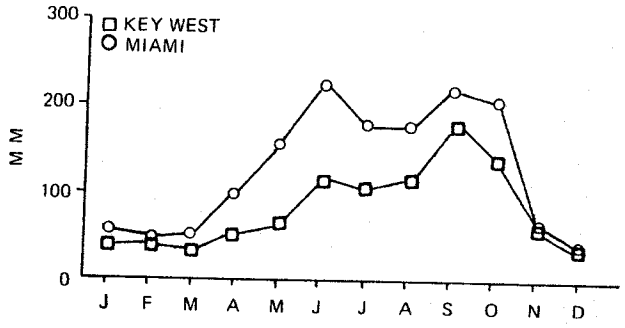


Figure 4. Monthly mean precipitation for Key West and Miami (NOAA 1981). Data base is 29 years for Key West; 38, Miami.

Table 4

Monthly wind speed (km/hr) and direction for Miami and Key West (NOAA 1981).

Month[a]	Miami		Key West	
	Mean speed (km/hr)	Direction	Mean speed (km/hr)	Direction
January	15.3	NNW	19.5	NE
February	16.3	ESE	19.6	SE
March	16.9	SE	20.3	SE
April	17.2	ESE	20.6	ESE
May	15.4	ESE	17.4	ESE
June	13.2	SE	15.6	SE
July	12.7	SE	15.9	ESE
August	12.7	SE	15.4	ESE
September	13.2	ESE	16.3	ESE
October	15.0	ENE	18.2	ENE
November	15.4	N	19.5	ENE
December	14.8	N	19.5	NE
Yearly	14.8	ESE	18.2	ESE

[a]Climate data base for Miami = 38 years; Key West = 29 years.

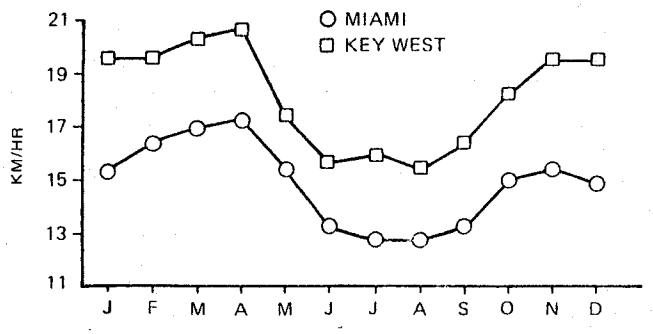


Figure 5. Monthly mean wind velocity for Key West and Miami (NOAA 1981). Data base is 29 years for Key West; 38, Miami.

season exists from 1 June to 30 November. Thirteen major hurricanes have passed across the reef tract and struck the Florida Keys since 1894. Criteria for a major hurricane include one or more of the following: 200-km/hr wind speed; winds reaching out 160 km from the hurricane eye; barometric pressure of 716.28 mm of mercury or less; and/or tide surge of 2.7 m or greater. The Florida Keys has a greater probability of hurricane impact (one in seven) than any other Florida coastal area (Florida Department of Natural Resources 1974). Facts pertaining to hurricane impacts on coral reefs will be detailed in the reef ecology chapter. Table 5 summarizes major hurricanes that have crossed the reef tract since 1873.

2.3 SOLAR RADIATION

Peak solar radiation occurs between 0900 and 1500 hr in Florida (Barnes and Taylor 1973). Transmittance through the water column is greatest at solar noon; albedo (reflection) is significant during early morning and late afternoon. According to Hanson and Poindexter (1972), maximum solar energy was expended at the air-sea interface from 1000 to 1400 hr; most of the energy was expended in heating the water column. Gordon and Dera (1969) studied solar radiation attenuation between Key Largo and Great Abaco Island, Bahamas, and found that in the surface layers (0-5 m) the attenuation (diffusion coefficient) was 0.11-0.57 Kd/m between Miami and the Florida Current. Hanson and Poindexter (1972) reported that the amount of solar radiation impinging on the bottom at 13 m ranged between 5% and 17%; zenith angle, cloud cover, wave action, and turbidity all influenced transmittance. Kanwisher and Wainwright (1967) reported that Florida reef corals required between 200 and 700 footcandles (fc) of solar illumination for autotrophic self-reliance (compensation point). On clear days these values correlated with a depth of about 30 m.

2.4 SEAWATER TEMPERATURE

The most extensive data base for reef seawater temperatures appears in Vaughan (1918). These data came from several lighthouses and Ft. Jefferson, Dry Tortugas, and are summarized in Table 6 and Figures 6-10. More recent data from a patch reef in Biscayne National Park are presented in Table 7 and Figure 11. Temperature extremes are from 14° to 38° C; most annual ranges are from 18° to 30° C. Mean values are above 18° C, the threshold temperature generally accepted for structural reef development by reef building corals (Wells 1956). Temperature variability (range and standard deviation) is greater during the winter. In recent winters (since 1976), polar air masses have cooled coastal waters, causing fish kills and coral mortalities. Areas that have suffered the greatest harm from thermal stresses are off Loggerhead Key, Dry Tortugas (staghorn coral thickets), and patch reefs off Plantation Key (Hens and Chickens and The Rocks). Cold water masses are created in Florida Bay during the winter passage of polar

mass of animals which undoubtedly flourished upon the great submarine plateau at a time when the Gulf Stream found its way out of the Gulf of Mexico with less velocity than it now has as it passes through the narrow Straits of Bemini. At that time it spread itself fan-shaped over the southern part of Florida and the Bahama Bank, and flowed more gently northerly and easterly along the coast, with the additional reinforcement of the westerly equatorial, flowing north of the Great Antilles to the eastward of Cuba. The Bahama Bank then probably consisted of a series of banks like Salt Key Bank, separated by channels like the Santarem and St. Nicholas, which were undoubtedly kept open by the same currents as now form the Old Bahama Channel. These channels, like those between the keys on the Florida side, have gradually become filled with the detritus driven into them by the trade winds, until the bank has been formed in its present state of consolidation. Yet it must not be forgotten that, while in the western part of the Caribbean, the Gulf of Mexico, and Florida a dead level prevails, at Havana, Hayti, and Barbados we have reefs elevated to a great height, and others at considerable elevation on certain of the Greater and Lesser Antilles.

The somewhat capricious distribution of coral reefs may perhaps be explained by the action of the great equatorial currents. The larger reefs occur in regions to which these currents bring in the track of their course abundant supplies of food for the reef-building animals. On the eastern coast of Africa, of Central America, or of Australia, for instance, extensive colonies of coral reefs flourish, while on the western coast of the same continents, in similar latitudes, but not bathed by such powerful equatorial currents, the supply of food seems insufficient for more than the isolated patches of corals existing there.

Other naturalists, as Semper[1] and Murray,[2] and later, Studer, have already attempted to explain the formation of coral reefs, in part at least, on grounds differing essentially from those to which Darwin ascribed them, and similar in the main to those

[1] Semper, C. Zeits. f. Wiss. Zool., 1863, XIII. p. 558.

[2] Murray, John. Proc. R. S. Edinb., No. 107, 1880, X. p. 505, On the Structure and Origin of Coral Reefs and Islands.

here brought forward. Mr. Murray's "observations of the reefs at Tahiti[1] support the view that they have been built from the shore seawards, and that the lagoons have been and are still being formed by the removal of the inner and dead portions of the coral reef by the solvent action of sea-water. . . . The food supply for the masses of living coral on the outer slope of the reef is brought by the oceanic currents sweeping past the islands, — a fact which explains the more vigorous growth of the reef on the windward sides. It is maintained by Mr. Murray that the whole of the phenomena of the Tahiti reefs may be fully explained by reference to the processes at present in action, and without calling in the aid of subsidence, as is done by Darwin and Dana; and it is further argued that the form of atoll and barrier reefs generally can be explained on the same principles."

Undoubtedly, Darwin's theory of reef formation presents a sound and admirable exposition of the grander causes which have brought about the elevation or subsidence of large tracts to a level favorable for coral growth; but at the time he wrote upon this subject, the formation of extensive limestone banks, built up by the animals living on the bottom, and constantly strengthened and increased by the attendant phenomena of winds and currents, was little understood. These facts have been brought into notice and emphasized by recent deep-sea explorations. Darwin, however, when examining maps of the West Indies, had been struck by the probable connection between the areas of deposition of the great banks marked upon the charts and the course of the sea-currents. He naturally explained the steep slopes, abruptly dropping from comparatively shallow plateaux to great depths, by what is known to occur wherever great masses of sediment are found, and he therefore considered these plateaux to be submerged mountains. Such they are, in a certain sense; not wholly built, however, as Darwin supposes, of sediment, but in great part also of the remains of the innumerable animals living and dying upon them. The nucleus of these banks has probably been formed around the shores of promontories subjected to the most active play of the great oceanic currents.

[1] Voyage of the "Challenger," Narrative of the Cruise, p. 781. 1885.

CHAPTER 2

THE ENVIRONMENT

2.1 CLIMATE

The climate of southeast Florida is characterized as subtropical marine in Miami and tropical maritime in Key West (NOAA 1981). The region is heavily influenced by the adjacent marine environments; the Florida Current, Gulf of Mexico, and Atlantic Ocean affect the terrestrial and marine climates during different seasons. Daily average air temperatures in Key West range from lows of 18.8° C during January to highs of 31.9° C in August (NOAA 1981). Compared to those of Key West, Miami air temperatures are measurably lower in winter and slightly lower during summer (Table 2 and Figures 2 and 3). There is a dry season from November to April in Miami and November to May in Key West. Key West averages 1,007.4 mm of precipitation annually; Miami, 1,518.9 mm (Table 3 and Figure 4). Key West's weather station is within 0.5 km of the coast and is more representative of the reef situation. Throughout most of the year southeast and east-southeast winds prevail, and velocities normally range from 10 to 20 km/hr; wind velocity is less during the summer (Table 4 and Figure 5).

2.2 HURRICANES

Severe hurricanes are common meteorological phenomena in southeast Florida. A formal hurricane

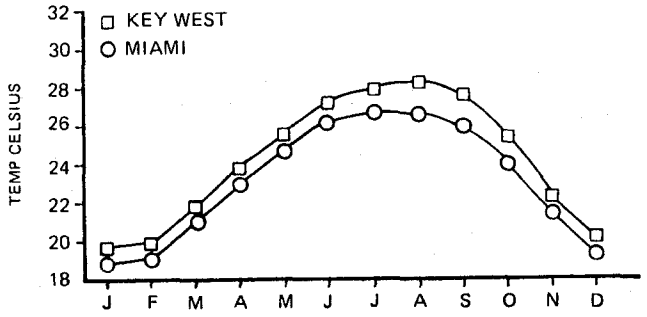


Figure 2. Monthly mean air temperature for Key West and Miami (NOAA 1981). Data base is 29 years for Key West; 38, Miami.

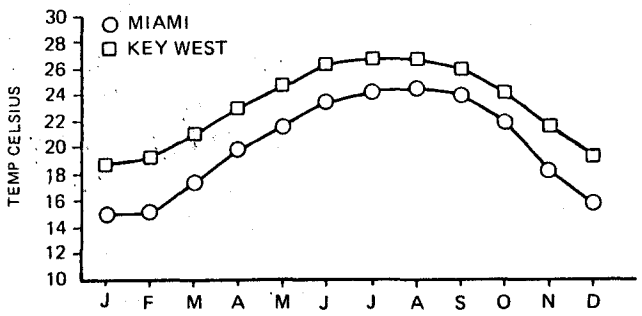


Figure 3. Monthly minimum air temperature for Key West and Miami (NOAA 1981). Data base is 29 years for Key West; 38, Miami.

Table 2

Monthly air temperatures (°C) for Miami and Key West (NOAA 1981).

Period[a]	Miami Range	Miami Mean	Key West Range	Key West Mean
January	14.8-24.2	19.6	18.8-24.2	21.5
February	15.0-24.8	19.9	19.2-24.8	22.0
March	17.2-26.4	21.8	21.0-26.3	23.7
April	19.6-28.2	23.9	23.1-28.1	25.6
May	21.5-29.6	25.6	24.7-29.6	27.2
June	23.3-31.1	27.2	26.2-31.1	28.6
July	24.2-31.7	27.9	26.7-31.8	29.2
August	24.3-32.2	28.3	26.6-31.9	29.3
September	23.9-31.3	27.6	25.9-31.0	28.4
October	21.7-29.2	25.4	24.0-28.9	26.4
November	18.1-26.6	22.3	21.4-26.4	23.9
December	15.6-24.8	20.2	19.2-24.7	21.9
Yearly	14.8-32.2	24.2	18.8-31.9	25.7

[a]Climate data base for Miami = 38 years; Key West = 29 years.

Table 3

Monthly precipitation (mm) for Miami and Key West (NOAA 1981).

Month[a]	Miami mean	Key West mean
January	54.6	42.4
February	49.5	47.0
March	52.6	39.6
April	91.4	55.1
May	155.4	63.8
June	228.6	115.6
July	175.5	104.4
August	170.7	113.5
September	222.0	186.4
October	207.8	141.5
November	69.1	67.8
December	41.7	38.6
Yearly total	1,518.9	1,015.7

[a]Climate data base for Miami = 38 years; Key West = 29 years.

At the time when Darwin wrote, and when we knew little of the limestone deposits formed by the accumulation of the *débris* of mollusks, echinoderms, polyps, and the like, upon folds of the earth's crust, the formation of the basal parts of barrier reefs was difficult of explanation. The evidence gathered by Murray, Semper, and myself, partly in districts which Darwin had already examined, and partly in regions where his theory of reef formation never seemed to find its proper application, has in a measure removed this difficulty. It all tends to prove that we must look to many other causes than those of elevation and subsidence for a satisfactory explanation of coral-reef formation. All-important among these causes are the prevailing winds and currents, the latter charged with sediment which helps to build extensive plateaux from lower depths to levels at which corals can prosper. This explanation, tested as it has been by penetrating the thickness of the beds underlying the coral reefs, seems a more natural one, for many of the phenomena at least, than that of the subsidence of the foundation to which the great vertical thickness of barrier reefs has been hitherto referred. Still, it is difficult to account for the great depth of some of the lagoons — forty fathoms — on any other theory than that of subsidence.

If, however, we have succeeded in showing that great submarine plateaux have gradually been built up in the Gulf of Mexico and the Caribbean by the decay of animal life, we shall find no difficulty in accounting for the formation of great piles of sediment on the floors of the Pacific and Indian Oceans, provided these banks lie in the track of a great oceanic current. Certainly the coral reefs of the Caribbean and the Gulf of Mexico, of Florida and the Bahamas, are distributed upon banks which lie directly in the path of the great Atlantic equatorial currents and of the Gulf Stream, — banks which we know to have been formed by the agency of these currents.

The fact that the coral reef at the extremity of Florida is the most recent of the coral formations found on the Florida shores plainly shows that these reefs, as well as those of Yucatan, Cuba, the Bahamas, and the Caribbean Sea, though not all of the same age, were yet of modern origin, since we find them

still in an active state of formation. Even the elevated reefs of Cuba and of the other West India Islands, though older, probably belong, nevertheless, to the most recent deposits of the kind we know. The difficulty of explaining the constant renewal of the coral faces of the atolls of the Pacific, and their present condition, on the supposition of their having existed from the time of the early tertiaries, was one of the main causes which led Darwin to seek for some other agency, like subsidence, to explain the renovating process of the original structure. In some instances coral reefs have unquestionably been uplifted. I have seen the elevated reefs of Cuba, of San Domingo, and other West India Islands, and of Barbados[1] (Figs. 39, 46), which are perhaps the most striking examples of

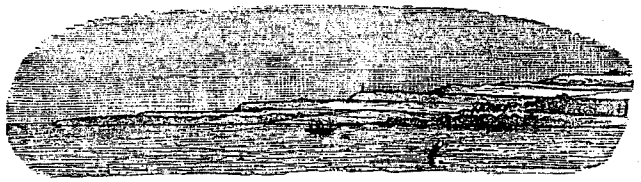


Fig. 46. — Terraces near Fort Charles Light House, Barbados.

elevated reefs. They are too well known to need more than a passing notice here. The terraces they form show plainly the successive stages of arrest in the agency of elevation, and there is no difficulty in accounting for their existence especially in a volcanic region like the West Indies; but that there should have been an extensive area of subsidence, in which the rate of subsidence was so evenly balanced with the rate of coral growth as to create and maintain the necessary conditions for reef formation, is less easy of explanation.

The cap of rhizopod earth for which Barbados is noted dates back to a time when the volcanic centre round which the coral reefs have grown in more recent times was still at a considerable depth below the level of the sea. This large accumulation of rhizopodial earth is an excellent example in favor of the theory

[1] The trachytic cone forming the base upon which the successive terraces of Barbados have been elevated is seen to crop out on the surface in the northeastern part of the island.

tested), medicine (artificial bones), geology, reef fisheries management, aquaria, mariculture techniques, and archaeology.

Revenue from all these activities reenters the south Florida economy and generates employment for many other people in the service sectors. The corals' greatest value, however, is as a living resource, and not as an item of commerce. Their habitat value and attraction to divers are worth far more than as an item of commerce. While coral reefs remain on the seafloor, they are like a good investment: they continue to generate monies through the marine protein harvested there and the divers who come to enjoy them. As curios, they bring a smaller dividend to a fewer number of people.

of Mr. Murray, that the inorganic material held in suspension in the sea became precipitated on the sides of volcanic peaks or slopes, and thus forms little by little the base or plateau upon which coral reefs eventually grew. If this be true, it is not necessary to resort to Darwin's theory of extensive areas of elevation or of subsidence in order to explain the formation of atolls or of fringing reefs. In the tropics and in regions situated in the path of great oceanic currents which carry along their course an immense amount of pelagic life, serving as food for the animals living upon the bottom, we have all the elements of the gradual accumulation of submerged land, which, when it rises to a certain level, becomes the foundation upon which reefs are formed. In fact, as has been well pointed out by Mr. Murray, we should have in an area of elevation as well as one of subsidence all the elements necessary for the construction of atolls.

In a very interesting article on the Bermudas, Rein[1] has taken very much the same view of their gradual building up, and explains the present condition of things by causes greatly differing from those adduced by Darwin to account for the apparent atoll shape of the groups.

The islands composing the Tortugas (Fig. 38) are Loggerhead, Bird, Garden, Long, Sand, Middle, and East Keys. These are always above the level of the sea, while Southwest Key and Bush Key are exposed only at low water, and North Key and Northeast Key have disappeared. These insignificant islands are the outcrops of extensive submarine banks. Loggerhead Key, not more than three fourths of a mile in length, is the top of a bank about five miles in length, extending to the three-fathom line, with an average width of three fourths of a mile, and has extensive coral sand flats running in prolongation of the northern and southern extremities of the key. Between this and the Garden Key and Long Key Bank, there are a few shoals running more or less parallel with Loggerhead Bank, the largest of which are Brilliant and White Shoals. Garden Key and Long Key Bank form a rectangular shoal of nearly the

[1] Rein, J. J. Beiträge zur Physikalischen Geographie der Bermuda Inseln. Bericht. Senckenb. Naturf. Gesell., 1869–70 (Mai, 1870), pp. 140–158.

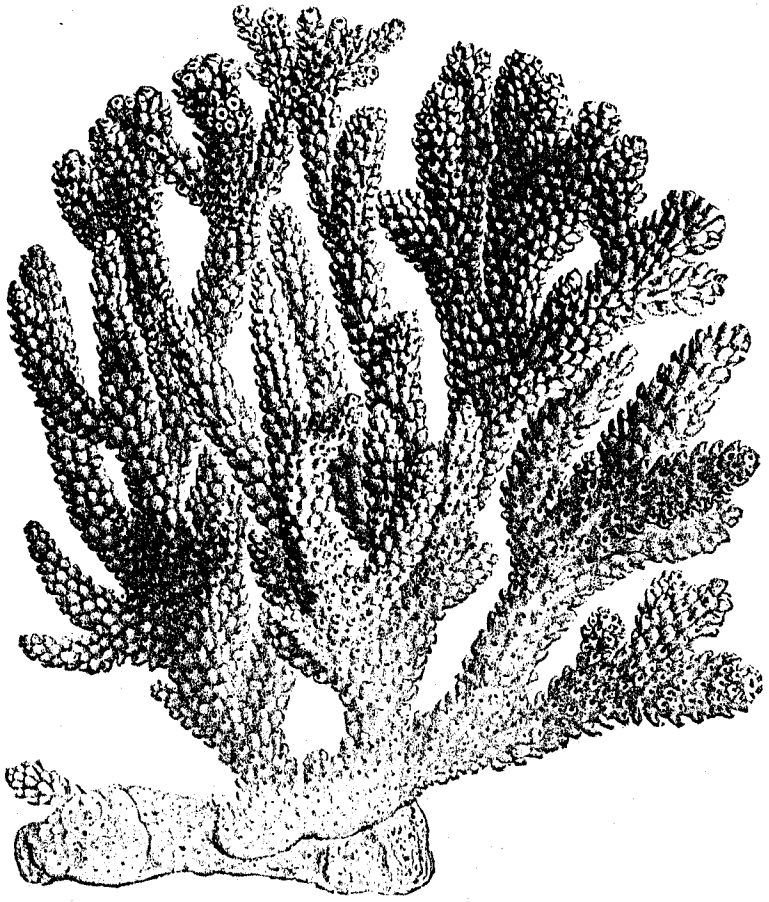


Fig. 11. MADREPORA PROLIFERA (Agassiz.)

industry until 1950. During that period collectors used either grappling hooks from boats or hand harvested while reef diving. The industry changed with the advent of scuba diving and the increased interest by the general public in the marine environment. There was increased demand for coral by tourists as well as for export to northern markets. No quantitative data exist on the magnitude or economics of the coral harvest. It is suspected that commercial coral harvest at no time employed more than 20 individuals working on a part-time seasonal basis. In 1973 and 1975 Florida enacted statutes making it illegal to collect, sell, or damage stony corals (Millepora and Scleractinia) and two species of sea fan (*Gorgonia*) within State waters. In 1976, the Federal Government (Bureau of Land Management) wrote regulations under the authority of the Outer Continental Shelf Lands Act to protect corals and reefs in the area under federal jurisdiction (beyond the 3-mi limit in the Atlantic). The Fifth Circuit Court of Appeals, however, ruled that these regulations can only be applied when active mineral or petroleum exploration or production is occurring in the immediate vicinity of the coral. Currently, the Gulf of Mexico and South Atlantic Fishery Management Councils are preparing a management plan for corals and coral reefs in the region between North Carolina and the Texas-Mexican border.

Today, coral being sold is foreign. From 1977 to 1979, 200,000 pieces of coral were imported with a dockside value of $31,500. Retail markup would place the value of imported coral at about $95,000. Most of this coral came from the Philippines, where collecting and selling coral is illegal, but enforcement is difficult because of the thousands of islands belonging to this nation.

Economically, Florida coral reefs directly or indirectly generate an estimated $30 million-$50 million annually within the Monroe County region. These monies come from all aspects of fishing, diving, education, and research. Commercial fishing in particular depends heavily on the coral reef habitats. Most of the sought-after species spend all or part of their lives in the reefs. For some species, the coral reefs are a nursery area where juveniles mature into adults. Many species breed and/or feed within the confines of the coral reef. Resident fish populations may only seek shelter and refuge in the reef and feed in the nearby surrounding grass flats or the open sea. The life history patterns of individual species vary, but the reef is a critical link to the success of these species. Table 1 presents commercial landings of reef-related species in Monroe County for 1980.

Diving as a sport and hobby attracts more than a million people to the Florida Keys annually. These divers rent and purchase equipment, charter tours to the reefs, and purchase food and lodging. Tourists come from as nearby as Homestead and Miami, and as far away as Europe and Canada. A 1979 *Skindiver* magazine survey indicated that the Florida Keys was the most popular diving location in the United States among traveling divers. The survey reported that the average diver spent about $718 per trip. There are 40 businesses

Table 1

Commercial landings of reef-related species in Monroe County, 1980 (NMFS 1981).

Species	Weight (lb)	Value ($)
Ballyhoo	311,724	85,871
Jacks	29,881	2,674
Dolphin	89,977	33,099
Grouper & scamp	509,794	451,014
Hogfish	34,184	17,965
Jewfish	32,646	5,312
Shark	175,643	18,365
Snappers		
Lane	15,526	6,890
Mangrove	240,117	127,530
Mutton	160,469	131,419
Red	15,532	20,820
Vermilion	915	861
Yellowtail	735,104	730,744
Triggerfish	105	19
Warsaw grouper	3,371	1,324
Spiny lobster	4,656,018	10,132,913
Spanish lobster	28,199	67,814
Total	7,039,205	11,834,634

in Monroe County devoted entirely to tourist diving. For the most part this activity is a nonconsumptive form of reef usage. Most tourists come to experience the reef environment firsthand and to observe fish. Some divers do spearfish and catch lobsters. Spearfishing is banned in some marine parks and sanctuaries, i.e., John Pennekamp Coral Reef State Park, Key Largo National Marine Sanctuary (JPCRSP–KLNMS), and Ft. Jefferson National Monument. Much of the tourist diving is concentrated offshore of Key Largo in JPCRSP–KLNMS, off Big Pine Key at Looe Key National Marine Sanctuary (LKNMS), and off Key West.

Besides diving, there are glass-bottom boat tours that allow the nondiver to enjoy the reef firsthand without getting wet. Charter airplanes also fly tourists over the reefs. Tourist gift shops market many reef-related souvenirs, from colorful T-shirts to postcards.

All levels of education, from elementary to graduate school (including youth organizations, scouts, sea camps, and diving schools), bring students to the coral reefs to supplement classroom experiences. Special publications, documentaries, and movies about the coral reefs are produced. These are an economic and educational benefit to the Nation.

Economic impacts of applied and basic research on coral reef communities include equipment rentals, air fills, and lodging. Potential commercial applications of this research will benefit pharmacology (anti-cancer compounds from various reef organisms are being

same length as that of Loggerhead, with an average width of nearly two miles, the great sand flats of this shoal being those of the Long and Bush Key tract. The Southwest Channel, with a depth varying from ten to twelve fathoms, separates Loggerhead Bank from the Bird, Garden, and Long Key Bank. This, in its turn, is separated from the still greater North, Northeast, East, and Middle Key Bank by the Southeast Channel, with a depth of about nine fathoms, while the Northwest Channel separates Loggerhead Bank from the North Key Bank, with an average depth of from seven to ten fathoms. The Eastern Bank is irregularly horseshoe-shaped, convex to the east, and partly surrounds a great interior bay, which has an average depth of about seven fathoms. The flood tides run from the south through the Southwest and South channels in a northeasterly direction, the ebb tide flowing in the opposite direction. The strongest tidal current passes through the Southwest Channel.

An examination of sections of the Tortugas from the west to the east shows the gradual rise of the mound forming the Tortugas, as we pass from the west side of the Loggerhead Bank to a line extending through the southwest slope of the same bank, and across to the main bank of the group; the mound falls slowly on the eastern slope as we cut across the east end of East Key Bank, till we finally come to the low elevation forming the southeast slope of East Key Bank. The action of the tides through the Southeast and Northwest channels is well shown in the fact that they keep open the passages between Long Key and Loggerhead banks, and between the former and North Key Bank, and also the secondary channels separating Bird Key, Garden Key, and Long Key. These are undoubtedly the last traces of the deeper and wider channels, probably once running parallel to the Southeast Channel. They have gradually been filled up since the sand flats of Bush Key began to form, so that the free circulation of the tides through them has been prevented. The presence of a few large heads of mæandrinas and astræans, as well as the luxuriant growth of *Madrepora prolifera* (Fig. 47) near low-water mark, on the two sides of these channels, now changed into sand flats, seems to indicate a

lighthouse. LeCompte (1937) described some Tortugas reefs. Wells (1933, unpublished) contains considerable information on the Tortugas reefs. A fire destroyed the Tortugas Laboratory in 1937; it was never rebuilt.

Verrill (1902), Smith (1943, 1948, 1971), Vaughan and Wells (1943), and Wells (1956) are the relevant scleractinian taxonomic and systematic references. During the recent period (1950 to present) there has been a great proliferation of scientific literature dealing with Florida coral reefs. Growth rates of coral species were detailed by Broecker and Thurber (1965), Shinn (1966), Jaap (1974), Landon (1975), Emiliani et al. (1978), Dodge (1980), and Hudson (1981). Population dynamics of scleractinian corals were reported by Dustan (1977a). Brooks (1963), Halley (1979), Davis (1982), and Porter et al. (1982) added to Tortugas information.

Ecological studies and reviews include Smith et al. (1950), Voss and Voss (1955), Jones (1963, 1977), Glynn (1973), Hudson et al. (1976), Hudson (1981), Goldberg (1973a, 1973b), Antonius (1974a), Kissling (1975), and Shinn (1975). Coral reef fish studies included Springer and McErlean (1962a, 1962b), Starck (1968), Starck and Davis (1966), Bohlke and Chaplin (1968), Emery (1973), and Jones and Thompson (1978). Reef morphology and physiography were reported by Stephenson and Stephenson (1950), Shinn (1966), Kissling (1965), Starck and Schroeder (1965), Starck (1966), Straughan (1978), Turmel and Swanson (1971), Weeks (1972), Hannau and Mock (1973), and Avent et al. (1977).

Geological literature includes Ginsburg (1956), Brooks (1963), Alt and Brooks (1965), Hoffmeister and Multer (1968), Duane and Meisberger (1969), Enos (1970), Multer (1971), Raymond (1972), Ginsburg (1973), Enos (1974), Gleason (1974), Hoffmeister (1974), Enos (1977), Lighty (1977), Lighty et al. (1978), Shinn (1980), Mitchell-Tapping (1981), and Ghiold and Enos (1982). Geographical research includes work by Ginsburg and Shinn (164), Marszalek et al. (1977), Marszalek (1981, 1982), Reed (1980), and Stoddart and Fosberg (1981).

Guidebooks or general references to Florida reefs include Hoffmeister et al. (1964), Ginsburg (1972a, 1972b), Zeiller (1974), Voss (1976), Greenberg (1977), Colin (1978a), and Kaplan (1982). Hurricane impacts on Florida reefs have been documented by Springer and McErlean (1962a), Ball et al. (1967), Perkins and Enos (1968), and Shinn (1975). The effect on coral reefs by other meteorological phenomena was studied by Jaap (1979), Walker (1981), and Roberts et al. (1982). Physical and chemical oceanography adjacent to the reef tract includes studies by Hela (1952), Chew (1954), Stommel (1959), Wennekens (1959), McCallum and Stockman (1964), Gordon and Dera (1969), Hanson and Poindexter (1972), Lee (1975), Lee and Mayer (1977), Lee and Mooers (1977), and Leming (1979).

The Octocorallia were reported on by Goldberg (1973a, 1973b), Opresko (1973), Cairns (1977), and Wheaton (1981). Underseas parks were reported on by Voss et al. (1969), Spotte (1972), Tzimoulis (1975), and Jameson (1981). Florida Current plankton was reported on by Bsharah (1957). Emery (1968) discussed coral reef plankton. Coral predators and boring and rasping biota were reported by Robertson (1963), Ebbs (1966), Antonius (1974b), Hein and Risk (1975), and Hudson (1977). Physiology of reef corals, particularly the symbiotic relationships of corals with zooxanthellae, was studied by Kanwisher and Wainwright (1967), Kriegel (1972), Chalker (1976, 1977), and Chalker and Taylor (1978). Reports on the impact of human activities include McCloskey and Chesher (1971), Hubbard and Pocock (1972), Straughan (1972), Voss (1973), Antonius (1974b, 1976, 1977), Courtenay et al. (1974), Griffin (1974), Jaap and Wheaton (1975), Manker (1975), Shinn (1975), Chan (1976), Britt and Associates (1977), Davis (1977a), Dustan (1977b), and Bright et al. (1981). Coral reef growth rates in Florida were reported by Hoffmeister and Multer (1964), Shinn et al. (1977), and Shinn (1980).

Echinoid distributions in John Pennekamp Coral Reef State Park were studied by Kier and Grant (1965). Miller et al. (1977) reported on diatoms in the park. Jameson (1981) reported on the biology, geology, and cultural resources in deeper regions of the Key Largo National Marine Sanctuary. Workshop and symposia literature includes Stursa (1974) and Taylor (1977). Shinn (1979) detailed collecting-permit requirements for biological and geological sampling in the Keys' area.

1.5 ECONOMIC SIGNIFICANCE

Exploitation of Florida's reef resources began with the Caloosa Indians, who harvested marine protein (fishes, lobsters, and conchs), shells, and coral for trading. Excavated middens occasionally contain coral artifacts. During the mid-17th to late-19th centuries, the Florida reefs posed a significant navigational hazard to Europeans and Americans. Today, salvagers recover gold, silver, and artifacts from the numerous shipwrecks adjacent to the reefs. Many reefs are named for shipwrecks. Looe Key Reef is named for the 44-gun British Frigate, the HMS *Looe*, which was wrecked on the reef the morning of 5 February 1744. Molasses Reef is named for an unknown vessel laden with molasses that foundered there.

Early Florida Keys' settlers had a thriving enterprise of luring unsuspecting ships onto the reefs with false beacons. They then claimed salvage rights on the wreck, salvaged the cargos, and auctioned them off. Wood from the vessels was also salvaged. Many of the older homes in Key West are constructed with salvaged ship timbers. In an effort to reduce the shipwrecks, early coral reef work was directed toward mitigating the hazards. This resulted in the lighthouse construction between 1825 and 1886 on the most dangerous reefs. These lighthouses significantly changed the nature of the Keys' economy. Fishing, cigar making, sponge harvesting, and agriculture replaced shipwrecking as the major economic endeavor at Key West.

Commercial sale of coral began in Key West around 1830 and remained a poorly organized cottage

more active tidal circulation through them formerly than is now taking place. An examination of the cross-sections in the direction of the prevailing winds, and in the direction of the tides, shows at a glance the mound-shaped mass which forms the base, rising from the general level of twenty-five to thirty fathoms, with its abrupt side facing the east. There are also seen the deep furrows, more or less broad, which have been scooped out of this mass by the action of the currents, such as those passing through the Southwest Channel.

The corals which give to the reefs their peculiar physiognomy are the extensive patches of Madrepora (principally *M. cervicornis*), the clusters of the two common species of Porites (*P. furcata* and *P. clavaria*) (Fig. 48) covering more or less the shallow tracts of coarse sand, and *Mæandrina areolata* growing between the patches of marine lawns formed by a species of Thalassia, with occasional patches of Anadyomene. In other parts of the reefs large holothurians (Mülleria) lie scattered on the bottom, while in somewhat deeper regions are pockets filled with large Diadematidæ. Immense masses of nullipores (Udotea and Halimeda, Figs. 49, 50) and corallines grow on the shallowest flats, on the tops of the branches of madrepores which have died from exposure to the air, either because they have grown up to the surface and so have become exposed by extreme low tides, or because strong winds have blown the water from the flats. The destructive effect which an extremely low tide has on a growing reef is well shown on the flats to the southward of Fort Jefferson, where the upper part of the branches of a certain size reaching up to a given level are frequently killed off by low tides. Exposure to the action of the sun even for a very short time is sufficient to kill them. The extreme sensitiveness of all corals to atmospheric action is well known, so that it becomes plain, as has been



Fig. 48. — Porites clavaria. (Agassiz.)

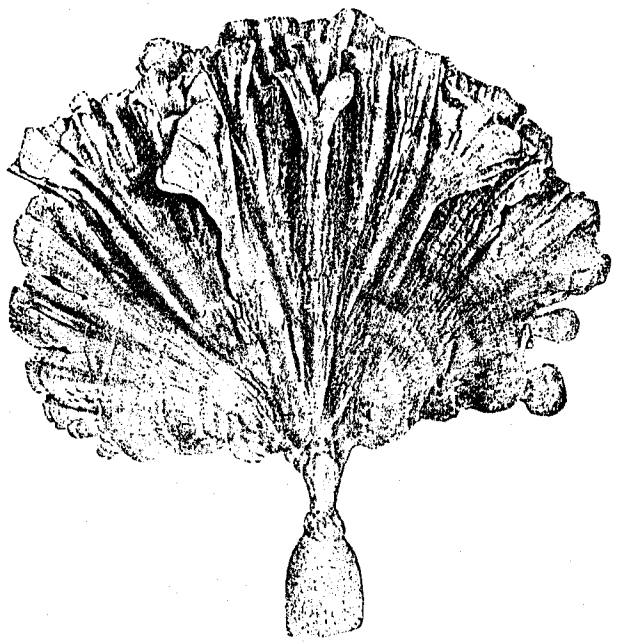


Fig. 49. — UDOTEA FLABELLATA. (Agassiz.)

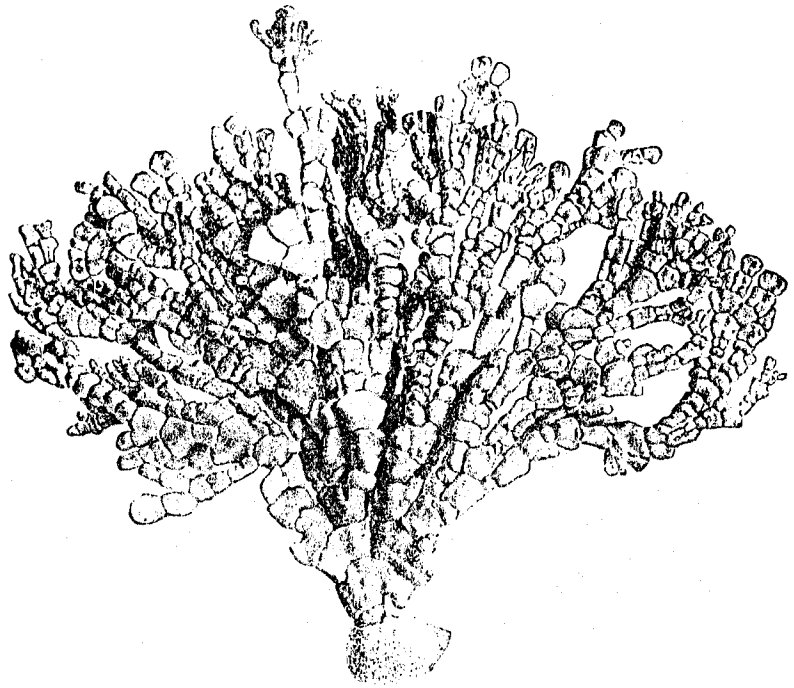


Fig. 50. — HALIMEDA TRIDENS. (Agassiz.)

The Keys or islands act as barriers to cross shelf water transport from shallower bays and sounds. These bays are very shallow, hence much influenced by meteorological events. Temperature, salinity, and turbidity can be significantly affected. Heavy rainfall, drought, and winter cold fronts are the major influences. Coral reef distribution patterns reflect the extent of water exchange between the bays and sounds and the Atlantic. The larger northern Keys (Elliott and Largo) have extensive reef development off their coasts; the middle Keys, which are smaller and more separated, have numerous channels communicating with Florida Bay (Plate 1a) and exhibit less reef development than the upper or lower Keys. The influence of Florida Bay on water quality negatively affects reef development in the middle Keys area.

Major bank reefs off the Florida Keys include Carysfort, Elbow, Key Largo Dry Docks, Grecian Rocks (Plate 3a), French (Plate 1b), Molasses, Alligator, Tennessee, Sombrero, Looe Key (Plate 2a and b), Eastern, Middle, and Western Sambos, American Shoals, Eastern and Western Dry Rocks, Rock Keys, and Sand Key. Dry Tortugas is studded with various coral reefs (Davis 1979, 1982).

Off the west coast of Florida, tropical reef development is nonexistent. Ledges and outcroppings are a special rocky habitat which supports an association of hardy corals and other biota; however, they do not construct three-dimensional reefs. The Florida Middle Ground (a fossil reef formation about 157 km northwest of Tampa Bay), while exhibiting higher diversity in coral species, is not an active coral reef comparable with those found off southeast Florida. These areas in the eastern Gulf of Mexico, however, are critical habitats that should be provided with rational management, especially since important fisheries are found in association with the gulf live bottom communities.

1.3 COMMUNITY DISTRIBUTION

The Florida Keys possess coral reef communities similar to those found in the Caribbean and other tropical Atlantic areas. The reefs are bathymetrically distributed from less than 1 to 41 m deep. Large-scale synoptic mapping of the Keys' reefs has been recently completed (Marszalek et al. 1977; Marszalek 1981, 1982). Caution should be exercised when interpreting these maps, as they use mapping units based on geological and biological criteria, and in some cases errant interpretation could occur due to their large scale and criteria used.

The basic pattern of marine communities in southeast Florida (where commercial development has not occurred) is one of a shoreline dominated by mangroves, rocky intertidal, or sedimentary environments. From the intertidal zone to Hawk Channel is a mosaic of environments including sediments, seagrass exposed Pleistocene rock, and some patch reefs. Seaward of Hawk Channel, patch reef abundance and frequency increase and bank reefs begin to occur. Seagrass is often abundant and sediment is coarser. Seaward of the bank reefs the sea bottom (where it has been investigated) consists of sediments, sponge habitats, and rubble, with occasional rocky outcrops that generally parallel the basic reefs.

The coral reefs, seagrasses, and mangroves are all integrated into the coastal ecosystem of southeastern Florida. Motile species and trophic energy webs are integrated and interrelated among the three communities.

1.4 HISTORICAL RESUME' OF FLORIDA CORAL REEF RESEARCH

Arbitrarily, coral reef research can be chronologically placed into three periods: early (to 1900), middle (1900 to 1950), and recent (1950 to present). Early research was descriptive and taxonomic, and was stimulated by the need to provide safe navigation for marine commerce. National security also had some influence in that the Caribbean Sea prior to 1860 was frequented by pirates and European naval powers. During the age of discovery, the Florida coastline was crudely mapped by the Spanish and English. Agassiz (1852, 1869, 1880, 1885, 1888), LeConte (1857), Hunt (1863), and Pourtales (1863-1869, 1871, 1878, 1880) provided the earliest reef descriptions and details about the coast. They also initiated systematic description of the many organisms found in and near the coral reefs.

During the middle period, establishment of the Tortugas Laboratory on Loggerhead Key by the Carnegie Institution was the most significant factor benefiting coral reef studies during the first half of the twentieth century. Alfred G. Mayer and his colleagues conducted much fundamental coral reef research from the Tortugas Laboratory. Mayer (1914, 1916, 1918) determined the thermal tolerances of tropical marine organisms in general and reef coral in particular. T. Wayland Vaughan was the most prolific Carnegie reef researcher, reporting on the geology of Tortugas, south Florida, and the Bahamas (Vaughan 1909, 1910, 1912, 1914a, 1914b, 1914c, 1914e, 1915a; Vaughan and Shaw 1916). He studied the taxonomy and growth rates of scleractinian corals (Vaughan 1911, 1914d, 1915b), summarized seawater temperatures at reef tract lighthouses (1918), and reported on the Tortugas current structure (1935). Other students of scleractinian corals include Duerden (1904), postlarval development in *Siderastrea radians*; Matthai (1916), systematics; Boschma (1925, 1929), postlarval development in *Manicina areolata*; Wells (1932), thermal tolerance knowledge; and Yonge (1935a, 1935b, 1937), *M. areolata* autecology, taxonomy of *Siderastrea* spp., and mucus production in stony corals. Other reef-related research from the Carnegie laboratory includes work by Cary (1914, 1916, 1918a, 1918b), Octocorallia; Taylor (1928), algae; deLaubenfels (1936), Porifera; and Longley and Hildebrand (1941), fish. Another first for the Tortugas laboratory was that the first underwater color photographs of coral reefs were taken by Longley at Tortugas. Dole (1914) and Dole and Chambers (1918) reported on salinity at Tortugas and off Fowey Rocks

stated already by Darwin, Dana, and others, that no coral reef can grow above the level of the lowest tides, and that all subsequent additions of material must be due to accumulation of sediment transported by the action of the tides and prevailing winds.

Next come the clusters of coral heads, huge masses of astræans and of mæandrina, very limited in their distribution at the Tortugas, as well as the more or less extensive patches of *Madrepora palmata* (Fig. 51), and finally what is known as broken ground, namely, the outer edge of the reef occupied mainly by clusters of gorgoniæ (Fig. 52), which also reach upward into the shallower region. Occasional patches may be seen of astræans, madrepores, and other reef-builders, which have extended below the depths at which they generally flourish, where they are soon killed or choked by the accumulation of fine coral sand and coralline sand or ooze of the deeper waters. This sediment fills the broad and narrow flat channels dividing the three great banks which compose the Tortugas, or separate the inner shoals, banks, and islands. Finally come the lines of broken coral heads and branches, mixed with dead corallines, shells of mollusks, old serpulæ tubes,[1] gorgoniæ stalks, and the like. These form a low dike, as it were, to be little by little pounded up by the breakers into smaller fragments, and carried, either by the winds, or waves, or currents, into the interior of the reefs, there to form sand flats of more or less coarse materials, until on the western faces of the banks the finest detritus is deposited in very steep slopes, constantly shifting like those of sand dunes, and, like them, running forward and backward at the will of the winds and waves. This continues until the particles have become cemented together by the action of the carbonic acid contained in excess in the salt water surrounding the reefs, and by the gluing of the slight amount of animal matter which holds these particles together. Some of the slopes (according to General Wright, of the Engineers) are as great as thirty-three degrees.

All this fine material, composed of fragments of every animal

[1] Serpulæ often form incrusting masses of considerable extent, acting, as has been noticed by Darwin, much as the patches of nullipores do in protecting decayed and dead corals from being too rapidly broken to pieces by the action of the waves.

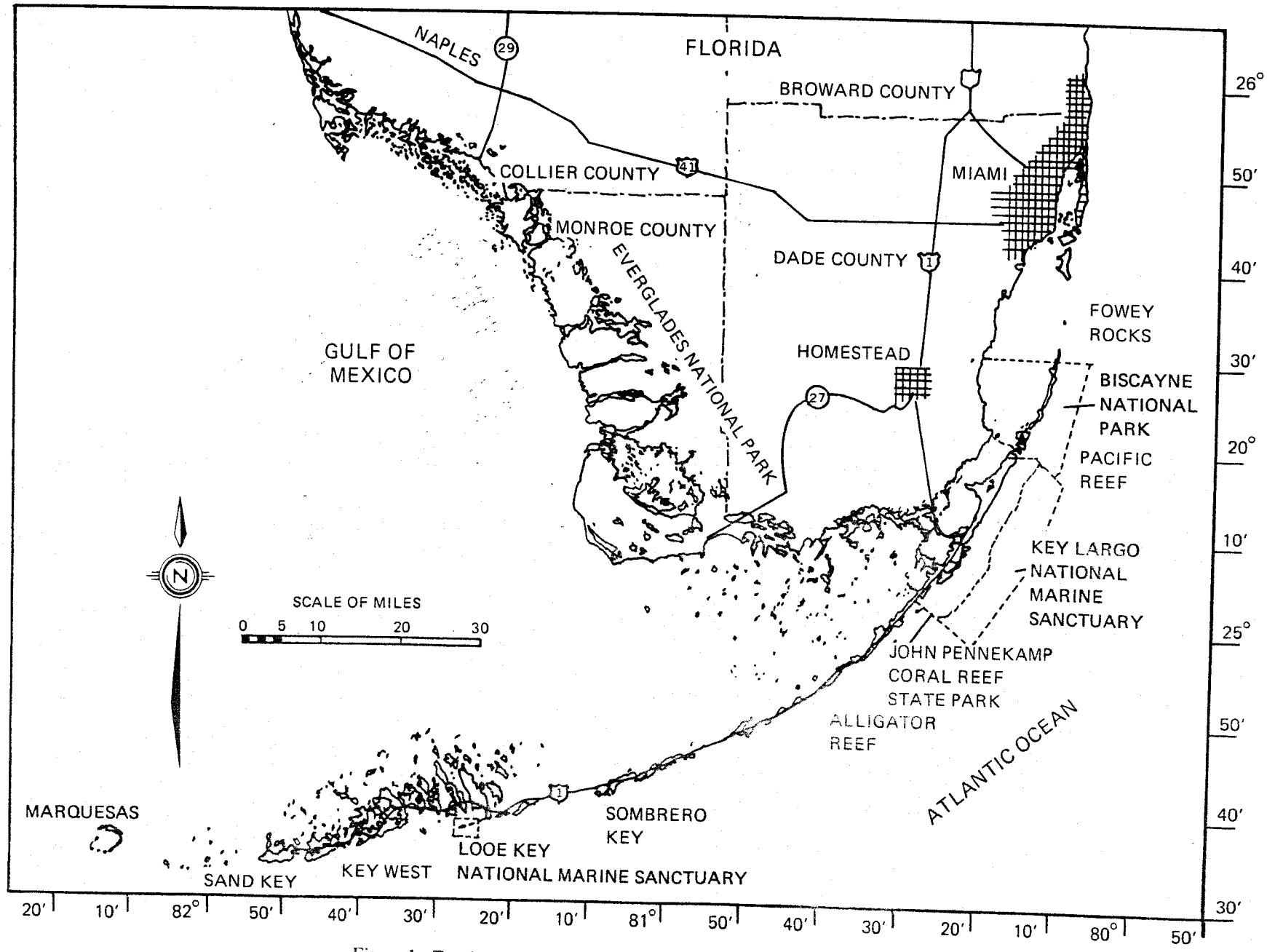


Figure 1. Tropical coral reef communities off south Florida.

and plant with a calcareous skeleton, of course prevents the growth of corals in positions which are not well scoured, either by the action of the tides or by that of the prevailing winds. The corals when alive are gradually buried under this mass of material constantly passing over them, and held in suspension. They flourish, therefore, only where the disturbing elements are reduced to a minimum; namely, on steep banks, or on the slopes which are scoured by tides, or on flats at considerable depths, over which a large body of water can freely pass, whether brought by the tides or driven by the winds. In such cases the corals can grow gradually towards the surface as fast as the sediment deposited has closed up the circulation of the lower levels. The quantity of calcareous matter held in suspension in the water in the vicinity of a reef, and on the reef itself, is very great. The breakers pounding upon the exposed slopes of the reefs destroy, even on calm days, large quantities of corals which have been weakened by the borings of mollusks, annelids, echinoderms, and sponges. On windy or stormy days the powdered fragments are driven far and wide, turning the surrounding water to chalk color for a considerable distance from the reef. It is not an uncommon thing, after a blow, to come upon this water discolored by the fine calcareous silt, to a distance of six to ten miles from the outer reef. After a prolonged storm I have seen between two and three inches of fine silt deposited in the interval between two tides. The limitation of coral-reef growth to shallow depths may be due to the fact that the ooze held in suspension rapidly sinks towards the bottom, the surface water remaining clear. The rapidity with which the corals are choked readily explains why they must of necessity have a limited vertical distribution depending upon local causes. This is well shown along the sections of the Tortugas. Off the Marquesas, and along the line of the main reef, we find corals living and flourishing at a much greater depth, and there seems to be no simpler explanation of the limited bathymetrical range than that of the baneful action of the silt near all reefs. That the silt is carried on the bottom by currents and waves is well known, and on the bottom of the Gulf Stream, to the north of the Straits of Bemini, we have a huge muddy bot-

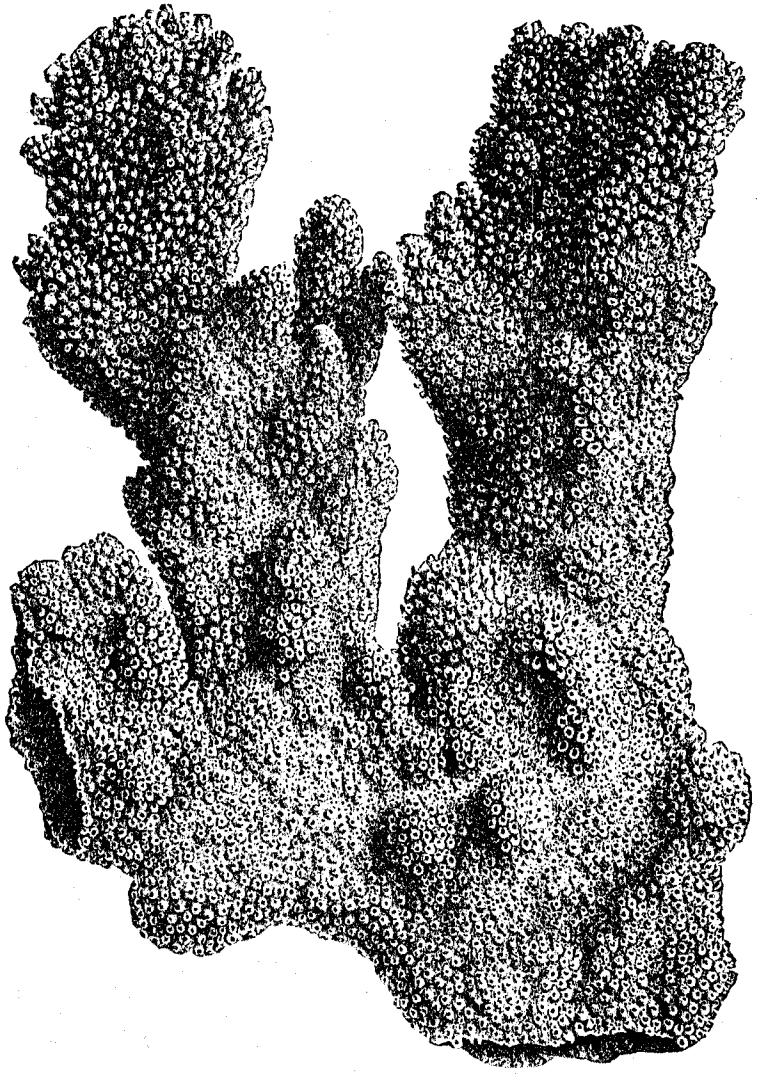


FIG. 51. — MADREPORA PALMATA. (AGASSIZ.)

CHAPTER 1

CHARACTERIZATION OF THE RESOURCE

1.1 OVERVIEW

Coral reefs are highly complex and diverse communities of biota, a phenomenon of the tropics and subtropics limited by such factors as suitable substratum, temperature, light, and sedimentation. In simplest terms coral reefs are concentrated complexes of corals and other organisms that construct a limestone structure in shallow water. In the initial building process, a set of primary framework builders set down the first structure; later colonizers add to the volume. Skeletal breakdown by physical and biological actions creates carbonate sediments, which are recycled by other biological processes or are cemented to the reef framework through biological or geochemical processes.

The coral reef complex found off southeast Florida represents a mosaic that exhibits extreme variability in all parameters used to evaluate biological communities. Coral reefs provide a wide spectrum of vocational and recreational activities. Many important fisheries are directly tied to these reef communities; a reef's principal resource value (economically) is as a highly productive habitat: it concentrates marine protein in a localized area. Coral reefs also play a significant role in the tourist industry of southeast Florida.

While the level of reef usage is increasing as southeast Florida experiences rapid population growth, management of these reef communities tends to lag or is unresponsive to the problems described herein.

Scientific and lay literature has reported real and potential threats to southeast Florida coral reefs (Straughn 1972; Voss 1973; Davis 1977a; Dustan 1977b; Bright et al. 1981). Impacts have included vessel groundings and sinkings, oil spills, anchor damage, beach renourishment dredging, fishery activities (lobster trap recovery), tropical fish and invertebrate collecting, shipwreck salvage, and diving-related activities. Individually these acts do not greatly affect the resource vitality, but the chronic and synergistic nature of some of these acts is cause for concern.

The goal of this document is to serve as a reference for those interested and concerned individuals responsible for environmental management of the resource, as well as those seeking a better understanding of Florida's coral reefs.

1.2 CORAL REEF DISTRIBUTION

Although the tropical coral reef communities found off southeast Florida (Figure 1) are the emphasis of this report, a brief summary of coral reef distributions throughout Florida will aid in understanding this resource. From the Georgia border to near Fort Pierce on the Atlantic coast, in depths of 15-50 m, *Oculina* (pretzel coral) bank communities are the dominant coral community (Avent et al. 1977; Reed 1980). These are low-diversity coral assemblages, but important fishery habitat. Grouper find refuge, feed, and breed in and near these structures. From Stuart (St. Lucie Inlet) to near Palm Beach is a transitional community of *Oculina* bank flora and fauna and hardier elements of the tropical reef biota. This region is characterized by the convergence of the temperate and subtropical climate zones. From Palm Beach southward to Miami (Cape Florida) elements of the tropical coral reef biota become increasingly important in a north-to-south gradient; however, the building of three-dimensional reef structures does not occur. This area is characterized as an octocoral-dominated hardground community (Goldberg 1973a). The two stony corals most responsible for reef building (*Acropora palmata*, elkhorn coral, and *Montastraea annularis*, star coral) rarely occur here, and currently do not actively build reefs. *Acropora palmata* was once an important reef builder in this area, but it ceased building reefs about 4,000 years before present (YBP) (Lighty 1977; Lighty et al. 1978). Today only a few isolated colonies are found north of Fort Lauderdale.

The region of maximum coral reef development is restricted to south and west of Cape Florida, offshore of the Florida Keys archipelago (Figure 1). This small chain of islands extending from Soldier Key to Dry Tortugas exhibits a diverse pattern of hardgrounds, patch reefs, and bank reefs from 25 m to 13 km offshore. This is the only shallow water ($<$ 10 m) tropical coral reef ecosystem found on the Continental Shelf of North America, and has been referred to as "The Florida Reef Tract" (Vaughan 1914a). This discontinuous assemblage of reefs forms an arc paralleling the Keys' coastline in a general southwesterly trend. Landward, the reefs are bounded by the Keys and a series of shallow embayments (Biscayne Bay, Card and Barnes Sounds, and Florida Bay); seaward of the reefs are the Straits of Florida and the Florida Current. The Florida Current, a subsystem of the Gulf Stream, plays an important role in the existence and maintenance of coral reefs off southeast Florida. It modifies the environment by moderating winter temperatures. The current's source is tropical; hence, its waters are significantly warmer than resident shelf water masses during the winter, thereby modifying winter thermal conditions such that offshore reef development is not hindered by extremely cold weather that occasionally occurs when cold fronts intrude into southeast Florida. Inshore patch reefs, however, are more vulnerable to cold extremes caused by winter weather. The current system is dynamic, and eddies or meanders bring considerable volumes of water into the reef environment. This brings plankton, a food source, and new recruitment from nonresident populations to the reefs. The significance of the Florida Current cannot be overestimated when considering coral reef existence off southeast Florida.

tom river carrying its silt to the steep slope south of Hatteras, depositing occasionally a few patches of green sand along the sides of its course, while the upper waters are perfectly clear and of the deepest blue.

Corals alone cannot supply all the sand we know to be carried by the Gulf Stream. We must add to this the mass of silt, mud, and sand which come from pelagic animals, and which is distributed by the winds and waves, to be spread uniformly over large areas, as is well shown from the distribution of the immense mass of calcareous ooze over the whole of the bottom between Florida and Cuba. This mass undoubtedly owes its existence in part to the silt which the Gulf Stream brings from the southeastern edge and slope of the Yucatan Bank, in part to the accumulation of the pelagic fauna which the same great current sweeps along its course. The amount of work done by the animals living upon the reef in preparation for the grinding process of the breakers is very great. All writers upon the reefs have referred to the destructive agency of boring mollusks, annelids, and echinoderms, that riddle the coral branches and heads with holes, and prepare the way for their fracture into larger or smaller fragments.

The echinoderms found upon the flats seem to live almost exclusively upon the organic matter and foraminifera they find mixed with the coral sand, upon which they feed, and which fills their digestive cavity. Their action, however, while an important one, in that they reduce the sand to a smaller size, is yet very slight as compared to the action of the breakers upon the sea-face of the reef. Darwin and others have referred to this agency of the echinoderms as one among those at work in triturating the corals. By some observers, these animals are supposed to be browsing on the living coral. This is not the case either with holothurians and Diadematidæ or with clypeasteroids: living on flats, they swallow the sand as they find it. But with Cidaris and Echinometra, which dig out holes in the coral rock, the case is different. H. H. Guppy has also observed the holothurians full of sand on the flats of the reefs of the Solomon Islands.

The Loggerhead, Bird, and Bush Key banks, which protect

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This publication is dedicated to all who seek the truth, especially Taylor Alexander; lost friends Lin Brown and Frank Wescott; and especially Karilyn.

each other to a certain extent from the action of the strong winds opposed to the prevailing trade-winds, present a more normal growth than that of the North Key Bank, which is particularly exposed to the full fury of the northers; they must counteract to a great extent the action of the trade-winds. The distribution of the broken ground, the position of the masses of *Madrepora cervicornis*, and the trend of the sand flats, all alike show the conflicting action to which the two slopes of this great bank have been subjected. This counterbalancing action of the northers and of the trade-winds is also well shown by its effect on the position of the islands themselves. During the prevalence of southeasterly winds, East Key, Sand Key, and Middle Key extend bodily to the westward, the materials for their growth being washed from the eastern shores. The opposite takes place during the prevalence of northers. The outline of Loggerhead Key is also constantly shifting, and according to the officers of the Lighthouse Board, none of the landmarks furnished by these islands can be relied upon in the location of buoys.

What takes place upon the shores of the islands also takes place, of course, upon the flats. Owing to the action of the winds and waves, the whole mass of the surface of the reef is kept in more or less active movement, according to the depth of water on the flats and to their position. The coarser materials covering the flats and shore lines, and made up of large-sized fragments, are gradually changing to the coarse sand which forms the flats nearer the outer edge of the reefs; and this, in its turn, is changed into the fine silt which fills the channels, and eventually limits the growth of the corals to regions where they can find permanent lodging, and are not immediately under the influence of this shifting sand and silt. The quality of the sand forming the beaches at different points on the keys and flats depends entirely on its position. It will be coarser or finer, according to the exposure of the beach, and the finest sand is found in the most sheltered places, where the silt has free chance to settle. (See Fig. 53 for a view of a characteristic coral sand beach at Key West.) The scarcity of fossils in the coral limestones of the reef has already been dwelt

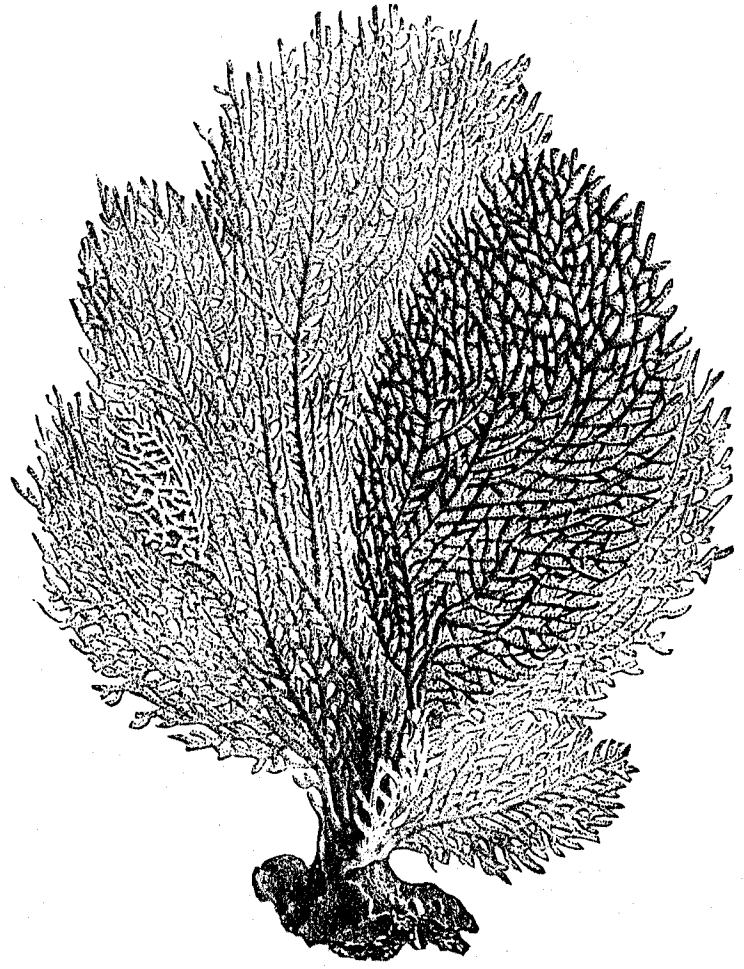


Fig. 52.—RHIPIDIGORGIA FLABELLUM. (Agassiz.)

CONVERSION FACTORS

Metric to U.S. Customary

Multiply	By	To Obtain
millimeters (mm)	0.03937	inches
centimeters (cm)	0.3937	inches
meters	3.281	feet
kilometers (km)	0.6214	miles
square meters (m^2)	10.76	square feet
square kilometers (km^2)	0.3861	square miles
hectares (ha)	2.471	acres
liters (l)	0.2642	gallons
cubic meters (m^3)	35.31	cubic feet
cubic meters (m^3)	0.0008110	acre-feet
milligrams (mg)	0.00003527	ounces
grams (g)	0.03527	ounces
kilograms (kg)	2.205	pounds
metric tons (mt)	2,205.0	pounds
metric tons (mt)	1.102	short tons
kilocalories (kcal)	3.968	BTU
Celsius degrees	$1.8(C^\circ) + 32$	Fahrenheit degrees

U.S. Customary to Metric

inches	25.40	millimeters
inches	2.54	centimeters
feet (ft)	0.3048	meters
fathoms	1.829	meters
miles (mi)	1.609	kilometers
nautical miles (nmi)	1.852	kilometers
square feet (ft^2)	0.0929	square meters
square miles (mi^2)	2.590	square kilometers
acres	0.4047	hectares
gallons (gal)	3.785	liters
cubic feet (ft^3)	0.02831	cubic meters
acre-feet	1,233.0	cubic meters
ounces (oz)	28.35	grams
pounds (lb)	0.4536	kilograms
short tons (ton)	0.9072	metric tons
BTU	0.2520	kilocalories
Fahrenheit degrees	$0.5556 (F^\circ - 32)$	Celsius degrees

upon, and their absence is readily accounted for by the constant disturbance of the shore-line deposits, which reduce little by little the larger fragments of shells and corals, or echinoderms, to a breccia, or again to oölite or fine sand. This is nowhere so well seen as on the shore line of Key West to the north of Fort Taylor. (Fig. 53.) There the outer reef is sufficiently distant to allow waves of considerable size to break upon this coast, and then strike to a low line of shore rocks. These rocks are completely riddled by larger or smaller cavities made by boring mollusks, annelids, sea-urchins, etc., or left by fossils or fragments of corals which have fallen out. Thus weakened, large masses are easily undermined by the water, which washes around them with considerable force. They fall off, become then broken into smaller and finer pieces, which are again reground in their turn, and are finally either re-soldered into finer breccia or coarse oölite, or into the finest oölite or sand, according to the composition of the rock. This is then cemented again to the shore line, forming a new line, more or less regularly stratified, dipping towards the sea, and, when exposed to the action of the air, soon coated with a thin film of hard limestone. This hardens, and forms the ringing crust of the rocks found everywhere on the keys. This coating is formed with great rapidity. An exposure between two tides is sufficient to form such a thin coating, as I have repeatedly had occasion to observe in the deposition of finer oölitic sands which fill the rock-pockets just within reach of the waves at high tide. A process of undermining similar to what has been observed at Key West takes place along all the coral-rock shores which happen to be exposed to the action of the sea. From the description of Rein and others, this undermining action, operating on a very much larger scale on æolian deposits of considerable altitudes, must be the principal agent in the formation of some of the peculiarly characteristic features of the Bermuda Islands. On the east and west shore of Loggerhead, near the northern extremity, we can trace admirably the successive layers of the coral limestone which have been deposited and have had an opportunity to harden between the tides, forming what appear to be stratified beds, with their outcrops running as a gen-

ABBREVIATIONS

BNP	Biscayne National Park
CG	(U.S.) Coast Guard
DER	Department of Environmental Regulation (Florida)
DNR	Department of Natural Resources (Florida)
DOA	Department of Administration (Florida)
DOS	Department of State (Florida)
EPA	(U.S.) Environmental Protection Agency
FWS	(U.S.) Fish and Wildlife Service
GS	(U.S.) Geological Survey
JPCRSP	John Pennekamp Coral Reef State Park
KLNMS	Key Largo National Marine Sanctuary (originally referred to as Key Largo Coral Reef Marine Sanctuary in early General Management Plan developed by NOAA)
LKNMS	Looe Key National Marine Sanctuary
MMS	Minerals Management Service
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
NPS	National Park Service
PHC	Petroleum hydrocarbons
Std. Dev. or SD	Standard deviation
USACE	U.S. Army Corps of Engineers
YBP	Years Before Present

eral thing parallel to the bend of the shore or at a slight angle from it, and dipping on the one side to the eastward and on the other to the westward.

The bank to the west of the Tortugas has large heads of astræans (Fig. 54) and madrepores growing up on it at a depth

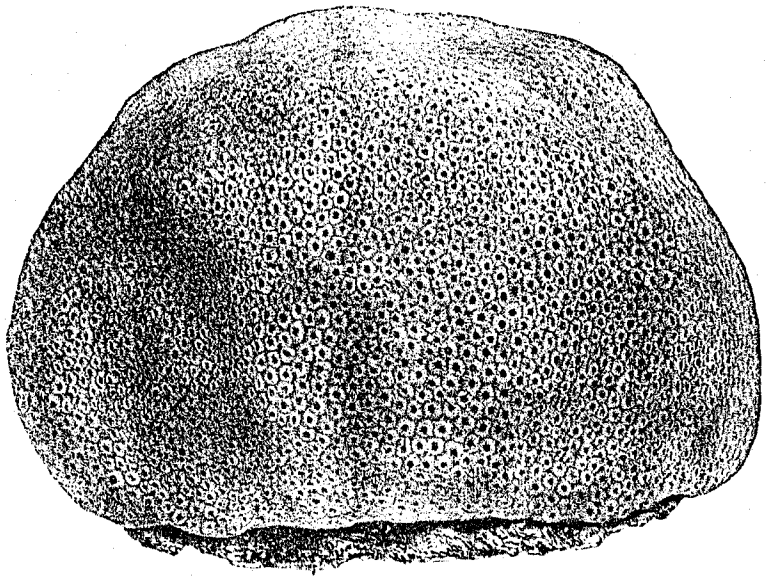


Fig. 54. — Orbicella annularis. (Agassiz.)

of from six to seven fathoms. Gorgoniæ are still found at a somewhat greater depth. This bank is an excellent specimen of an isolated coral patch, such as must have formed the basis of all the keys and reefs. In time it will undoubtedly form a new reef, flush with the surface, to the westward of the Tortugas. The greatest depth at which reef-building corals have been observed to grow is in the Southwest Channel on the steep banks of White Shoal, and in the channel to the southwest of Bird Key, where madrepores grow to a depth of about ten fathoms.[1] As a general rule, however, the corals are choked

[1] Murray found off the slope of the reef at Tahiti that "the whole of the space from the edge of the reef to a depth of about thirty-five fathoms was covered with a most luxuriant growth of corals, with the exception of one or two small spaces where there was white coral sand."

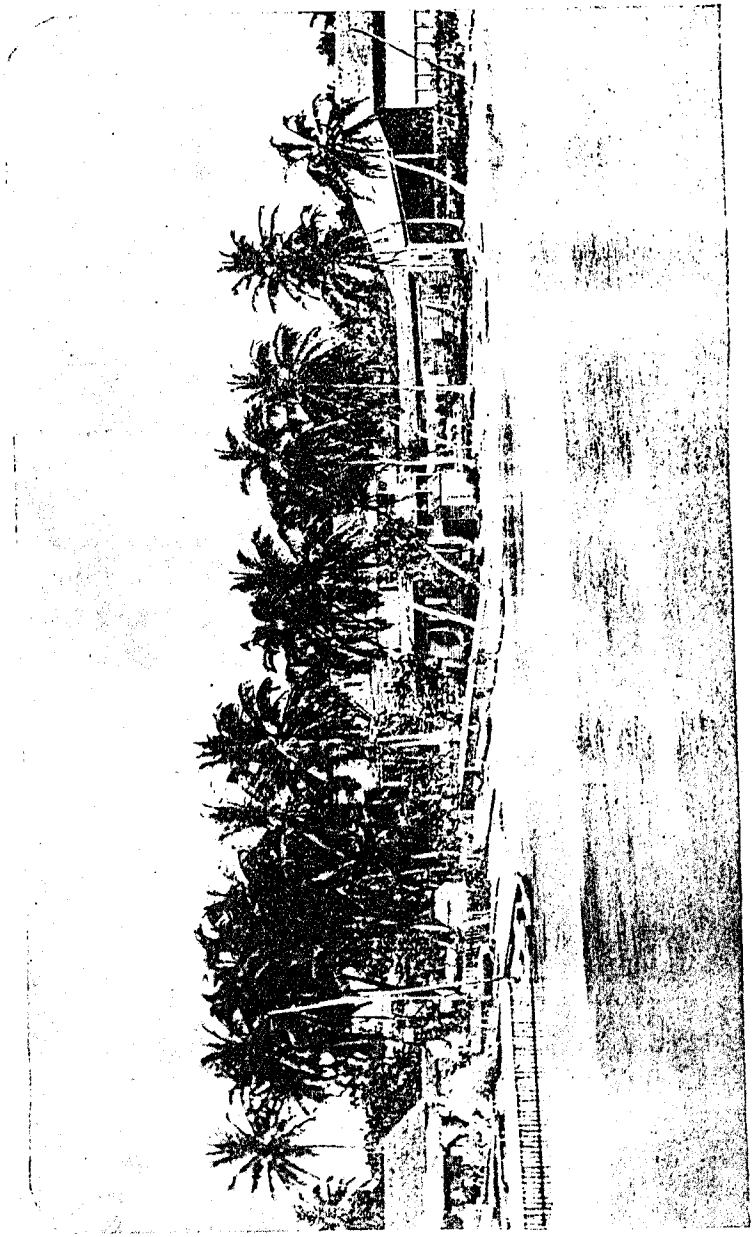


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below six fathoms by the ooze, and their place is taken by gorgonians.

All estimates of the age of the southern extremity of Florida, or of the reef alone, must necessarily be very defective. The great age assigned by Professor Agassiz to the northern part of the peninsula may not be exaggerated, if it be understood as including the time at which the Vicksburg limestone forming its backbone was deposited. But the extension of the coral reefs proper so far north in Florida has never been proved. The rate of growth of the reef-builders is very rapid, and it is quite possible that the reef-builders of the Florida Reef began at once all along the line extending from Key West to Cape Florida, and quickly reached the surface, forming at first a barrier somewhat less compact than the present line of reef. Uncertain as we are respecting the time at which the various parts of the reef reached the surface, we can only say that in Florida, limiting the estimate strictly to the depth at which corals grow, it would probably take from one thousand to twelve hundred years for corals to rise from the seven-fathom line to the surface. This would give us no clue whatever to the actual age of the reef, because it is difficult to determine how far the width of any coral reef is due to the growth of coral. But supposing the reef to have an average width of half a mile, and its lateral growth to be say four or five times more rapid than its vertical increase, we should get at least twenty thousand years as the age of the outer reef. It is quite possible for a great width of reef to be forming at one time, and to spread laterally with rapidity if the plateau upon which it grows is of the right depth. Take, for instance, the width of flats upon which madrepores flourish. A plateau at favorable depth would very soon be covered by them; they would spread rapidly until they reached the edge beyond which no corals could thrive, on account of the depth.

Thus we see, from the sections and a study of the distribution of the corals, that at the present day material is constantly added to the knoll forming the Tortugas; that this material is derived either from the animals and plants living upon the reef, or from the pelagic animals which die while passing through

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the channels; and that we can find nowhere any trace of elevation. Here the calcareous material has evidently been heaped up to its highest point by the influence of the waves or winds. Furthermore, we see growing to the westward of the Tortugas a knoll similar to that which has formed the Tortugas themselves, and which will form, in the course of time, an island or a series of islands like them to the westward. It is further evident, also, that the Alacran Reef has been built up in the same way, and that its peculiar atoll shape is due to the action of the prevailing winds and currents, and not to any subsidence of the great Yucatan plateau.

The character of the fauna and flora of the Tortugas is interesting as corroborating the comparatively recent age at which the reef has been formed. We find, as we go north along the keys, that the nearer we come to the mainland of Florida, the greater the number of plants characteristic of the mainland. As we reach islands more or less inaccessible, or islands merely formed by flats which have reached low-water mark, the vegetation consists almost wholly of mangroves. Yet at the Tortugas, in spite of the narrow channel which separates them from the Marquesas, I saw but a single diminutive mangrove plant, while a few bay-cedars, as they are called, a vine with a thick white flower, and Bermuda grass have alone found their way there, although the Tortugas are in the direct line of the prevailing winds from the Marquesas. One of the species of land shells common at Key West has already found its way to the Tortugas. The group is visited by pelicans, cranes, humming-birds, plovers, and a few land birds. It being the winter season when I visited the place, the insects were few in number. No terrestrial reptiles have been found on the Tortugas, while at Key West there are many of the frogs, toads, lizards, and snakes characteristic of the southern spit of the mainland, — all this showing that the Tortugas reefs have not been above the level of the sea long enough to have received as yet the fauna or flora characteristic of the more northern line of keys.

The explanation given here of the formation of huge deposits of limestone from the limestone carcasses of invertebrates takes

for granted that the most favorable conditions for their support exist; and this condition we assume to be an abundance of food, brought to them by the great oceanic currents passing over the regions where these submarine plateaux are forming. We know as yet too little of the fauna of the oceanic basins to be able to affirm how far the population of the bottom depends upon the food it receives from oceanic currents. We can only judge by analogy. No marine fauna has been explored which equals in variety or in the number of its individuals that of the Caribbean and of the Gulf of Mexico, from the depth of two hundred and fifty to about one thousand fathoms. It has proved richest in the districts most favorably situated with regard to the currents and the food supply they bring in their track. It is but natural to extend this effect to other oceanic currents, and in their track we may therefore expect to find the most favorable conditions for the support of an immense fauna. In fact, the question of food is of the utmost importance to the distribution, not only of marine, but of terrestrial animals; and the absence or presence of an abundant supply of suitable nourishment must of necessity be an all-important factor in the character and variety of the fauna of any place or period, — far more influential, perhaps, than the many obscure physical causes upon which we are so apt to explain the distribution of animal life. On the continental ledges, where the shore detritus is gradually accumulated, bringing with it a large amount of animal and vegetable food, we find the most populous fauna near the hundred-fathom line. When, in addition to the action of the influences which have accumulated the shore detritus, we have a continental shore or plateau bathed by a great and powerful current, bringing with it an abundance of pelagic life, we may expect a superabundant supply of food, and consequently a fauna of unusual richness and variety. The fauna of the Pourtalès Plateau, of the hundred-fathom slope to the westward of the Tortugas, of the northeastern slope of the Yucatan plateau, of the windward side of the Lesser Antilles, and of the continental slope of the eastern coast of the United States below the hundred-fathom line, are all examples of such districts supporting a marine fauna of sur-

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passing richness. In a similar way, we may expect to find in the track of the Pacific equatorial current the most favorable conditions for the support of a rich and varied marine fauna. The "Challenger" found, perhaps, no richer dredging fields than off the coast of Japan, which lie directly in the track of the Japanese stream; the fauna of the Kuro Siwo may be considered as the Pacific equivalent of the Florida and Caribbean fauna.

In past geological times the effect of the currents in determining the distribution of the marine invertebrates must have been as marked as it is at the present day. As long as we had a great equatorial current running practically unbroken round the world, and only slightly deflected by the continental islands of Central America and of the East Indies, which stood in the path of this equatorial belt, it was natural that we should have a very extensive geographical range for all the tropical marine forms. It was only after the complete shutting off or comparative isolation of the Atlantic from the Pacific that different physical conditions began to exist simultaneously, which were of the greatest importance in reducing the supply of food to the animals on the west coast of the continental barriers, and in extending towards the north, as far as the temperature would allow, a supply of food far more abundant than that with which the fauna of the eastern coast was supplied before such a break of continuity existed. As this separation of the Atlantic and Pacific probably took place late in the cretaceous period, and was perhaps not completed till the middle tertiary, we shall naturally expect to find the marine fauna of the earlier geological periods of the Old and the New World to be very similar, and consisting of many identical species. These older faunæ flourished on the shores and continental shelves which were washed either by the equatorial currents, or by branches extending both north and south along the then existing continents and continental islands; and where we now find rich fossiliferous deposits we may feel assured that the beds at the time of their formation were either formed along a continental shelf, or lay in the track of a primary or a secondary marine current, which supplied an abundance of pelagic food indirectly necessary for the support of any rich marine fauna.

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THREE CRUISES OF THE BLAKE, VOL. I.

BULLETIN

OF THE

MUSEUM OF COMPARATIVE ZOÖLOGY

AT

HARVARD COLLEGE, IN CAMBRIDGE.

VOL. XIV.

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A Contribution to American Thalassography.

THREE CRUISES

OF THE

UNITED STATES COAST AND GEODETIC SURVEY

STEAMER "BLAKE"

IN THE GULF OF MEXICO, IN THE CARIBBEAN SEA, AND ALONG THE ATLANTIC COAST OF THE UNITED STATES, FROM 1877 TO 1880.

BY

ALEXANDER AGASSIZ.

IN TWO VOLUMES.

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PREFACE

This profile of the coral reef community of south Florida is one in a series of community profiles that treat coastal and marine habitats important to humans. Coral reefs are highly productive habitats which provide living space and protection from predation for large populations of invertebrates and fishes, many of which have commercial value. Coral reefs also provide an important economic benefit by attracting tourists to south Florida.

The information in the report can give a basic understanding of the coral reef community and its role in the regional ecosystem of south Florida. The primary geographic area covered lies seaward of the coast from Miami south and west to the Dry Tortugas. References are provided for those seeking indepth treatment of a specific facet of coral reef ecology. The format, style, and level of presentation make this synthesis report adaptable to a variety of needs such as the preparation of environmental assessment reports, supplementary reading in marine science courses, and the education of participants in the democratic process of natural resource management.

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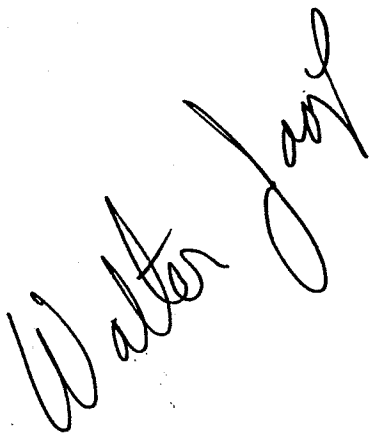
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THE ECOLOGY OF THE SOUTH FLORIDA CORAL REEFS: A COMMUNITY PROFILE

by

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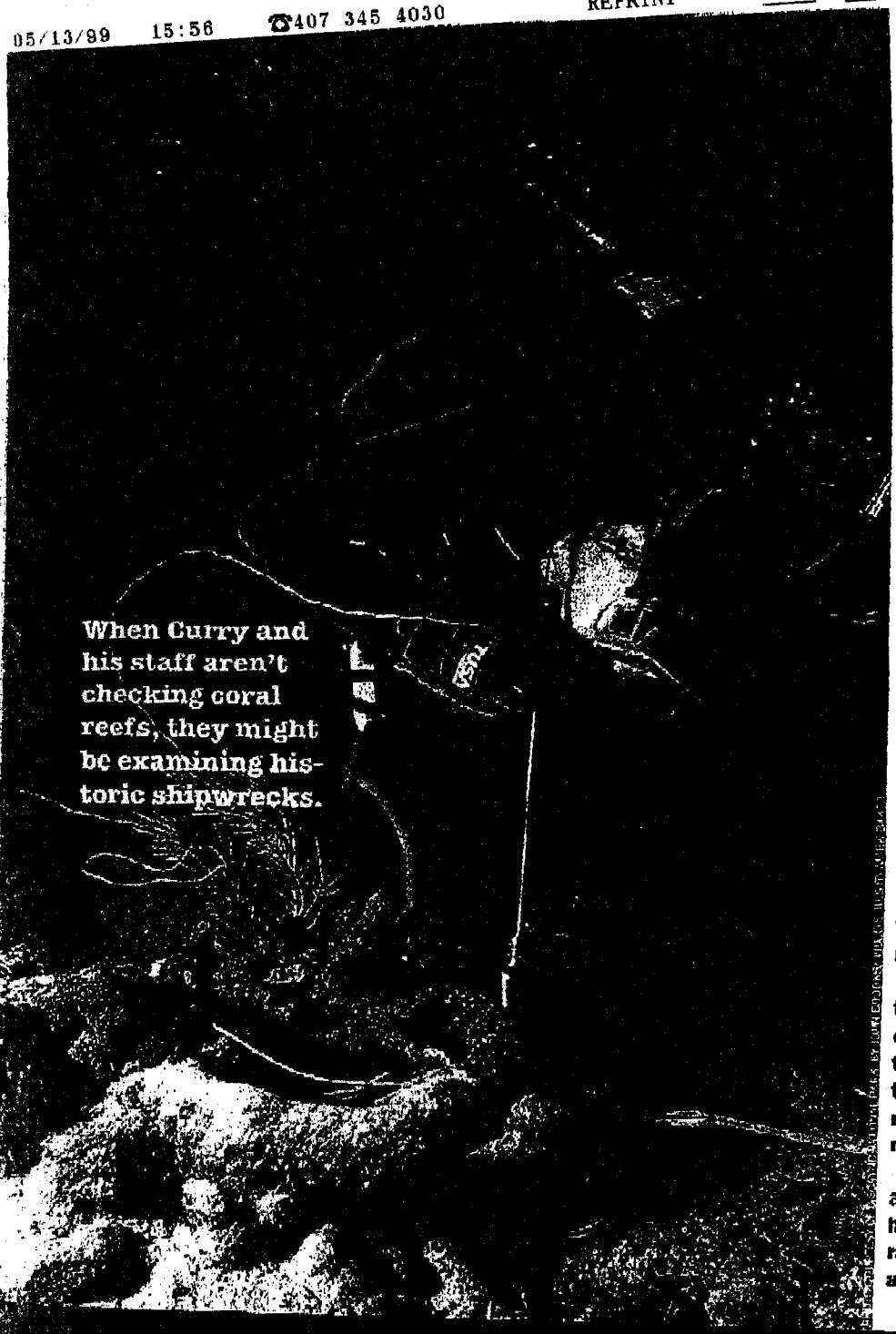
Prepared for

National Coastal Ecosystems Team
Division of Biological Services
Research and Development
Fish and Wildlife Service
U.S. Department of the Interior
Washington, D.C. 20240

and

Gulf of Mexico OCS Regional Office
Minerals Management Service
U.S. Department of the Interior
Metairie, Louisiana 70010


Science with Attitude
Contact kids
CTW
CHILDREN'S TELEVISION WORKSHOP JULY/AUGUST 1999
Coasters
Take You
for a Ride!
Mount
Rushmore
Gets a Face-Lift
Junior
Lifeguards
Make a
Splash



When Curry and his staff aren't checking coral reefs, they might be examining historic shipwrecks.

Some Like It Wet!

Richard Curry: Science Coordinator, Biscayne National Park, FL

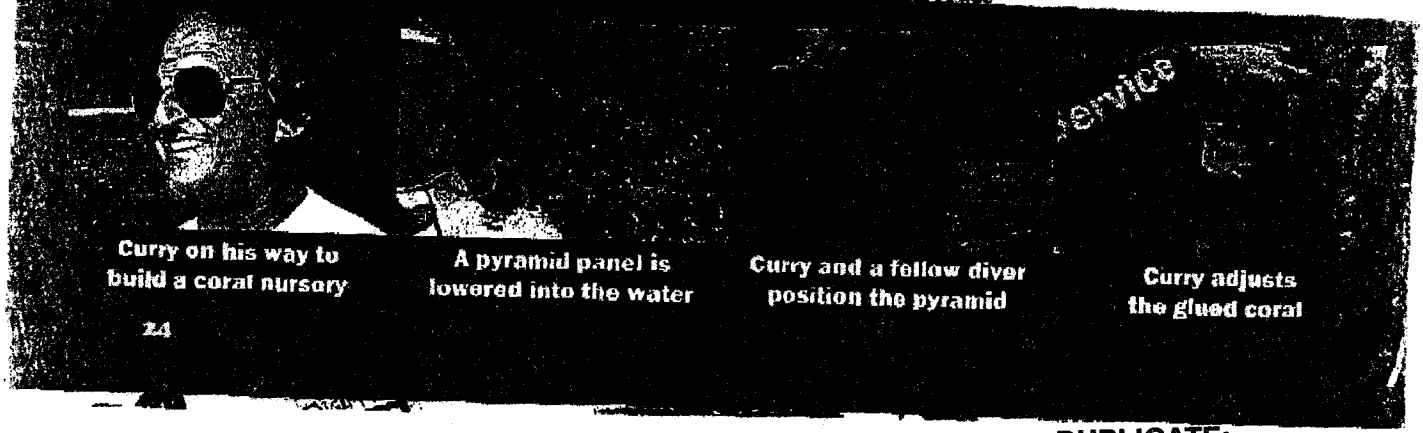
Richard Curry is all wet. That's because 95 percent of his "office" is underwater! Biscayne is one of America's five undersea national parks. Curry spends much of his time studying and repairing the park's coral reefs: underwater ridges that are home to fish, plants and other marine life.

Lots of things can be dangerous to the coral reefs. "Anchors that drop on the reefs cause the most damage," Curry told CONTACT KIDS. Fishing lines, spear guns and debris from boats are also to blame for broken coral.

Damaged coral reefs can throw off the whole marine ecosystem. It's Curry's job to make sure that doesn't happen. To help reverse the problem, he started his own coral reef recovery program.

Growing coral is no easy task. First, Curry places mini concrete pyramids underwater. He glues damaged coral to the pyramids. When the coral matures, Curry attaches it to a real coral reef.

So far, the program's been a success. "One of the sites has had a 100-percent survival rate," says Curry. Spoken like a proud papa! ◆



Curry on his way to build a coral nursery

A pyramid panel is lowered into the water

Curry and a fellow diver position the pyramid

Curry adjusts the glued coral

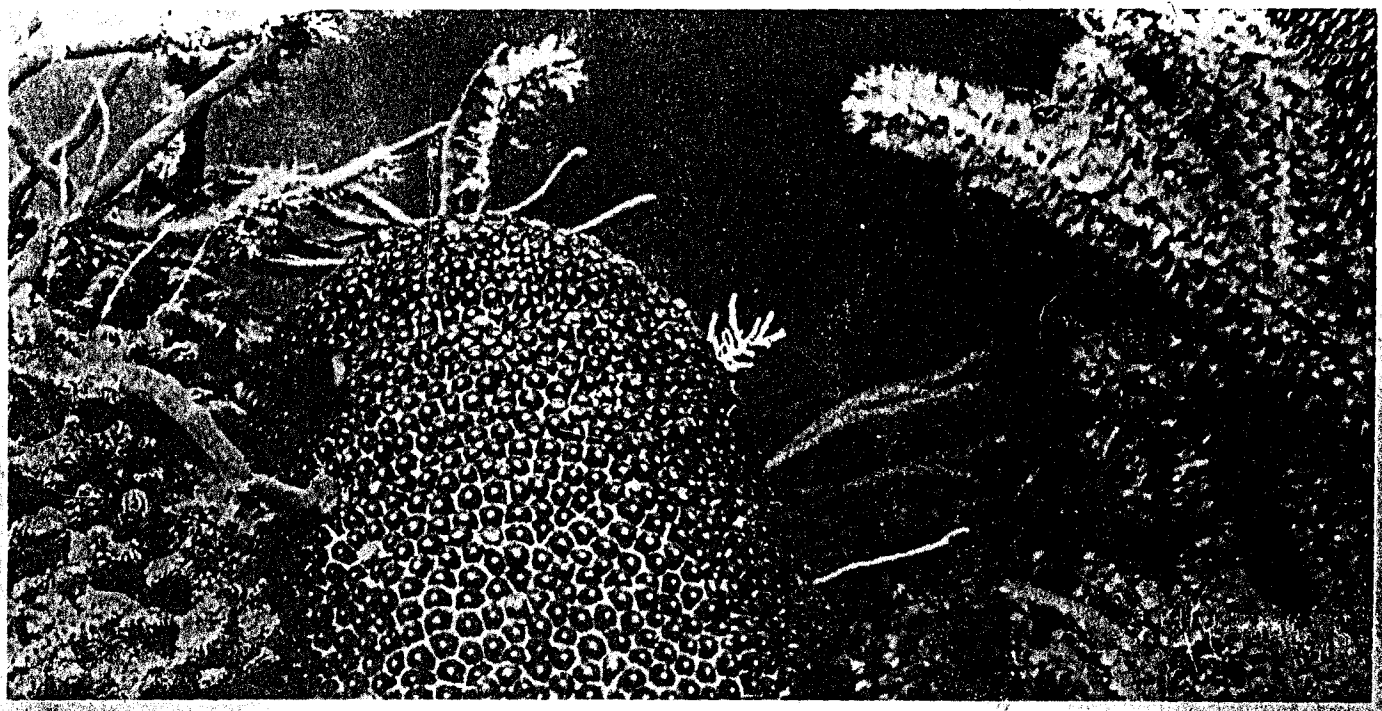
DUPLICATE:
Original in
Museum Archives
BSC-118

W. Jaap

FWS/OBS-82/08
August 1984

Minerals Management Service
MMS 84-0038

THE ECOLOGY OF THE SOUTH FLORIDA CORAL REEFS: A Community Profile







U.S. Department of the Interior

Fish and Wildlife Service
Minerals Management Service

Date: 9/28/98
Sender: Caroline Rogers
To: bob@wayback.er.usgs.gov, dennis.hubbard@oberlin.edu, Jimmy Johnston, BISC Science, Richard Curry, Brendalee Phillips
cc: Russ Hall, Nick Funicelli
Priority: Normal
Subject: GC proposal

Here is the latest version of our proposal(attached in Word and RTF). This is the best I can do under the circumstances (still in recovery mode here with only intermittent generator power,lots of unhappy electronics, and lots of very hot, sticky people). The proposal must be finished in 2 days (I leave on Thursday for 8 days). If you want me to make changes, PLEASE make it very clear just what you want changed--do not insert a few words here and there and send it back to me so I have to hunt for the changes you've made! You can insert words within brackets or with asterisks next to them so I know what you have changed. If you feel a whole paragraph needs to be rewritten, please supply the new paragraph and let me insert it in the text.

We are still working on the budget.

Denny--please send me your one page CV on e mail, with a copy to Nick.

Thanks to all of you for providing excellent text for this proposal. I regret that it hasn't been possible for me to be in touch with you more as I have worked on it. We are feeling lucky that the storm didn't do more damage. Hope it hasn't disrupted Bob's or Jimmy's lives too much!

Caroline

If you can't read these attachments, let me know. My computer will be off for part of the afternoon but Ii'll try to keep checking e mail messages when I can.


gc.rtf


gc.doc

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
562	GL	14.05	19.87	W				4.8			
563	GL	17.77	21.54	W				9.0			
564	GL	16.71	21.55	W				3.0			
565	YE	18.45	22.04	W				5.6			
566	GR	18.52	22.06	W				5.6			
567	GR	18.60	24.58	W				5.0			
568	GR	21.33	22.04	W				5.6			
569	GL	21.10	23.31	W				8.0			
570	GL	20.10	24.87	W				9.4			
571	GL	17.30	25.30	W				8.2			
572	GL	16.49	26.70	W	6.0	6.2	4.6	6.6	0.2	-1.6	2.0
573	YE	12.00	26.32	W				7.4			
574	GL	27.40	10.26	W				10.2			
575	GL	10.10	29.67	W				6.0			
576	GL	10.54	28.89	W				11.8			
577	GR	13.81	29.67	W				3.6			
578	GR	13.79	29.62	W				5.2			
579	GR	16.09	28.81	W				4.0			
580	GL	16.24	28.87	W				2.2			
581	GL	14.16	29.72	W				4.2			
582	GL	15.24	30.20	W				8.4			
583	GL	14.13	24.78	W				3.6			
584	GL	15.25	23.92	W				7.0			
585	GL	16.17	23.98	W				4.0			
586	GR	14.70	23.65	W				10.2			
587	GL	14.35	27.26	W				8.0			
588	GL	19.49	29.11	W		5.6	5.8	6.4		0.2	0.6
589	GR	19.00	28.07	W				9.0			

BISC Science Files: Biscayne Section: Coral Reefs: Ecology: General

DUPLICATE
Original in
Museum Archive
BISC-118

Version: Sept. 28
TITLE: Changes in coral reef structure and function over different spatial and temporal scales: a case study in four U.S. National Parks

BRD PRINCIPAL CONTACT:
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OBJECTIVES/JUSTIFICATION
This project addresses coral reefs in national parks in the US Virgin Islands [Virgin Islands National Park (VIIS)and Buck Island Reef National Monument (BUIS)] and in Florida [Dry Tortugas National Park (DRTO) and Biscayne National Park (BISC)]. These reefs are subject to a range of different anthropogenic and natural stresses. The overall objective is to detect changes in coral reef structure over different spatial and temporal scales and to relate changes in structure to changes in function, specifically calcification rates. Selected biological, physical and chemical aspects of reefs in 4 national parks will be examined. The project is envisioned at three spatial scales: 1) remote sensing (Responsibility: J. Johnston, BRD National Wetlands Research Center, Mapping Division): production of maps showing distribution of coral reefs based on most recent data available; 2) single reef zones: determination of calcification rates (Responsibility: R. Halley, Geologic Division—Coastal and Marine Program) for areas of reefs characterized by quantitative underwater videos (Responsibility: C. Rogers, BRD-FCSC); physical oceanography—current studies (Responsibility: DK Hubbard, Oberlin College); 3) coral colonies: a) in situ examination of density of coral juveniles ("recruits") along transects within reef zones described in #2 (Responsibility: C. Rogers, BRD-FCSC); b) coral cores (Responsibility: Oberlin College). The t emporal component of the project includes a comparison of a time series of aerial photos for detection of structural changes in coral reefs, examination of coral cores for past calcification rates, and measurements of reef function (calcification) over 24 hour periods during the winter and summer.

Need:
This proposal describes a series of mapping, monitoring, and research tasks relevant to the President's Executive Order on Coral Reef Protection (June 11,1998). The U.S. and International Coral Reef Initiatives have drawn attention to the continuing deterioration of coral reefs worldwide. Coral reefs are the primary emphasis of the DOI Inventory and Monitoring Program for the Virgin Islands (USVI) and Florida, and one of the important ecosystems cited in the Geologic Division strategic plan (Bohlen et al. 1998). They have been the focus of several recent USGS workshops (e.g., Field et a l. 1998)..

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
486	GL	28.10	10.97	W			7.4	8.6			1.2
487	GL	28.56	12.72	W			15.0	17.6			2.6
488	GL	28.66	13.27	W			5.2	5.6			0.4
489	GL	28.10	8.65	W			12.6	14.8			2.2
490	GL	28.72	7.28	W			9.8	ns			
491	GR	28.05	4.64	W			13.0	15.2			2.2
492	YE	28.43	6.60	W			10.4	ns			
534	GL	32.95	8.29	W				5.4			
535	GR	31.44	1.23	W				49.4			
536	GR	28.60	8.09	W				9.2			
537	GL	28.27	8.17	W				5.0			
538	GR	26.98	6.77	W				13.0			
539	GR	27.47	6.86	W				4.8			
540	GL	26.20	13.34	W				10.8			
541	GR	26.75	10.75	W				10.4			
542	GL	28.12	13.25	W				4.6			
543	GL	25.65	11.05	W				5.2			
544	GR	20.85	11.93	W				14.2			
545	GR	22.84	10.24	W				12.6			
546	GL	23.71	13.85	W				6.4			
547	WO	19.37	13.33	W				8.6			
548	GL	20.60	15.83	W				10.0			
549	GL	21.60	15.62	W				6.0			
550	GL	22.93	18.65	W				5.0			
551	GL	17.75	15.75	W				16.0			
552	GR	17.10	16.65	W				13.0			
553	GL	16.50	16.79	W				10.4			
554	YE	16.77	16.13	W				9.2			
555	YE	19.10	18.19	W				4.8			
556	GR	19.66	18.40	W				8.6			
557	GL	22.00	18.08	W				8.6			
558	YE	21.90	17.99	W				12.2			
559	GL	21.85	17.96	W				3.0			
560	GR	18.85	20.30	W				9.6			
561	YE	18.28	19.66	W				7.8			

Recent assessments of the status of coral reefs worldwide conclude that 10% of the reefs have been destroyed, 60% will be lost within the next 40 years, and only 30% can be considered stable (Wilkinson 1992). Although some scientists argue that existing data are inadequate to draw these conclusions because most of the world's reefs have not been studied, it is clear that the amount of living coral on many reefs in the Caribbean and western Atlantic has declined while the abundance of algae has increased (Ginsburg 1994). Our current knowledge is inadequate to determine if this shift to greater algal abundance is just part of a natural cycle although most scientists conclude that some of the changes may be unprecedented and irreversible.

Background: Natural stresses such as hurricanes and coral diseases as well as anthropogenic factors such as increased runoff, damage from boats, and sewage input have killed corals and altered the relative abundances of reef organisms. Coral reefs are among the ecosystems which could be most vulnerable to changes in climate, although rising sea level could actually benefit reefs which have already reached the surface. Increased CO_2 could lower calcification rates with far-reaching effects on reef structure (Pennisi 1998). Though not the most abundant organisms on Caribbean reefs, corals create the reef's physical structure, providing habitat for fishes and other organisms. Corals provide clues to the present and to the past. They are sensitive to several physical factors associated with future climate---elevated CO_2, higher temperatures, and increased UV radiation. They respond to increased temperatures and UV radiation by "bleaching" (losing color). When corals bleach, they cease reproduction and their growth rates decrease (e.g., Szmant and Gassman 1990).

Coral skeletons contain a record of past environmental conditions. For example, they have annual (or near annual) growth bands because skeletal densities vary with cooler and warmer temperatures. Through examination of coral cores ("sclerochronology" studies) one can learn about calcification rates in the past and compare those to present rates.

Monitoring of reef structure and function at selected reefs in the four parks is the central focus of this project. Existing data are severely limited both spatially and temporally, with insufficient data from widely separated geographic areas over long periods of time. To address these scale deficiencies, we have included a remote sensing component to this proposal and the examination of coral cores for information on past environmental conditions. Use of these two tools may partially make up for the lack of monitoring data from decades ago. The project includes the evaluation of remote sensing as a tool for tracking changes in coral reef structure, including rearrangement of shallow zones (reef crests) by hurricanes. We will find out if it is possible to use aerial photos to track the widespread mortality of the primary reef-building species Acropora palmata (elkhorn coral) which was documented over the last 2 decades.

We propose to measure parameters of carbon budgets to assess reef conditions. For many years carbon budgets of reefs have been studied by measuring geochemical parameters of carbon utilization (Smith, 1973). The techniques used to make these measurements have been greatly refined during

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
451	GR	16.39	22.50	W			6.8	8.4			1.6
452	GR	14.50	22.45	W			10.2	13.8			3.6
453	GL	15.80	20.59	W			8.8	7.8			-1.0
454	GL	15.93	20.57	W			8.0	10.2			2.2
455	GL	16.32	20.74	W			9.4	9.6			0.2
456	GL	17.70	21.87	W			9.2	11.4			2.2
457	GL	20.53	24.55	W			12.2	13.4			1.2
458	GL	20.49	24.20	W			6.8	6.2			-0.6
459	GL	19.90	22.99	W			5.6	8.0			2.4
460	YE	20.15	19.85	W			5.2	5.8			0.6
461	WO	19.75	19.07	W			8.2	9.4			1.2
462	GR	19.90	18.99	W			12.2	14.4			2.2
463	GL	17.61	18.57	W			5.2	7.4			2.2
464	GL	16.32	19.10	W			5.2	7.0			1.8
465	GL	15.85	17.77	W			7.6	10.4			2.8
466	GL	21.80	16.68	W			10.4	11.2			0.8
467	GL	22.44	16.83	W			14.2	16.4			2.2
468	GL	23.39	14.58	W			10.8	12.8			2.0
469	GL	23.12	14.89	W			9.4	10.2			0.8
470	WO	22.65	13.88	W			8.8	10.2			1.4
471	GL	20.30	14.90	W			10.4	12.6			2.2
472	GL	19.10	14.56	W			6.8	7.6			0.8
473	GL	18.65	14.45	W			4.8	6.0			1.2
474	YE	24.08	13.54	W			5.4	6.2			0.8
475	YE	23.03	11.23	W			5.2	7.0			1.8
476	GL	23.95	10.80	W			12.4	13.4			1.0
477	GL	23.97	10.97	W			5.8	7.2			1.4
478	GR	25.40	13.40	W			7.8	9.6			1.8
479	GL	26.63	14.22	W			10.2	12.8			2.6
480	GL	26.53	14.45	W			6.2	7.2			1.0
481	YE	28.00	13.24	W			12.0	12.0			0.0
482	YE	27.45	12.86	W			9.0	10.0			1.0
483	GL	24.00	8.17	W			5.2	6.0			0.8
484	GR	26.78	8.40	W			18.6	19.2			0.6
485	GL	27.21	9.32	W			11.2	12.0			0.8

the past two decades because they are, in part, also the techniques used for measuring global atmospheric CO_2 exchange with the ocean. These refined procedures can now be used again to study coral reefs (Buddemeier and Kinzie 1998).

On many reefs, a variety of natural and human stresses have caused a shift in the carbon balance between carbon used for constructing carbonate skeletons and carbon used to grow fleshy tissues of algae ("macroalgae"). In some extreme cases coral reefs have been almost entirely overgrown by algae (Hughes 1994). We propose to measure this balance using geochemical techniques and to characterize reefs with a range of live coral cover. Two important outcomes of these measurements is an improved understanding of the CO_2 contribution of coral reefs to the atmosphere and a methodology to assess the direct impact of increased CO_2 on coral reefs.

PROCEDURES/METHODS:

Rationale for Selection of Study Sites

Long-term monitoring sites were established on reefs in all of these parks under an NPS program which began in 1988, and the DOI Inventory & Monitoring (I&M) program has supported additional work in the USVI parks and Dry Tortugas National Park. Several sets of aerial photos are available for all of these sites. Information on changes in coral reefs at Dry Tortugas comes from comparison of a map produced by Agassiz in 1881 with one from 1976 (Davis 1982).

The coral reef monitoring which NPS and BRD have conducted in national parks in the USVI and Florida in conjunction with state and university scientists is one of only a few long-term monitoring programs in the Caribbean and western Atlantic (Connell 1997). Data on cover by coral and algae are available for all 4 parks, and effects of different stresses have been documented for some reefs. Underwater videotapes which provide a statistically quantifiable and permanent visual record of reef characteristics are available for reefs in the I & M program.

A major task for Year 1 will be the selection of each study site based on the need to include reefs with a range of different reef types with variations in coral cover. (Aerial photos obtained for the remote sensing portion of the project will be examined in making site selections.) At least one of our sites on St. John will be Lameshur Bay, for which we have the longest data set. (This site is also under consideration for inclusion in a "marine reserve" within park waters) . We may also select Hawksnest Bay for which we have information on siltation effects and coral growth rates (Hubbard ***) because it is a shallow reef exhibiting some signs of recovery in elkhorn coral populations. At least one study site at Buck Island will also be in an elkhorn zone. Deeper reef zones will be examined at either Biscayne or Dry Tortugas National Park. Coral cover at the Lameshur Bay reef is now only 12%, and we will select at least one reef with relatively high coral cover for comparison (over 40% is high for the Caribbean/western Atlantic).

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
414	GL	10.52	26.30	W		5.4	ns	6.4			
415	GL	10.59	27.35	W		5.2	6.8	9.0		1.6	2.2
416	GR	12.34	27.27	W		3.8	4.4	7.0		0.6	2.6
418	GR	19.85	29.24	W		9.4	9.8	10.4		0.4	0.6
419	YE	20.00	29.42	W		6.0	6.0	8.0			2.0
420	GL	18.79	28.97	W		6.2	6.8	8.0		0.6	1.2
421	GL	10.58	28.95	W		8.8	9.6	ns		0.8	
422	WO	13.79	29.79	W		8.4	10.2	14.0		1.8	3.8
423	YE	16.70	29.35	W		8.2	ns	8.0			
424	GL	16.60	29.35	W		10.2	12.0	13.0		1.8	1.0
425	GL	10.15	28.85	W			9.6	10.0			0.4
426	YE	14.70	30.23	W			5.8	6.6			0.8
427	WO	13.20	30.05	W			6.8	7.6			0.8
428	GR	13.40	29.93	W			4.8	ns			
430	GL	13.97	28.20	W			3.4	ns			
431	GL	13.85	28.28	W			5.0	6.0			1.0
432	GL	11.25	25.79	W			5.2	5.4			0.2
433	GR	16.10	27.30	W			8.0	10.6			2.6
434	GR	16.19	27.58	W			5.8	5.8			0.0
435	GR	16.92	27.66	W			3.8	5.0			1.2
436	GR	19.00	28.76	W			9.2	9.2			0.0
437	WO	19.50	27.00	W			9.8	11.8			2.0
438	GR	26.00	26.79	W			6.2	7.0			0.8
439	GR	19.43	26.76	W			4.2	5.8			1.6
440	GR	19.45	26.40	W			7.8	9.2			1.4
441	GR	18.60	26.85	W			22.0	28.4			6.4
442		17.94	26.42	W			4.8	6.2			1.4
443	GR	17.32	26.13	W			8.0	12.0			4.0
444	GR	18.10	25.95	W			7.8	8.0			0.2
445	GR	17.41	25.80	W			8.4	16.0			7.6
446	GR	16.94	25.55	W			3.8	ns			
447	GR	14.45	24.81	W			5.2	5.4			0.2
448	GR	13.90	25.59	W			4.2	6.2			2.0
449	GL	14.42	23.95	W			3.6	5.0			1.4
450	GR	19.40	25.65	W			21.2	25.0			3.8

1. REMOTE SENSING: CORAL REEF MAPPING TASKS

We propose to map and quantify the spatial distribution (geographic extent) of coral reefs in all four parks and to attempt to document changes in reef structure over time (1940's to present) using high resolution photography. The locations, geometry., and distribution of reefs will be mapped using state of the art precision optics and camera systems that can produce very high spatial resolution images (1:24,000 scale or greater). These aerial photographs will be taken at fixed intervals to ensure sufficient overlap and sidelaps for stereoscopic interpretation (Stereoscopic interpretation will follow the U.S. Fish and Wildlife Service's National Wetlands Inventory Mapping protocols using 10X magnification). Due to distortions inherent in aerial photography, objects are usually not represented in their actual position or configuration. Photogrammetry is often used to remove these distortions and produce georeferenced map information. The results are three dimensional models of the earth surface, or vector line data, for features of interest that are registered to a real world coordinate system.

The advantage of low-altitude natural color and infrared photography is that it provides sufficient high spatial resolution to detect features measuring less than one square meter. Aerial photography is currently in use for this type of mapping. Lastly, very large scale imagery allows for identification of actual coral reefs and is easily analyzed/interpreted. Photography can be used to map coral reefs to depths of 20 meters, the depth range where the majority of the coral reefs occur. The major disadvantage is that it is difficult to map and measure the steep slopes of some reefs. All photographs used will be scanned and georectified, so they can be used as a base map for zoom transferring photo interpretations. Where necessary, ground truthing, using divers with global positioning systems (GPS), will be undertaken to verify extent and types of reefs mapped. Additionally, where available or economically feasible, other data sets from laser and acoustic imaging systems, e.g. satellites, sonar, and LIDAR will be used to validate maps and provide quality control.

Additionally, a mapping classification system will be developed based on geomorphic type, ecological makeup, and environmental conditions. We hope to standardize our system with the one that The Nature Conservancy's Conservation Data Center in the USVI has been developing on marine ecosystems. Our protocols will adhere to those developed by the U.S.G.S. GAP and NOAA's C-CAP, which are hierarchical and community based.

Once the maps are finalized, they will be digitized and/or scanned using ARC/INFO software. These digitized data will provide data on acreage (areal extent) on types of coral reefs mapped. To document coral reef changes over time (1940's to present), a search will be conduct by the U.S.G.S. Mapping Division to identify historical high resolution photography. Following procedures described above, maps will be developed that depict historical distribution for the 1940's - 50's, 60's - 70's, and 90's depending on availability of photography. These maps will be digitized and compared to develop statistics and maps that portray changes over the past 50 years. We are especially interested in finding out if the mortality of Acropora palmata, the

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
221	GR	19.79	27.74	W	5.8	12.0	12.2	15.4	6.2	0.2	3.2
222	GL	17.93	27.20	W	4.8	ns	ns				
223	GR	17.59	26.71	W	7.2	9.5	ns	11.0	2.3		
224	GR	18.47	26.32	W	4.6	8.0	8.6	9.4	3.4	0.6	0.8
225	GR	17.31	25.97	W	10.8	10.0	10.4	ns	-0.8	0.4	
226	GL	12.03	24.62	W	5.0	8.0	7.8	9.8	3.0	-0.2	2.0
227	GR	21.69	19.83	W	10.0	13.0	ns	13.0	3.0		
228	GR	21.77	19.91	W	4.4	ns	ns	ns			
229	YE	18.35	15.65	W	5.0	11.0	12.0	ns	6.0	1.0	
230	YE	18.45	15.43	W	2.8	ns	ns	ns			
231	GR	18.82	13.86	W	3.0	6.0	6.5	7.8	3.0	0.5	1.3
232	GR	17.08	16.00	W	4.8	8.0	9.5	11.0	3.2	1.5	1.5
233	GR	21.09	11.47	W	4.0	6.8	8.0	9.8	2.8	1.2	1.8
234	GL	24.12	10.87	W	6.0	8.4	12.5	ns	2.4	4.1	
235	GL	27.57	13.65	W	3.4	5.2	9.0	10.0	1.8	3.8	1.0
236	GR	28.43	14.34	W	4.4	9.2	11.5	12.4	4.8	2.3	0.9
237	GR	28.25	11.53	W	7.2	11.6	17.0	20.2	4.4	5.4	3.2
238	GR	32.24	10.39	W	4.8	ns	ns	ns			
239	GR	34.75	8.95	W	11.0	17.2	19.0	20.4	6.2	1.8	1.4
240	GR	33.25	8.02	W	11.6	10.4	10.6	11.0	-1.2	0.2	0.4
241	GR	33.33	7.89	W	3.6	6.0	6.5	6.8	2.4	0.5	0.3
242	GR	31.83	6.24	W	3.8	7.6	9.5	12.0	3.8	1.9	2.5
243	GR	33.69	8.21	W	6.2	8.4	12.0	13.4	2.2	3.6	1.4
244	YE	32.80	9.65	W	4.4	ns	6.5	6.8			0.3
245	GR	33.23	10.20	W	9.4	15.0	22.0	21.8	5.6	7.0	-0.2
246	GL	32.38	8.02	W	9.2	9.4	15.0	16.8	0.2	5.6	1.8
247	GR	32.89	8.38	W	4.6	5.8	10.0	9.6	1.2	4.2	-0.4
248	YE	31.83	5.31	W	6.4	9.0	10.0	10.2	2.6	1.0	0.2
249	YE	27.60	5.04	W	5.8	7.6	8.5	7.6	1.8	0.9	-0.9
250	GR	27.44	5.25	W	6.2	ns	ns	ns			
251	GR	28.00	5.36	W	5.0	7.8	ns	ns	2.8		
252	GR	27.50	6.95	W	4.4	6.4	ns	ns	2.0		
253	GL	26.77	9.87	W	12.6	ns	ns	ns			
254	YE	25.83	9.36	W	5.0	6.2	ns	ns	1.2		
255	YE	26.35	10.24	W	6.8	8.2	7.0	11.4	1.4	-1.2	4.4

major reef building coral in shallow water, can be tracked over the last few decades.

We will acquire existing datasets on coral reef development and mapping from the National Park Service's Virgin Islands unit, and the NOAA C-CAP program and the Florida Marine Research Institute reef tract mapping within the Florida Keys. These data will be compared to and analyzed in conjunction with the results from this study to develop a consistent mapping effort and status and trends products

2. REEF STRUCTURE: QUANTITATIVE CHARACTERIZATION

As one component of the DOI Inventory and Monitoring Program, BRD scientists are developing specific protocols for monitoring bottom (benthic) cover, particularly cover by corals and algae. Divers use digital video cameras in underwater housings to produce videotapes along transects (For details, see Study Plan on Development of a Protocol for Using Videography to Monitor Coral Cover available from the FCSC). The video tapes can be quantitatively analyzed using image analysis software and data on cover by corals, algae, and other organisms can be analyzed statistically. A subset of transects can be monitored over time (annually is usually sufficient) to look for changes in abundance of coral and other organisms. To the extent feasible, the calcification studies described in the next section will be conducted on transects or sections of transects for which data over the last several years are available. When this is not possible, the video method will be used to characterize the area for which calcification rates area being determined.

The videotape will also record incidence of coral bleaching and coral diseases while supplemental information on these conditions can be recorded by the diver serving as a buddy for the diver doing the videotaping. (Note that the teams of scientists working on reef calcification and reef structure components of this proposal will be working together in the field)

Coral recruitment:

Survival of coral reefs requires that coral colonies reproduce both sexually and asexually through fragmentation. Coral colonies which have succumbed to diseases, storms, and bleaching must be replaced eventually by new colonies if reefs are to persist. Numerous studies have shown that the most abundant coral "recruits" do not come from the major reef-constructing species, Acropora palmata (elkhorn coral) and Montastraea annularis (star coral). These two species produce few sexual recruits. The presence of recruits of star and elkhorn coral are generally considered good indicators of the reef's condition. We propose to record the density of coral recruits in situ along the transects selected for videotaping and calcification studies. Small coral colonies (less than 5 cm) are generally not readily identifiable from videotapes.

3. REEF FUNCTION: CALCIFICATION

Carbonate sediment production, photosynthesis, and respiration will be

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
186	GR	26.72	12.60	W	8.0	ns	ns	ns			
187	GR	24.63	13.25	W	6.0	6.0	7.0	7.8	0.0	1.0	0.8
188	GR	24.50	13.73	W	10.0	14.2	16.0	18.6	4.2	1.8	2.6
189	GR	23.25	12.70	W	11.0	ns	ns	ns			
190	GR	22.00	11.87	W	8.0	10.0	13.0	ns	2.0	3.0	
191	YE	21.30	11.60	W	7.0	9.2	ns	ns	2.2		
192	YE	22.19	10.80	W	9.0	ns	ns	ns			
193	GR	26.20	5.73	W	7.0	9.2	12.0	13.2	2.2	2.8	1.2
194	GR	20.00	12.66	W	9.0	11.6	ns	ns	2.6		
195	GR	16.30	16.85	W	9.0	13.0	ns	ns	4.0		
196	GR	13.20	21.35	W	9.0	10.4	13.5	15.0	1.4	3.1	1.5
197	GR	13.50	21.25	W	7.0	7.0	10.0	ns	0.0	3.0	
198	GR	13.43	20.92	W	10.0	13.0	ns	ns	3.0		
199	GR	13.52	19.90	W	7.0	9.5	10.5	12.0	2.5	1.0	1.5
200	GR	14.67	22.25	W	9.0	9.2	10.0	10.4	0.2	0.8	0.4
201	GL	13.25	27.54	W	7.6	10.2	ns	9.0	2.6		
202	GL	13.44	27.53	W	7.8	10.0	10.0	12.4	2.2	0.0	2.4
203	GL	13.43	27.50	W	4.8	6.0	7.0	8.4	1.2	1.0	1.4
204	GR	16.10	26.87	W	31.4	35.0	38.2	42.0	3.6	3.2	3.8
205	GL	19.79	27.37	W	11.6	16.0	ns	ns	4.4		
206	GL	20.34	27.59	W	11.2	12.5	ns	ns	1.3		
207	GR	17.79	28.20	W	5.2	12.0	14.8	17.0	6.8	2.8	2.2
208	GL	12.43	24.18	W	5.2	ns	ns	ns			
209	GL	12.48	24.10	W	3.0	5.0	ns	ns	2.0		
210	GR	12.68	24.00	W	6.6	10.5	9.4	10.0	3.9	-1.1	0.6
211	GR	12.70	24.41	W	3.0	14.5	ns	ns	11.5		
212	GR	13.26	24.46	W	7.8	ns	9.0	ns			
213	GR	14.86	24.30	W	5.2	8.2	6.8	7.2	3.0	-1.4	0.4
214	GL	14.97	24.29	W	18.0	17.0	17.4	18.4	-1.0	0.4	1.0
215	GR	15.33	27.61	W	3.0	ns	5.8	7.0			1.2
216	GL	16.59	27.79	W	7.0	10.0	8.2	10.0	3.0	-1.8	1.8
217	GR	17.42	28.80	W	7.6	9.0	ns	18.0	1.4		
218	YE			W	5.6	ns	ns	ns			
219	YE	19.87	28.64	W	4.2	ns	8.6	7.4			-1.2
220	GL	19.74	28.45	W	3.4	ns	6.6	8.2			1.6

measured seasonally (summer and winter) at selected study sites to determine seasonal and areal variation in tissue/carbonate production and to derive average annual production rates. These parameters will be calculated from total alkalinity, pH, calcium concentrations, salinity, irradiance, temperature, wind and current speed, and air-sea CO_2 and O_2 fluxes measured along transects across reefs. Transects will be located parallel to unidirectional current flow across a given reef, characterized using a series of current meters, with sample stations positioned at the upstream and downstream ends of each transect. (If transects are not feasible because of local current conditions, portions of reefs will be enclosed in clear mylar and flow will be controlled with a water pump.) Geochemical and physical parameters (including water temperature) will be measured at each station along a transect at different times (and irradiances) during the day and night to determine daily variations in production and to derive average daily production rates.

Total alkalinity and pH will be used to calculate calcification and net photosynthesis using the alkalinity anomaly technique of Smith and Key (1975) such that calcification (C) = half the change in total alkalinity, and net photosynthesis (P) = total carbon - calcification. Total carbon will be calculated using carbonate system equations from Millero (1979). Calcium measurements will provide an independent measure of calcification for comparison. Air-sea CO_2 fluxes will be measured directly at each station inside of a floating bell (Frankignoulle 1988, Gattuso et al. 1993, Kayanne et al. 1995) using the procedure and calculations of Frankignoulle (1988). Air-sea O_2 fluxes will be determined by measuring atmospheric and water pO_2 and calculating fluxes as described in Wanninkhof (1992). Differences in oxygen and carbon metabolism between upstream and downstream stations will be corrected for O_2 and CO_2 exchange with the atmosphere as described in (Gattuso et. al., 1993).

Productivity and metabolic rates per unit area will be calculated using the difference in concentration between upstream and downstream stations, the volume of water transported along a transect, and the transect area such that the change in concentration of a parameter (delta $C/m_2/s$) = ($C/m3 \times m3/hr)/m_2$ (Barnes and Devereux, 1984). Seasonal production rates will be used to calculate average annual production rates.

Comparison of these data with previous productivity estimates and calcification rates, as well as calcification rates determined from coral cores (Hudson et. al., 1976; Dodge et. al, 1983; Dodge, et. al, 1992) would indicate whether long-term (decades) changes are occurring on the reefs.

Coral cores:

Skeletons of some coral species (including Montastraea annularis) provide a record of the environmental conditions under which the corals grew. We propose to examine coral cores which have already been collected from the parks to look for any changes in calcification (deposition of the coral skeleton) which would indicate short-term or long-term changes in environmental conditions. Cores will be used to construct a history of

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
151	GL	33.71	10.46	W	5.8	5.8	ns	ns	0.0		
152	GL	33.50	10.98	W	3.4	5.0	8.0	ns	1.6	3.0	
153	GR	34.45	11.14	W	9.2	9.6	ns	ns	0.4		
154	GL	35.87	10.95	W	6.4	14.6	17.0	17.2	8.2	2.4	0.2
155	GL	33.42	8.15	W	5.6	8.2	10.5	11.6	2.6	2.3	1.1
156	GR	33.58	8.48	W	28.8	31.0	33.0	34.0	2.2	2.0	1.0
157	YE	33.20	4.53	W	13.0	13.4	14.5	13.6	0.4	1.1	-0.9
158	GR	31.50	1.35	W	42.4	50.0	52.0	50.0	7.6	2.0	-2.0
159	YE	28.52	4.41	W	6.8	8.0	9.5	10.6	1.2	1.5	1.1
160	GR	28.50	4.44	W	8.0	11.4	12.5	14.0	3.4	1.1	1.5
161	GL	28.22	5.69	W	8.0	9.8	12.5	13.6	1.8	2.7	1.1
162	GL	28.30	6.27	W	5.2	10.0	10.0	ns	4.8	0.0	
163	GR	28.34	6.36	W	7.4	12.0	ns	13.0	4.6		
164	GL	28.65	6.22	W	6.0	8.8	11.0	10.4	2.8	2.2	-0.6
165	GL	30.00	5.54	W	3.8	8.0	9.5	10.4	4.2	1.5	0.9
166	GL	29.93	4.33	W	3.6	ns	9.0	8.8			-0.2
167	GL	30.05	4.33	W	6.2	ns	7.5	ns			
168	GR	25.81	6.24	W	9.4	12.2	14.0	15.8	2.8	1.8	1.8
169	GL	27.35	5.28	W	5.8	ns	12.0	ns			
170	GR	24.05	8.84	W	11.6	13.4	17.0	ns	1.8	3.6	
171	GR	24.89	7.47	W	5.0	10.0	9.5	ns	5.0	-0.5	
172	GR	24.25	9.46	W	6.2	ns	17.0	17.6			0.6
173	YE	24.58	11.12	W	9.0	9.8	9.0	8.6	0.8	-0.8	-0.4
174	YE	24.80	11.24	W	10.8	ns	ns	ns			
175	GL	24.75	12.02	W	12.6	15.0	19.0	21.6	2.4	4.0	2.6
176	GR	26.00	10.89	W	7.2	ns	11.0	11.8			0.8
177	GL	26.25	11.30	W	21.4	24.2	ns	ns	2.8		
178	GR	26.95	10.84	W	11.4	18.0	ns	ns	6.6		
179	GR	27.05	10.72	W	6.8	7.2	7.4	9.8	0.4	0.2	2.4
180	GL	27.38	9.41	W	8.2	11.2	ns	ns	3.0		
181	GR	27.69	9.54	W	11.6	ns	24.8	25.8			1.0
182	GL	27.59	8.25	W	8.8	17.0	ns	ns	8.2		
183	GR	27.57	8.21	W	3.6	7.0	ns	ns	3.4		
184	YE	28.85	7.98	W	12.0	12.2	13.5	13.0	0.2	1.3	-0.5
185	YE	28.69	8.05	W	5.8	7.2	9.5	9.4	1.4	2.3	-0.1

climate conditions over as long a period as possible. We will not be collecting new cores from any of the sites.

Dr. Robert Halley, who has primary responsibility for this portion of the study, will do pilot studies in the Florida Keys National Marine Sanctuary (with funds he has already secured) prior to conducting the first experiments in VIIS in the summer of 1999.

Physical Oceanography

Coral reefs require good current velocities for their growth and survival. Currents transport larvae of corals, fishes and other reef organisms from upstream areas. They also carry sediments, oil, and other pollutants to the reefs. A knowledge of water flow patterns in different bays and over different reefs increases our understanding of the vulnerability of reefs to several anthropogenic stresses and the potential sources of larvae for replenishment of damaged reefs. If monitoring reveals increases in algae and other indicators of stress (coral bleaching) knowledge of current patterns may be useful in identifying the source of the stresses(e.g., runoff from coastal development). Currents will be measured using current meters at each of the study sites.

Relationship to Goals of BRD/CGRP

The proposed work relates to the goals of the BRD/CGRP in several ways. First the proposed measures of air-sea CO_2 fluxes not only provides basic data for determining the degree to which coral reefs contribute to atmospheric CO_2, but they also provides a way to evaluate the sensitivity of coral reef carbon budgets to future atmospheric CO_2 levels (Goal 1). Second, carbon-budget measurements on reefs will help determine the combined effects of global change and environmental contamination on reefs (Goal 2). Third, the project is being addressed at several spatial and temporal scales in an effort to learn more about responses of coral reefs to global change (Goal 3). Fourth,the proposed experiments provide a test to determine to what degree careful management of sediment and nutrient input to reefs (which affects the relative abundances of algae and living coral) could offset effects of increased global CO_2 (Goal 4)

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ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
116	GL	21.59	16.01	W	5.6	10.0	ns	ns	4.4		
117	GL	21.16	15.40	W	6.6	16.4	16.8	19.0	9.8	0.4	2.2
118	GL	20.95	15.13	W	5.6	8.0	ns	ns	2.4		
119	YE	20.86	15.37	W	3.8	5.4	ns	ns	1.6		
120	YE	19.89	15.92	W	4.6	9.0	10.0	ns	4.4	1.0	
121	GL	19.19	15.28	W	11.0	13.0	14.0	21.2	2.0	1.0	7.2
122	GR	18.33	16.80	W	6.6	15.0	18.4	22.0	8.4	3.4	3.6
123	GL	17.80	16.20	W	7.2	7.0	9.0	ns	-0.2	2.0	
124	GL	17.90	16.00	W	14.2	19.0	20.0	ns	4.8	1.0	
125	GL	16.67	17.10	W	5.8	8.0	9.4	ns	2.2	1.4	
126	GR	18.40	17.02	W	9.0	12.0	11.8	14.0	3.0	-0.2	2.2
127	GR	19.40	16.12	W	5.2	11.0	11.6	5.8	5.8	0.6	-5.8
128	GR	21.68	16.65	W	8.0	10.8	13.6	15.6	2.8	2.8	2.0
129	GL	23.20	15.38	W	8.6	12.2	17.4	15.6	3.6	5.2	-1.8
130	GR	22.90	15.97	W	6.8	9.8	12.0	13.4	3.0	2.2	1.4
131	GR	23.30	15.75	W	5.4	6.6	ns	8.4	1.2		
132	GR	24.08	16.31	W	3.4	7.6	8.5	9.8	4.2	0.9	1.3
133	GR	24.27	18.27	W	5.2	7.8	ns	11.6	2.6		
134	GR	26.20	16.16	W	3.6	ns	ns	ns			
135	GL	26.91	15.97	W	7.6	9.4	ns	ns	1.8		
136	GL	25.89	15.67	W	3.6	5.2	ns	ns	1.6		
137	GL	25.90	15.75	W	7.8	9.6	ns	ns	1.8		
138	GR	26.03	15.86	W	5.8	6.0	8.5	9.8	0.2	2.5	1.3
139	YE	26.09	14.80	W	8.2	11.0	ns	11.2	2.8		
140	GL	26.98	14.65	W	4.8	8.5	10.0	11.0	3.7	1.5	1.0
141	GL	28.72	12.83	W	13.4	16.0	ns	ns	2.6		
142	GR	28.80	12.50	W	14.6	16.6	22.0	22.6	2.0	5.4	0.6
143	YE	29.50	12.61	W	9.2	8.8	10.0	9.8	-0.4	1.2	-0.2
144	GR	29.36	12.62	W	4.0	7.0	9.0	10.0	3.0	2.0	1.0
145	GR	29.38	12.98	W	11.4	17.6	23.0	23.0	6.2	5.4	0.0
146	GL	29.10	12.30	W	7.2	10.6	14.0	15.8	3.4	3.4	1.8
147	GR	28.28	11.09	W	10.0	ns	ns	ns			
148	GR	28.75	10.57	W	28.4	33.0	34.0	34.8	4.6	1.0	0.8
149	GL	30.55	10.97	W	13.6	ns	ns	ns			
150	GR	30.70	10.20	W	74.2	ns	ns	ns			

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ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
81	GR	17.83	23.50	W	5.6	10.0	ns	ns	4.4		
82	GR	17.41	22.68	W	3.8	ns	ns	ns			
83	GL	17.19	22.75	W	10.8	14.4	ns	ns	3.6		
84	GR	14.67	22.25	W	9.8	20.0	ns	ns	10.2		
85	GR	16.89	21.74	W	7.2	11.0	ns	ns	3.8		
86	GR	17.82	22.40	W	8.8	10.8	ns	14.0	2.0		
87	GR	17.90	22.12	W	4.8	9.6	ns	ns	4.8		
88	GR	17.92	21.87	W	7.0	14.6	ns	ns	7.6		
89	GR	18.28	22.21	W	4.2	6.8	ns	11.4	2.6		
90	GL	21.30	24.98	W	6.8	15.0	18.8	17.0	8.2	3.8	-1.8
91	GR	18.85	20.78	W	9.2	10.6	ns	13.6	1.4		
92	GL	20.73	23.87	W	8.6	ns	ns	ns			
93	YE	19.75	22.29	W	8.4	9.2	ns	10.2	0.8		
94	GL	19.43	21.45	W	8.8	8.4	ns	9.6	-0.4		
95	GL	19.57	20.58	W	6.0	11.0	ns	ns	5.0		
96	GR	16.77	20.57	W	6.0	ns	11.0	14.0			3.0
97	GR	13.30	20.53	W	4.8	8.0	ns	ns	3.2		
98	GL	13.40	20.35	W	10.2	10.8	ns	ns	0.6		
99	GR	15.54	19.27	W	7.4	11.6	15.6	ns	4.2	4.0	
100	GR	16.90	18.23	W	9.4	29.2	33.4	ns	19.8	4.2	
101	GL	18.03	18.31	W	6.4	ns	8.4	9.6			1.2
102	GR	19.30	18.46	W	4.6	5.4	7.4	8.6	0.8	2.0	1.2
103	YE	19.55	18.32	W	7.2	10.0	ns	ns	2.8		
104	GL	16.67	18.43	W	3.2	ns	7.4	9.4			2.0
105	YE	17.63	18.12	W	4.6	8.2	9.0	10.0	3.6	0.8	1.0
106	GR	17.59	18.22	W	6.4	9.4	11.4	11.0	3.0	2.0	-0.4
107	GL	18.05	17.70	W	6.2	11.6	12.6	14.0	5.4	1.0	1.4
108	GR	20.90	17.85	W	6.2	8.4	10.0	10.0	2.2	1.6	0.0
109	GR	21.02	17.86	W	6.4	9.4	10.8	11.4	3.0	1.4	0.6
110	GL	21.58	17.48	W	4.4	13.0	14.0	17.0	8.6	1.0	3.0
111	GL	22.00	18.05	W	6.8	9.8	ns	8.6	3.0		
112	GR	22.62	17.09	W	12.8	17.2	20.4	34.4	4.4	3.2	14.0
113	GL	22.59	16.90	W	7.6	9.2	ns	ns	1.6		
114	GR	21.90	16.03	W	8.6	13.4	14.0	15.0	4.8	0.6	1.0
115	GL	21.67	16.09	W	4.0	8.0	12.6	15.0	4.0	4.6	2.4

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Szmant, A.M., Gassman, N.J. 1990. The effects of prolonged bleaching on the tissue biomass and reproduction of the reef coral Montastrea annularis. Coral Reefs 8: 217-224.
Wanninkhof, R. 1992. Relationship between wind speed and gas exchange over the ocean. Journal of Geophysical Research 97:7373-7382.
Wilkinson, C. 1992. Coral reefs of the world are facing widespread devastation: can we prevent this through sustainable management practices? Proc. Of the 7th Int. Coral Reef Sym 1: 11-21.

EXPECTED PRODUCTS:

Maps will be produced at a scale of 1:24,000 or greater to identify regional patterns and trends, and will conform to U.S. Geological Survey Mapping Standards. Maps will be produced in both digital and hard copy atlas formats. Digital format will be available on the Internet. Photographs, which will be scanned and georectified, will be available through the Internet and hard copy.CD-ROMS and digital tapes of maps and photographs will also be produced for distribution.

Other products include CDs with archived videotransect data (and appropriate metadata) and diskettes with results of image analyses.

TECHNOLOGY/INFORMATION TRANSFER:

All three of the major components of this proposal include development of protocols which will be transferable to other agencies and individuals with an interest in mapping and monitoring of coral reefs as well as calculations of effects of increased CO_2 associated with climate change.

DATA MANAGEMENT:

Data (maps and photographs) will be documented using the NBII Metadata Standard, and these metadata will be served through the National Wetlands Research Center's NBII Clearinghouse Node.Bibliographic metadata for all information and products will be added to the Biological Resource Division's Bibliographic Metadata Database at http://biology.usgs.gov/pubs.

PERSONNEL: (from the initiating Center)

Nicholas Funicelli, Caroline S. Rogers, Ginger Garrison, Jeff Miller
Florida Caribbean Science Center:
Dr. Funicelli is the Principal Contact for BRD. Dr. Rogers has primary responsibility for studies on reef structure. She will be assisted by Ms. Ginger Garrison. Jeff Miller is

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
46	GR	11.00	29.50	W	5.0	10.5	9.8	10.6	5.5	-0.7	0.8
47	GR	11.66	29.53	W	5.4	8.6	ns	7.6	3.2		
48	GR	11.87	28.68	W	2.5	6.5	6.0	7.8	4.0	-0.5	1.8
49	GR	14.46	29.62	W	2.5	ns	6.0	6.4			0.4
50	YE	14.99	30.35	W	6.1	8.6	11.4	13.0	2.5	2.8	1.6
51	GR	15.35	30.50	W	9.6	12.2	ns	ns	2.6		
52	GR	18.50	31.03	W	3.8	5.6	7.0	8.4	1.8	1.4	1.4
53	GR	19.80	30.55	W	4.8	ns	8.8	13.4			4.6
54	GR	17.00	29.55	W	5.0	9.0	9.8	12.0	4.0	0.8	2.2
55	GR	16.75	29.50	W	9.8	ns	ns	ns			
56	GR	13.08	28.45	W	4.0	ns	6.8	7.4			0.6
57	GR	10.43	27.90	W	5.2	13.0	8.8	ns	7.8		
58	GR	10.35	27.75	W	4.2	7.0	ns	ns	2.8		
59	GR	12.85	26.26	W	8.8	12.0	ns	ns	3.2		
60	GR	13.95	26.60	W	4.8	9.0	11.2	11.8	4.2	2.2	0.6
61	GR	14.26	26.59	W	3.8	6.5	8.2	9.0	2.7	1.7	0.8
62	GR	16.67	27.44	W	4.4	7.2	9.4	10.4	2.8	2.2	1.0
63	GR	17.13	27.81	W	4.4	8.0	ns	ns	3.6		
64	YE	17.56	27.47	W	6.2	10.8	11.6	12.8	4.6	0.8	1.2
65	GR	20.35	27.84	W	7.6	10.4	12.4	14.6	2.8	2.0	2.2
66	GR	20.38	27.82	W	3.2	5.6	7.8	6.6	2.4	2.2	-1.2
67	GR	20.34	27.03	W	5.4	4.4	ns	5.6	-1.0		
68	GR	16.48	26.61	W	7.2	11.0	13.2	16.0	3.8	2.2	2.8
69	GR	12.50	25.70	W	3.6	5.5	ns	7.8	1.9		
70	GR	12.39	25.75	W	2.8	ns	ns	ns			
71	GR	10.47	26.50	W	5.2	14.0	15.4	15.8	8.8	1.4	0.4
72	GR	10.40	26.35	W	5.6	ns	6.6	ns			
73	GR	10.35	26.30	W	8.4	12.5	12.6	11.4	4.1	0.1	-1.2
74	GR	10.31	26.15	W	3.8	ns	6.6	6.8			0.2
75	GR	10.66	26.00	W	7.2	13.0	14.8	14.0	5.8	1.8	-0.8
76	GR	15.19	25.65	W	8.8	14.0	14.8	18.4	5.2	0.8	3.6
77	GR	17.72	26.18	W	7.2	10.0	13.8	15.6	2.8	3.8	1.8
78	GR	18.03	26.57	W	7.0	10.2	10.4	11.6	3.2	0.2	1.2
79	YE	19.59	25.47	W	8.8	ns	ns	ns			
80	GL	16.31	24.15	W	17.0	22.2	ns	ns	5.2		

the lead field person.

COOPERATORS/PARTNERS:

Within the U.S.G.S., the Geology and Mapping Divisions will be partners and provide personnel, equipment, and expertise for certain tasks to conduct this research effort. The National Park Service will be cooperating with us at all sites. The National Oceanic and Atmospheric Administration's Coastal Change Analysis Program and Coastal Services Center, EPA's Environmental Monitoring and Assessment Program, National Aeronautics and Space Administration's Commercial Remote Sensing and Earth Enterprise Programs, Florida's Department of Environmental Protection's Marine Research Institute, Virgin Islands Department of Natural Resources, and the National Park Service will be cooperating in the mapping and trend analysis (change) tasks. Major contributors/collaborators include:

- Jimmy Johnston, USGS, BRD, Nat. Wetlands Res. Center, 700 Cajundrome Blvd, Lafayette, LA 70506; p318 266-8556; f266-8616 (Remote sensing/mapping)
- Robert Halley,USGS, Center for Coastal Geology, St. Petersburg, Fl p813 893-3100; f893-3333 (Carbon budget, calcification studies)

Dennis Hubbard, Oberlin College, 44293 Rt 511E, Oberlin, Ohio 44074; (phone and fax 440 774-5180 (Physical oceanography, coral cores)

FACILITIES/EQUIPMENT/STUDY AREAS:

For map production and trend (change) analysis, work will be performed by the Spatial Analysis Branch of the National Wetlands Research Center. The Branch has the necessary photogrammetic and cartographic equipment for mapping; UNIX workstations, scanners, GPS, and digitizing equipment for geographic information system (GIS) analyses, and an Internet server (NBII Clearinghouse Node) to distribute data. The BRD field station in the USVI has a Whaler and a diesel boat plus all necessary dive gear to support field work in St. John. We hope to use National Park Service boats in Biscayne National Park and at Buck Island Reef National Monument. Current meters will probably be supplied by the USGS Coastal and Marine Program in St. Petersburg. Oberlin College will supply lab space, office support, and some technician time.

LEGAL AND POLICY-SENSITIVE ASPECTS:
Research permits will be necessary for each of the 4 parks. Supt. Russ Berry, Virgin Islands National Park, P.O. Box 710, USVI 00830; ph 340 693-8950.
Supt. Joel Tutein, Buck Island Reef National Monument, 2100 Church St. #100, Christiansted, St. Croix, USVI 00820. ph 340 773-1460; Supt. Richard Ring, Everglades National Park, 40001 State Road 9336, Homestead, Fl 33030, ph 305 242-7848. Supt. Richard Frost, Biscayne National Park, P.O. Box 1369, Homestead, Fl 33090.

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
6	GL	29.03	13.88	W		4.8	6.5	6.6		1.7	0.1
7	GR	28.80	14.80	W		8.6	9.0	9.6		0.4	0.6
8	GR	28.46	14.75	W		8.8	12.0	ns		3.2	
9	GL	27.45	15.57	W		8.6	11.0	12.0		2.4	1.0
10	YE	27.48	15.48	W		9.0	11.0	11.8		2.0	0.8
11	GL	27.30	15.90	W		10.8	12.0	11.8		1.2	-0.2
12	GR	27.34	16.00	W		10.0	ns	ns			
13	GL	26.69	16.19	W		9.0	ns	ns			
14	GR	26.50	16.35	W		9.0	10.0	12.6		1.0	2.6
15	GL	25.95	16.12	W		9.2	12.0	14.2		2.8	2.2
16	GL	25.35	16.83	W		5.6	ns	ns			
17	GL	26.18	17.50	W		15.4	ns	15.0			
18	GL	25.77	17.53	W		15.0	7.2	9.0		-7.8	1.8
19	GL	24.40	16.30	W		9.2	11.4	11.8		2.2	0.4
20	GL	25.20	14.27	W		8.0	10.0	11.0		2.0	1.0
21	GL	26.40	13.07	W		7.0	9.5	10.8		2.5	1.3
22	YE	25.57	13.19	W		4.2	6.5	6.0		2.3	-0.5
23	GL	30.09	10.65	W		11.8	13.5	13.8		1.7	0.3
24	GL	26.03	11.28	W		22.0	21.0	19.2		-1.0	-1.8
25	GL	25.04	12.10	W		7.6	10.0	11.6		2.4	1.6
26	GL	24.19	12.45	W		12.0	12.8	17.0		0.8	4.2
27	YE	21.59	12.30	W		10.4	11.5	12.4		1.1	0.9
28	GR	24.35	8.09	W		10.0	ns	ns			
29	GR	24.00	8.83	W		17.0	20.0	20.0		3.0	0.0
30	GR	20.19	13.70	W		9.0	10.0	15.0		1.0	5.0
31	GR	21.27	12.42	W		12.2	ns	16.6			
32	GL	18.60	14.10	W		7.2	9.0	8.0		1.8	-1.0
33	GL	17.27	17.93	W		7.4	9.2	ns		1.8	
34	GL	17.20	17.90	W		6.2	7.6	ns		1.4	
35	GR	17.08	18.30	W		5.8	7.0	7.8		1.2	0.8
36	GL	16.17	19.40	W		5.6	ns	ns			
42	YE	10.36	29.85	W	5.5	6.0	5.8	5.8	0.5	-0.2	0.0
43	GR	10.25	29.90	W	5.5	11.4	12.0	14.0	5.9	0.6	2.0
44	YE	10.30	29.75	W	1.4	ns	ns	ns			
45	YE	10.18	29.75	W	4.0	ns	8.4	8.4			0.0

WORK AND REPORTING SCHEDULE:

1. Develop Coral Reef Mapping Protocols and GAP Classification System	6/1/1999 - 5/30/2000
2. Search by Mapping Division for Historical Aerial Photography	6/1/1999 - 12/31/1999
3. Award Contract for Aerial Photography Acquisition for Florida Keys	9/30/1999
4. Prepare Florida Keys Coral Reef Maps (Historical and Recent)	8/1/1999 - 9/30/2001
5. Award Contract for Aerial Photography Acquisition for Virgin Islands	9/30/2000
6. Prepare Virgin Islands Coral Reef Maps (Historical and Recent)	8/1/2000 - 9/30/2002
7. Conduct GIS Analyses on Trend/Changes of Coral Reefs	1/1/2000 - 12/31/2002
8. Prepare NBII Node for Data	1/1/2003 - 9/30/2003

For the reef structure and function portions of this proposal, year 1 will be devoted to selecting study sites and doing a pilot study on St. John. Twice a year in years 2 and 3 work will be conducted on St. John. Work will be done on Buck Island in year3 and in Biscayne in year 4. Dry Tortugas reefs will be studied in year 5. Annual progress reports will be prepared with the final reports being submitted within 4 months of project completion.

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
504	YE	16.94	17.83	E			8.2	8.8			
505	GL	16.99	17.83	E			6.4	7.8			1.4
506	GL	18.66	21.80	E			8.4	8.8			0.4
507	GL	18.31	18.66	E			5.0	5.4			0.4
508	GL	17.40	17.78	E			4.4	5.6			1.2
509	GL	22.18	23.15	E			5.0	6.4			1.4
510	GL	26.84	14.43	E			4.2	4.6			0.4
511	GL	30.44	17.86	E				11.6			
512	YE	29.11	12.05	E				3.8			
513	GR	27.17	10.36	E				5.8			
514	YE	26.16	15.30	E				6.0			
515	GL	26.70	15.32	E				3.8			
516	GL	25.96	10.60	E				12.0			
517	GL	27.05	12.05	E				5.8			
518	GR	12.62	23.53	E				5.4			
519	GL	25.00	14.08	E				9.2			
520	GL	26.41	20.59	E				10.0			
521	GR	27.38	17.03	E				7.0			
522	GL	21.50	16.25	E			3.8	5.6			1.8
523	YE	22.85	12.79	E				6.2			
524	GL	21.32	18.33	E				3.2			
525	GL	19.13	16.49	E				7.0			
526	GL	19.23	16.54	E				3.4			
527	GR	14.42	23.00	E			20.0	23.0			3.0
528	GR	23.03	12.00	E				14.0			
529	GL	15.17	26.77	E				5.0			
530	GR	18.62	16.87	E				4.2			
531	WO	12.00	29.83	E				10.2			
532	GL	11.98	29.65	E				12.8			
533	GL	11.67	29.62	E				4.0			
1	GL	25.04	9.00	W		5.6	7.0	8.2		1.4	1.2
2	GL	25.66	8.64	W		3.0	5.0	6.4		2.0	1.4
3	GL	25.39	9.30	W		5.0	9.5	8.2		4.5	-1.3
4	GL	27.20	11.30	W		4.2	6.0	7.0		1.8	1.0
5	GL	28.65	13.00	W		13.0	14.0	14.0		1.0	0.0

PERSONNEL QUALIFICATIONS:

James B. Johnston, Ph.D.

E-mail: jimmy_johnston@usgs.gov

James B. Johnston, Ph.D. 1973. Biology, University of Southern Mississippi. Chief, Spatial Analysis Branch.

Dr. Johnston seeks ways to improve responsiveness and efficiency of decision making by establishing partnerships among Federal, state, and local governments and the private sector to protect and restore coastal habitats and the fish and wildlife resources they support. He is interested in applying state-of-the-art technologies (geographic information systems, remote sensing, expert systems, and information management systems) to monitor, map, analyze, and predict habitat changes and impacts; implementing innovative research and developmental studies that address resource issues related to the protection, restoration, and management of natural resources; and establishing educational and public outreach programs to encourage protection, conservation, and management of wetlands and other aquatic habitats.

Representative Publications:

Johnston, J.B., M.C. Watzin, J.A. Barras, and L.R. Handley. 1995. Gulf of Mexico coastal wetlands: case studies of loss trends. Pages 269-272 in E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac, eds. Our *Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems.* U.S. Department of the Interior, National Biological Service, Washington, DC.

Ji, W., and J.B. Johnston. 1994. Coastal ecosystem decision support GIS: functions and methodology. Marine Geodesy 18:229-241.

Johnston , J.B., D.W. Field, and A.J. Reyer. 1992. Disappearing coastal wetlands. Pages 53-58 in Stemming the Tide of Coastal Fish Habitat Loss. National Coalition for Marine Conservation, Savannah, GA.

Johnston, J.B. 1990. Wetland and Wildlife Management in the Gulf of Mexico Region. In Proceedings of the Conference on Environmental and Economic Status of the Gulf of Mexico. Environmental Protection Agency. New Orleans, LA. 5 pp. (In press)

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
364	GL	24.69	20.10	E		4.0	6.0	7.3		2.0	1.3
365	GL	24.83	20.70	E		5.8	6.4	7.4		0.6	1.0
366	GR	24.57	11.29	E		4.0	ns	5.2			
367	GL	24.95	11.00	E		4.5	5.4	5.4		0.9	0.0
368	GL	25.90	11.54	E		4.2	6.0	7.4		1.8	1.4
369	GL	26.88	10.59	E		7.6	9.0	10.0		1.4	1.0
370	GR	20.75	13.65	E		16.0	14.0	17.6		-2.0	3.6
371	GL	26.42	13.75	E		3.8	5.0	8.2		1.2	3.2
372	GL	26.04	13.68	E		4.4	ns	6.0			
373	GR	27.47	15.03	E		5.8	7.6	9.8		1.8	2.2
374	GL	30.80	19.81	E		8.2	11.0	11.2		2.8	0.2
375	GR	30.00	16.83	E		18.8	ns	17.0			
376	GL	31.05	19.23	E		18.0	21.4	22.0		3.4	0.6
377	GL	31.47	18.60	E		15.0	17.0	17.2		2.0	0.2
378	GR	31.20	18.43	E		4.8	7.4	7.6		2.6	0.2
379	YE	30.06	18.32	E		8.6	ns	9.8			
380	GR	29.80	17.99	E		11.0	ns	ns			
381	GR	15.03	22.93	E		11.4	ns	12.4			
382	GR	30.32	17.35	E		8.6	ns	8.6			
383	WO	30.26	17.24	E		4.8	ns	5.0			
384	GR	22.29	22.25	E		17.8	22.0	24.8		4.2	2.8
385	GL	28.55	16.75	E		6.4	6.0	ns		-0.4	
386	GL	29.49	13.75	E		3.5	4.2	8.2		0.7	4.0
387	GL	29.50	13.39	E		4.0	6.0	7.4		2.0	1.4
493	YE	1.91	31.79	E			13.4	14.0			
494	GL	9.38	24.49	E			9.0	9.8			0.8
495	WO	12.92	27.97	E			21.6	26.6			5.0
496	GL	13.54	29.11	E			5.8	7.8			2.0
497	GL	12.10	22.38	E			8.2	7.4			-0.8
498	GL	13.23	22.94	E			8.0	9.0			1.0
499	YE	13.09	26.03	E			8.2	9.6			
500	GL	12.96	21.93	E			9.2	13.0			3.8
501	GR	31.18	19.50	E		21.2	26.0	29.2		4.8	3.2
502	GL	15.29	19.02	E			11.2	10.6			-0.6
503	GL	16.39	18.52	E			8.8	9.0			0.2

Lawrence R. Handley, M.S.

E-mail: larry_handley@usgs.gov

Lawrence R. Handley, M.S. 1973. Geography, University of Arkansas. Ph.D. candidate, 1987, Geography, University of California, Berkeley. Cartography, aerial photo interpretation, geographic information systems, global positioning systems, geomorphology, 4-color process printing.

Handley supervises the acquisition of aerial photography, the photointerpretation of wetland and upland habitats for present and historical time periods, and the cartographic representation of the photointerpretation on base maps. Research and other projects focus on the determination of mapping and photointerpretation accuracy, the use of GPS in base map development, the comparison of PC-based GIS software packages, seagrass photointerpretation and mapping, the use of aerial video in mapping, and introducing wetlands mapping and GIS to secondary school educators via workshops.

Representative Publications:

Handley, L.R. 1995. Seagrass distribution in the northern Gulf of Mexico. Pages 273-275 in E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M. Mac, eds. Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals and Ecosystems. National Biological Service, Washington, DC.

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Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
328	GL	19.69	20.35	E		3.8	5.4	6.2		1.6	0.8
329	GL	18.75	17.45	E		4.8	ns	6.6			
330	YE	18.70	17.25	E		9.8	ns	ns			
331	GR	15.35	25.43	E		5.6	ns	ns			
332	YE	19.10	23.00	E		7.0	7.0	7.4		0.0	0.4
333	GL	20.54	18.20	E		8.2	9.4	10.6		1.2	1.2
334	GL	20.95	17.66	E		3.4	ns	4.8			
335	GL	19.18	16.64	E		6.4	4.0	ns		-2.4	
336	YE	18.58	19.31	E		4.6	4.0	4.8		-0.6	0.8
337	YE	17.85	17.58	E		8.0	ns	8.2			
338	YE	17.88	17.60	E		6.8	8.0	9.2		1.2	1.2
339	GL	18.00	17.58	E		13.0	15.0	16.4		2.0	1.4
340	YE	18.01	16.96	E		7.6	7.0	6.2		-0.6	-0.8
341	GL	18.45	16.13	E		11.6	14.0	16.0		2.4	2.0
342	GR	21.69	23.14	E		10.8	ns	12.0			
343	GR	19.80	14.94	E		4.4	5.0	7.0		0.6	2.0
344	GL	19.63	15.00	E		6.8	7.0	8.4		0.2	1.4
345	GR	19.80	14.85	E		2.4	14.0	3.0		11.6	-11.0
346	GR	20.30	14.41	E		8.4	ns	9.6			
347	GR	24.35	17.89	E		12.0	ns	ns			
349	GL	21.95	16.60	E		5.6	ns	7.8			
350	GL	22.67	17.25	E		4.0	ns	6.4			
351	GR	23.39	18.43	E		11.4	13.0	13.4		1.6	0.4
352	GR	28.70	11.27	E		17.0	21.0	25.6		4.0	4.6
353	GR	25.40	21.30	E		10.8	ns	ns			
354	GR	16.90	19.72	E		8.0	7.8	9.0		-0.2	1.2
355	GR	18.00	17.44	E		8.0	7.4	6.8		-0.6	-0.6
356	GL	16.43	21.13	E		14.0	13.2	17.6		-0.8	4.4
357	GL	20.95	22.04	E		6.0	7.0	7.4		1.0	0.4
358	WO	23.15	12.30	E		3.0	10.0	12.6		7.0	2.6
359	GL	23.03	13.18	E		4.8	7.0	8.0		2.2	1.0
360	GR	22.79	14.64	E		7.8	7.4	6.4		-0.4	-1.0
361	YE	22.75	14.43	E		6.0	ns	5.2			
362	GL	22.69	14.59	E		6.4	6.6	8.0		0.2	1.4
363	GL	22.09	13.80	E		10.0	9.0	9.8		-1.0	0.8

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Hartley is responsible for installation, configuration and overall maintenance of software, hardware, and networking for geographic information system operations. His specific duties include managing and coordinating GIS projects, performing image analysis, developing prototype GIS products, troubleshooting, quality control, personnel management and training, and interacting with clients. Hartley also serves as the Project Leader for the Louisiana GAP Program.

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Habitat change in Delta National Wildlife Refuge
GIS analyses around the Caddo Lake, TX area
CWPPRA GIS analysis for Bayou LaBranche, Bayou Sauvage, and Raccoon Island
Hurricane Andrew survey data LA Dept. of Wildlife and Fisheries
Bird survey data for LA Dept. of Wildlife and Fisheries
Vegetation Survey for LA Dept. of Wildlife and Fisheries
Louisiana GAP Project (Co-PI)

Representative Publication:

Ramsey, E.R., III, and S. Hartley. 1994. National Wetlands Research Center uses visual true color classification in waterfowl habitat mapping. Earth Observation Magazine, February: 28-30.

Appendix B

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
34	GR	28.85	12.38	E	3.6	8.4	ns	ns	4.8		
35	GL	28.93	13.21	E	11.2	10.5	18.0	23.0	-0.7	7.5	5.0
36	YE	29.13	11.71	E	15.0	ns	ns	ns			
37	GL	30.15	12.03	E	6.0	12.2	15.2	19.4	6.2	3.0	4.2
38	GR			E	6.2	7.2	ns	ns	1.0		
39	GR	25.39	16.93	E	4.6	11.8	12.0	ns	7.2	0.2	
40	GR	23.48	17.33	E	5.8	9.5	ns	12.0	3.7		
41	GR	22.36	21.39	E	6.4	10.2	13.0	ns	3.8	2.8	
301	GL	13.30	28.24	E		28.2	ns	33.6			
302	YE	14.33	27.69	E		10.8	12.0	14.4		1.2	2.4
303	GR	14.25	27.29	E		3.2	ns	4.6			
304	YE	13.17	27.18	E		6.8	7.6	7.6		0.8	0.0
305	YE	11.70	26.27	E		8.0	9.4	10.8		1.4	1.4
306	GR	13.76	25.78	E		5.6	8.2	9.4		2.6	1.2
307	GR	13.78	25.75	E		3.8	5.2	6.0		1.4	0.8
308	GR	13.47	25.78	E		6.2	2.8	5.0		-3.4	2.2
309	YE	13.23	25.33	E		6.2	ns	8.2			
310	GR	12.60	25.50	E		9.4	ns	11.2			
311	GL	12.41	20.87	E		8.4	10.2	14.0		1.8	3.8
312	GL	13.62	20.93	E		7.2	8.4	10.6		1.2	2.2
313	GL	13.50	20.98	E		5.0	5.8	8.8		0.8	3.0
314	GR	17.48	23.28	E				14.2			
315	GL	15.05	25.50	E		4.2	ns	5.2			
316	GL	16.55	22.41	E		13.2	14.6	16.0		1.4	1.4
317	GL	16.86	22.35	E		4.4	ns	6.2			
318	GL	16.47	21.16	E		13.2	ns	ns			
319	GL	14.97	20.20	E		4.4	ns	6.2			
320	GL	14.05	19.59	E		10.0	11.4	11.8		1.4	0.4
321	GR	13.50	19.53	E		10.6	ns	10.8			
322	GL	13.00	19.95	E		10.2	11.2	12.0		1.0	0.8
323	GL	15.37	18.36	E		7.2	9.2	10.3		2.0	1.1
324	YE	16.98	19.96	E		6.8	7.6	7.4		0.8	-0.2
325	GL	17.95	20.55	E		9.2	8.6	11.0		-0.6	2.4
326	GL	15.98	20.70	E		5.6	ns	8.6			
327	GR	17.40	20.45	E		4.2	ns	4.4			

DUPLICATE:
Original in
Museum Archives
BSC-118

Species, Location, Size and Growth of Commercial Sponges at Black Point

ID#	Species	NE	SW	SECT	Jul-93	Oct-93	Jun-94	Oct-94	GR 1	GR 2	GR 3
1	YE	29.47	17.60	E	7.6	ns	6.8	ns			
2	GR	29.67	19.50	E	9.8	ns	5.0	ns			
3	GR	29.80	19.33	E	7.2	14.7	21.0	25.0	7.5	6.3	4.0
4	GR	27.55	14.40	E	8.6	14.8	18.2	22.4	6.2	3.4	4.2
5	GR	27.70	11.98	E	8.8	12.0	ns	ns	3.2		
6	GR	28.82	10.54	E	7.8	15.4	19.4	23.2	7.6	4.0	3.8
7	YE	28.14	17.96	E	7.4	8.4	ns	ns	1.0		
8	GR	27.11	19.50	E	3.2	5.0	ns	ns	1.8		
9	GR	26.40	16.40	E	4.8	ns	ns	ns			
10	GR	24.85	18.58	E	28.8	35.6	36.4	34.4	6.8	0.8	-2.0
11	GR	10.99	24.91	E	7.8	10.4	11.0	12.2	2.6	0.6	1.2
12	GR	12.73	22.93	E	10.6	22.2	ns	10.0	11.6		
13	GR	12.18	23.35	E	4.4	7.8	9.0	10.0	3.4	1.2	1.0
14	GR	12.09	22.96	E	7.8	13.4	17.0	22.0	5.6	3.6	5.0
15	YE	12.94	22.16	E	6.0	ns	ns	9.8			
16	GR	13.39	22.62	E	8.6	10.0	10.0	10.2	1.4	0.0	0.2
17	YE	13.92	22.40	E	4.4	6.0	6.0	ns	1.6	0.0	
18	GR	13.11	23.14	E	3.4	ns	ns	ns			
19	GR	13.84	23.33	E	4.0	7.5	7.8	8.0	3.5	0.3	0.2
20	GR			E	10.8	ns	ns	ns			
21	GR	14.15	21.52	E	8.4	9.4	8.2	ns	1.0	-1.2	
22	GR	20.23	18.01	E	6.6	10.4	11.6	16.8	3.8	1.2	5.2
23	GR	16.55	17.35	E	3.8	ns	9.0	11.6			2.6
24	GR			E	6.6	ns	ns	ns			
25	GR	19.56	14.00	E	15.8	ns	ns	ns			
26	GR	25.24	15.68	E	4.6	8.0	10.8	13.0	3.4	2.8	2.2
27	YE	25.98	14.20	E	9.6	10.2	10.0	10.4	0.6	-0.2	0.4
28	GR	27.18	14.50	E	3.4	ns	ns	18.0			
29	YE	25.72	13.80	E	7.8	9.8	11.8	11.6	2.0	2.0	-0.2
30	GR	20.20	13.49	E	8.8	ns	10.8	8.0			-2.8
31	GR	26.67	12.76	E	9.8	15.6	10.6	11.0	5.8	-5.0	0.4
32	GR	21.79	12.93	E	12.0	ns	ns	ns			
33	GR			E	4.0	ns	ns	ns			

Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
496	GL	12.33	25.10	W			3.2	3.0	3.2	5.0			-0.2	0.2	1.8
497	GL	19.65	14.48	W	62.0	57.4	59.8	52.4	48.6	49.6	-4.6	2.4	-7.4	-3.8	1.0
498	GL	22.85	12.05	W					7.4	8.0					0.6
499	GR	22.06	11.90	W					48.6	52.2					3.6
500	GL	23.89	11.66	W					3.4	5.0					1.6
R10	GL	24.44	10.13	W	3.2	2.8	ns	3.2	ns	ns	-0.4				
R11	GL	33.23	9.24	W		3.4	ns	ns	ns	ns					
R12	RE	32.31	2.97	W		3.0	ns	ns	ns	9.0					
R13	GL	27.49	11.70	W		4.6	ns	ns	ns	ns					
R14	RE	17.05	15.33	W		9.4	10.0	10.4	10.6	11.2		0.6	0.4	0.2	0.6
R15	GL	17.40	15.95	W		9.8	11.0	13.6	12.0	ns		1.2	2.6	-1.6	
R16	RE	16.55	16.68	W		3.4	ns	ns	ns	2.8					
R17	GR	24.25	13.10	W		6.0	ns	ns	ns	ns					
R18	RE	15.70	18.63	W		9.2	10.0	8.6	9.0	9.4		0.8	-1.4	0.4	0.4
R19	GL	20.92	20.92	W		4.6	4.6	5.8	8.0	8.0		0.0	1.2	2.2	
R2	GL	20.53	19.33	W		17.6	19.8	22.0	23.0	26.0		2.2	2.2	1.0	3.0
R20	RE	17.63	21.23	W		3.6	ns	ns	ns	5.2					
R21	RE	18.00	21.40	W		8.0	ns	ns	ns	ns					
R23	GR	18.37	23.05	W		2.6	ns	ns	ns	ns					
R24	RE	14.25	29.52	W		8.8	11.1	ns	8.8	8.8		2.3			0.0
R26	RE	12.14	26.35	W		2.4	ns	ns	ns	ns					
R27	RE	21.67	13.84	W		2.8	ns	6.0	5.4	ns				-0.6	
R28	RE	24.88	7.69	W		4.5	6.0	ns	ns	ns		1.5			
R29	GR	29.89	12.55	W		2.2	3.0	4.0	4.4	4.8		0.8	1.0	0.4	0.4
R3	GR	20.03	20.10	W		7.4	9.0	ns	ns	ns		1.6			
R30	GR	30.16	12.91	E		4.6	4.6	5.8	ns	#483		0.0	1.2		
R31	GR	24.54	11.55	E		3.8	7.0	ns	ns	ns		3.2			
R32	GL	17.47	19.74	E		7.8	7.0	9.6	ns	ns		-0.8	2.6		
R33	GR	16.67	17.68	E		4.4	8.0	ns	ns	ns		3.6			
R35	GL	13.69	22.94	E		15.8	16.0	20.6	22.0	25.0		0.2	4.6	1.4	3.0
R4	GL	19.45	21.87	W		3.6	7.0	5.8	8.0	ns		3.4	-1.2	2.2	
R6	RE	11.81	25.75	W		4.8	ns	ns	ns	ns					
R7	RE	20.98	21.38	W		2.4	4.0	4.8	4.2	ns		1.6	0.8	-0.6	
R9	GL	14.07	24.23	W		18.0	ns	ns	ns	ns					

Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
460	GL	25.54	11.50	E	23.6	26.0	25.4	25.8	27.0	28.0	2.4	-0.6	0.4	1.2	1.0
461	GL	26.34	10.83	E				6.0	6.8	8.2				0.8	1.4
463	GL	9.94	25.65	E				3.6	ns	ns					
464	GL	4.71	30.81	E				2.8	3.4	3.0				0.6	-0.4
465	GL	35.64	9.88	W				6.8	5.0	7.8				-1.8	2.8
466	GL	21.37	23.00	W				5.6	ns	ns					
467	GL	20.93	24.60	W				5.6	ns	ns					
468	GL	20.99	18.59	W				3.8	3.2	3.0				-0.6	-0.2
469	GL	20.90	17.50	W				6.0	6.8	8.6				0.8	1.8
470	GL	16.38	23.36	W	24.6	24.8	22.0	30.0	30.0	31.0	0.2	-2.8	8.0	0.0	1.0
471	GL	16.80	28.11	W				3.8	3.0	4.2				-0.8	1.2
472	GL	15.63	29.39	W				3.6	3.0	2.2				-0.6	-0.8
473	GL	14.73	26.83	W				5.0	3.0	4.0				-2.0	1.0
474	GL	16.40	26.06	W				3.6	3.2	6.0				-0.4	2.8
475	GR	23.58	12.66	W				6.0	ns	ns					
476	WO	29.43	6.48	W	38.2	ns	39.0	39.4	39.0	43.0			0.4	-0.4	4.0
477	GL	30.35	6.12	W				15.6	17.0	17.0				1.4	0.0
478	GL	27.08	7.45	W				4.8	6.0	6.4				1.2	0.4
479	GL	24.19	10.69	W				5.0	4.6	5.6				-0.4	1.0
480	GL	11.84	25.78	W				7.2	7.0	7.4				-0.2	0.4
481	GL	23.68	9.57	W				13.0	13.8	14.8				0.8	1.0
482	GL	17.00	24.46	E	19.2	23.0	22.4	25.4	26.4	26.6	3.8	-0.6	3.0	1.0	0.2
483	GL	30.40	12.95	E					5.8	7.2					1.4
484	GL	28.98	11.28	E					5.4	ns					
485	YE	24.29	12.04	E						12.6					
486	GL	26.53	16.98	E	25.2	30.2	30.6	35.2	36.6	37.8	5.0	0.4	4.6	1.4	1.2
487	GL	24.25	15.27	E	45.8	47.0	46.0	ns	46.0	45.2	1.2	-1.0			-0.8
488	GL	17.10	19.75	E					7.8	9.0					1.2
489	GL	12.70	25.97	E	41.6	41.4	42.0	47.0	46.0	46.0	-0.2	0.6	5.0	-1.0	0.0
490	GL	8.30	27.63	E					9.8	10.2					0.4
491	GL	2.65	30.42	E	8.4	ns	7.2	9.8	9.8	ns			2.6	0.0	
492	GL	1.03	30.85	W	45.0	46.0	48.0	45.8	45.4	48.1	1.0	2.0	-2.2	-0.4	2.7
493	GL	10.50	28.09	W		3.0	ns	ns	6.0	ns					
494	GL	17.97	27.96	W	4.0	ns	ns	ns	6.4	8.0					1.6
495	WO	12.64	25.15	W					12.4	16.6					4.2

TITLE: **MEASURING METABOLISM OF REEFS IN VIRGIN ISLANDS NATIONAL PARK AND BISCAYNE NATIONAL PARK: SIGNS OF TROUBLE?**

Submitted to: Dr. Russ Hall
Dr. Nick Funicelli
Florida Caribbean Science Center
USGS, Biological Resources Division
Prepared by: Dr. Caroline Rogers
June 2, 1999

OBJECTIVES and JUSTIFICATION:

Need – Over the last two decades, a variety of natural and human stresses have caused severe degradation of many reefs in the Caribbean and western Atlantic, including those within Virgin Islands National Park (VINP) and Biscayne National Park (BNP). Reefs are exhibiting declines in living coral and increases in algae. Calcification rates are changing because of a shift in the carbon balance between carbon used for constructing carbonate skeletons and carbon used to grow fleshy tissues of algae ("macroalgae"). To date, monitoring programs in VINP (e.g., Rogers et al. 1997) and BNP (e.g., Porter and Meier 1992) have focused on reef structure (e.g., abundances or cover of organisms) rather than reef function ("metabolism"). Calcification, the most fundamental process of all, involves the deposition of calcium carbonate, primarily by corals and coralline algae, which creates the 3-dimensional structure of the reef (see Hallock 1997). Scientists debate whether reefs are sources or sinks of CO_2, although most consider reefs as sources of CO_2 over the time frame of interest to human beings because CO_2 is released during the production of calcium carbonate (Hallock 1997, Hubbard 1997). Another essential process is productivity (photosynthesis and respiration) of reef organisms, including the zooxanthellae within the stony coral tissues and non-symbiotic algae (both turfs and macroscopic algae, or "macroalgae"). In this proposal we refer to calcification and productivity as reef "metabolism". There is an urgent need to determine the calcification rates of selected reefs within these national parks and to find out if these reefs are actively accreting or if they are unable to maintain their structure because the balance has shifted away from the major framework building organisms, including the scleractinian corals, to non-calcifying (or only weakly-calcifying) organisms (see Kinsey 1985).

Presently, we know of no efforts to monitor calcification rates on reefs as indicators of reef condition. We need to determine if measurements of

Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
424	GL	18.42	22.60	W		10.4	15.0	15.8	16.0	16.8		4.6	0.8	0.2	0.8
425	GL	18.33	23.36	W			7.0	5.0	ns	ns			-2.0		
426	GL	17.20	24.20	W			7.4	7.8	10.4	12.0			0.4	2.6	1.6
427	GL	15.84	24.20	W	32.6	31.6	33.8	35.0	35.6	36.4	-1.0	2.2	1.2	0.6	0.8
428	GL	14.87	24.33	W			7.0	4.8	5.4	6.4			-2.2	0.6	1.0
429	GL	17.20	27.62	W	9.8	11.6	27.0	18.0	19.6	21.0	1.8	15.4	-9.0	1.6	1.4
431	GL	14.88	25.84	W				11.2	ns	12.2					
432	GL	30.90	19.58	E			3.8	4.6	3.8	5.2			0.8	-0.8	1.4
433	GL	28.80	12.42	E			5.4	ns	6.2	7.0					0.8
434	GL	27.70	15.18	E			45.0	43.8	ns	ns			-1.2		
435	GR	27.49	15.15	E			5.8	7.0	6.6	6.6			1.2	-0.4	0.0
436	GL	27.40	13.09	E	49.0	52.0	51.4	53.4	54.4	55.1	3.0	-0.6	2.0	1.0	0.7
437	GL	27.79	11.80	E	4.2	ns	8.4	ns	8.0	9.3					1.3
438	GL	26.30	12.75	E	21.4	25.0	25.4	27.6	32.0	32.4	3.6	0.4	2.2	4.4	0.4
439	GL	26.25	12.92	E	29.4	28.6	29.0	31.2	33.6	35.1	-0.8	0.4	2.2	2.4	1.5
440	GL	25.85	14.41	E	8.0	ns	5.8	7.2	7.8	8.0			1.4	0.6	0.2
441	GL	24.67	15.49	E			3.0	ns	ns	ns					
442	GL	22.60	13.02	E	13.4	14.0	14.2	15.2	ns	ns	0.6	0.2	1.0		
443	GL	24.04	17.04	E			4.8	ns	3.0	ns					
444	GL	22.33	16.66	E			14.2	14.4	14.0	14.8			0.2	-0.4	0.8
445	GL	22.20	13.25	E			4.6	4.0	3.6	4.4			-0.6	-0.4	0.8
446	GL	18.72	17.58	E			4.2	4.0	3.8	2.6			-0.2	-0.2	-1.2
447	GL	16.69	17.65	E			9.4	9.8	9.8	10.2			0.4	0.0	0.4
448	GL	16.82	19.74	E			6.4	7.2	7.0	7.0			0.8	-0.2	0.0
449	GR	18.93	23.75	E			24.5	23.0	26.0	24.0			-1.5	3.0	-2.0
450	GR	15.78	22.85	E			30.4	30.6	31.0	32.6			0.2	0.4	1.6
451	GL	15.20	21.03	E			11.0	13.2	ns	ns			2.2		
452	GL	13.92	22.74	E		8.8	9.0	10.0	11.0	10.4		0.2	1.0	1.0	-0.6
453	GL	14.66	25.22	E			8.2	10.0	9.6	10.0			1.8	-0.4	0.4
454	GL	11.43	22.40	E	7.8	7.4	ns	9.4	9.4	10.2	-0.4			0.0	0.8
455	GL	11.80	25.77	E			10.8	11.4	11.8	11.0			0.6	0.4	-0.8
456	GL	10.29	22.21	E			3.6	ns	ns	ns					
457	GL	9.59	23.15	E			6.2	5.2	5.6	5.4			-1.0	0.4	-0.2
458	GL	8.25	23.88	E	48.8	50.0	46.0	49.2	49.0	50.0	1.2	-4.0	3.2	-0.2	1.0
459	GL	3.03	30.40	E	15.4	16.0	14.0	15.2	15.0	15.0	0.6	-2.0	1.2	-0.2	0.0

calcification rates and photosynthesis are useful tools for quantifying differences among reefs as well as changes on reefs over time (for example, before and during/after bleaching episodes or runoff events). We plan to test and adapt methods which have recently been used successfully in seagrass beds in Florida Bay (Halley and Yates 1999). We propose to measure reef metabolism in Virgin Islands National Park and Biscayne National Park on reefs with a range of live coral cover during times of low and high water temperatures (winter and late summer/fall). Bleaching episodes, such as the most severe on record in 1998, are usually associated with higher than normal water temperatures. Water temperatures in both parks have exceeded 30 C, the temperature above which the symbiosis between corals and their zooxanthellae breaks down (Glynn and D'Croz 1990). We hope to measure reef metabolism before and during bleaching episodes. Additional outcomes of these measurements are an improved understanding of the CO_2 contribution of coral reefs to the atmosphere and a methodology which can help to assess the direct impact of increased CO_2 on coral reefs.

Background: Natural stresses such as hurricanes and coral diseases as well as anthropogenic factors such as increased runoff, damage from boat anchors and groundings, and sewage input have killed corals and altered the relative abundances of reef organisms. In some extreme cases coral reefs have been almost entirely overgrown by algae (Hughes 1994). Coral reefs are also among the ecosystems which could be most vulnerable to changes in climate because increased atmospheric CO_2 could lower calcification rates with far-reaching effects on reef structure (Pennisi 1998, Kleypas et al. 1999). The current warming trend in sea water temperatures also poses serious threats to reefs because corals exist near the maximum temperatures they can tolerate (e.g, Hubbard 1997). Corals are also especially sensitive to elevated CO_2 and increased UV radiation (Brown 1997). Though not the most abundant organisms on Caribbean reefs, corals create the reef's physical structure, providing habitat for fishes and other organisms.

Corals provide clues to the present and to the past. They respond to increased temperatures and UV radiation by "bleaching" (losing color). When corals bleach, they cease reproduction and their growth rates decrease (e.g., Szmant and Gassman 1990). Coral skeletons contain a record of past environmental conditions. For example, they have annual (or near annual) growth bands because skeletal densities vary with cooler and warmer temperatures. Through examination of coral cores ("sclerochronology" studies) one can learn about calcification rates in the past and compare those to present rates (e.g., Hudson et al. 1976).

Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
336	GL	15.73	19.09	E						3.6					
337	GR	19.14	23.06	E						28.6					
338	GR	19.60	22.30	E						10.4					
339	GL	18.87	17.55	E						10.8					
340	GL	22.23	13.28	E						5.4					
341	GL	23.37	12.95	E	32.4	33.6	30.6	36.0	36.4	40.0	1.2	-3.0	5.4	0.4	3.6
342	GL	25.43	18.03	E						2.4					
343	YE	25.23	13.33	E					3.8	4.4					0.6
344	GL	24.75	11.41	E						7.8					
345	GL	24.61	11.85	E						5.6					
346	GL	25.65	12.60	E						10.2					
347	GR	27.10	16.66	E	49.2	57.4	58.0	68.4	70.2	74.0	8.2	0.6	10.4	1.8	3.8
401	GL	31.30	2.23	W			6.0	6.6	6.4	6.8			0.6	-0.2	0.4
402	GL	34.55	7.44	W			8.2	9.0	9.0	9.6			0.8	0.0	0.6
403	GL	30.43	7.30	W	40.0	ns	ns	43.8	40.0	42.0				-3.8	2.0
404	GL	27.62	7.13	W			6.4	7.4	8.0	7.6			1.0	0.6	-0.4
405	GL	28.16	9.80	W	42.8	44.0	46.8	46.0	48.0	46.8	1.2	2.8	-0.8	2.0	-1.2
406	WO	23.25	8.95	W	43.0	43.0	37.8	43.0	45.8	49.8	0.0	-5.2	5.2	2.8	4.0
407	GL	24.40	10.08	W	2.0	ns	8.6	8.4	10.0	10.2			-0.2	1.6	0.2
408	GR	24.62	9.93	W	8.8	12.0	12.8	13.0	11.0	13.2	3.2	0.8	0.2	-2.0	2.2
409	GL	22.88	10.79	W			6.8	7.2	ns	ns			0.4		
410	GL	23.50	12.04	W			6.0	7.2	8.0	9.3			1.2	0.8	1.3
411	GL	27.05	14.79	W		5.2	ns	5.2	5.6	6.8				0.4	1.2
412	WO	22.56	16.28	W	17.0	17.0	23.0	24.0	27.0	29.8	0.0	6.0	1.0	3.0	2.8
413	GL	24.15	17.54	W			4.0	6.2	7.0	9.0			2.2	0.8	2.0
414	GL	19.98	17.65	W			4.6	ns	5.8	ns					
415	GL	19.00	18.21	W			4.8	4.6	5.8	7.4			-0.2	1.2	1.6
416	GL	19.40	18.74	W			4.2	5.0	5.0	5.4			0.8	0.0	0.4
417	GL	21.13	18.95	W			13.2	13.4	19.8	17.0			0.2	6.4	-2.8
418	GL	23.06	20.19	W			3.4	3.4	4.4	4.2			0.0	1.0	-0.2
419	GL	22.85	20.14	W			5.6	5.4	6.8	6.6			-0.2	1.4	-0.2
420	GL	22.58	20.75	W	5.4	ns	ns	8.2	ns	ns					
421	GL	22.00	20.50	W	4.2	ns	ns	5.4	7.0	6.4				1.6	-0.6
422	GL	14.37	19.70	W	22.0	20.2	21.2	22.6	23.4	25.8	-1.8	1.0	1.4	0.8	2.4
423	GL	19.00	21.36	W	11.4	18.8	ns	14.4	16.0	17.1	7.4			1.6	1.1

Monitoring of reef metabolism at selected reefs in Virgin Islands National Park and Biscayne National Park is the central focus of this 2-year project. Detailed information on the structure of each study site will be correlated with the measurements of reef metabolism. (This information is available for some reefs from the USGS/NPS Inventory & Monitoring Program.) Existing data on reef structure and function are severely limited both spatially and temporally, with insufficient data from widely separated geographic areas over long periods of time. To begin to address these scale deficiencies, we will be looking at reefs in subtropical and tropical areas, and we will be examining coral cores for information on past environmental conditions.

PROCEDURES/METHODS:

Selection of Study Sites

Some of the study sites for this project will be areas for which long-term data (both biological and environmental) are already available. Long-term monitoring sites were established on reefs in Virgin Islands National Park and Biscayne National Park under an NPS program which began in 1988, and the DOI Inventory & Monitoring (I&M) program has supported additional work in VINP. Other sites will be chosen to ensure that data are obtained from a variety of different reef types and from sites of particular management concern.

The coral reef monitoring programs which NPS and BRD have conducted in these two parks in conjunction with state and university scientists are some of the few long-term monitoring programs in the Caribbean and western Atlantic (Connell 1997). Data on cover by coral and algae are available for both VINP and BNP, and effects of different stresses have been documented for some reefs. Underwater videotapes which provide a statistically quantifiable and permanent visual record of reef structure are available from both parks.

A major task for Year 1 will be the selection of each study site based on the need to include reefs with a range of different reef types with variations in coral cover. Reefs in Biscayne National Park generally have less than 5% living coral while some sites in St. John have live cover in excess of 20%. Initially, we will focus on reefs for which data on reef structure are already available. On St. John, we will study sites in Lameshur and Newfound bays , for which we have the longest data sets (10 and 9 years respectively). These sites are also under consideration for inclusion in a "marine reserve" within park waters. Transects in Newfound Bay would have the highest coral cover of all the study sites (23%) while those in Lameshur have a coral cover of about 10%. We may also select Hawksnest Bay for which we have information on siltation effects and coral

Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
301	GR	27.05	14.25	W	24.0	27.2	33.6	40.0	42.0	45.6	3.2	6.4	6.4	2.0	3.6
302	GR	25.53	9.45	W					47.2	40.2					-7.0
303	GL	27.23	6.42	W					5.8	6.0					0.2
304	GL	28.11	6.83	W					7.8	8.4					0.6
305	GL	29.38	8.25	W	30.0	31.0	31.8	33.0	34.2	35.0	1.0	0.8	1.2	1.2	0.8
306	GR	19.82	18.92	W						8.2					
307	GR	19.70	19.00	W						5.2					
308	YE	12.91	29.08	W						8.4					
309	GL	15.14	27.31	W						4.4					
310	GL	20.35	21.73	W						6.0					
311	GL	20.45	20.85	W						27.2					
312	GL	17.94	20.05	W						5.8					
313	GL	15.67	18.65	W						2.8					
314	GL	21.38	21.20	W						5.8					
315	GL	21.65	20.63	W						4.4					
316	GL	20.55	19.23	W						4.2					
317	GL	24.63	17.30	W						6.6					
318	GL	23.54	10.83	W						3.8					
319	GL	27.58	14.63	W						6.8					
320	GL	24.55	8.80	W						34.6					
321	GL	28.13	9.72	W						46.8					
322	GL	26.45	5.83	W						10.0					
323	GL	26.22	6.70	W						5.6					
324	GR	27.84	7.13	W	25.0	ns	27.8	28.4	35.0	35.0			0.6	6.6	0.0
325	GR	28.30	8.84	W	26.0	29.0	30.6	32.0	36.2	36.0	3.0	1.6	1.4	4.2	-0.2
326	GR	28.55	6.90	W						25.8					
327		27.83	6.40	W						23.4					
328	GL	27.27	6.28	W						10.8					
329	WO	29.69	3.95	W						25.0					
330	GL	34.58	7.45	W						9.8					
331	GL	2.72	30.54	E						11.6					
332	GL	9.85	26.29	E						8.4					
333	GL	10.45	23.92	E						20.2					
334	GL	10.40	23.96	E						3.2					
335	GL	11.70	23.19	E						4.2					

growth rates (Hubbard et al. 1987) because it is a shallow reef exhibiting some signs of recovery in elkhorn coral (Acropora palmata) populations. This primary reef-building species was decimated throughout the Caribbean in the 1980's by white band disease.

Reef Function: Calcification and Productivity

Carbonate sediment production, photosynthesis, and respiration will be measured in winter (when temperatures are lowest) and late summer/fall (when temperatures are highest) to determine seasonal and areal variation in tissue/carbonate production and to derive average annual production rates. These parameters will be calculated from total alkalinity, pH, calcium concentrations, salinity, irradiance, temperature, wind and current speed, and air-sea CO_2 and O_2 fluxes measured along transects across reefs.

We propose to work with our primary collaborators, Dr. Robert Halley and Dr. Kim Yates, from the USGS Geologic Division to measure parameters of carbon budgets to assess reef conditions. For many years carbon budgets of reefs have been studied by measuring geochemical parameters of carbon utilization (Smith, 1973). The techniques used to make these measurements have been greatly refined during the past two decades because they are, in part, also the techniques used for measuring global atmospheric CO_2 exchange with the ocean. These refined procedures can now be used again to study coral reefs (Buddemeier and Kinzie 1998).

Dr. Halley and Dr. Yates have developed prototypes of two geochemical monitoring systems including a Submersible Habitat for Analyzing Reef Quality (S.H.A.R.Q.) and an In Site Biogeochemical Analysis System (I.B.A.S) for measurement of geochemical changes associated with benthic and water column carbonate sediment production and metabolic activity, respectively (see Halley and Yates for details). To measure reef metabolism, we will use two primary experimental approaches: 1) upstream-downstream transects across broad sections of the reef, and 2) metabolism of small reef areas enclosed within the SHARQ (see also Rogers 1979).

For upstream-downstream measurements, transects will be located parallel to unidirectional current flow across a given reef. Current velocities will be measured with current meters. Sample stations will be positioned at the upstream and downstream ends of each transect.

Geochemical and physical parameters (including water temperature) will be measured at each station along a transect at different times (and irradiances) during the day and night to determine daily variations in production and to

Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
244	GL	27.94	7.77	W	27.8	28.0	30.8	29.0	ns	28.8	0.2	2.8	-1.8		
246	GL	27.86	6.24	W	18.2	19.9	21.2	23.5	24.0	25.0	1.7	1.3	2.3	0.5	1.0
247	GL	27.88	6.30	W	19.0	20.6	22.0	24.0	24.0	24.2	1.6	1.4	2.0	0.0	0.2
248	GL	28.69	6.54	W	10.0	8.2	11.0	13.5	13.8	13.8	-1.8	2.8	2.5	0.3	0.0
249	YE	28.53	6.92	W	9.6	ns	18.0	22.0	25.0	30.6			4.0	3.0	5.6
250	GL	28.72	7.00	W	7.6	ns	10.0	14.0	ns	9.8			4.0		
251	GL	28.77	6.63	W	4.0	ns	6.0	9.0	9.0	10.2			3.0	0.0	1.2
253	GL	28.11	6.82	W	5.0	ns	ns	ns	ns	ns					
254	GL	30.31	6.15	W	9.4	11.6	12.0	ns	ns	ns	2.2	0.4			
257	GL	29.70	11.08	W	21.8	ns	ns	ns	ns	ns					
258	GL	29.89	10.35	W	26.4	25.0	ns	ns	ns	ns	-1.4				
259	GL	30.80	9.80	W	38.8	ns	ns	ns	ns	ns					
260	WO	31.09	8.69	W	11.0	ns	ns	ns	ns	ns					
261	GL	32.75	8.35	W	34.6	32.2	36.8	36.0	37.0	36.4	-2.4	4.6	-0.8	1.0	-0.6
262	GL	32.11	7.64	W	14.2	18.8	16.6	18.0	19.0	19.0	4.6	-2.2	1.4	1.0	0.0
263	GL	32.20	7.66	W	23.6	22.2	24.0	27.5	28.0	27.8	-1.4	1.8	3.5	0.5	-0.2
264	GL	32.22	7.50	W	32.4	ns	ns	ns	ns	ns					
265	GL	31.83	7.42	W	4.2	ns	ns	ns	ns	ns					
266	GL	33.25	9.14	W	11.8	11.6	14.8	15.8	19.0	19.0	-0.2	3.2	1.0	3.2	0.0
267	GL	34.00	10.17	W	23.4	ns	24.8	28.0	27.0	27.4		1.4	3.2	-1.0	0.4
268	GL	32.48	9.85	W	27.2	26.2	28.4	30.0	32.0	31.8	-1.0	2.2	1.6	2.0	-0.2
269	GL	33.48	5.55	W	45.2	44.0	47.2	48.0	49.0	49.0	-1.2	3.2	0.8	1.0	0.0
270	GL	33.40	5.14	W	49.2	ns	ns	ns	ns	ns					
271	WO	31.79	5.05	W	45.8	46.0	ns	ns	ns	ns	0.2				
272	GL	30.95	3.37	W	9.4	ns	10.8	12.6	ns	ns			1.8		
273	GL	30.85	3.05	W	20.6	ns	20.8	24.0	24.0	23.0			3.2	0.0	-1.0
274	WO	29.66	3.95	W	13.4	5.0	18.8	20.0	23.0	ns	-8.4	13.8	1.2	3.0	
275	GL	27.25	6.40	W	3.0	3.0	ns	5.0	ns	ns	0.0				
276	GL	27.23	6.29	W	2.4	4.2	ns	6.4	9.0	12.0	1.8			2.6	3.0
277	GL	16.69	21.90	W	3.6	ns	ns	ns	ns	ns					
278	GL	17.70	24.39	W	3.0	ns	ns	5.8	ns	ns					
279	GL	17.16	26.56	W	2.4	ns	ns	ns	ns	ns					
280	GL	22.43	11.52	W	4.2	ns	ns	8.5	10.0	ns				1.5	
281	GL	14.27	20.25	W	5.2	ns	ns	ns	ns	ns					
282	GL	14.20	20.29	W	14.8	15.0	18.0	16.0	15.2	16.6	0.2	3.0	-2.0	-0.8	1.4

derive average daily production rates. Recording thermistors are already in place on several reefs in VINP and BNP.

Total alkalinity and pH will be used to calculate calcification and net photosynthesis using the alkalinity anomaly technique of Smith and Key (1975) such that calcification (C) = half the change in total alkalinity, and net photosynthesis (P) = total carbon - calcification. Total carbon will be calculated using carbonate system equations from Millero (1979). Calcium measurements will provide an independent measure of calcification for comparison. Air-sea CO_2 fluxes will be measured directly at each station inside a floating bell (Frankignoulle 1988, Gattuso et al. 1993, Kayanne et al. 1995) using the procedure and calculations of Frankignoulle (1988). Air-sea O_2 fluxes will be determined by measuring atmospheric and water pO_2 and calculating fluxes as described in Wanninkhof (1992). Differences in oxygen and carbon metabolism between upstream and downstream stations will be corrected for O_2 and CO_2 exchange with the atmosphere as described in (Gattuso et. al. 1993).

Productivity and metabolic rates per unit area will be calculated using the difference in concentration between upstream and downstream stations, the volume of water transported along a transect, and the transect area such that the change in concentration of a parameter (delta $C/m^2/s$) = $(C/m3 \times m3/hr)/m^2$ (Barnes and Devereux 1984). Seasonal production rates will be used to calculate average annual production rates. Comparison of these data with previous productivity estimates and calcification rates, as well as calcification rates determined from coral cores (Hudson et. al. 1976; Dodge et. al. 1984; Dodge, et. al. 1992) would indicate whether long-term (decades) changes are occurring on the reefs.

We plan to use both the upstream-downstream method and the SHARQ in both national parks. In some cases, upstream-downstream techniques may not be feasible because of local current conditions (i.e., currents are too weak or too complex)., or because reef zones are not wide enough to allow detection of changes. In other situations, for example, where the reef has very high relief, it will be more difficult to use the SHARQ. The IBAS will be used to measure metabolism of the water column and to enable quantification of benthic and water column contributions to overall metabolism. Dr. Robert Halley and Dr. Kimberly Yates, our primary collaborators, have successfully done pilot studies of seagrass beds in Florida Bay using these techniques and plan to test them out on reefs soon.

In the fall of 1998, severe bleaching occurred on the reefs around St. John and within Biscayne National Park. We hope to take measurements during future

Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
198	GL	20.57	14.41	W	20.4	19.8	20.4	19.2	22.0	20.4	-0.6	0.6	-1.2	2.8	-1.6
199	GL	21.41	15.40	W	3.8	ns	ns	ns	ns	ns					
202	GL	19.85	21.58	W	44.8	45.8	49.3	46.0	50.0	ns	1.0	3.5	-3.3	4.0	
203	GL	20.28	20.89	W	38.6	ns	ns	ns	ns	ns					
204	GL	19.64	18.91	W	17.0	19.0	19.4	19.8	23.0	21.0	2.0	0.4	0.4	3.2	-2.0
205	GL	19.77	19.06	W	5.2	7.2	ns	ns	ns	ns	2.0				
206	GL	19.73	19.02	W	3.4	ns	ns	ns	ns	ns					
207	GL	19.76	18.99	W	3.6	4.4	9.3	ns	ns	ns	0.8	4.9			
208	GL	20.48	21.66	W	5.6	6.8	9.0	9.8	11.0	13.1	1.2	2.2	0.8	1.2	2.1
209	GL	20.34	21.68	W	4.8	ns	ns	ns	ns	ns					
210	GL	21.18	22.67	W	10.0	8.9	6.0	16.6	17.0	16.6	-1.1	-2.9	10.6	0.4	-0.4
213	GL	22.65	19.69	W	7.8	8.8	9.8	11.8	ns	14.8	1.0	1.0	2.0		
214	GL	23.81	18.08	W	16.2	ns	ns	ns	ns	ns					
215	GL	24.55	19.91	W	8.4	9.4	12.0	11.6	ns	14.0	1.0	2.6	-0.4		
216	GL	24.34	18.25	W	10.0	10.0	11.0	ns	12.0	ns	0.0	1.0			
217	GL	23.60	14.17	W	42.8	39.0	37.4	19.0	ns	ns	-3.8	-1.6	-18.4		
218	WO	22.48	16.30	W	15.6	ns	20.8	23.5	25.0	15.1			2.7	1.5	-9.9
220	GL	20.65	16.41	W	9.4	10.2	12.2	15.2	16.2	17.4	0.8	2.0	3.0	1.0	1.2
221	WO	21.13	14.44	W	26.6	29.9	32.0	35.0	39.0	38.2	3.3	2.1	3.0	4.0	-0.8
222	GL	22.23	12.04	W	18.8	23.0	23.0	26.5	29.0	28.0	4.2	0.0	3.5	2.5	-1.0
223	GR	22.10	12.00	W	45.0	47.4	46.0	52.0	ns	ns	2.4	-1.4	6.0		
224	GL	22.88	12.08	W	4.6	ns	ns	ns	ns	ns					
225	GL	26.60	9.38	W	19.6	22.0	24.0	24.8	26.0	27.4	2.4	2.0	0.8	1.2	1.4
226	GR	25.55	9.47	W	40.0	39.6	44.8	49.0	ns	ns	-0.4	5.2	4.2		
229	GL	24.85	9.07	W	42.6	31.8	ns	ns	ns	ns	-10.8				
231	GR	24.42	9.03	W	9.4	11.6	13.2	18.0	17.0	20.1	2.2	1.6	4.8	-1.0	3.1
232	GL	25.55	13.44	W	26.4	25.4	26.2	27.5	26.0	26.0	-1.0	0.8	1.3	-1.5	0.0
233	GL	26.45	14.23	W	44.4	44.0	46.4	48.0	50.0	48.4	-0.4	2.4	1.6	2.0	-1.6
235	GL	27.14	14.38	W	30.8	33.8	39.6	44.0	47.0	48.8	3.0	5.8	4.4	3.0	1.8
236	GL	27.65	12.44	W	20.0	ns	ns	ns	ns	ns					
237	GL	27.43	13.58	W	18.0	17.8	ns	23.5	25.0	25.4	-0.2			1.5	0.4
238	GL	26.84	11.85	W	17.8	17.0	18.6	21.5	24.0	25.0	-0.8	1.6	2.9	2.5	1.0
239	GL	26.95	11.30	W	32.2	22.0	32.0	34.0	37.0	36.4	-10.2	10.0	2.0	3.0	-0.6
241	GL	28.60	9.63	W	53.8	54.8	56.0	56.0	57.0	55.0	1.0	1.2	0.0	1.0	-2.0
243	GL	27.96	7.93	W	6.2	ns	9.4	13.0	14.0	14.4			3.6	1.0	0.4

bleaching events to determine the effects of zooxanthellae loss (which results in bleaching) on productivity and calcification rates.

Reef Structure

It is essential that we have pertinent data on the structure of the transects to accompany the metabolism rates we measure (with both the upstream-downstream technique and the SHARQ). At some study sites, we intend to install the SHARQ over transects for which we already have very detailed information on relative abundances of different organisms ("reef structure"). At other sites, we will collect quantitative information using videography (Rogers and Miller submitted manuscript).

Coral Cores

Skeletons of some coral species (including Montastraea annularis) provide a record of the environmental conditions under which the corals grew. We propose to examine coral cores which have already been collected from the parks to look for any changes in calcification (deposition of the coral skeleton) which would indicate short-term or long-term changes in environmental conditions. Cores will be used to construct a history of climate conditions over as long a period as possible. We will not be collecting new cores from any of the sites.

The proposed work represents a major study of reef metabolism or "function" as opposed to reef "structure" which is the subject of most monitoring projects. It addresses the fundamental processes required for reef development. The work also relates to the goals of BRD's Global Climate Change Program in several ways. First the proposed measurement of air-sea CO_2 fluxes not only provide basic data for determining the degree to which coral reefs contribute to atmospheric CO_2, but they also provide a way to evaluate the sensitivity of coral reef carbon budgets to future atmospheric CO_2 levels (Goal 1). Second, carbon-budget measurements on reefs will help determine the combined effects of global change and environmental contamination on reefs (Goal 2). Third, the project is being addressed at several spatial and temporal scales in an effort to learn more about responses of coral reefs to global change (Goal 3). Fourth, the proposed experiments provide a basis for a better understanding of how careful management of sediment and nutrient input to reefs (which affects the relative abundances of algae and living coral) could offset effects of increased global CO_2 (Goal 4)

Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
160	GL	25.22	7.13	W	12.0	ns	ns	15.0	15.0	15.1				0.0	0.1
161	GL	23.90	8.57	W	15.4	16.4	19.8	22.2	23.0	26.8	1.0	3.4	2.4	0.8	3.8
163	GL	23.09	9.33	W	32.0	35.6	38.4	ns	ns	ns	3.6	2.8			
164	GL	23.71	9.07	W	8.2	8.8	ns	ns	ns	ns	0.6				
165	GL	24.43	8.93	W	34.0	27.0	35.6	35.6	ns	ns	-7.0	8.6	0.0		
166	GL	21.35	11.97	W	51.0	ns	ns	ns	ns	ns					
167	GL	22.63	11.12	W	5.0	ns	ns	ns	10.4	ns					
168	GL	20.82	12.46	W	21.8	24.8	29.0	33.2	35.0	36.6	3.0	4.2	4.2	1.8	1.6
169	GL	20.68	12.34	W	15.2	ns	ns	ns	ns	ns					
170	GL	20.17	12.65	W	19.0	18.8	22.4	17.0	23.0	ns	-0.2	3.6	-5.4	6.0	
171	GL	19.85	12.63	W	23.2	24.0	24.4	25.0	26.0	25.4	0.8	0.4	0.6	1.0	-0.6
173	GL	19.26	14.77	W	9.8	ns	ns	ns	ns	ns					
174	GL	18.14	15.02	W	8.0	8.4	12.0	12.0	12.6	14.4	0.4	3.6	0.0	0.6	1.8
175	GL	17.45	17.49	W	4.0	5.0	7.2	7.4	7.4	7.8	1.0	2.2	0.2	0.0	0.4
176	GL	17.73	17.33	W	5.8	5.2	7.0	5.2	8.0	7.4	-0.6	1.8	-1.8	2.8	-0.6
177	GL	15.06	18.32	W	24.2	26.4	ns	ns	ns	ns	2.2				
179	GL	15.39	19.66	W	3.6	ns	ns	ns	ns	ns					
180	GL	12.50	22.24	W	17.4	20.0	ns	21.0	19.4	21.4	2.6			-1.6	2.0
181	GL	13.63	22.87	W	33.2	39.0	43.3	43.0	44.4	44.0	5.8	4.3	-0.3	1.4	-0.4
182	GL	12.99	24.67	W	5.0	6.2	8.0	8.8	9.2	9.6	1.2	1.8	0.8	0.4	0.4
183	GL	13.23	24.84	W	19.0	21.0	25.0	28.0	23.8	24.6	2.0	4.0	3.0	-4.2	0.8
184	GL	11.97	24.92	W	8.6	10.6	12.0	11.8	16.6	12.8	2.0	1.4	-0.2	4.8	-3.8
185	GL	12.09	25.41	W	4.0	ns	ns	ns	ns	ns					
186	GL	12.22	26.60	W	20.0	21.0	25.0	26.0	27.4	30.0	1.0	4.0	1.0	1.4	2.6
187	GL	9.73	29.06	W	7.0	ns	ns	ns	ns	ns					
188	GL	12.85	29.14	W	6.4	ns	ns	ns	ns	ns					
189	GL	14.43	30.54	W	48.0	47.8	50.2	49.8	55.2	55.4	-0.2	2.4	-0.4	5.4	0.2
190	GL	13.95	26.30	W	9.2	ns	ns	10.4	10.8	13.1				0.4	2.3
191	GL	17.39	19.50	W	10.6	12.0	20.0	11.8	9.2	ns	1.4	8.0	-8.2	-2.6	
192	GL	18.35	18.68	W	12.0	ns	ns	ns	ns	ns					
193	GL	18.50	18.58	W	2.0	ns	ns	ns	ns	ns					
194	GL	17.93	20.05	W	6.0	7.0	7.6	8.6	9.0	ns	1.0	0.6	1.0	0.4	
195	GL	15.54	20.60	W	3.4	ns	ns	ns	ns	ns					
196	GR	19.81	16.57	W	24.0	25.8	ns	ns	ns	ns	1.8				
197	GL	20.29	14.72	W	30.0	30.0	32.0	32.0	33.0	34.0	0.0	2.0	0.0	1.0	1.0

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Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
118	GL	8.32	27.79	E	7.4	9.2	9.4	10.4	9.8	24.2	1.8	0.2	1.0	-0.6	14.4
119	GL	6.13	29.26	E	24.8	ns	ns	ns	ns	ns					
120	GL	6.42	28.33	E	13.2	13.6	13.2	ns	ns	ns	0.4	-0.4			
121	GL	17.13	29.04	W	16.6	ns	ns	ns	ns	ns					
122	GL	17.30	28.50	W	70.4	69.0	ns	74.0	ns	ns	-1.4				
123	GL	19.37	29.30	W	14.6	ns	ns	ns	ns	ns					
124	GL	18.85	29.67	W	9.8	10.0	ns	ns	ns	ns	0.2				
125	GL	17.86	27.47	W	10.4	12.0	ns	14.4	16.0	16.3	1.6			1.6	0.3
127	GL	5.30	26.55	E	14.0	15.8	ns	ns	ns	ns	1.8				
128	GL	4.65	29.21	E	35.4	38.0	37.6	43.6	45.0	45.0	2.6	-0.4	6.0	1.4	0.0
131	GL	2.55	30.50	E	35.4	35.0	36.0	36.0	37.0	39.0	-0.4	1.0	0.0	1.0	2.0
132	GL	2.49	30.54	E	36.2	36.0	29.8	ns	ns	ns	-0.2	-6.2			
134	GL	17.75	27.47	W	24.4	23.6	27.0	26.0	27.0	28.0	-0.8	3.4	-1.0	1.0	1.0
136	GL	16.70	28.09	W	9.8	ns	ns	ns	ns	ns					
137	GL	16.66	26.43	W	23.0	25.0	30.0	33.0	36.2	37.3	2.0	5.0	3.0	3.2	1.1
138	GL	16.25	26.13	W	35.0	48.2	48.0	44.0	46.2	48.3	13.2	-0.2	-4.0	2.2	2.1
139	GL	16.50	26.18	W	9.6	ns	ns	ns	ns	ns					
140	GL	16.32	26.04	W	3.6	4.8	6.5	7.4	8.6	11.0	1.2	1.7	0.9	1.2	2.4
141	GL	15.99	26.30	W	9.6	10.6	27.0	ns	ns	ns	1.0	16.4			
142	GL	15.40	25.87	W	20.8	ns	ns	ns	ns	ns					
143	GL	16.43	24.98	W	15.8	ns	ns	ns	ns	ns					
144	GL	17.04	25.65	W	12.2	11.6	12.0	13.8	17.2	17.0	-0.6	0.4	1.8	3.4	-0.2
147	WO	17.40	23.55	W	23.0	ns	ns	ns	27.0	ns					
148	GL	17.17	23.99	W	4.2	ns	ns	ns	ns	ns					
149	GL	20.83	24.08	W	22.6	ns	ns	ns	ns	ns					
150	GL	32.00	1.00	W	65.2	57.0	ns	ns	ns	ns	-8.2				
151	GL	29.10	3.00	W	41.0	41.0	44.4	46.0	46.8	47.4	0.0	3.4	1.6	0.8	0.6
152	GL	28.80	3.23	W	68.0	ns	64.6	ns	ns	ns					
153	WO	27.30	5.28	W	10.0	9.0	9.6	12.2	14.0	16.4	-1.0	0.6	2.6	1.8	2.4
154	GL	26.44	5.84	W	8.0	9.0	9.0	8.8	ns	9.8	1.0	0.0	-0.2		
155	GL	26.42	5.95	W	12.6	ns	ns	ns	ns	ns					
156	GL	25.74	6.51	W	4.6	4.0	7.0	5.0	4.6	5.6	-0.6	3.0	-2.0	-0.4	1.0
157	GL	25.84	6.47	W	19.4	16.8	20.0	18.8	20.0	19.4	-2.6	3.2	-1.2	1.2	-0.6
158	GL	26.00	6.75	W	15.4	18.2	22.2	24.2	26.0	28.6	2.8	4.0	2.0	1.8	2.6
159	GL	26.16	6.70	W	2.4	1.0	ns	ns	ns	ns	-1.4				

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Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
79	GL	25.53	12.51	E	5.6	ns	ns	ns	ns	ns					
81	GL	25.59	11.33	E	12.4	12.6	12.2	13.2	12.2	13.0	0.2	-0.4	1.0	-1.0	0.8
82	GL	25.13	11.02	E	13.6	14.8	14.6	18.6	20.2	23.0	1.2	-0.2	4.0	1.6	2.8
83	GL	24.76	11.57	E	5.4	7.0	6.2	8.6	ns	8.0	1.6	-0.8	2.4		
84	YE	24.25	12.04	E	8.0	9.0	9.0	11.2	11.8	12.4	1.0	0.0	2.2	0.6	0.6
85	GL	24.81	13.34	E	7.2	8.6	7.6	9.6	10.8	11.4	1.4	-1.0	2.0	1.2	0.6
86	GL	24.73	13.40	E	23.4	24.4	23.8	29.2	30.4	32.0	1.0	-0.6	5.4	1.2	1.6
87	GL	23.64	14.21	E	38.6	40.0	36.8	41.8	41.0	39.8	1.4	-3.2	5.0	-0.8	-1.2
88	GL	23.19	14.07	E	7.2	7.0	6.0	6.2	5.8	5.6	-0.2	-1.0	0.2	-0.4	-0.2
91	GL	25.27	13.59	E	14.1	16.2	16.6	18.6	20.8	20.6	2.1	0.4	2.0	2.2	-0.2
92	GL	25.02	13.90	E	5.6	ns	ns	ns	ns	ns					
93	GL	20.55	14.29	E	20.4	18.2	16.5	16.8	16.4	17.4	-2.2	-1.7	0.3	-0.4	1.0
94	GL	20.70	15.85	E	14.8	ns	ns	ns	ns	ns					
95	GL	19.89	16.40	E	18.8	ns	ns	ns	ns	ns					
96	WO	19.23	14.62	E	60.4	ns	65.2	70.0	73.0	73.0			4.8	3.0	0.0
97	GL	19.18	14.62	E	12.0	ns	ns	ns	ns	ns					
98	GL	16.60	19.80	E	31.6	34.0	31.8	35.6	38.0	36.6	2.4	-2.2	3.8	2.4	-1.4
99	GL	14.65	19.82	E	30.8	31.8	30.0	32.4	33.0	33.2	1.0	-1.8	2.4	0.6	0.2
100	GL	16.81	19.64	E	5.8	6.8	5.4	ns	ns	ns	1.0	-1.4			
101	GL	15.67	19.19	E	9.8	ns	ns	ns	ns	ns					
102	GL	15.88	18.20	E	9.2	ns	ns	ns	ns	ns					
103	GR	14.55	18.63	E	36.6	39.4	36.4	40.2	41.0	41.0	2.8	-3.0	3.8	0.8	0.0
104	GL	14.63	18.38	E	48.2	ns	ns	ns	ns	ns					
105	GL	14.26	19.91	E	10.6	12.0	12.2	17.0	18.0	18.4	1.4	0.2	4.8	1.0	0.4
106	WO	13.44	20.43	E	15.4	16.0	16.0	ns	23.0	22.2	0.6	0.0			-0.8
107	GL	13.72	21.58	E	15.4	18.4	17.6	20.4	21.0	23.0	3.0	-0.8	2.8	0.6	2.0
108	GL	13.30	21.62	E	21.2	23.0	22.4	27.4	28.0	27.4	1.8	-0.6	5.0	0.6	-0.6
109	GL	12.59	22.15	E	19.4	21.6	22.2	24.6	ns	ns	2.2	0.6	2.4		
110	GL	12.15	21.95	E	14.8	16.2	15.4	18.0	18.0	19.0	1.4	-0.8	2.6	0.0	1.0
112	GL	10.40	24.09	E	14.8	15.6	15.0	19.0	19.0	21.0	0.8	-0.6	4.0	0.0	2.0
113	GL	10.07	24.67	E	13.0	15.8	15.0	20.8	23.0	24.2	2.8	-0.8	5.8	2.2	1.2
114	GL	10.02	24.50	E	9.6	10.4	9.6	11.8	13.0	15.0	0.8	-0.8	2.2	1.2	2.0
115	GL	10.08	24.04	E	20.8	22.8	21.0	24.4	24.0	25.4	2.0	-1.8	3.4	-0.4	1.4
116	GL	9.89	24.15	E	11.2	12.0	21.6	13.0	13.0	14.0	0.8	9.6	-8.6	0.0	1.0
117	GL	9.54	24.78	E	7.8	ns	ns	ns	ns	ns					

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Smith, S. V., and Key, G. S., 1975, Carbon dioxide and metabolism in marine environments. Limnology and Oceanography 20:493-495.
Szmant, A.M., Gassman, N.J. 1990. The effects of prolonged bleaching on the tissue biomass and reproduction of the reef coral Montastrea annularis. Coral Reefs 8: 217-224.

Wanninkhof, R. 1992. Relationship between wind speed and gas exchange over the ocean. Journal of Geophysical Research 97:7373-7382.

EXPECTED PRODUCTS:

Scientific papers based on this research will be submitted to peer-reviewed journals. Presentations on the work will be made at national or international conferences, including the 9th International Coral Reef Symposium in 2000.

Other products include CDs with archived videotransect data (and appropriate metadata) and diskettes with results of image analyses. Investigators' Annual Reports will be submitted to VINP and BNP. A video of the procedures used to measure reef metabolism will be produced.

TECHNOLOGY/INFORMATION TRANSFER:

This proposal includes development of protocols which will be transferable to other agencies and individuals with an interest in measuring reef metabolism and in calculating the of effects of increased CO_2 associated with climate change. The video of the methods used will be made available upon request.

DATA MANAGEMENT:

Data will be documented using the NBII Metadata Standards. Bibliographic metadata for all information and products will be added to the Biological Resource Division's Bibliographic Metadata Database at http://biology.usgs.gov/pubs.

PERSONNEL: (from the initiating Center)
Nick Funicelli
Caroline Rogers
Ginger Garrison
Jeff Miller
Steve Walsh

Appendix A

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
35	GL	8.24	30.35	E	2.0	ns	ns	ns	ns	ns					
36	GL	8.56	28.43	E	12.8	ns	ns	ns	ns	ns					
38	GL	12.75	25.65	E	28.4	32.0	30.4	35.0	37.0	36.0	3.6	-1.6	4.6	2.0	-1.0
39	GL	12.83	25.73	E	23.4	25.0	25.6	31.0	31.0	31.0	1.6	0.6	5.4	0.0	0.0
40	GL	12.95	27.70	E	23.2	24.2	23.4	24.2	24.0	24.0	1.0	-0.8	0.8	-0.2	0.0
41	GL	14.77	24.21	E	3.0	ns	ns	ns	ns	ns					
42	GL	17.79	20.19	E	13.4	14.6	12.4	14.6	14.0	13.6	1.2	-2.2	2.2	-0.6	-0.4
43	GL	18.85	17.57	E	9.8	ns	9.6	12.2	10.0	10.0			2.6	-2.2	0.0
44	GL	19.45	17.39	E	20.0	ns	ns	ns	ns	ns					
45	GL	19.20	17.19	E	12.4	14.6	6.2	17.4	17.4	19.0	2.2	-8.4	11.2	0.0	1.6
46	GL	20.50	17.95	E	11.8	13.0	12.8	14.6	15.0	16.0	1.2	-0.2	1.8	0.4	1.0
47	GL	21.39	18.11	E	12.6	11.2	12.8	13.8	13.0	14.0	-1.4	1.6	1.0	-0.8	1.0
48	GL	20.02	18.22	E	1.0	ns	ns	ns	ns	ns					
49	GL	21.70	17.77	E	7.4	18.6	18.4	ns	25.0	26.8	11.2	-0.2			1.8
50	GL	21.60	17.33	E	55.0	56.4	54.4	56.6	57.0	56.4	1.4	-2.0	2.2	0.4	-0.6
51	GL	22.05	17.99	E	1.0	ns	ns	ns	ns	ns					
52	GL	22.03	17.26	E	1.0	ns	ns	ns	5.4	ns					
53	GL	22.97	16.97	E	8.8	10.0	10.6	14.0	13.6	15.2	1.2	0.6	3.4	-0.4	1.6
55	GL	24.40	15.38	E	1.0	ns	ns	ns	ns	ns					
57	WO	25.75	16.57	E	51.2	48.4	51.0	55.8	57.4	60.0	-2.8	2.6	4.8	1.6	2.6
59	GL	27.25	17.45	E	7.2	8.4	8.2	9.8	9.6	10.4	1.2	-0.2	1.6	-0.2	0.8
60	GL	27.53	17.80	E	7.4	8.8	9.6	11.2	11.4	12.6	1.4	0.8	1.6	0.2	1.2
62	GL	28.30	17.20	E	9.6	6.2	ns	ns	ns	ns	-3.4				
63	GL	30.40	17.19	E	4.2	ns	ns	ns	ns	ns					
64	GL	30.55	16.30	E	25.0	ns	ns	ns	ns	ns					
65	GL	30.60	17.05	E	8.8	ns	ns	ns	ns	ns					
66	GL	29.55	14.41	E	55.0	57.4	55.6	59.2	58.6	62.4	2.4	-1.8	3.6	-0.6	3.8
67	GR	28.37	15.16	E	6.0	7.2	7.0	ns	ns	6.4	1.2	-0.2			
68	GL	27.49	15.19	E	42.6	45.4	42.6	33.2	ns	ns	2.8	-2.8	-9.4		
69	GL	28.19	12.96	E	5.2	ns	ns	29.8	ns	ns					
71	GL	29.13	11.25	E	1.0	ns	ns	ns	ns	ns					
72	GR	29.25	10.70	E	43.4	48.6	43.0	45.4	45.0	46.0	5.2	-5.6	2.4	-0.4	1.0
73	GL	28.29	11.50	E	7.4	ns	6.6	9.4	9.8	10.8			2.8	0.4	1.0
75	GL	26.09	13.45	E	58.2	60.0	59.6	63.6	65.8	67.3	1.8	-0.4	4.0	2.2	1.5
78	GL	25.60	12.60	E	7.4	8.0	9.0	ns	10.2	10.0	0.6	1.0			-0.2

Doug Weaver
Others from FCSC

COOPERATORS/PARTNERS:

- Our primary partners are the Geology Division of USGS and the National Park Service (Biscayne National Park and Virgin Islands National Park). All will be providing personnel, equipment, and expertise for certain tasks to conduct this research effort.

- Robert Halley, USGS, Center for Coastal Geology, St. Petersburg, Fl p 813 893-3100; f893-3333 (Carbon budget, calcification studies)
- Kimberly Yates, USGS, Center for Coastal Geology(Carbon budget, calcification studies)
- Richard Curry, Biscayne National Park (scientific support in BNP)
- Dennis Hubbard, Oberlin College, 44293 Rt 511E, Oberlin, Ohio 44074; (phone and fax 440 774-5180 (Physical oceanography, coral cores)

BRD PRINCIPAL CONTACT

Dr. Nicholas Funicelli
Chief, Coastal and Marine Ecology Branch
Florida Caribbean Science Center
Gainesville, Florida

FACILITIES/EQUIPMENT/STUDY AREAS:

The BRD field station in the USVI has a Whaler and a diesel boat plus all necessary dive gear to support field work in St. John. Biscayne National Park will support the operations there with one Biological Technician, boats, lab space, current meters, Hydrasondes, etc. The USGS Center for Coastal Geology will supply all necessary equipment for the SHARQ experiments. The 24 hour measurement sessions will probably require rental of a boat large enough to support 4 people.

LEGAL AND POLICY-SENSITIVE ASPECTS:
Research permits will be necessary for both parks. Supt. Russ Berry, Virgin Islands National Park, P.O. Box 710, USVI 00830; ph 340 693-8950.
Supt. Richard Frost, Biscayne National Park, P.O. Box 1369, Homestead, Fl 33090.

Species, Location, Size and Growth of Commercial Sponges at Billy's Point

ID#	Species	NE	SW	SECT	Jul-92	Jan-93	Jul-93	Oct-93	Apr-94	Jul-94	GR 1	GR 2	GR 3	GR 4	GR5
1	WO	29.93	18.85	E	52.2	51.4	50.4	57.0	59.0	61.2	-0.8	-1.0	6.6	2.0	2.2
2	GL	29.79	18.92	E	10.0	ns	ns	ns	ns	ns					
3	WO	29.98	19.76	E	26.8	29.0	26.8	32.0	34.0	37.0	2.2	-2.2	5.2	2.0	3.0
4	GL	19.14	18.40	E	16.2	19.0	15.6	18.4	20.2	21.4	2.8	-3.4	2.8	1.8	1.2
5	GL	28.60	18.29	E	17.2	19.8	14.0	21.2	21.4	22.2	2.6	-5.8	7.2	0.2	0.8
6	GL	27.70	19.05	E	38.6	39.8	ns	ns	ns	ns	1.2				
7	GL	27.45	18.91	E	3.0	ns	ns	ns	ns	ns					
8	GL	27.10	19.20	E	33.0	35.2	25.0	35.8	35.4	35.8	2.2	-10.2	10.8	-0.4	0.4
9	GL	22.21	21.37	E	15.8	ns	ns	ns	ns	ns					
10	GL	22.41	19.05	E	28.2	43.0	34.0	36.2	36.6	38.0	14.8	-9.0	2.2	0.4	1.4
11	GL	23.63	19.02	E	13.8	ns	ns	ns	ns	ns					
12	WO	23.10	18.20	E	63.2	67.2	65.4	70.8	72.6	72.0	4.0	-1.8	5.4	1.8	-0.6
13	GL	23.30	18.39	E	17.8	ns	ns	ns	ns	ns					
14	GL	23.40	18.12	E	20.0	ns	ns	ns	ns	ns					
15	GR	23.09	18.29	E	1.0	ns	ns	ns	ns	ns					
16	GL	22.28	18.53	E	6.2	ns	ns	ns	ns	ns					
17	WO	19.55	22.50	E	7.8	9.8	8.6	12.0	10.0	9.4	2.0	-1.2	3.4	-2.0	-0.6
18	GL	19.13	23.25	E	43.2	30.2	28.8	36.0	33.0	30.0	-13.0	-1.4	7.2	-3.0	-3.0
19	GL	19.32	24.03	E	11.8	12.4	ns	ns	ns	ns	0.6				
20	GL	17.33	24.26	E	1.0	ns	ns	ns	ns	ns					
22	GL	15.22	26.11	E	9.0	ns	ns	ns	ns	ns					
23	GL	15.39	26.63	E	21.2	ns	ns	42.4	ns	ns					
24	GL	14.36	26.16	E	15.8	18.6	18.8	21.8	22.0	22.6	2.8	0.2	3.0	0.2	0.6
25	GL	14.36	25.70	E	8.0	8.8	6.6	7.6	ns	5.8	0.8	-2.2	1.0		
26	GL	13.24	27.39	E	14.2	ns	ns	ns	ns	ns					
27	GL	13.40	28.10	E	10.0	12.4	20.1	ns	ns	ns	2.4	7.7			
28	GL	13.10	26.90	E	57.4	63.0	61.0	63.2	61.2	65.0	5.6	-2.0	2.2	-2.0	3.8
29	GL	12.75	27.15	E	37.2	39.6	38.4	41.0	40.0	42.4	2.4	-1.2	2.6	-1.0	2.4
30	GL	12.52	28.53	E	15.8	ns	6.8	19.0	18.8	19.8			12.2	-0.2	1.0
31	GL	12.57	28.24	E	10.0	ns	ns	ns	ns	ns					
32	GL	11.98	28.41	E	7.8	ns	ns	ns	ns	ns					
33	WO	10.94	28.89	E	14.6	17.0	20.4	ns	22.0	22.8	2.4	3.4			0.8
34	WO	9.50	30.20	E	45.8	49.2	ns	65.0	67.0	70.0	3.4			2.0	3.0

BUDGET

Year 1		**Matching Contributions**			
BRD Salaries		*GD Salaries*		*NPS Salaries*	
Rogers (4 pp)	15,655	Halley (8 pp)	40,624	Curry (3 pp)	7,118
Garrison (2 pp)	4,745	Yates (8 pp)	17,424	Tech (2 pp)	3,000
Miller (6 pp)	11,358	Thompson (4pp)	12,952		
FCSC emp. (4 pp)	8,000				
FCSC emp. (2 pp)	4,000				
Equipment					
Current meters		provided			
Boat rental for 24 hr sessions	8,400				
Supplies					
Fuel, videotapes, air fills, stakes	7,500				
Travel to BNP					
Rogers (one week)	1,500	Halley	4,400		
Miller (2 pp)	5,500	Yates	4,400		
FCSC employee (2 pp)	4,750	Thompson	4,400		
Travel to VINP					
		Halley	5,200		
		Yates	5,200		
		Thompson	5,200		
TOTALS	71,408		99,800		10,118

Table 8. Recruitment of Commercial Sponges at Black Point.

Species	Oct'93	Jun'94	Oct'94	Total
S. graminea	70	41	36	147
S. tubulifera	45	17	18	80
S. barbara	20	10	9	39
H. lachne	3	4	2	9

Table 8. Recruitment of Commercial Sponges at Black Point. The number of new recruits into the study plots are presented for each species. Only sponges less than 10 cm circumference that are recorded for the first time during a particular sampling period are considered recruits.

Year 2		**Matching funds**			
BRD Salaries		*GD Salaries*		*NPS Salaries*	
Rogers (6 pp)	23,478	Halley (8 pp)	40,624	Curry	7,118
Garrison (2 pp)	4,745	Yates (8 pp)	17,424	Tech	3,000
Miller (6 pp)	11,358	Thompson	12,952		
FCSC biologist	8,000				
FCSC biologist	4,000				
Equipment					
Boat Rental	8,400				
Supplies					
Fuel, videotapes, air fills, stakes	5,000				
Travel to BNP					
Rogers (one week)	1,500	Halley	4,400		
Miller (2 pp)	5,500	Yates	4,400		
FCSC employee (2 pp)	4,750	Thompson	4,400		
Travel to VINP					
		Halley	5,500		
		Yates	5,500		
		Thompson	5,500		
TOTALS	76,731		99,800		10,118

Note: The budget is based on two 2-week field sessions each year in each park. Three BRD employees (VINP) or two BRD employees and one NPS technician (BNP) would work in the field with three GD employees (VINP) for each sampling period.

Table 7. Sponge Mortality at Black Point

Sample Period	Present start	Present end	Lost	Mortality (sponges/mo)
S. graminea				
Jul'93-Oct'93	85	80	5	1.7
Oct'93-Jun'94	153	131	22	2.8
S. tubulifera				
Jul'93-Oct'93	172	154	18	6.0
Oct'93-Jun'94	188	154	34	4.3
S. barbara				
Jul'93-Oct'93	43	38	5	1.7
Oct'93-Jun'94	50	42	8	1.0
H. lachne				
Jul'93-Oct'93	0	0	0	0.0
Oct'93-Jun'94	3	3	0	0.0

Table 7. Sponge Mortality at Black Point. Many of the commercial sponges, particularly the small cryptic recruits, are often not seen dudring a prticular sampling period but appear during the next one. Sponges are considered lost if they do not appear for two successive monitoring periods. The rates of sponge mortality (sponges/month) are calculated only for those sponges not seen for two successive sampling periods, and therfore, mortality rates over the last sampling period are not included.

WORK AND REPORTING SCHEDULE

To encompass the range of reefs which we hope to monitor for calcification and productivity rates we will need to extend the work over two years. There will be two field sessions in the winter and late summer/fall of each year in VINP and BNP. Each field session will be 2 weeks long.

Table 6. Average Monthly Growth Rates of Commercial Sponges at Black Point

	Jul'93-Oct'93			Oct'93-Jun'94			Jun'94-Oct'94		
Species	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**
S. graminea	1.0	0.7	69	0.2	0.2	111	0.3	0.3	151
S tubulifera	1.2	0.8	136	0.2	0.2	124	0.3	0.4	145
S. barbara	0.7	0.5	30	0.1	0.1	34	0.1	0.3	42
H. lachne				0.2		2	0.3	0.2	8

Table 6. Average Monthly Growth Rates of Commercial Sponges at Black Point. Mean growth rates of commercial sponges (mean) are calculated as the increase in circumference (cm) of individual sponges measured at the beginning and end of each sample period. Mean, standard deviations (sd) and the total number of sponges (n) are given for each species.

(1)

DRAFT

File name: spcalcif
May 24, 1999 Version
[10:00 AM]

TITLE: MEASURING METABOLISM OF REEFS IN VIRGIN ISLANDS NATIONAL PARK AND BISCAYNE NATIONAL PARK: SIGNS OF TROUBLE?

OBJECTIVES and JUSTIFICATION:

Need—Over the last two decades, a variety of natural and human stresses have caused severe degradation of many reefs in the Caribbean and western Atlantic, including those within Virgin Islands National Park (VINP) and Biscayne National Park (BNP). Reefs are exhibiting declines in living coral and increases in algae. Calcification rates are changing because of a shift in the carbon balance between carbon used for ← reference? constructing carbonate skeletons and carbon used to grow fleshy tissues of algae ("macroalgae"). To date, monitoring programs in VINP (e.g., Rogers et al. 1997) and BNP (e.g., Meier and Porter) have focused on reef structure (e.g., abundances or cover of organisms) rather than reef function ("metabolism"). Calcification, the most fundamental process of all, involves the deposition of calcium carbonate, primarily by corals and coralline algae, which creates the 3-dimensional structure of the reef. Another essential process is productivity (photosynthesis and respiration) of reef organisms, including the zooxanthellae within the stony coral tissues and non-symbiotic algae (both turfs and macroscopic algae, or "macroalgae"). In this proposal we refer to calcification and productivity as reef "metabolism". There is an urgent need to determine the calcification rates of selected reefs within these national parks and to find out if these reefs are actively accreting or if they are unable to maintain their structure because the balance has shifted away from the major framework building organisms, including the scleractinian corals, to non-calcifying (or only weakly-calcifying) organisms.

definition!
not specific specific
need!

Presently, we know of no efforts to monitor calcification rates on reefs as indicators of reef condition. We need to determine if measurement of calcification rates and photosynthesis are useful tools for quantifying differences between reefs as well as changes on reefs over time (for example, before and during/after bleaching episodes or runoff events). We plan to test and adapt methods which have recently been used successfully in seagrass beds in Florida Bay (Halley and Yates ref?) We propose to measure reef metabolism in Virgin Islands National Park and Biscayne National Park on reefs with a range of live coral cover during times of low and high water temperatures (winter and late summer/fall). Bleaching episodes, ~~such as the most severe on record in~~ 1998, are usually associated with higher than normal water temperatures. We hope to measure reef metabolism before and during bleaching episodes. Additional outcomes of these measurements are an improved understanding of the CO_2 contribution of coral

why specifically during bleaching events?

what is the outcome?

Table 5. Species Composition at Black Point

Species	Jul'93		Oct'93		Jun'94		Oct'94	
	# present	% total	# present	% total	# present	% total	# present	%total
S. graminea	85	28%	153	39%	168	43%	210	44%
S tubulifera	172	57%	188	48%	163	42%	199	41%
S. barbara	0	0%	3	1%	7	2%	10	2%
H. lachne	43	14%	50	13%	50	13%	61	13%
Total	300		394		388		480	

Table 5. Species Composition at Black Point. The number of sponges located within the study plots at Black Point during each sampling period are listed for the four commercial species. The relative contribution of each species to the total number of commercial sponges at the site is also presented.

reefs to the atmosphere and a methodology which can help to assess the direct impact of increased CO_2 on coral reefs.

Background: Natural stresses such as hurricanes and coral diseases as well as anthropogenic factors such as increased runoff, damage from boat anchors and groundings, and sewage input have killed corals and altered the relative abundances of reef organisms. In some extreme cases coral reefs have been almost entirely overgrown by algae (Hughes 1994).

what about overfishing and removal of herbivores?

Coral reefs are also among the ecosystems which could be most vulnerable to changes in climate because increased CO_2 could lower calcification rates with far-reaching effects on reef structure (Pennisi 1998 , Kleypas et al. 1999). Though not the most abundant organisms on Caribbean reefs, corals create the reef's physical structure, providing habitat for fishes and other organisms.

Important point

Corals provide clues to the present and to the past. They are also sensitive to several physical factors associated with future climate---elevated CO_2, higher temperatures, and increased UV radiation. They respond to increased temperatures and UV radiation by "bleaching" (losing color). When corals bleach, they cease reproduction and their growth rates decrease (e.g., Szmant and Gassman 1990).

?

How?

Poorly worded. How can something be sensitive to smth that has not happened

Q do they stop calcifying?

Coral skeletons contain a record of past environmental conditions. For example, they have annual (or near annual) growth bands because skeletal densities vary with cooler and warmer temperatures. Through examination of coral cores ("sclerochronology" studies) one can learn about calcification rates in the past and compare those to present rates (refs.).

Monitoring of reef metabolism at selected reefs in Virgin Islands National Park and Biscayne National Park is the central focus of this 2-year project. Detailed information on the structure of each study site will be correlated with the measurements of reef metabolism. (This information is available for some reefs from the USGS/NPS Inventory & Monitoring Program.) Existing data on reef structure and function are severely limited both spatially and temporally, with insufficient data from widely separated geographic areas over long periods of time. To begin to address these scale deficiencies, we will be looking at reefs in subtropical and tropical areas, and we will be examining coral cores for information on past environmental conditions..

Poorly worded.

PROCEDURES/METHODS:

Rationale for Selection of Study Sites

Table 4 Recruitment of Commercial Sponges at Billy's Point

Species	Oct'93	Apr'94	Jul'94	Total
S. graminea	16	8	25	49
S. tubulifera	1	0	1	2
S. barbara	0	2	1	3
H. lachne	0	1	0	1

Table 4. Recruitment of Commercial Sponges at Billy's Point. The number of new recruits into the study plots are presented for each species. Only sponges less than 10 cm circumference that are recorded for the first time during a particular sampling period are considered recruits.

Some of the study sites for this project will be areas for which long-term data (both biological and environmental) are already available. Long-term monitoring sites were established on reefs in Virgin Islands National Park and Biscayne National Park under an NPS program which began in 1988, and the DOI Inventory & Monitoring (I&M) program has supported additional work in VINP. Other sites will be chosen to ensure that data are obtained from a variety of different reef types and from sites of particular management concern.

The coral reef monitoring which NPS and BRD have conducted in these two parks in conjunction with state and university scientists are some of the few long-term monitoring programs in the Caribbean and western Atlantic (Connell 1997). Data on cover by coral and algae are available for both VINP and BNP, and effects of different stresses have been documented for some reefs. Underwater videotapes which provide a statistically quantifiable and permanent visual record of reef characteristics are available for reefs in both of these parks.

A major task for Year 1 will be the selection of each study site based on the need to include reefs with a range of different reef types with variations in coral cover. Reefs in Biscayne National Park generally have less than 5% living coral while some sites in St. John have live cover in excess of 20%. Initially, we will focus on reefs for which data are already available. On St. John, we will study sites in Lameshur and Newfound bays, for which we have the longest data sets (10 and 9 years respectively). These sites are also under consideration for inclusion in a "marine reserve" within park waters. Transects in Newfound Bay would have the highest coral cover of all the study sites (23%) while those in Lameshur have a coral cover of about 10%. We may also select Hawksnest Bay for which we have information on siltation effects and coral growth rates (Hubbard et al. 1987) because it is a shallow reef exhibiting some signs of recovery in elkhorn coral (*Acropora palmata*) populations. This primary reef-building species was decimated throughout the Caribbean in the 1980's by white band disease.

Managers of Biscayne National Park have recommended the following sites:
Richard—please recommend specific study sites in BNP if possible, sites which might help answer "managment concerns"—it could actually be cool to look at calcification at one of the areas which is recovering from a boat grounding -- just a thought

REEF FUNCTION: CALCIFICATION AND PRODUCTIVITY

Carbonate sediment production, photosynthesis, and respiration will be measured in winter (when temperatures are lowest) and late summer/fall (when temperatures are highest) to determine seasonal and areal variation in tissue/carbonate production and to derive average annual production rates. These parameters will be calculated from total alkalinity, pH, calcium concentrations, salinity, irradiance,

Table 3. Sponge Mortality at Billy's Point

Sample Period	Present start	Present end	Lost	Mortality (sponges/mo)
S. graminea				
Jul'93-Oct'93	186	175	11	3.7
Oct'93-Apr'94	205	184	21	3.5
S. tubulifera				
Jul'93-Oct'93	19	16	3	1.0
Oct'93-Apr'94	16	13	3	0.5
S. barbara				
Jul'93-Oct'93	2	2	0	0.0
Oct'93-Apr'94	2	2	0	0.0
H. lachne				
Jul'93-Oct'93	15	15	0	0.0
Oct'93-Apr'94	14	14	0	0.0

Table 3. Sponge Mortality at Billy's Point. Many of the commercial sponges, particularly the small cryptic recruits, are often not seen dudring a prticular sampling period but appear during the next one. Sponges are considered lost if they do not appear for two successive monitoring periods. The rates of sponge mortality (sponges/month) are calculated only for those sponges not seen for two successive sampling periods, and therfore, mortality rates over the last sampling period are not included.

temperature, wind and current speed, and air-sea CO_2 and O_2 fluxes measured along transects across reefs.

We propose to work with our primary collaborators, Dr. Robert Halley and Dr. Kim Yates, from the USGS Geologic Division to measure parameters of carbon budgets to assess reef conditions. For many years carbon budgets of reefs have been studied by measuring geochemical parameters of carbon utilization (Smith, 1973). The techniques used to make these measurements have been greatly refined during the past two decades because they are, in part, also the techniques used for measuring global atmospheric CO_2 exchange with the ocean. These refined procedures can now be used again to study coral reefs (Buddemeier and Kinzie 1998).

Dr. Halley and Dr. Yates have developed prototypes of two geochemical monitoring systems including a Submersible Habitat for Analyzing Reef Quality (S.H.A.R.Q.) and an In Site Biogeochemical Analysis System (I.B.A.S) for measurement of geochemical changes associated with benthic and water column carbonate sediment production and metabolic activity, respectively (see Halley and Yates for details). To measure reef metabolism, we will use two primary experimental approaches: 1) upstream-downstream transects across broad sections of the reef ( ), and 2) metabolism of small reef areas enclosed within the SHARQ (see also Rogers 1979).

For upstream-downstream measurements, transects will be located parallel to unidirectional current flow across a given reef, characterized using a series of current meters, with sample stations positioned at the upstream and downstream ends of each transect.

Geochemical and physical parameters (including water temperature) will be measured at each station along a transect at different times (and irradiances) during the day and night to determine daily variations in production and to derive average daily production rates. Recording thermistors are already in place on several reefs in VINP and BNP.

Total alkalinity and pH will be used to calculate calcification and net photosynthesis using the alkalinity anomaly technique of Smith and Key (1975) such that calcification (C) = half the change in total alkalinity, and net photosynthesis (P) = total carbon - calcification. Total carbon will be calculated using carbonate system equations from Millero (1979). Calcium measurements will provide an independent measure of calcification for comparison. Air-sea CO_2 fluxes will be measured directly at each station inside of a floating bell (Frankignoulle 1988, Gattuso et al. 1993, Kayanne et al. 1995) using the procedure and calculations of Frankignoulle (1988). Air-sea O_2 fluxes will be determined by measuring atmospheric and water pO_2 and calculating fluxes as described in Wanninkhof (1992). Differences in oxygen and carbon metabolism between upstream and downstream stations will be corrected for O_2 and CO_2 exchange with the atmosphere as described in

Table 2. Average Monthly Growth Rates of Commercial Sponges at Billy's Point

	Jul'93-Oct'93			Oct'93-Apr'94			Apr'94-Jul'94		
Species	**mean**	**sd**	**n**	**mean**	**sd**	**n**	**mean**	**sd**	**n**
S. graminea	0.5	1.1	167	0.1	0.3	175	0.2	0.4	179
S tubulifera	0.9	1.0	15	0.2	0.4	12	0.2	0.9	14
S. barbara	1.0		2	0.6		2	0.8	1.0	3
H. lachne	1.3	0.6	12	0.3	0.3	14	0.5	0.6	16

Table 2. Average Monthly Growth Rates of Commercial Sponges at Billy's Point. Mean growth rates of commercial sponges (mean) are calculated as the increase in circumference (cm) of individual sponges measured at the beginning and end of each sample period. Mean, standard deviations (sd) and the total number of sponges (n) are given for each species.

(Gattuso et. al., 1993).

Productivity and metabolic rates per unit area will be calculated using the difference in concentration between upstream and downstream stations, the volume of water transported along a transect, and the transect area such that the change in concentration of a parameter (delta $C/m_2/s$) = $(C/m3 \times m3/hr)/m_2$ (Barnes and Devereux, 1984). Seasonal production rates will be used to calculate average annual production rates.

Comparison of these data with previous productivity estimates and calcification rates, as well as calcification rates determined from coral cores (Hudson et. al., 1976; Dodge et. al, 1983; Dodge, et. al, 1992) would indicate whether long-term (decades) changes are occurring on the reefs.

We plan to use both the upstream-downstream method and the SHARQ in both national parks. In some cases, upstream-downstream techniques may not be feasible because of local current conditions (i.e., currents are too weak or too complex)., or because reef zones are not wide enough to allow detection of changes. In other situations, for example, where the reef has very high relief, it will be more difficult to use the SHARQ. The IBAS will be used to measure metabolism of the water column and to enable quantification of benthic and water column contributions to overall metabolism. Dr. Robert and Dr. Kimberly Yates, our primary collaborators, have successfully done pilot studies of seagrass beds in Florida Bay using these techniques and plan to test them out on reefs soon.

In the fall of 1998, severe bleaching occurred on the reefs around St. John and within Biscayne National Park [### is this true, Richard???]. We hope to take measurements during future bleaching events to determine the effects of zooxanthellae loss (which results in bleaching) on productivity and calcification rates.

REEF STRUCTURE

It is essential that we have pertinent data on the structure of the transects to accompany the metabolism rates we measure (with both the upstream-downstream technique and the SHARQ). At some study sites, we intend to install the SHARQ over transects for which we already have very detailed information on relative abundances of different organisms ("reef structure"). At other sites, we will collect quantitative information using videography (Rogers and Miller submitted manuscript).

Coral cores:

Skeletons of some coral species (including Montastraea annularis) provide a record of the environmental conditions under which the corals grew. We propose to examine coral cores which have already been collected from the parks to look for any changes in calcification (deposition of the coral skeleton) which would indicate short-term or long-

Table 1. Species Composition at Billy's Point

Species	Oct-93		Apr-94		Jul-94	
	# present	% total	# present	% total	# present	% total
S. graminea	204	87	195	85	217	84
S. tubulifera	16	7	14	6	20	8
S. barbara	2	1	3	1	5	2
H. lachne	14	6	18	8	17	7
Total	236		230		259	

Table 1. Species Composition at Billy's Point. The number of sponges located within the study plots at Billy's Point during each sampling period are listed for the four commercial species. The relative contribution of each species to the total number of commercial sponges at the site is also presented.

term changes in environmental conditions. Cores will be used to construct a history of climate conditions over as long a period as possible. We will not be collecting new cores from any of the sites.

The proposed work represents a major study of reef metabolism or "function" as opposed to reef "structure" which is the subject of most monitoring projects. It addresses the fundamental processes required for reef development. The work also relates to the goals of BRD's Global Climate Change Program in several ways. First the proposed measures of air-sea CO_2 fluxes not only provides basic data for determining the degree to which coral reefs contribute to atmospheric CO_2, but they also provides a way to evaluate the sensitivity of coral reef carbon budgets to future atmospheric CO_2 levels (Goal 1). Second, carbon-budget measurements on reefs will help determine the combined effects of global change and environmental contamination on reefs (Goal 2). Third, the project is being addressed at several spatial and temporal scales in an effort to learn more about responses of coral reefs to global change (Goal 3). Fourth, the proposed experiments provide a basis for a better understanding of how careful management of sediment and nutrient input to reefs (which affects the relative abundances of algae and living coral) could offset effects of increased global CO_2 (Goal 4)

TIMELINE

To encompass the range of reefs which we hope to monitor for calcification and productivity rates we will need to extend the work over two years. There will be two field sessions in the winter and late summer/fall of each year in VINP and BNP. Each field session will be 2 weeks long..

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PLEASE NOTE—I HAVE NOT CHECKED THE REFERENCES YET FOR ACCURACY, OMISSIONS, ETC.

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Bohlen, S. R., Halley, R. B., Hickman, S. J., Johnson, S. Y., Lowenstern, J.

or indirectly attributable to the effects of Hurricane Andrew.

Spomges measuring less than 10 cm circumference (1.5 cm radius) which were not present during the prior sampling are considered to be recruited into the population between sampling periods. Recruitment of new individuals into the study site at Black Point is shown in Table 8. Recruitment rates are higher during summer sampling periods than during winter, reflecting increased gamete production during the warmer months. The recruitment rate of new individuals into the study site during the past year is about three times greater that the mortality rate, resulting in a 60% increase in the total number of sponges between July, 1993 and October, 1994.

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BLACK POINT

The research plots were initially established at Black Point in July, 1993. Sponges were monitored at this site during October, 1993, June, 1994 and October, 1994. All commercial sponges found within the study plots since the start of this project are listed in Appendix B. Their location within the study plots are presented in Map 2. *S. graminea* is the dominant species, comprising 43.8% of the total and *S. tubulifera* accounts for only slightly less, making up 41.5% of the total. *S. barbara* and *H. lachne* are also present at this site accounting for 2.1% and 12.7 %, respectively, of all commercial sponges present in October, 1994 (see Table 5). The density of all commercial species at this site is 8000 sponges/ha.

Monthly growth rates of commercial sponges at Black Point are presented in Table 6. Growth rates between monitoring periods were highly variable. The rates include increases in sponge circumference due to new growth as well as decreases in circumference resulting from mechanical breakage due to storms, necrotic loss due to disease, predation or any combination of these factors.

Table 7 shows mortality rates for individual species during the second year of sampling. Losses are most likely due to a combination of factors such as mechanical dislodging and damage during storms, predation, disease and natural mortality. Mortality rates were lower during the second year than during the first, when high mortality was either direcly

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EXPECTED PRODUCTS:

Scientific papers based on this research will be submitted to peer-reviewed journals. Presentations on the work will be made at national or international conferences, including the 9th International Coral Reef Symposium in 2000.

Other products include CDs with archived videotransect data (and appropriate metadata) and diskettes with results of image analyses.
Investigators' Annual Reports will be submitted to VINP and BNP.
A video of the procedures used to measure reef metabolism will be produced.

TECHNOLOGY/INFORMATION TRANSFER:
This proposal includes development of protocols which will be transferable to other agencies and individuals with an interest in measuring reef metabolism and in calculating the of effects of increased CO_2 associated with climate change.
The video of the methods used will be made available upon request.

DATA MANAGEMENT:
Data will be documented using the NBII Metadata Standards. Bibliographic metadata for all information and products will be added to the Biological Resource Division's Bibliographic Metadata Database at http://biology.usgs.gov/pubs.

thickness, measurements of sediment depth will be taken at locations throughout the plots during normal monitoring. This may provide some indication of how sediments are shifting within the plots.

As before the storm, there is an extensive grass bed (*Thalassia testudinum*) surrounding the plot. There appears to be little or no effect of sediment transport on this area. Seagrasses thrive where sediments are deep and are relatively sparse in hardbottom areas where sediments are thin, usually less than 5 cm thick.

PERSONNEL: (from the initiating Center)
Nick Funicelli
Caroline Rogers
Ginger Garrison
Jeff Miller
Steve Walsh (need to check with him!)
Doug Weaver (need to check with him!)

COOPERATORS/PARTNERS:

- Our primary partners are the Geology Division of USGS and the National Park Service (Biscayne National Park—maybe VIIS?). Both will be providing personnel, equipment, and expertise for certain tasks to conduct this research effort.

- Robert Halley, USGS, Center for Coastal Geology, St. Petersburg, Fl p813 893-3100; f893-3333 (Carbon budget, calcification studies)
- Kimberly Yates, USGS, Center for Coastal Geology
- Richard Curry, Biscayne National Park
- Dennis Hubbard, Oberlin College, 44293 Rt 511E, Oberlin, Ohio 44074; (phone and fax 440 774-5180 (Physical oceanography, coral cores)

FACILITIES/EQUIPMENT/STUDY AREAS:

The BRD field station in the USVI has a Whaler and a diesel boat plus all necessary dive gear to support field work in St. John. Biscayne National Park will support the operations there with one Biological Technician, boats, lab space, current meters, Hydrasondes, etc. The USGS Center for Coastal Geology will supply all necessary equipment for the SHARQ experiments.

LEGAL AND POLICY-SENSITIVE ASPECTS:
Research permits will be necessary for both parks. Supt. Russ Berry, Virgin Islands National Park, P.O. Box 710, USVI 00830; ph 340 693-8950.
Supt. Richard Frost, Biscayne National Park, P.O. Box 1369, Homestead, Fl 33090.

BUDGET

Year 1		Matching Contributions			
BRD Salaries		*GD Salaries*		*NPS Salaries*	
Rogers (4 pp)		Halley (8 pp)		Curry (3 pp)	

BLACK LEDGE

There has been no recruitment of new sponges at this site over the past year. This site was originally picked because it had the physical characteristics of suitable sponge habitat - shallow, coarse sediment, good water circulation and sparse vegetative coverage - yet the density of commercial sponges in the area was low. Currents and waves accompanying Hurricane Andrew deposited a thick overburden of fine, marly sediment over the area which currently covers the study site. This resulted in a rapid change of the dominant benthic community type at this site from a hardbottom, filter-feeding community dominated by sponges and octacorals, with a sparse cover of seagrass and calcareous algae to a burrowing community dominated by the Terebellid worm, *Eupolymnia nebulosa.* However, we have recently observed that this storm sediment is slowly being redistributed. As sediment cover is thinning, the benthic community appears to be returning to pre-storm conditions.

There is little recruitment of other benthic organisms requiring a hard bottom to settle out. Octocorals that survived the storm appear healthy. Sponge more tolerant of sediment loads (i.e., *Chondrilla nucula* and *Haliclona* sp.) are reappearing in the plot. Although sediment patterns were not mapped, there appears to be some redistribution of sediment. No photographs of this site were available before Hurricane Andrew. The site was first established only days before the storm hit South Florida. Post-hurricane pictures reveal the extent of the sediment deposited by the storm. To quantify any further changes in sediment

Garrison (2 pp)		Yates (8 pp)		Tech (2 pp)	
Miller (6 pp)		Tech. (4 pp)			
FCSC emp. (4 pp)					
FCSC emp. (2 pp)					
Equipment					
Supplies					
Fuel, videotapes, air fills, stakes					
Travel to BNP					
Rogers (one week)		Halley			
Miller (2 pp)		Yates			
FCSC employee (2 pp)		Tech.			
Travel to VINP					

Year 2		Matching funds			
BRD Salaries		GD Salaries		NPS Salaries	
Rogers (6 pp)		Halley (8 pp)		Curry	
Garrison (2 pp)		Yates (8 pp)		Tech	
Miller (6 pp)		Tech.			
FCSC biologist					

loss of all reproductively mature sponges in the area during the hurricane removed another local source of recruits.

Subtle alteration in the habitat may be another reason why no new sponges have reestablished at the study site. We have observed that certain organisms that were not previously seen at the site or were rare are now common. Different species of algae (e.g., *Caulerpa* spp.) appear to be much more prevalent now than before the hurricane. This may be part of a successional process, a permanent change from pre-storm conditions, or merely a temporary situation resulting from increased nutrient fluxes from the less consolidated substrate.

FCSC biologist					
Equipment					
Supplies					
Fuel, videotapes, air fills, stakes					
Travel to BNP					
Rogers (one week)		Halley			
Miller (2 pp)		Yates			
FCSC employee (2 pp)		Tech.			
Travel to VINP					

Note: The budget is based on two 2-week field sessions each year in each park. Three BRD employees (VINP) or two BRD employees and one NPS technician (BNP) would work in the field with three GD employees (VINP) for each sampling period.

PELICAN BANK

Pelican Bank experienced 100% mortality due to the effects of Hurricane Andrew in August, 1992. The site has been continuously monitored to determine how quickly this site would be recolonized by commercial sponge in absence of competition for suitable habitat. Since the hurricane, only one grass sponge (*S. tubulifera*) has been observed at this site.

Prior to the summer of 1992, commercial sponge harvesters had established sponge drying racks at Pelican Bank. The spongers would bring their daily catch to this location for the initial curing process. The large number of reproductively mature sponges submersed in the waters during the first stage of the process probably resulted in the release of larvae and fragments into the area. Over the years, this may have potentially provided a rich source of new recruits over the area directly downcurrent from the drying racks. Tilmant (1978) has speculated that this process may have been responsible for the high density of sponges observed in this area. Once sponges were established in the area, normal growth and reproduction would sustain population levels in the absence of any major disturbance.

The sponge racks were removed from Pelican Bank by BNP shortly after the closure of the fishery in 1992. The passing of Hurricane Andrew over Biscayne Bay in August, 1992 resulted in the loss of all sponges at the study site directly south of Pelican Bank. The absence of new recruits at this site clearly supports Tilmant's speculation that the site may have been originally populated by larvae and fragments released during curing. In addition,

From: Shana Curry <mattnshana@mattsmith.net>
To: spm2u@mindspring.com <spm2u@mindspring.com>
Date: Thursday, May 27, 1999 11:00 PM
Subject: FW: proposal

-----Original Message-----
From: Caroline Rogers [SMTP:Caroline_Rogers@usgs.gov]
Sent: Monday, May 24, 1999 11:57 AM
To: richard@mattsmith.net
Subject: proposal

Hi Richard--

Hope you are having a great vacation. I don't think there is anything I absolutely have to have from you before I submit this proposal to Russ Hall (within the week). There are two things which would help, however-- Am I correct that there was severe bleaching in BNP in late summer/fall of 1998? Also, are there any particular reefs (of special importance to park managers, or sites with long-term data, NOT Porter's photostations please!) which you want me to list as study sites in this proposal?

If you can stand to skim through the attached, revised proposal, I would really appreciate your comments.

Cheers-

Caroline

or indirectly attributable to the effects of Hurricane Andrew.

Sponges measuring less than 10 cm circumference (1.5 cm radius) which were not present during the prior sampling are considered to be recruited into the population between sampling periods. Recruitment of new individuals into the study site at Billy's Point is shown in Table4. Recruitment rates are higher during summer sampling periods than during winter, reflecting increased gamete production during the warmer months. The number of sponges lost due to mortality is equal to the number of new individuals recruited into the site during this sampling period, maintaining population density over the course of one year.

DUPLICATE:
Original in
Museum Archives
B15C-118

BILLY'S POINT

Sponges were monitored at Billy's Point during July, 1993, October, 1993, April 1994 and July, 1994. All commercial sponges found within the study plots since the start of this project are listed in Appendix A. Their locations within the study plots are presented in Map 1. Species composition at this site has not changed significantly during the second year of the project (Goodness of Fit G-test, $p>0.1$). *S. graminea* is the dominant species, comprising approximately 84% of the total. *S. tubulifera, S. barbara* and *H. lachne* are also present at this site but their individual contribution to the total number of commercial sponges is less that 10% (see Table 1). Density of all commercial species at this site is 4300 sponges/ha.

Monthly growth rates of all four species at Billy's Point are presented in Table 2. Growth rates between monitoring periods were highly variable. The rates include increases in sponge circumference due to new growth as well as decreases in circumference resulting from mechanical breakage due to storms, necrotic loss due to disease, predation or any combination of these factors.

Table 3 shows mortality rates for individual species during the second year of sampling. Losses are most likely due to a combination of factors such as mechanical dislodging and damage during storms, predation, disease and natural mortality. Mortality rates were lower during the second year than during the first, when high mortality was either directly

species, tagged, measured and mapped by grid coordinates.

Monitoring of the research sites was interrupted during the first year by Hurricane Andrew in August, 1992. The effect of the hurricane on this project was documented in the First Annual Report, delivered in September, 1993. This report represents an continuation of the first years work.

INTRODUCTION

This is the second annual report submitted to South Florida Water Management District (SFWMD) by Biscayne National Park (BNP) as required by Contract C91-2547. The information contained in this report represents field work carried out by Biscayne National Park Resource Management staff from October, 1993 through October, 1994. These data were collected during the second year of a three year study of the growth, mortality and recruitment of four species of commercial sponges: *Hippospongia lachne, Spongia barbara, Spongia graminea, and Spongia tubulifera.* This research was initiated in November, 1991 by BNP and SFWMD. Funding for the project is through the Florida Surface Water Improvement and Management Program (SWIM). The objective of this three year study is to provide quantitative data on the population dynamics of the commercial sponge species in Biscayne Bay. These data will be used to reevaluate the status of commercial sponge harvesting in Biscayne Bay. The bay was closed to commercial sponging by the Florida Marine Fisheries Commission in December, 1991, but this decision will be revisited as information on the commercial species becomes available through this project.

The research protocol for this project was designed by BNP and approved by SFWMD. The research plan called for the establishment of permanent study sites at four locations in Biscayne Bay. Benthic community composition was surveyed and suitable research sites were established prior to the first monitoring period, July, 1992. At each site, two 10 x 30 meter plots were staked off and each commercial sponge within the plots was identified to

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Aronson

t spatial variability of coral assemblages a Reef Tract

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The structure and composition of coral reef communities is probably determined by the interaction of multiple forcing functions operating on a variety of scales. Hierarchical analyses of coral assemblages from other geographic locations have detected high variability at scales different from those in the present study. A multiscale analysis should, therefore, precede any management decisions regarding large reef systems such as the Florida Reef Tract.

Key words Scale · Coral reefs · Landscape ecology · Florida Keys · Caribbean · Hierarchical analysis.

nunities of the western Atlan- past two to three decades, but ses of this change remain problem is that small-scale vidual reefs have been erron- landscape and geographic reef coral assemblages vary tial prerequisite to devising k the dynamics of coral reefs r we quantify variation in the spur-and-groove habitats scales spanning five orders of rida Reef Tract. A video- was conducted to estimate t the following hierarchical patial scales: (1) among tran- .1-km scale), (2) among sites cale), (3) among reefs within 0- to 20-km scale), and (4) tract (50- to 100-km scale). variability among transects es within reefs. This means adequately represented the groove habitat of the reef as g reefs within sectors was ed with marginally signifi- ors. Estimates from an indi- ot adequately characterize stimates sufficiently repres- of the sector.

son
ville Boulevard, Dauphin
Department of Marine Sciences,
bile, Alabama 36688,

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Introduction

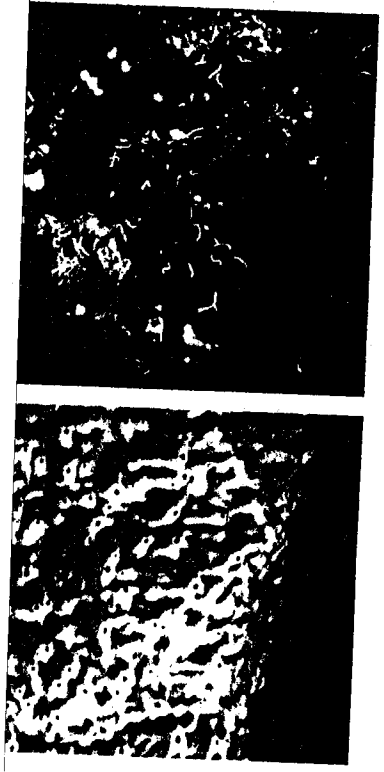
Ecologists have become increasingly aware that scales of measurement must be adjusted to suit the nature of the system to be studied and the hypotheses to be tested (Stommel 1963; Dayton and Tegner 1984; Menge and Olson 1990). Most ecosystems display variability that differs depending on the spatial and temporal scales of observation (O'Neill et al. 1986; Weins 1989; Underwood 1997). This scale dependence is often due to the interaction of processes possessing distinct rates and scales of effect (Allen and Hockstra 1992). Considerations of scale are germane to the dynamics of coral reef communities, in which processes operate over spatial scales from the submicroscopic to the global, and temporal scales from the instantaneous to the millennial (Hubbard 1988; Jackson 1991, Hatcher 1997).

Measuring the variability of coral assemblages across multiple scales can elucidate the range of scales at which different patterns occur (Reichelt and Bradbury 1984; Hatcher et al. 1987; Ogden et al. 1994). Surveying over a range of scales may also help uncover links between seemingly unrelated processes operating at different hierarchical levels of organization (Menge

Reef sites

dinoflagellates (Garson et al. 1998), but appearance and free-living rather than in Rico in 1987–88 (Vicente, 1990).

The occurrence of sponge bleaching The high latitude of the *Chondrilla* blea in cooler regions are also influenced by ments. Changes in symbiont levels are l their ability to survive in competitive re mental evidence that the alkaloids from from feeding on the sponge tissue.



Acknowledgements We thank K. Bancroft for

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199–202

Jane Fromont, Western Australian Muse
Mary Garson, University of Queensland

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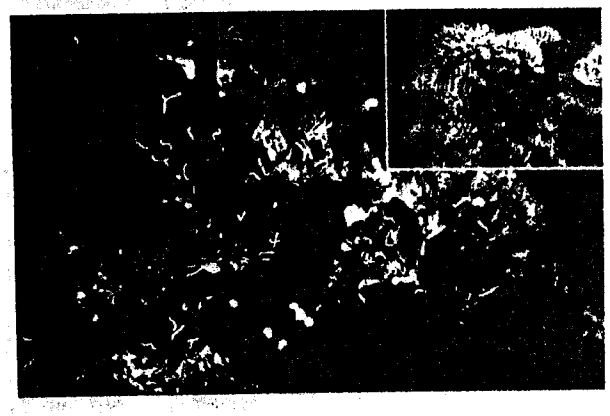
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Sponge bleaching on the West and East coasts of Australia

At Fremantle (32°04'S, 115°45'E) on the West coast of Australia *Chondrilla australiensis* (Fig. 1), a dominant sponge forming encrustations up to 1 m², was found bleached in February 1998. Individuals in full light to 6 metres depth had lost all colouration, whilst shaded individuals and those below 6 metres had not bleached. After three months sponges that had completely bleached had died and shaded individuals were beginning to colonise substrata that had been cleared by the bleaching event.

At Heron Island (23°27'S, 151°55'E) on the East coast of Australia *Haliclona* sp. (Fig. 2), a dominant species in the channel zone between 10–15 m depth was found bleached in June 1998, and bleached individuals were still apparent in September 1998. Neither species had been observed to bleach prior to 1998 in 2 and 5 years of monthly monitoring respectively, and no bleaching has occurred since this event.

First indications are that sponge bleaching is associated with stress or loss of phototrophic symbionts within the sponges. *Chondrilla nucula* from the Northern Hemisphere contains the cyanobacteria *Aphanocapsa feldmannii* (Gaino et al, 1976). *Haliclona* sp. contains dinoflagellates (Garson et al, 1998), but bleached individuals had few dinoflagellates which were unhealthy in appearance and free-living rather than intracellular. The single previous account of sponge bleaching occurred in Puerto Rico in 1987–88 (Vicente, 1990).

The occurrence of sponge bleaching reported here coincides with hard and soft coral bleaching worldwide in 1998. The high latitude of the *Chondrilla* bleaching suggests that sessile invertebrates with phototrophic symbionts occurring in cooler regions are also influenced by recent climatic anomalies, with implications for management of reef environments. Changes in symbiont levels are likely to impact on the secondary chemistry of the sponge species and hence on their ability to survive in competitive reef environments, thus altering present community structure. We have experimental evidence that the alkaloids from *Haliclona* sp. inhibit larval settlement, are toxic to corals, and deter reef fish from feeding on the sponge tissue.

Acknowledgements We thank K. Bancroft for the image of *Chondrilla australiensis* and A. E. Flowers for the image of *Haliclona* sp.

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Reef sites

REPORT

T. J. T. Murdoch · R. B.

Scale-dependen
along the Florid

Accepted: 19 July 1999

Abstract Coral reef comm
tic have changed over the
the magnitude and ca
controversial. Part of th
patterns observed on indi
eously extrapolated to
scales. Understanding ho
through space is an esse
sampling strategies to trac
through time. In this pape
cover of hard corals i
(13–19 m depth) at spatial
magnitude along the Fl
graphic sampling progra
variances in coral cover
levels and corresponding s
sects within sites (0.01- to
within reefs (0.5- to 2-km
sectors of the reef tract (
among sectors of the reef
Coral cover displayed low
within sites and among si
that transects from a site
variability of the spur-and-
a whole. Variability amo
highly significant, compar
cant variability among sect
vidual reef, therefore, did
nearby reefs, nor did those
ent variability at the scale

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SOUTH FLORIDA WATER MANAGEMENT DISTRICT
CONTRACT C91-2547

MONITORING OF THE RECRUITMENT, GROWTH AND MORTALITY OF COMMERCIAL SPONGES IN BISCAYNE NATIONAL PARK:

SECOND ANNUAL REPORT
NOVEMBER, 1994

Submitted by:
Resource Management Division
Biscayne National Park
November, 1994

and Olson 1990; Allen and Hoekstra 1992; L
Wu and Loucks 1995). Moreover, multiscale
may reveal domains, or ranges of scale, in
characteristics of a reef system are scale-in
(Weins 1989; Aronson 1994; Aronson and
1998). If the scales of interest fall within suc
independent domain, then research progra
optimized to reduce the effort required to sa
effectively (Underwood 1997).

Coral reefs of Florida and the Caribb
changed over the past two to three decad
magnitudes, scales, and causes of this chan
controversial (Ginsburg 1994; Hughes 1994
and Precht in press). In general, the cover of l
corals has declined and algal cover has increa
researchers have suggested that factors op
small spatio-temporal scales (meters to kilor
days to years), such as point-source nutrie
and ship groundings, could be primarily resp
the decline of coral populations along the F
Tract (Dustan and Halas 1987; Lapointe
1992; Ginsburg and Shinn 1994; Lapoi
Others assert that meso- to large-scale proc
to thousands of kilometers and decades to
such as larval transport, fishing pressure, d
breaks, and climate change, are equally or m
tant (Lessios 1988; Smith and Budden
Szmant and Forrester 1996; Roberts 1997). A
prerequisite to formulating and testing
about temporal dynamics is understandin
coral assemblages vary over multiple sp
at one time (Schneider 1994). Despite th
ance to nearshore food webs, few multisca
have been attempted for corals on reefs (
Edmunds and Bruno 1996; Hughes et
although studies of this sort are commo
reef fish (Sale 1980; Victor 1986; Doherty
1994).

Until recently, information regarding th
of Florida's reefs was derived primarily
scale surveys (e.g. Dustan and Halas 1987;
Meier 1992; Lapointe 1997). Surveys that
the entire reef tract are needed to determ
the patterns observed and the processes in
those small-scale studies can be extrapola
scales (Ogden et al. 1994). Furthermore, th
techniques used must have sufficient stati
to test the hypotheses, an issue that has
ignored in the contentious debates about
the Florida Reef Tract.

In this paper we test the hypothesis that
hard corals (Scleractinia plus Milleporin
Florida Reef Tract exhibits variability t
with the spatial scale of observation. We s
and groove habitats at 13–19 m depth o
1995 using a hierarchical sampling design
highlight the value of multiscale assessme

Fig. 3 Mean percent coral cover for nine sites within three intensely-sampled reefs on the Florida Reef Tract (three sites at each reef, ten video transects at each site). *Error bars* represent one standard error of the sample mean

Table 1 Results of two-level nested ANOVA on arcsine transformed proportional coral cover along the Florida Reef Tract, comparing the variation among reefs with the variation among sites within reefs and among transects within sites (error term). The denominator mean square for testing the effect of Reef, following Zar (1984) but contrary to Sokal and Rohlf (1981). The *F* test for Reef is highly significant despite being more conservative than if the variances had been pooled

Source	Sum of Squares	df	Mean Square	*F*	*P*
Reef	0.6451	2	0.3225	329.81	7.32 · 10
Site(Reef)	0.0059	6	0.0010	0.5607	0.760
Error	0.1413	81	0.0017		

s

lity among reefs to the variabil-
eefs and among transects within
s from nine sites on three reefs
ive species of hard corals were
sites. The cover of hard corals,
t of 45 000 point counts, varied
e three reefs (Fig. 3). The five
in descending order of overall
franksi, *Siderastrea siderea*, *M.*
and *Colpophyllia natans*. These
58.4% of the total cover. All
no other species accounted for
otal cover.

ities, showed similar patterns of scale dependence (Fig. 4). Sites were more similar to other sites on the same reef than they were to sites on either of the other reefs, with the exception of Tennessee Reef site M4 in Sambo Reef clustered together, and they were distinct from Carysfort Reef. In the Bray-Curtis analysis, sites within Carysfort Reef were more different from each other than Western Sambo and Tennessee Reefs were from each other.

on in mean coral cover among
nove habitat within the three
. Furthermore, coral cover was
among transects within sites,
l errors. A two-level nested
ted within reefs, revealed no
fects, but there was a highly
ect (Table 1). Among-transect
13.7% of the total variance
an square estimates; see for
997), among-site variation
e total variance, and among-
or 86.3% of the total. Tukey
se comparisons showed that
three reefs was significantly
ver on both other reefs

Sectors, reefs, and transects

The low variance among sites within reefs provided the rationale for collapsing the reef and site levels and using 10 transects from a single site to represent the spur-and-groove habitat of an entire reef. Comparison of the variation among sectors to the variation among reefs within sectors involved the analysis of 160 val

ultivariate point count data,
and Bray-Curtis dissimilar-

nd among-sector differences in the second
dition, we calculated the minimum detect-
he-transformed proportional coral cover
y, among sectors. The minimum detect-
e of the difference in coral cover that one
detect in future studies using the same
performed according to Zar (1984) and

e power was set at $(1 - \beta) = 0.80$ and the
$\alpha = 0.05$ to calculate minimum detect-
ted values of δ in the two analyses were
d coral cover for ease of interpretation.
transformed) lowest group mean in the
ck-transformed to actual percent cover,
culated between the back-transformed
ransformed) lowest group mean. Second,
(transformed) highest group mean, that
, and the difference was taken between
ed) highest mean and the back-trans-
tions were used to estimate the range of
ference in actual percent cover, corre-
group means in each of the ANOVAs

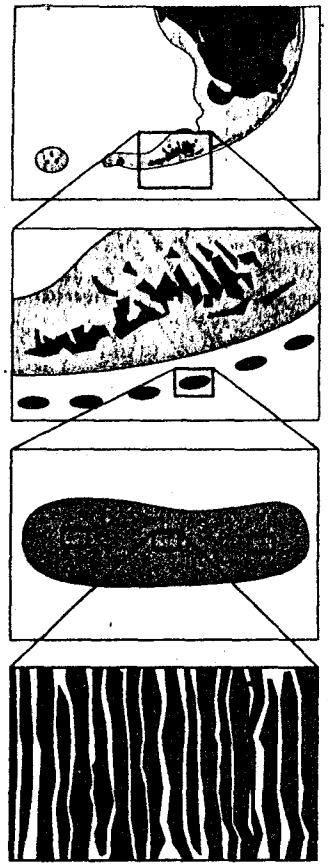


Fig. 2 Hierarchical levels and spatial scales of analysis

(1997). Divers stretched a 25-m long waterproof surveyor's tape down the middle of each of ten haphazardly selected spurs within the site to be sampled. Transects were generally 3–10 m apart. Care was taken to avoid laying the transect lines over sand or off the ends of spurs. Once each transect line was in place another diver slowly swam its length, videotaping a 0.4 m wide × 25 m long swath of the reef.

The transects were videotaped in plan view and at a constant height from the substratum using a high resolution (Hi-8) video camera. The camera was enclosed in a underwater housing and equipped with a wide-angle lens and two 50-W waterproof lights. A stainless steel rod projected forward from the camera housing. The rod was used as a guide so that the diver could maintain a set distance of 40 cm between the camera lens and the reef surface. A 15-cm gray plastic bar was mounted on the end of the rod. The plastic bar provided scale in the videotaped images. The camera was held perpendicular to the reef surface, with the scale bar maintained at a distance of less than 2 cm from the substratum.

The videotaped transects were analyzed in the laboratory with a Hi-8 video cassette recorder (VCR) wired to a high-resolution color monitor. Each video transect was sampled at 50 regularly spaced, non-overlapping frames, displayed by pausing the VCR. For each frame, one of ten clear plastic sheets marked with ten random points was laid over the monitor screen, and the sessile organisms or substrate types present under the points were identified and recorded. The videotape was then advanced to the next frame and a new sheet of dots haphazardly selected. Percent covers of coral species were calculated for each transect from the resulting set of 500 point counts. A sample size of ten transects, analyzed in this manner, allows statistically powerful, univariate and multivariate comparisons of coral cover among sites (Aronson et al. 1994; Aronson and Swanson 1997).

Point counts are biased against the inclusion of rare species, particularly when cover is low (Aronson et al. 1994; Hayek and Buzas 1997). To examine patterns of species presence and absence, we recorded all coral species appearing in each video transect. Rarefaction analysis in an earlier study showed that a sample of ten transects is inadequate to estimate coral species richness on western Atlantic reefs; therefore, ten additional transects of the same dimensions were surveyed visually in the field and the coral species recorded, providing a sufficient sample size of $N = 20$ (Aronson et al. 1994). Presence-absence data were only compared at the 10- to 20-km (reefs within sectors) and the 50- to 100-km (among-sector) scales. Time constraints did not permit us to sample ten visual transects at each of the three sites on Western Sambo, Tennessee, and Carysfort Reefs.

Statistical analysis

Univariate coral cover data from the transects were analyzed using a two-level nested analysis of variance (ANOVA) design. One ANOVA compared the variance among sites to the variance among reefs, with sites nested within reefs. Two additional ANOVAs compared the variance among reefs to the variance among sectors, with reefs nested within sectors; a separate ANOVA was calculated for each sectorial classification scheme. For the three intensively sampled reefs (i.e. Western Sambo, Tennessee, and Carysfort) the site that was chronologically the first sampled was used to represent that reef in the latter two ANOVAs. The error terms in the three ANOVAs represented estimates of the variance among transects.

Prior to ANOVA, the point count data were expressed as proportions. The data were then tested for conformity to the parametric assumptions of normality and homogeneity of variances, using the Lilliefors and F_{max} tests, respectively. Arcsine transformation was necessary to make the data satisfy the assumptions of ANOVA.

Cluster analysis was used to determine if sites within the three intensively sampled reefs were more similar to each other in the composition of their coral assemblages than they were to sites from other reefs. The point count data were pooled by coral species across transects within sites. Dissimilarity matrices were calculated for the nine sites (three on each reef), and the sites were clustered by the average linkage method. Two dissimilarity measures were used in separate cluster analyses: Euclidean distance and Bray-Curtis dissimilarity. Both are weighted toward the most abundant species, but the Bray-Curtis measure is a more robust, reliable measure (Faith et al. 1987).

The same approach was used to determine if spur-and-groove habitats on reefs within sectors were more similar to each other than to spur-and-groove habitats on reefs from other sectors. In this case the Euclidean distance and Bray-Curtis dissimilarity matrices were calculated from the vectors representing species-specific point count values on the 16 reefs, and the reefs were again clustered by the average linkage method. Since the Euclidean and Bray-Curtis measures are weighted toward the dominants, we performed a third cluster analysis of reefs, in which all species were weighted equally. The 16 reefs were analyzed based on the species presence-absence data, using a matrix of Jaccard dissimilarities and clustering by the average linkage method. All univariate and multivariate statistical calculations were performed using the SYSTAT 8.0 statistical package.

A power analysis was performed for each nested ANOVA. The power of the performed test was calculated to determine the probability of detecting among-reef differences in the first comparison (sites nested within reefs) a
(reefs within sectors). In ad
able difference, δ, in arcsi
among reefs and, separate
able difference is an estima
can reasonably expect to
design. Calculations were
Cohen (1988).

Following convention, th
significance level was set a
able differences. The calcul
converted to untransforme
First, δ was added to the
analysis, that value was ba
and the difference was ca
value and the observed (unt
δ was subtracted from the
value was back-transforme
the observed (untransform
formed value. These calcula
the minimum detectable di
sponding to the range of
(Aronson et al. 1994).

Results

Reefs, sites, and transec

To compare the variab
ity among sites within r
sites, 90 video transect
were analyzed. Thirty-f
recorded from the nine
estimated from a data s
considerably among th
most abundant species,
cover, were *Montastrae*
faveolata, *M. cavernosa*,
species accounted for
other species were rare:
more than 5.3% of the

There was little variat
sites in the spur-and-gr
intensively sampled reefs
relatively homogeneous
judging from the sma
ANOVA, with sites ne
significant among-site e
significant among-reef ef
variation accounted for
(calculated from the m
example Underwood
accounted for ~ 0% of t
reef variation accounted
HSD a posteriori pairw
coral cover on each of th
different from coral c
($P < 0.002$ in all cases).

Cluster analysis of the
using Euclidean distance

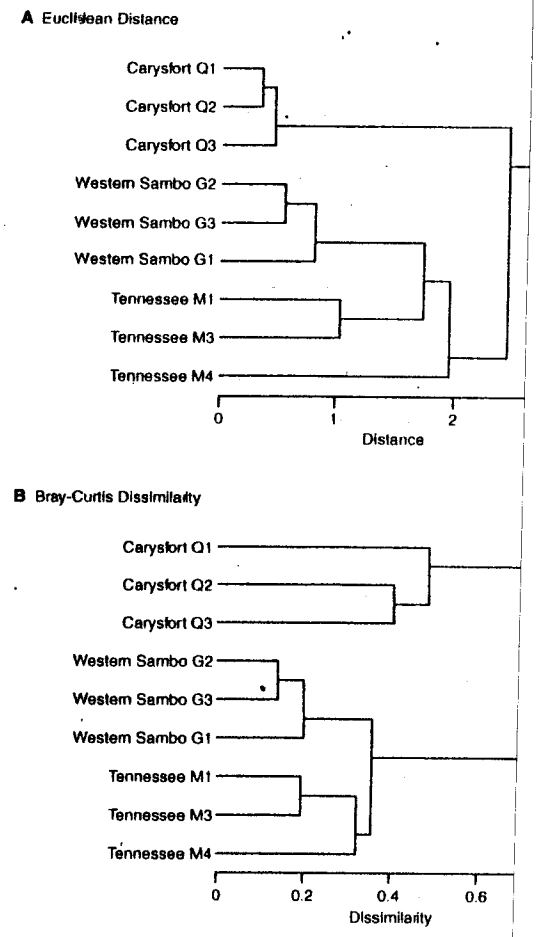


Fig. 4 A,B Cluster diagrams showing the relationships of s
specific coral cover among nine sites on three intensively s
reefs within the Florida Reef Tract. Sites were clustered
average linkage method based on: A Euclidean distance and
Curtis dissimilarity

transects from 16 reefs. Thirty-eight species of corals were recorded from the 16 reefs. Total cover, estimated from a data set of 80,000 point c showed substantial among-reef variation (Fig. 5 five dominant species were, in descending order, *tastraea franksi*, *M. faveolata*, *M. cavernosa*, *Sider siderea*, and *Millepora alcicornis*. Together th counted for 69.4% of the total coral cover. All species were rare: no other species accounted fo than 4.8% of the total cover.

Two-level nested ANOVAs, using both se classification schemes, detected highly significant ences among reefs and marginally significant ences among sectors (Table 2). Using the Kle Orlando (1994) sectorial classification scheme, a transect variation accounted for 17.6% of th

Study	Locality	Variability at level of			
		Transect	Site	Reef	Sector
This study	Florida Reef Tract	Low	Low	High	High
Edmunds and Bruno (1996)	Jamaica	Low		High	High
Hughes et al. (1999)	Great Barrier Reef	High	High	Low	Low

Rowan 1998). These differences determine which species will dominate under benign conditions and which will do better in the face of chronic stress or disturbance (Aronson and Precht in press). Patterns of spatial variability may be distinct at different taxonomic levels or for different functional groups (Bradbury and Loya 1978; Sullivan and Chappone 1993; Edmyer and Risk 1995; Hughes et al. 1999). possibilities we are currently exploring for the corals of the Florida Reef Tract.

Sampling strategies for science and management

Based on our results, surveys taken at different sites within the spur-and-groove habitat on a reef along the Florida Reef Tract should yield similar estimates of coral cover. In other words, the three reefs we sampled intensively appeared to exist within a domain of scales over which coral cover and species composition were relatively homogeneous (i.e. scale-independent). The common practice of sampling over a minimal area can be justified within the scale-independent domain of each reef (Wiens 1989; Underwood 1997). Since reefs differed from their neighbors, however, researchers and environmental managers in Florida should survey numerous reefs to determine the state of the coral assemblages at the 10- to 20-km scale and at larger scales. The direction and rate of change of the coral assemblage of each reef may be different from that of its neighbors (cf. Kay 1991; Edmunds and Bruno 1996).

Coral reef surveys are almost always limited by time and money, necessitating short, "snapshot" visits to individual reefs. Power analysis showed that an investigator can reasonably expect to detect differences on the order of 3–7% coral cover when comparing spur-and-groove habitats on up to ten reefs in the 13–19 m depth range along the Florida Reef Tract. using a sample size of ten transects per reef. If the study requires detection of smaller differences or involves more than ten reefs, then more transects may be necessary.

Complex patterns of change through time cannot be assessed by short-term, synoptic surveys such as the one described in this paper. Long-term, hypothesis-driven sampling is needed to detect relative changes in assemblage composition over different temporal scales in such systems. Until such time-series data are collected for the majority of the reefs along the Florida Reef Tract, it will not be possible to ascertain with

characteristics that probably in-
survival, including extreme
and salinity as well as high
ds (Ginsburg and Shinn 1964,
1992; Burns 1985; Shinn et al.
ivan 1994; Szmant and For-
y Reef (reef K), which is near
exhibited particularly low
erican Shoal and Alligator
ch are opposite islands and
osure to Florida Bay water,
gs. 1, 5). Thus, water from
id not depress coral cover
Middle Keys. The Middle
e treated as a unit for the

mewhat from those of Ed-
), who surveyed reefs in
o observed high alma-reef
(Table 4), their reefs were
kilometers, a spatial scale
riability. Patterns of vari-
n the Great Barrier Reef,
tudied coral colony abund-
gain, the spatial scales were
s covered 250–500 km in
posed to 50–100 km in the
ometers. The low among-
Hughes et al. (1999) could
mped distribution of reefs
e physical and biological
lity in reef coral assem-
ales and hierarchical levels
tions. Thus, although all
variability at some scale,
e scales of maximum and
r locales.

al variability among coral
within those assemblages
rtable. Corals exhibit in-
rphology, endosymbiosis,
al pattern, reproductive
survivorship relative to
urbance (Jackson 1979;
Jackson 1985; Tomascik
1997; Soong 1993; Edin-
one and Sullivan 1996;

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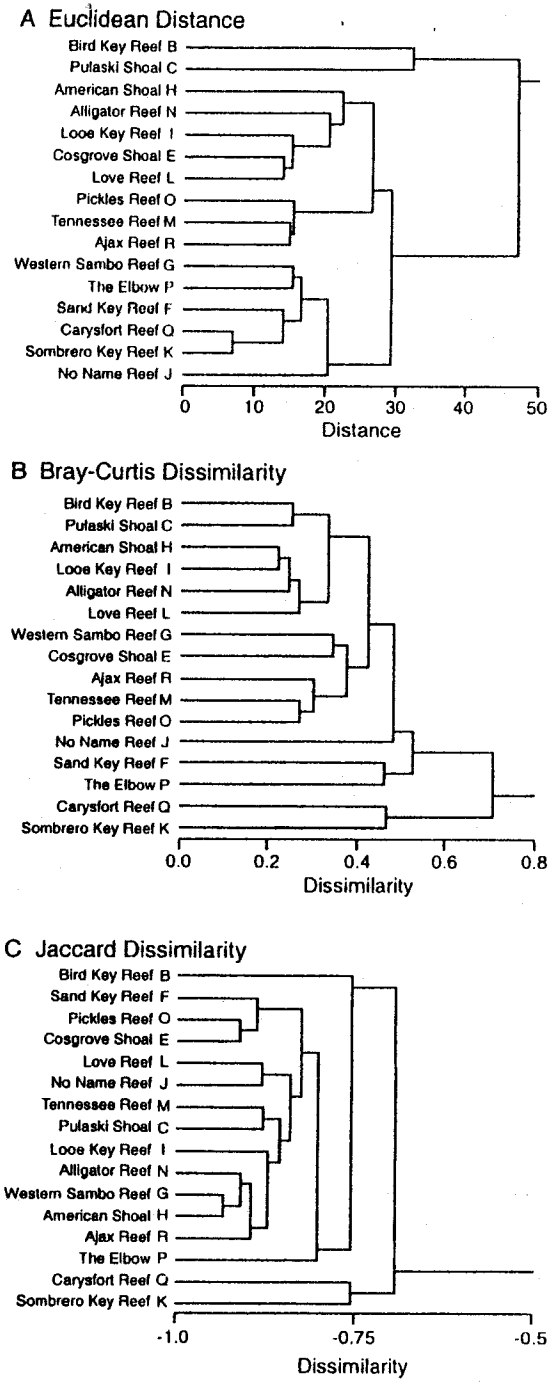


Fig. 6A–C Cluster diagrams showing the relationships among 16 reefs along the Florida Reef Tract. Sites were clustered by the average linkage method based on: **A** Euclidean distance calculated from species-specific coral cover, **B** Bray-Curtis dissimilarity calculated from species-specific coral cover, and **C** Jaccard dissimilarity calculated from species presence-absence data

Table 3 Results of one-way ANOVA on arcsine-transformed proportional coral cover, comparing variation among single sites at Western Sambo, Tennessee, and Carysfort Reefs to variation among transects within sites (error term) along the Florida Reef Tract

Source	Sum of Squares	df	Mean Square	F	P
Sites	0.2378	2	0.1189	53.897	3.74×10^{-10}
Error	0.0596	27	0.0022		

among sectors was $13.70 < \delta < 13.79\%$ cover, assuming a balanced, nested design and using the Klein and Orlando (1994) classification. In fact, the analysis detected a (possibly) significant difference of 13.94% cover between the Dry Tortugas and the Upper Keys. The minimum significant between-reef difference in coral cover, detected between Sand Key Reef (reef F) and Carysfort Reef (reef Q), was 2.8% (Tukey test, $P < 0.025$), which again agrees with Aronson et al. (1994). Similar results were obtained from calculations using the Shinn et al. (1989) classification.

Discussion

Patterns of variability at different scales

Coral assemblages of the Florida Reef Tract exhibited different degrees of variability in cover depending on the spatial scale surveyed. Coral cover varied little within and among sites on a single reef, yet it varied substantially from reef to reef. Had the Dry Tortugas sector not exhibited high coral cover, landscape-scale (among-reef) variation would have overwhelmed any intersectorial differences.

The higher coral cover observed in the Dry Tortugas could have been a result of their isolation from natural and anthropogenic sources of coral mortality from Florida Bay and the rest of the Florida Reef Tract. The Dry Tortugas are also exposed to gyres that may return locally-generated larvae to the sector, promoting coral recruitment (Lee et al. 1994, 1995). Research into the genetic variability of gorgonians indicates that populations in the Dry Tortugas are distinct from those along the rest of the Florida Reef Tract (D. Brazeau pers. comm.). The same could be true for one or more coral species, especially those with a short larval lifespan (see Carlon and Olson 1993).

The pattern of high reef-to-reef variability within sectors was presumably the result of environmental gradients acting at spatial scales equal to or larger than individual reefs but smaller than sectors. Such environmental gradients could be caused by water crossing the Florida Platform from the Atlantic Ocean and from Hawk Channel (Pitts 1994), or by water from Florida Bay reaching the reefs via passes between the Keys (Smith 1994). Water from Hawk Channel and Florida

Table 4 Variability of coral cover at different hierarchical levels in this and other studie

Bay possesses several cha
hibit coral growth and
variability in temperatur
nutrient and sediment loa
1994; Roberts et al. 1983,
1989; Chiappone and Sul
rester 1996). Sombrero K
a large pass to Florida Ba
coral cover, whereas An
Reef (reefs H and N), wh
therefore blocked from ex
had high coral cover (F
Florida Bay apparently
uniformly throughout the
Keys, therefore, cannot b
purpose of management.

Our results differed so
munds and Bruno (199
Jamaica. Although they als
variability in coral cover
separated by one to severa
on which we found low v
ation were also different
where Hughes et al. (1999)
ance at a variety of scales. A
different from ours: secto
Hughes et al. (1999), as op
present study, and their re
dreds of meters to tens of k
reef variability observed by
have been due to the clu
sampled within sectors. Ti
factors that underlie varia
blages may act at different s
in different geographic loc
three studies detected high
none could have predicted t
minimum variability at othe

This study examined spat
assemblages, but the species
are themselves biologically v
terspecific differences in mo
fragmentation rate, dispers
mode, recruitment rate, an
gradients of stress and dis
Highsmith 1982; Hughes an
and Sander 1987; Smith 1992
ger and Risk 1995; Chiapp

Table 7. Change in commercial sponge abundance and distribution from 1978 to 1991. Results of the present study are compared to baseline data gathered in 1978 (Tilmant, 1978). The ratio of historical to present commercial sponge densities (mean number of sponges/plot) and the direction of change (+ = increase, - = decrease) are presented. See text for details.

SITE	1978	1991	RATIO	CHANGE
A13	2.0	0	-	-
B9	15.6	0	-	-
B10	19.4	0	-	-
B11	4.6	1.0	4.6	-
B12	7.4	0	-	-
B13	16.2	0	-	-
B14	1.4	0	-	-
C9	7.6	0	-	-
C10	16.8	3.6	4.7	-
C11	2.0	4.2	0.5	+
C12	1.8	11.0	0.2	+
C13	7.0	2.0	3.5	-
C14	11.6	4.6	2.5	-
C15	6.0	7.2	0.8	+
D9	0	3.0	0	+
D10	1.8	3.0	0.6	+
D11	0.8	12.4	0.1	+
D12	1.8	11.4	0.2	+
D13	1.2	3.2	0.4	+
D14	2.2	13.6	0.2	+
D15	0	4.6	0	+
D16	0	9.2	0	+
E9	0.4	1.6	0.3	+
E11	0.2	6.8	0.03	+
E12	0	4.0	0	+
E14	0	8.2	0	+
E15	2.6	0	-	-
F9	0.8	0.6	1.3	-
F12	1.0	0	-	-
F13	0	2.8	0	+
F14	7.4	0	-	-
F15	2.4	10.8	0.2	+
G9	1.2	0	-	-
G10	2.4	0	-	-
G11	0.2	0.7	0.3	+
G12	0.6	1.2	0.5	+
G13	6.0	3.6	1.7	-
G14	0.2	25.8	0.008	+
H9	0.2	1.0	0.2	+

reefs are undergoing the most dramatic chang
assemblage structure (Rogers 1988; Ray and G
1991; Ogden et al. 1994). In Florida and the Carib
an independent sampling approach, with ten tra
haphazardly positioned in the spur-and-groove h
of the study reef at each sampling time, pr
a simple, inexpensive, statistically powerful alter
to the traditional repeated measures design, in
permanent transects or quadrats are resample
time (see also Aronson et al. 1994). It may a
desirable to collect long-term data on changes
condition or health of coral colonies, as well
processes such as recruitment, mortality, and
vory, but such decisions must depend on the hy
ses guiding the study.

Single factors rarely provide sufficient explan
in ecology. The goal of ecological analysis shoul
understand the relative contributions of multip
cesses to observed patterns (Quinn and Dunham
Thus, for example, although water from Floric
may affect reef development in the Middle and
Keys, it is by no means the only influence (e.g. L
et al. 1996, 1998). Multiple factors combine to
mine patterns of community composition alo
Florida Reef Tract. Multiscale analyses of comp
systems like the Florida Reef Tract are expensi
time-consuming, but they are crucial to realistic
and effective management.

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the University of South Alabama. This is Contribution 3
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DUPLICATE:
Original in
Museum Archives

Table 6. Size range of commercial sponges. Mean, median and range of sizes of individual commercial species. The longest horizontal dimension (cm) was measured for each sponge in the study area.

	Mean	Median	Range
H. lachne	11.4	10.0	1 - 40
S. tubulifera	11.1	10.0	1 - 45
S. barbara	6.1	5.0	1 - 19
S. graminea	6.3	4.0	1 - 20

Table 5. continued

SITE	*S. vesparia*	OTHER	TOTAL	DENSITY
F4	0	72	72	4583.7
F5	0	111	111	7066.5
F6	15	113	128	8148.7
F7	0	117	117	7448.4
F8	4	630	634	26903.5
F9	0	188	188	4787.4
F10	0	132	132	8403.4
F11	0	45	45	2864.8
F12	0	111	111	7066.5
F13	3	214	217	5525.9
F14	0	24	24	1527.9
F15	41	252	293	7461.2
G2	0	9	9	573.0
G4	0	43	43	2737.5
G5	0	62	62	3947.0
G6	7	113	120	5093.0
G7	4	123	127	8085.1
G8	0	90	90	5729.6
G9	1	303	304	19353.2
G10	1	13	14	891.3
G11	0	281	281	11926.4
G12	0	78	78	1986.3
G13	1	121	122	3106.7
G14	22	783	805	20499.1
H2	0	150	150	9549.3
H4	0	32	32	2037.2
H5	0	99	99	6302.5
H6	0	31	31	1973.5
H7	0	136	136	4838.3
H8	3	7	40	2546.5
H9	2	498	500	12732.4
H10	0	94	94	5984.2
H11	0	540	540	34377.4
I4	0	80	80	5093.0
I6	0	56	56	3565.1

Table 5. Abundance of noncommercial sponges. The mean number of loggerhead (S. vesparia) and other noncommercial sponges observed at each site. Noncommercial sponge density (sponges/ha) is highly variable throughout the study area.

SITE	*S. vesparia*	OTHER	TOTAL	DENSITY
A9	0	14	14	356.5
A10	0	1	1	63.7
A11	0	1	1	63.7
A12	0	3	3	191.0
B10	0	288	288	18334.6
B11	7	239	246	6137.0
B12	5	229	234	9931.3
B13	0	11	11	700.3
C3	0	51	51	3246.8
C4	0	7	7	445.6
C5	2	292	294	18716.6
C7	0	36	36	2291.8
C9	15	202	217	5525.9
C10	42	216	258	6569.9
C11	19	129	148	3768.8
C12	28	383	411	10466.0
C13	0	123	123	6951.9
C14	13	216	229	5831.4
C15	6	143	49	3794.2
D4	3	352	355	22600.0
D5	0	694	694	17672.5
D6	76	329	405	25783.0
D7	153	1597	1750	44563.3
D8	63	275	338	8607.1
D9	0	322	322	8199.6
D10	11	285	296	7537.6
D11	9	398	407	10364.2
D12	17	396	413	10516.9
D13	0	107	107	2724.7
D14	12	406	418	10644.3
D15	6	226	232	5907.8
D16	1	291	292	7435.7
E4	0	188	188	11968.4
E5	2	326	328	8352.4
E6	6	506	512	13037.9
E7	17	350	367	9345.6
E8	0	42	42	2673.8
E9	0	164	164	4176.2
E10	1	10	11	700.3
E11	2	247	249	6340.7
E12	4	149	53	3896.1
E13	0	44	44	1400.6
E14	10	366	376	9574.7
E15	0	6	6	382.0

Table 4. Density of commercial sponge species. Individual species densities (#/ha) and total commercial sponge density at each site where commercial sponges are present.

SITE	*H. lachne*	*S. barbara*	*S. tubulifera*	*S. graminea*	TOTAL
B11	0	50.9	76.4	0	127.3
C10	127.3	50.9	178.3	50.9	407.4
C11	127.3	203.7	152.8	50.9	534.8
C12	305.6	458.4	483.8	76.4	1324.2
C13	229.2	50.9	0	25.5	305.6
C14	50.9	178.3	356.5	0	585.7
C15	76.4	0	840.3	0	916.7
D4	66.7	0	127.3	0	191.0
D5	0	101.9	305.6	305.6	713.0
D6	0	63.7	318.3	0	382.0
D7	127.3	356.5	101.9	0	585.7
D8	127.3	738.5	458.4	1044.1	2368.2
D9	229.2	25.5	76.4	50.9	382.0
D10	0	127.3	254.7	0	382.0
D11	382.0	585.7	356.5	254.7	1578.8
D12	585.7	280.1	203.7	382.0	1451.5
D13	203.7	101.9	50.9	50.9	407.4
D14	305.6	636.6	687.5	101.9	1731.6
D15	25.5	254.7	305.6	0	585.7
D16	50.9	305.6	814.9	0	1171.4
E5	50.9	25.5	356.5	0	432.9
E6	0	356.5	458.4	0	814.9
E7	585.7	611.2	1044.1	458.4	2699.3
E9	101.9	50.9	50.9	0	203.7
E11	280.1	203.7	331.0	50.9	865.8
E12	254.7	76.4	152.8	25.5	509.3
E14	127.3	178.3	738.5	0	1044.1
F4	0	0	63.7	0	63.7
F8	85.3	0	0	0	76.4
F13	178.3	50.9	101.9	25.5	356.5
F15	25.5	178.3	76.4	1095.0	1375.1
G6	0	42.4	0	0	42.4
G11	84.9	0	0	0	85.3
G12	127.3	0	25.5	0	152.8
G13	229.2	25.5	152.8	50.9	458.4
G14	331.0	840.3	458.4	1655.2	3285.0
H9	0	25.5	101.9	0	127.4

THE UNIVERSITY OF MIAMI

A thesis submitted in partial fulfillment of
the requirements for the degree of
Master of Science

THE ECOLOGY AND DISTRIBUTION OF REEF-BUILDING CORALS ON FOUR SOUTH FLORIDA REEFS.

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Table 3. Commercial sponge density and habitat characteristics. Water depth, sediment thickness, bottom type and commercial sponge density (sponges/ha) are given for each site where commercial sponges occur.

SITE	DEPTH (m)	SEDIMENT (mm)	BOTTOM TYPE	DENSITY
B11	1.6	10	1	127.3
C10	2.5	50	3	458.4
C11	2.0	80	1	534.8
C12	2.1	30	1	400.6
C13	1.9	100	1	254.7
C14	1.7	40	1	585.7
C15	1.7	100	1	916.7
D4	2.3	200	4	191.0
D5	2.0	30	1	713.0
D6	2.0	60	3	382.0
D7	2.0	40	2	585.7
D8	1.6	30	2	368.2
D9	2.1	40	1	383.0
D10	2.4	10	1	382.0
D11	2.7	50	2	578.8
D12	2.7	30	1	451.5
D13	2.3	70	1	407.4
D14	1.7	140	1	731.6
D15	2.2	50	1	585.7
D16	2.5	160	3	171.4
E5	2.3	120	4	814.9
E7	2.7	30	2	699.3
E9	1.6	500	4	203.7
E11	3.3	60	2	865.8
E12	2.7	50	1	509.3
E14	2.5	100	1	44.1
F4	3.6	150	4	63.7
F8	3.4	60	4	85.3
F9	2.3	570	4	76.4
F13	3.1	80	4	356.5
F15	1.8	50	1	375.1
G6	3.6	150	3	42.0
G11	3.4	100	4	85.3
G12	3.4	40	2	152.8
G13	2.6	70	1	458.4
G14	2.1	20	1	285.0
H9	2.5	50	4	127.3

Table 2. Summary of the occurrence of sponges at sampling sites. The number of sites at which commercial sponges occur is presented for each species.. Frequency of commercial sponge sites is based on the total number of sites sampled. See Methods for details.

	# of sites	Frequency
H. lachne	29	0.31
S. barbara	30	0.32
S. tubulifera	33	0.35
S. graminea	17	0.18
Total Commercial	37	0.39
Total Noncommercial	79	0.84

BURNS, THOMAS PATRICK (M.S., BIOLOGICAL OCEANOGRAPHY)

THE ECOLOGY AND DISTRIBUTION OF REEF-BUILDING CORALS ON FOUR SOUTH FLORIDA REEFS. (May, 1983)

Abstract of a master's thesis at the University of Miami. Thesis supervised by Professor G. L. Voss.

Line-intercept transects in three depth-zones between the surface and 18 m on four consecutive shelf-edge reefs in South Florida (25° 29' to 25° 22' N) were used to study the structure and diversity of the hermatypic coral (Scleractinia) community. Low diversities, low coral cover and colony abundance, and the small size of colonies indicated that this area is not an optimum habitat for reef-corals. Temperature sensitive acroporids and other shallow fore-reef species were scarce and small. Species diversity, evenness, and Shannon-Wiener diversity in most cases increased with depth. Montastrea annularis and other corals reached greater abundance and size in the deep fore-reefs. The results suggest that cold surface water in winter is the major control of the distribution of hermatypic corals with depth on these reefs. The shallowest zone is stressed more frequently and severely by water temperatures below the tolerance levels of all but the hardiest corals. Differences in the abundance of several species and diversity among the four neighboring reefs indicate that exposure to environmental stress varies within the 13 km from Triumph to Pacific Reef. Hydrodynamic conditions varying with the location of reefs may determine magnitudes of stress or frequencies of disturbance from cold or sediment-laden bay water flowing out of tidal passes.

Table 1. continued

Site	Latitude (d.m.s)	Longitude (d.m.s)	Depth (m)	Sediment (mm)	Bottom Type
H1	25.39.30	80.11.32	3.0	500	1
H2	25.38.24	80.11.32	4.6	300	2
H3	25.37.18	80.11.32	2.7	500	4
H4	25.36.12	80.11.31	4.1	500	4
H5	25.35.04	80.11.31	4.0	500	4
H6	25.34.01	80.11.31	3.0	300	4
H7	25.32.55	80.11.37	2.9	200	4
H8	25.31.47	80.11.31	2.5	60	4
H9	25.30.45	80.11.34	2.5	50	4
H10	25.29.31	80.11.38	1.5	100	4
H11	25.28.32	80.11.34	2.2	100	4
I1	25.39.31	80.10.19	4.9	500	1
I4	25.36.12	80.10.18	1.6	500	4
I6	25.34.01	80.10.18	2.0	500	4

THE UNIVERSITY OF MIAMI

THE ECOLOGY AND DISTRIBUTION OF REEF-BUILDING CORALS ON FOUR SOUTH FLORIDA REEFS.

BY

Thomas Patrick Burns

A THESIS

Submitted to the Faculty
of the University of Miami
in partial fulfillment of the requirements for
the degree of Master of Science

Coral Gables, Florida

May, 1983

Table 1. continued

Site	Latitude (d.m.s)	Longitude (d.m.s)	Depth (m)	Sediment (mm)	Bottom Type
E3	25.37.18	80.15.10	2.5	700	4
E4	25.36.16	80.15.11	3.4	110	4
E5	25.35.08	80.15.08	2.7	220	2
E6	25.33.58	80.15.08	2.3	120	4
E7	25.32.53	80.15.09	2.7	30	2
E8	25.31.50	80.15.13	2.8	170	4
E9	25.30.39	80.15.10	1.6	500	4
E10	25.29.42	80.15.05	3.6	150	4
E11	25.28.32	80.15.10	3.3	70	2
E12	25.26.13	80.15.13	2.5	100	1
E14	25.25.11	80.15.09	2.5	100	1
E15	25.24.10	80.15.08	2.4	100	4
E16	25.23.00	80.15.10	0.8	500	4
F3	25.37.18	80.13.57	3.0	340	4
F4	25.36.14	80.13.58	3.6	150	4
F5	25.35.07	80.13.55	2.6	60	1
F6	25.33.57	80.13.53	3.2	20	1
F7	25.32.52	80.13.52	3.8	400	4
F8	25.31.46	80.14.01	3.4	60	4
F9	25.30.44	80.12.46	2.3	570	4
F10	25.29.39	80.13.59	3.1	70	4
F11	25.28.36	80.13.55	3.4	50	4
F12	25.27.24	80.13.57	3.4	200	4
F13	25.26.20	80.13.57	3.1	80	4
F14	25.25.15	80.14.03	3.1	70	4
F15	25.24.06	80.13.56	1.8	50	1
G2	25.38.26	80.12.46	4.1	500	4
G3	25.37.18	80.12.44	3.3	280	4
G4	25.36.11	80.12.42	4.0	500	4
G5	25.35.05	80.12.44	3.9	200	4
G6	25.33.59	80.12.41	3.6	150	3
G7	25.32.56	80.12.45	3.8	300	4
G8	25.31.49	80.12.44	2.9	100	4
G9	25.30.42	80.12.43	2.6	70	4
G10	25.29.37	80.12.44	1.5	100	4
G11	25.28.30	80.12.48	3.4	100	4
G12	25.27.24	80.12.44	3.4	40	2
G13	25.26.18	80.12.44	2.6	70	1
G14	25.25.12	80.12.44	2.1	20	1

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Table 1. Location, water depth, sediment depth and bottom type at study sites. Water depth, sediment depth and vegetative coverage (bottom type) are listed along withthe Loran C coordinates fo each study site. See Methods for details.

Site	Latitude (d.m.s)	Longitude (d.m.s)	Depth (m)	Sediment (mm)	Bottom Type
A9	25.30.46	80.19.59	0.8	250	4
A10	25.29.36	80.19.53	0.9	310	4
A11	25.28.29	80.19.59	1.1	110	4
A12	25.27.25	80.19.51	1.3	350	4
B8	25.31.48	80.18.47	2.0	20	3
B9	25.30.40	80.18.45	0.8	120	4
B10	25.29.40	80.18.48	1.1	60	4
B11	25.28.29	80.18.47	1.6	10	1
B12	25.27.26	80.18.49	1.6	50	2
B13	25.26.18	80.18.50	1.4	60	1
B14	25.25.15	80.18.50	1.5	60	4
B15	25.24.08	80.18.49	1.6	90	1
C3	25.37.12	80.17.35	0.9	300	4
C4	25.36.14	80.17.35	2.0	600	4
C5	25.35.06	80.17.35	2.0	50	4
C6	25.34.00	80.17.35	1.0	20	4
C7	25.32.55	80.17.34	2.0	100	3
C8	25.31.48	80.17.35	1.5	10	4
C9	25.30.43	80.17.33	1.6	50	2
C10	25.29.31	80.17.34	2.5	50	3
C11	25.28.31	80.17.37	2.0	80	1
C12	25.27.24	80.17.35	2.1	30	1
C13	25.26.13	80.17.35	1.9	100	1
C14	25.25.08	80.17.35	1.7	40	1
C15	25.24.05	80.17.31	1.7	100	1
C16	25.23.00	80.17.35	0.7	500	4
D3	25.37.18	80.16.22	1.8	10	4
D4	25.36.12	80.16.23	2.3	200	4
D5	25.35.06	80.16.22	2.0	30	1
D6	25.34.03	80.16.20	2.0	60	3
D7	25.32.59	80.16.23	2.0	40	2
D8	25.31.51	80.16.22	1.6	30	2
D9	25.30.47	80.16.24	2.1	40	1
D10	25.29.41	80.16.22	2.4	20	1
D11	25.28.33	80.16.18	2.7	50	2
D12	25.27.26	80.16.23	2.7	30	1
D13	25.26.16	80.16.25	2.3	70	1
D14	25.25.11	80.16.22	1.7	140	1
D15	25.24.06	80.16.22	2.2	50	1
D16	25.22.58	80.16.24	2.5	160	3

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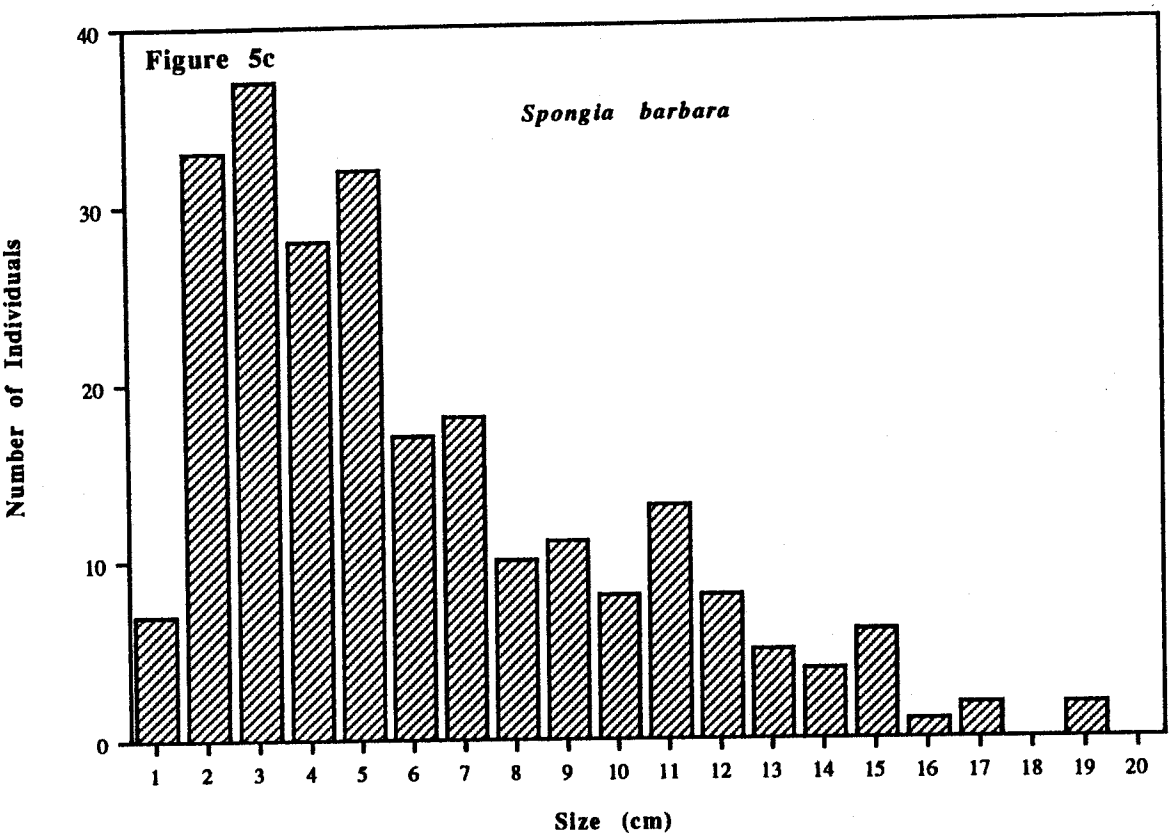
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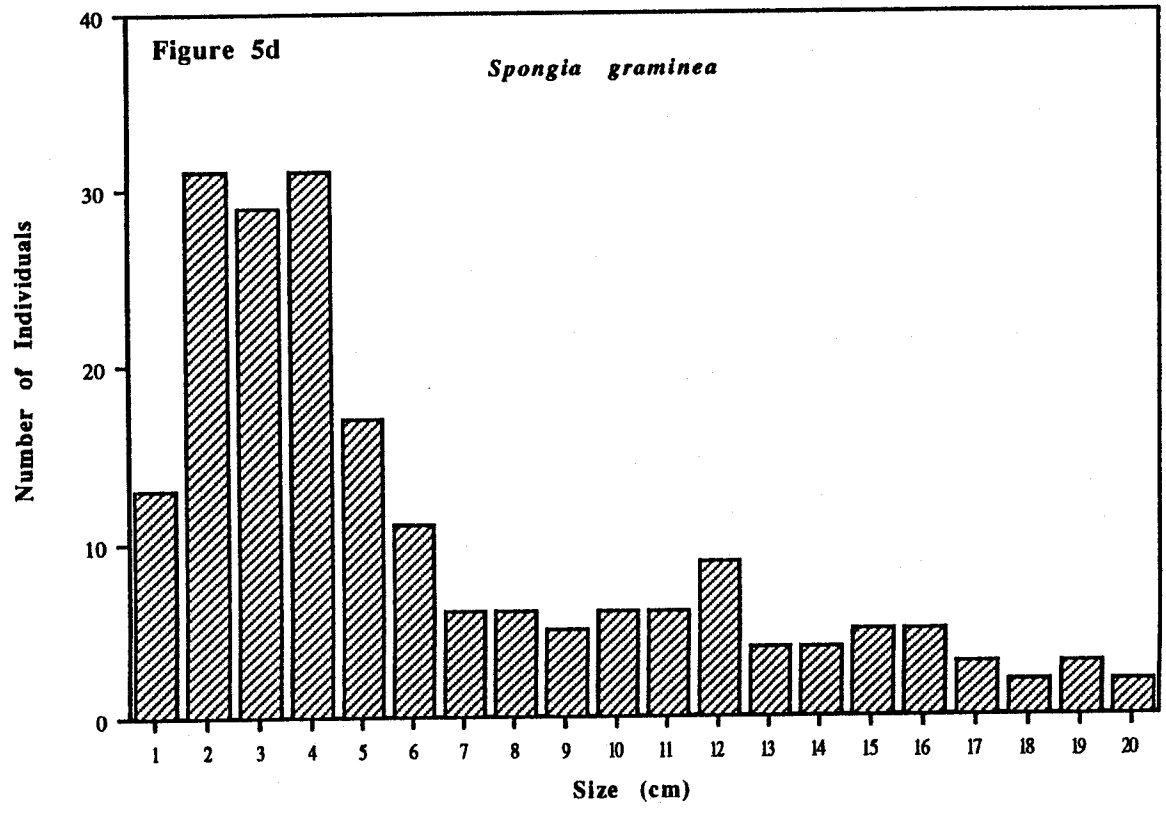
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Figure 5c
Spongia barbara
Number of Individuals
0
10
20
30
40
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Size (cm)


Figure 5d
Spongia graminea
Number of Individuals
0
10
20
30
40
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20
Size (cm)

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Figure 7. Mean coral cover and number of colonies per transect for selected species at Triumph Reef. 26

Figure 8. Relative abundance of corals: Triumph Reef. 28

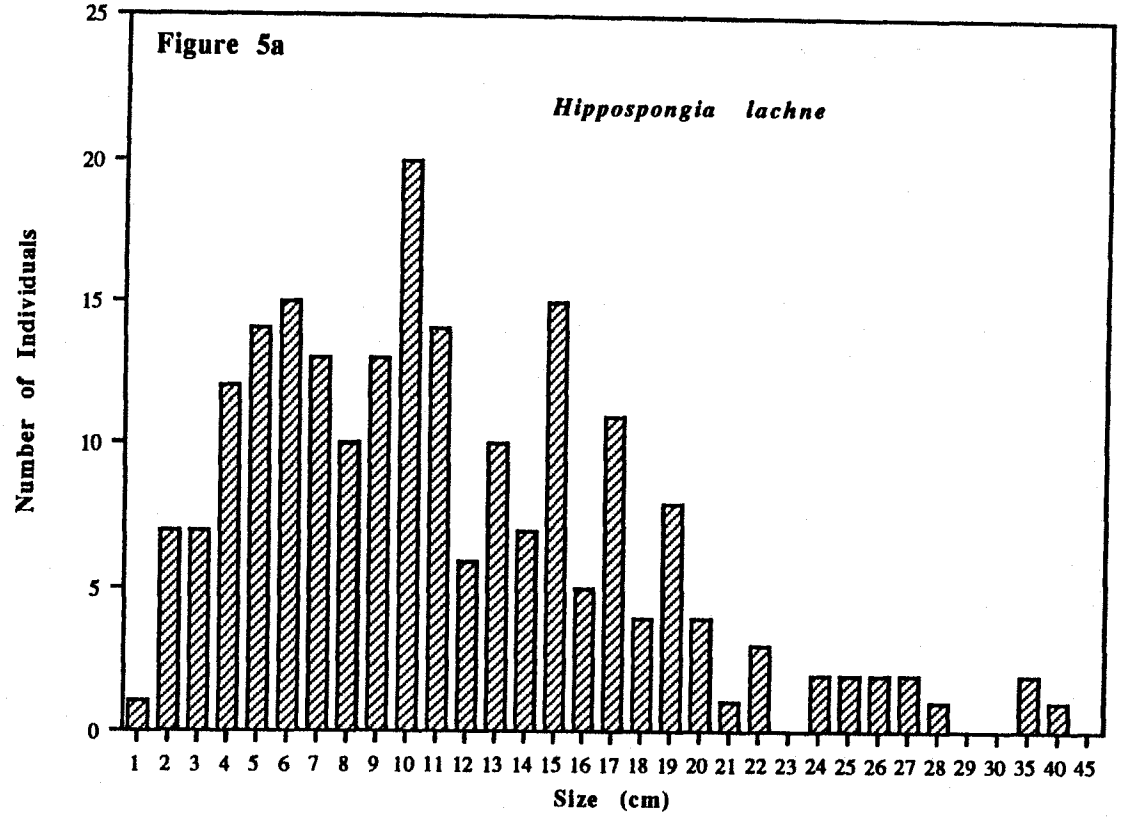
Figure 9. Relative abundance of corals: Long Reef. 37

Figure 10. Mean coral cover and number of colonies per transect for selected species at Long Reef. 39

Figure 11. Relative abundance of corals: Ajax Reef. 44

Figure 12. Mean coral cover and number of colonies per transect for selected species at Ajax Reef. 46

Figure 13. Relative abundance of corals: Pacific Reef. 51


Figure 5a
Hippospongia lachne
Number of Individuals
0
5
10
15
20
25
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 35 40 45
Size (cm)

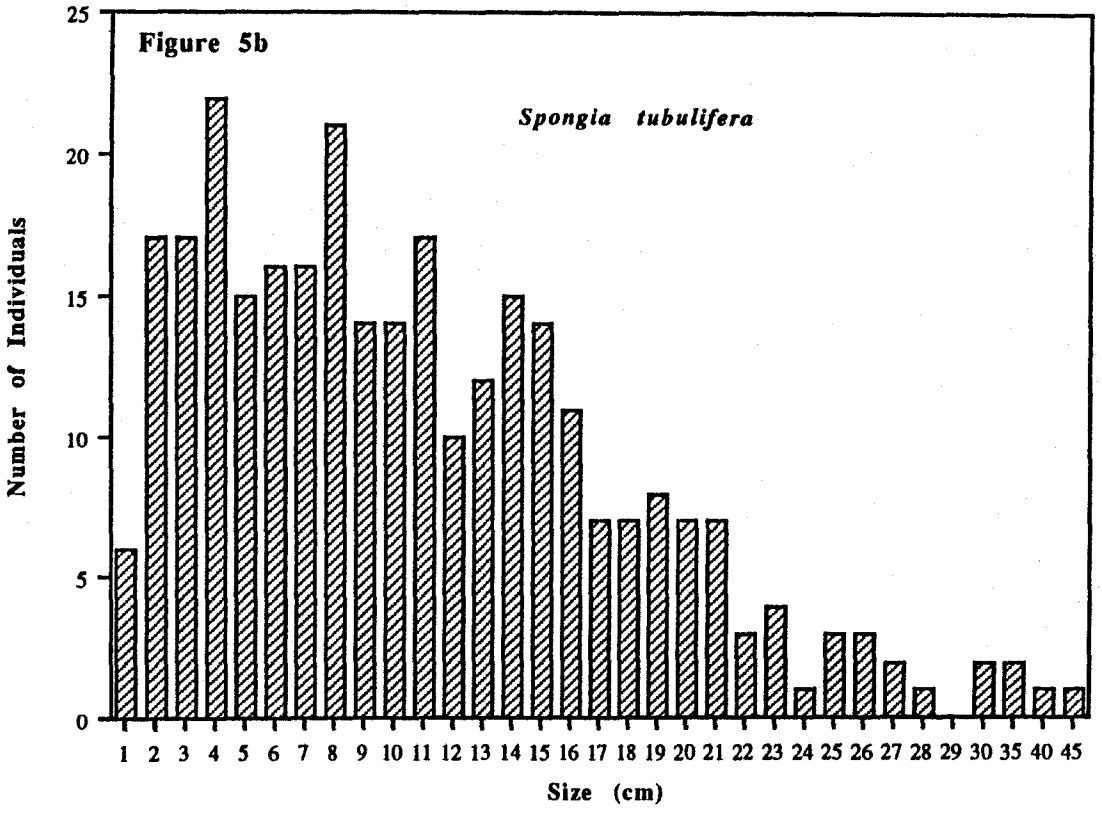

Figure 5b
Spongia tubulifera
Number of Individuals
0
5
10
15
20
25
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 35 40 45
Size (cm)

Figure 14. Mean coral cover and number of colonies per transect for selected species at Pacific Reef.
53

Figure 15. Size-frequency distributions of all colonies.
58

Figure 16. Size-frequency distributions by depth-zone for a) Siderastrea siderea, b) Dichocoenia stokesii
62

c) Montastrea annularis d) Montastrea cavernosa
63

Figure 17. Dendrogram showing clustering based on Bray-Curtis Similarity of coral cover in the reef-zones.
66

Figure 18. Percent of surface light at reef substrate by depth for Abaco Is. Bahamas (Storr, 1964).
70

Figure 19. Cover and number of colonies of a) Acropora cervicornis, b) Diploria clivosa c) Agaricia agaricites, and d) Dichocoenia stokesii in the shallow fore-reefs.
81

Figure 20. Percent of Total Species Richness vs. Evenness for the three reef-zones on all reefs.
83

Figure 21. Profile of Carysfort Reef (Key Largo, FL).
86

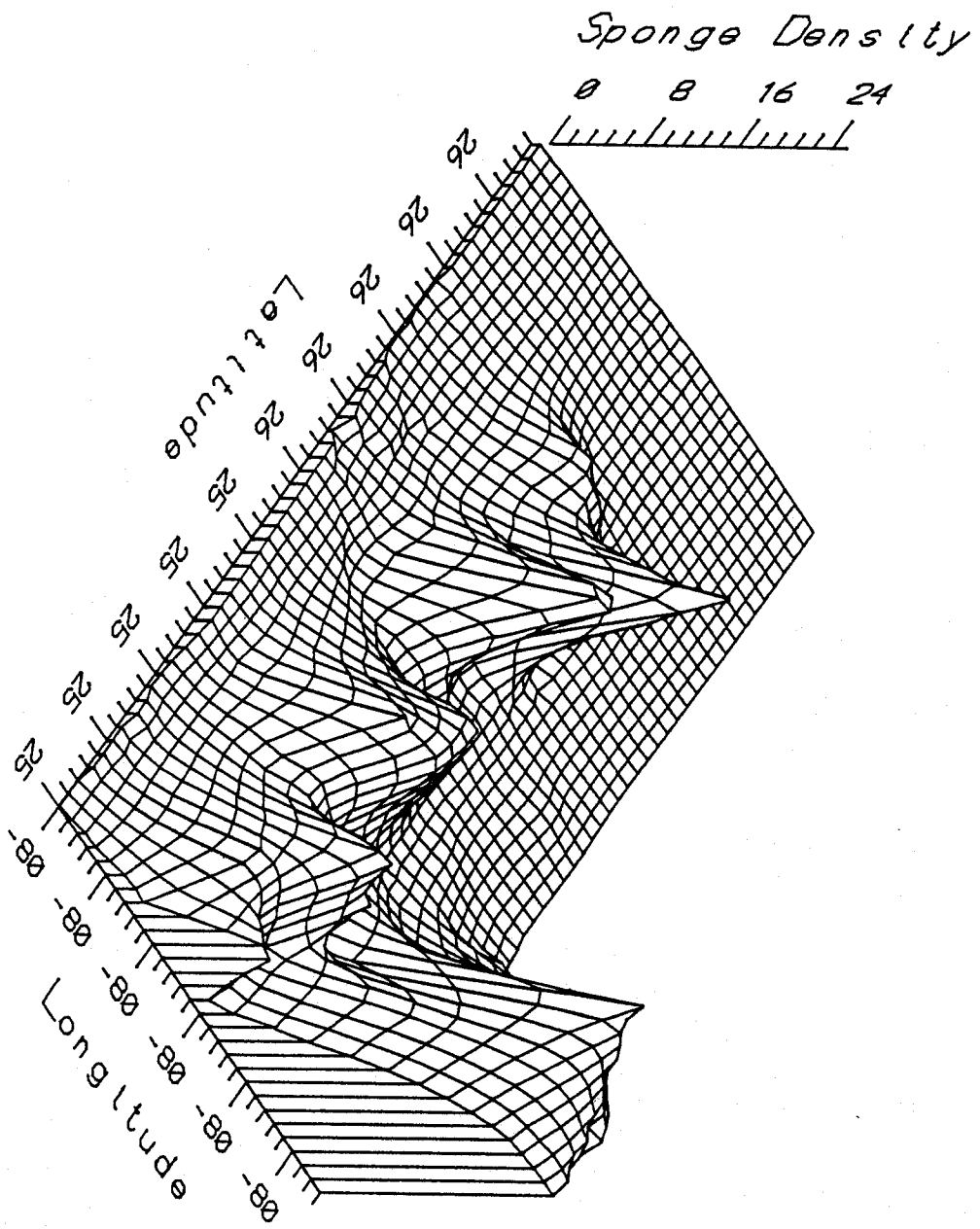
Figure 5. Size-frequency distribution of commercial sponges in Biscayne National Park. The greatest horizontal dimension of each sponge was measured an plotted against the frequency of occurrence for *H. lachne* (a), *S. tubulifera* (b), *S. barbara* (c) and *S. graminea* (d).

INTRODUCTION

The abundance and diversity of life on coral reefs is startling. Attracting our attention with an urbanesque landscape of color, shape, and motion, the coral reef holds it with the complexity of its interactions. Compelled, naturalists and scientists have described the reefs of the world and have used them as natural laboratories for investigating interactions between organisms, and between these organisms and their environment.

One expression of this complexity is the distribution of coral reef organisms in the available space on the reef. Hermatypic corals, primitive animals with microscopic, single-celled algae living within their tissues, are unevenly distributed on coral reefs. One of the earliest explanations for the distribution of corals was the decrease in light with increased depth (Edmondson, 1928, Verwej, 1931). Motoda (1935) and Kawaguti (1941), recognizing the importance of the symbiotic algae to hermatypic corals, concluded that on deeper areas of Palao's reefs changes in light with depth would play a major role in coral distributions.

As part of the Great Barrier Reef Expedition, that explored the world's largest reef system from 1925 to 1929, Marshall and Orr (1931) proposed that the distribution of corals was a result of variations in sedimentation. Manton (1931) and Stephenson *et al.* (1931) found that the seaward slope of reefs had a richer fauna and grew more actively than other areas of the reef. Abe (1937), at the Palao Tropical Biology


Sponge Density
0 8 16 24
Latitude
26 26 26 26 25 25 25 25 25
Longitude
-80 -80 -80 -80 -80 -80

Station, expressed the belief that the coral community on the reef flat was controlled by water movement and secondarily, its effect on sedimentation.

Recent work has more explicitly acknowledged the number of complex factors affecting the distribution of corals with depth. Sheppard (1982) has comprehensively reviewed the efforts of modern science to document the distribution of corals on reef slopes above the depth at which light is limiting and to determine the controls upon that distribution. Storr (1964, Bahamas), Morelock and Koenig (1967, Mexico), Scatterday (1974, Bonaire), Loya (1976, Puerto Rico) and Bak (1977, Curacao) have proposed that corals are distributed within distinct sedimentary environments brought about by different wave-energies and exposure to currents. Turbidity was correlated with reduced coral cover (Roy and Smith, 1971). Geister (1977) generalized changes in the coral community with changing wave-energies. Antonius (1981) suggested that cold,upwelling water limits the depth of corals on reefs off Venezuela.

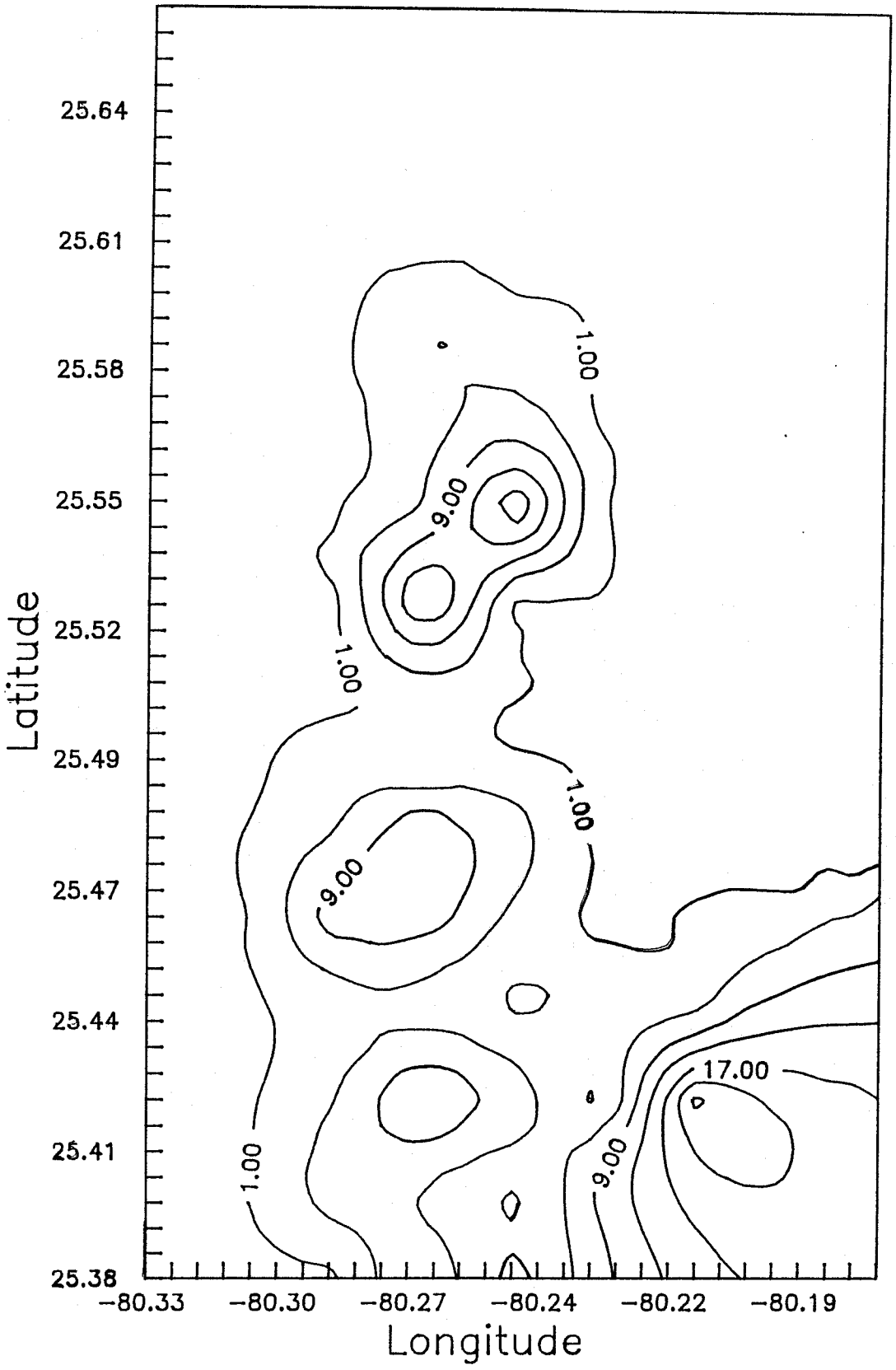
On any reef the coral community at different depths will experience different levels of light, silt, wave-exposure, current-speeds, and temperature. Reefs in different locations will be affected by these variables to different degrees. The Gulf Stream provides the reefs of South Florida with warm oceanic water necessary for hermatypic coral survival. Vaughan (1918), however, suggested that the reefs north of Key Largo, Florida were near the limit of coral tolerance to low temperatures. He presented data that showed little difference in the ten-day means between 1879 and 1899, but extreme low temperatures decreased by three degrees to 15°C at Fowey Rocks (Vaughan, 1918).

Figure 4. Topographic plot of commercial sponge density in Biscayne National Park. Sponge densities are plotted over the coordinates of the study area.

There are differences among the reefs of South Florida. Some of the best developed reefs are in the Key Largo National Marine Sanctuary (Pennekamp) (Ginsburg and Shinn,1964, Marszalek et al., 1977). Shinn (1963,1980) has described the zonation and geologic history of a reef there. Voss (in press) has described the bottom-dwelling communities on these reefs and Jaap (1981) documented the zonation of hard corals on several of its deep reefs. Between Carysfort Reef in Pennekamp and Fowey Rocks are the reefs of Biscayne National Park. These reefs were qualitatively described by Voss et al. (1969) who noted that they were mostly bare coral rock. Tilmant et al. (in prep.) have been studying the patch reefs in the park, many of which have large and numerous hermatypic corals.

The purposes of this investigation were to quantify the hermatypic coral community on four shelf-edge reefs at their northernmost limit and to test the hypotheses that their distribution varies with depth and among reefs. Knowing the distribution we may better understand how the environment effects hermatypic corals.

Sponge Density in Biscayne NP



MATERIALS AND METHODS

Study Area

Originally established as Biscayne National Monument in 1968, Biscayne National Park (BNP) now comprises 104,000 acres (42,120 hectares) of southern Biscayne Bay, mangrove-covered coral islands, and the Florida Reef Tract. The original boundaries included four of the northernmost reefs of the arcuate, discontinuous, bank-barrier reef (Davis, 1928), that extends from the Dry Tortugas 360 km to Fowey Rocks, which lies 6.5 km to the north of Triumph Reef. These four reefs, Pacific, Ajax, Long, and Triumph, were the sites of this study. They lie south to north, respectively, on a line running almost due north between the latitudes 25°22'N and 25°29'N, a distance of 13 km (Fig. 1).

These limestone ridges, the products of past reef-growth, lie on the shallow shelf edge. East of the 18 m depth-contour that marks the boundary of the park, the bottom slopes to the deep shelf edge and then drops off to a depth of about 824 m (2500 ft.). The Florida Current flows within the narrow channel between the Florida peninsula and the Bahamas Bank, the shallow platform from which rise the Bahama Islands. The current creates almost ideal oceanic conditions the whole length of the Florida reef tract.

Field Methods

A preliminary visual survey of the study reefs using SCUBA led to a division of each reef into 3 sampling areas. This was suggested by apparent differences in the community and the topography in 3 ranges of

Figure 3. Contour plot of commercial sponge density in Biscayne National Park. Commercial sponge density contours are plotted over the coordinates of the study area. Highest densities occur in the axis of the hard bottom area (see Fig. 2) and decrease with distance from the center. Sponge density values on the contour lines are the mean of 5 random surveys of 78.5 m^2 plots.

Figure 1

Map of Biscayne National Park and surrounding area showing the location of the four study reefs.

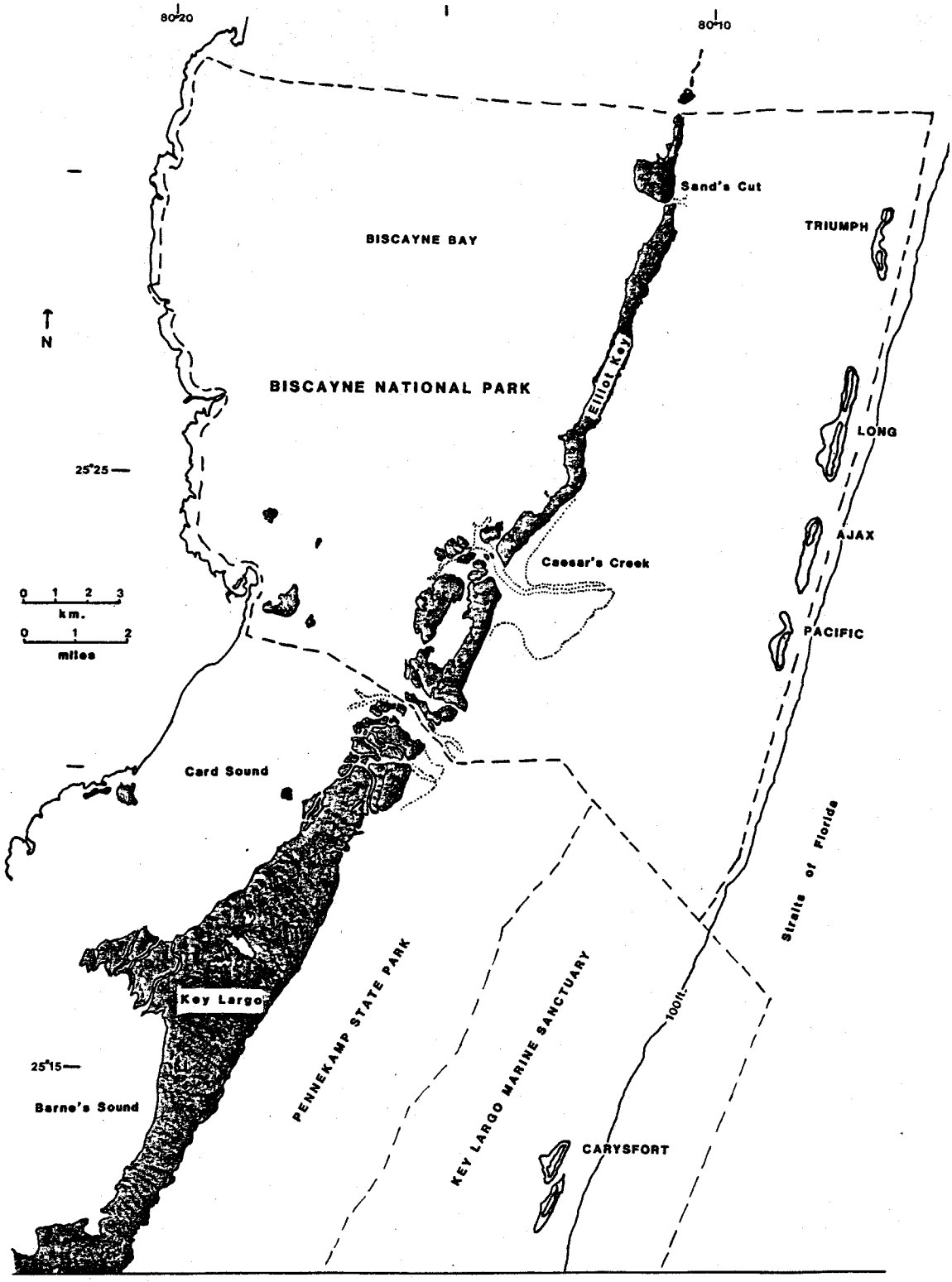

80°20
80°10
Sand's Cut
TRIUMPH
BISCAYNE BAY
N
BISCAYNE NATIONAL PARK
Elliot Key
LONG
25°25
AJAX
Caesar's Creek
0 1 2 3
km.
0 1 2
miles
PACIFIC
Card Sound
Key Largo
PENNEKAMP STATE PARK
KEY LARGO MARINE SANCTUARY
100 ft.
Straits of Florida
25°15
Barne's Sound
CARYSFORT

Figure 2. Commercial sponge distribution in hard bottom and seagrass communities. Commercial sponge sites (+) are located in areas of shallow sediment and sparse vegetation (shaded area). Few commercial sponges are found in the seagrass community which covers most of the bay bottom.

depth: < 6 m, 6-12 m, and 12-18 m (Fig. 2). Randomly placed line-intercept transects within these zones were used to test the null hypotheses that there were no differences between zones. Stratified random sampling reduces the variability of the samples and is preferred to a strictly random or systematic placement of samples where there is marked zonation (Stoddart, 1972, Greig-Smith, 1964).

The line-intercept method (Loya,1978) was chosen because of its use in Caribbean coral-reef studies (Porter, 1972, Loya, 1976,Ott, 1975). In this method one stretches a line between two points and measures the amount of line that overlaps the organisms of interest. Comparisons of this method with other sampling methods have found insignificant differences in the quantitative estimation of measures of abundance (Kinzie and Snider, 1978, Weinberg, 1981, Dodge et al., 1982). Its ease of use allowed a greater area to be sampled. It is desirable to reach a reasonable compromise between the accuracy of a large survey and the precision of a detailed analysis of a smaller, possibly unrepresentative area (Kinzie and Snider,1978).

The most efficient transect length was determined by species/transect length curves (Loya,1978). The plotted data for initial transects showed a leveling off of the number of species encountered by 20 m , and this was chosen as the transect length (Fig. 3). The number of samples needed to approximate the population mean was estimated by plotting sample means against the number of transects. The curves of mean coral cover, number of species, and number of colonies versus the number of transects leveled off by 8 transects (Fig. 4). This was chosen as the number of transects to be used in each depth zone.

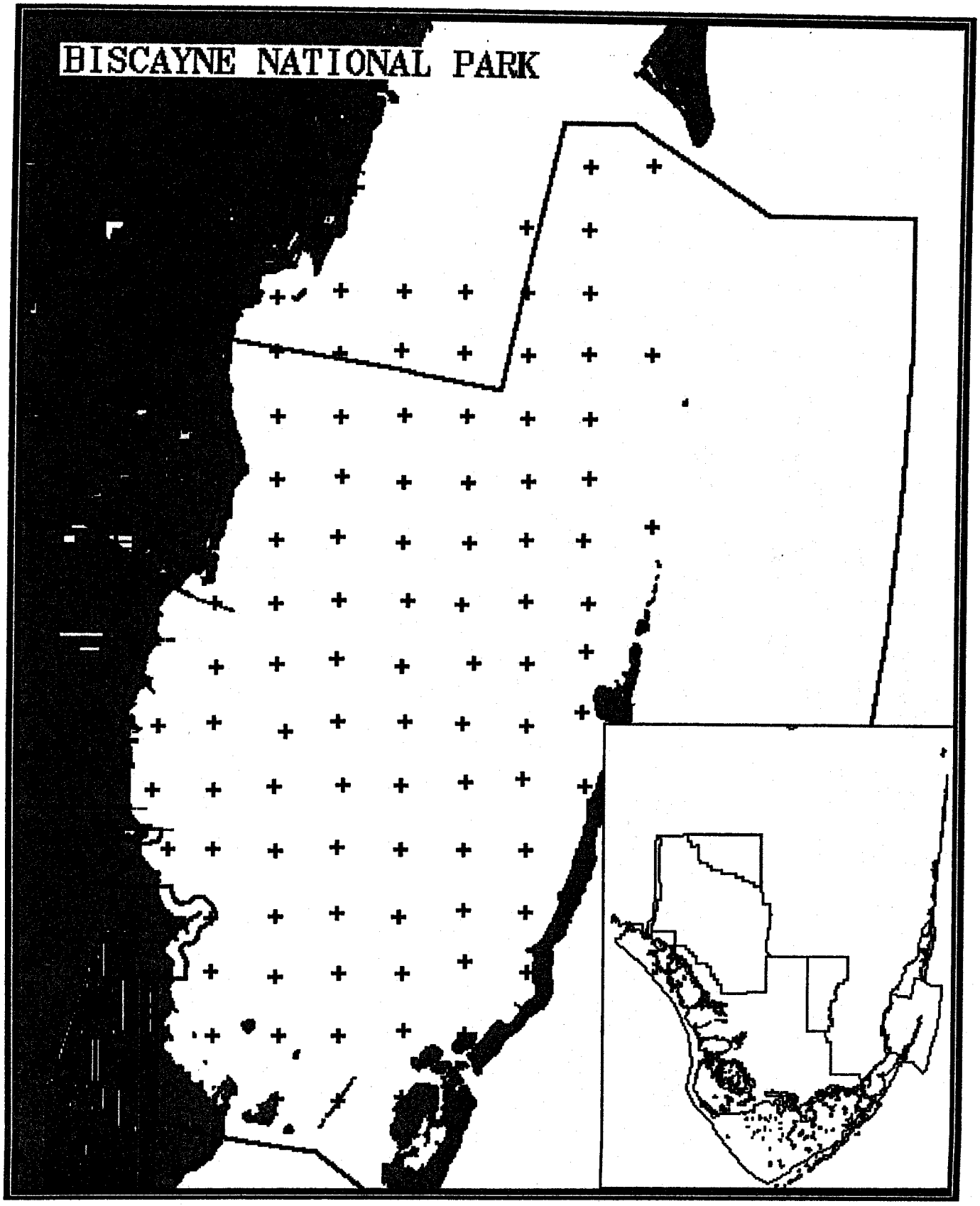
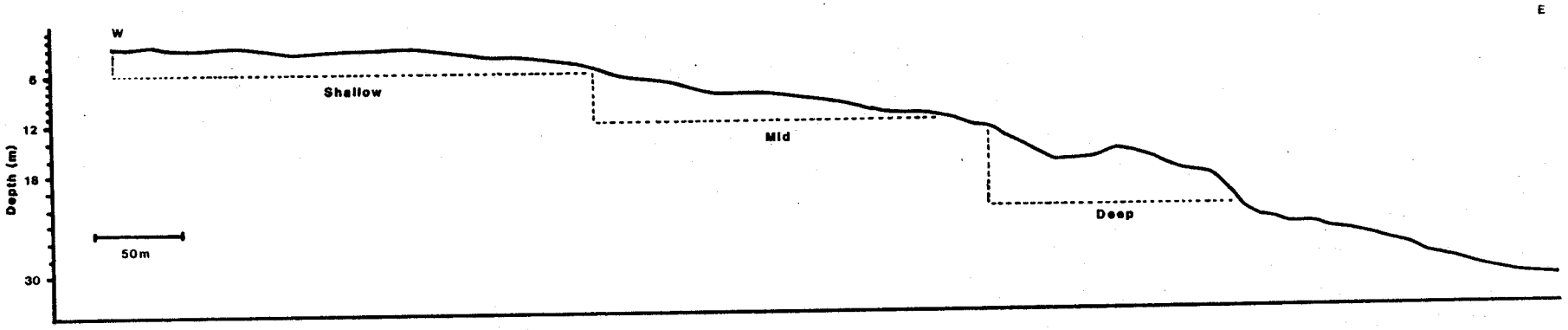

BISCAYNE NATIONAL PARK

Figure 2

Profile of Ajax Reef showing stratification of reef into depth-zones.

Figure 1. Location of survey sites within Biscayne National Park. Survey sites (+) are located at the intersections of a 2 km grid over the southern part Biscayne Bay in Biscayne National Park

AJAX REEF



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Figure 3

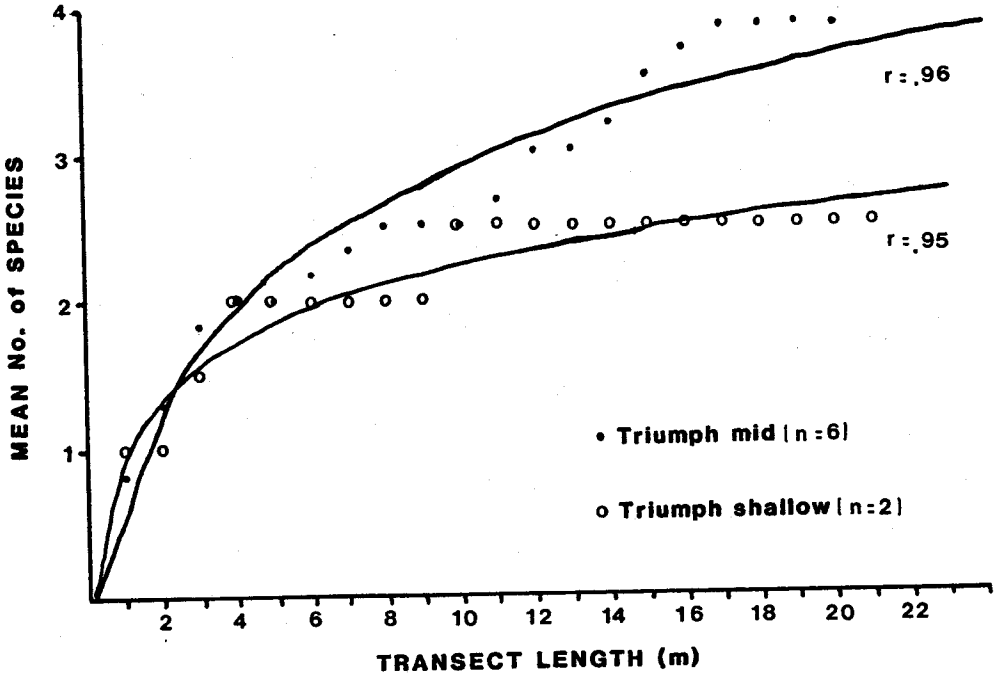
The cummulative mean number of species as a function of transect length.

RECOMMENDATIONS

1. To determine whether further loss of commercial sponge habitat in Biscayne Bay is occurring, BNP should establish monitoring areas in the transition zone along the western edge of the hard bottom areas. Visual surveys and sponge density counts should be accompanied measurements of sediment depth and estimates of vegetative coverage. Monitoring these sites on a bi-annual basis should be adequate for determining whether the affected area is expanding.

2. Further experimental work should be conducted to determine the population dynamics of the commercial sponges in Biscayne Bay. Monitoring sponge growth, recruitment and mortality over several years will provide better estimates of growth rates, reproduction and the potential for population growth.

3. Biscayne National Park should remain closed to all commercial sponge harvesting. BNP Resource Management Division and the Florida Marine Fisheries Commission should reassess the effect of the sponge fishery the sponge populations.and reconsider this decision only after information on the age structure and population dynamics of the commercial sponge species within BNP becomes available.


MEAN No. of SPECIES
TRANSECT LENGTH (m)
r = .96
r = .95
• Triumph mid (n = 6)
o Triumph shallow (n = 2)
1
2
3
4
2
4
6
8
10
12
14
16
18
20
22

CONCLUSIONS

The results of the sampling of commercial sponge populations in Biscayne Bay indicate that distribution and abundance of sponges within the bay is highly variable. Only 40% of the bay bottom is suitable habitat for commercial sponges. We found a highly significant correlation among sponge distribution, sediment depth and vegetatiive coverage. Commercial sponge habitat is characterized by a relatively shallow overburden of coarse sediment with sparce vegetation consisting mostly of calcareous green algae. The abundance of sponges within this area is highest near the center of the bay and is greatly reduced in areas where sediment depth and vegetation limit larval attachment and growth. A transition zone occurs the edge of the hard bottom community along a north-south axis in the center of south Biscayne Bay. There has been a 21% loss in bottom area colonized by commercial sponges since 1978. This may be due to increased development of the areas adjacent to the bay.

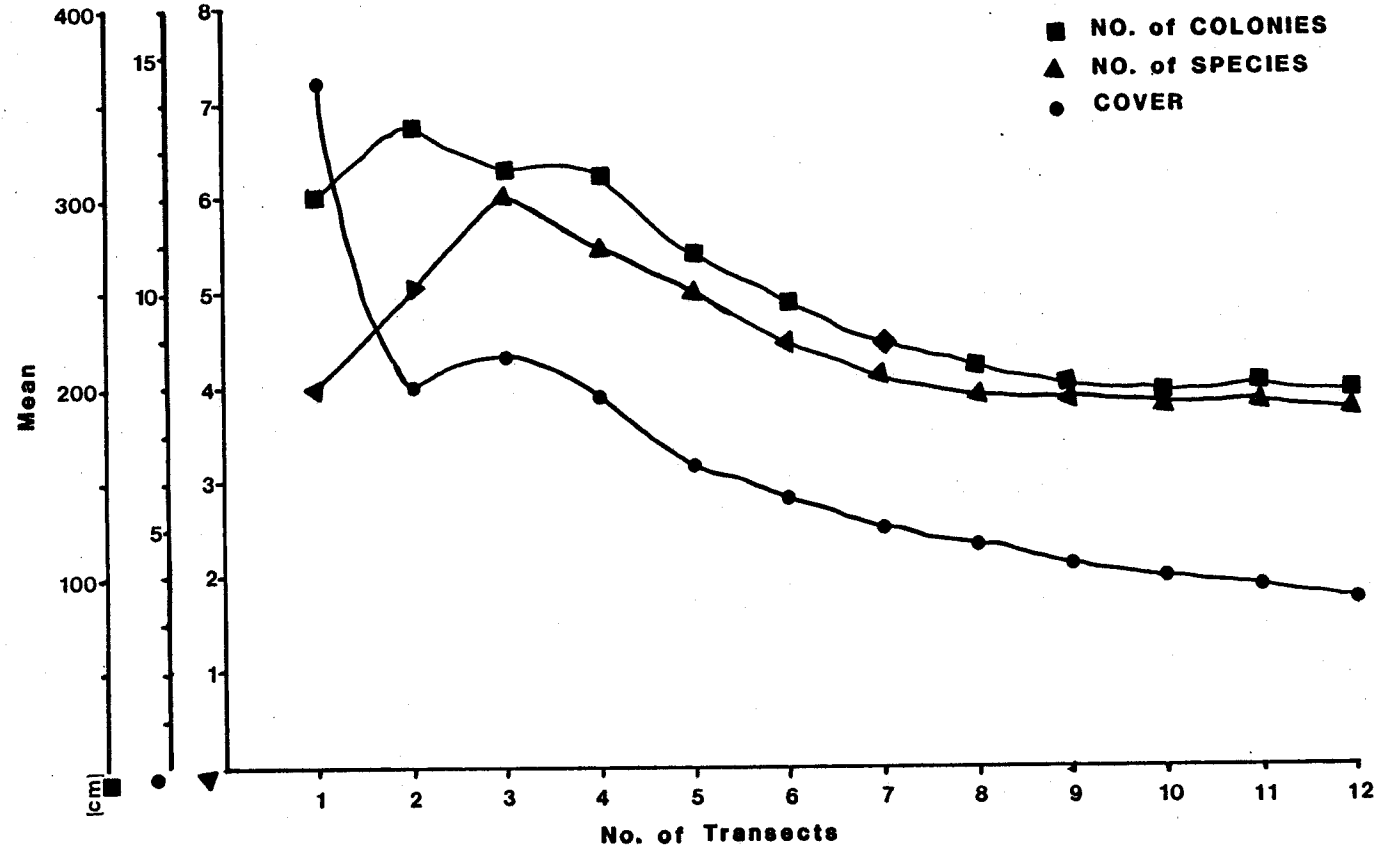
The density of commercial sponges in the bay has not significantly change from that reported in a previous survey in 1978 (Tilmant, 1978). However, it is possible that the sponge density at that time was underestimated, since only the large, conspicuous sponges were included in the census (Tilmant, personal communication). The size structure of the commercial sponge populations indicate that most of the individuals are below reproductive age. The skewed size-frequency distribution toward smaller sizes may be due to natural biological and physical constraints on growth and mortality or may reflect the selective removal of larger individuals from the population by commercial spongers. The loss of reproductively active individuals to commercial harvesting may lead to a decline in the abundance of commercial sponges in the bay.

Figure 4

The mean coral cover, colony abundance, and number of species per transect as a function of the number of transects.

The recruitment rate of a species (the rate at which new individuals settle in a population and survive to reproductive maturity) must exceed the mortality rate in order for the species to be reproductively successful. Larvae must find attachment space in suitable area large enough to allow development of adequate numbers of individuals of large enough size to sustain reproduction in the population at a viable level. It is probable that for sponges, reproductive efficiency depends on long survival of a few individuals following heavy mortality in the early stages. Estimates of growth rates of *H. lachne* in the northern Gulf of Mexico (Storr, 1964) and the Florida Keys (Moore, 1910) indicate that it takes from three to four years for this sponge to reach commercial size (12.7 cm diameter). Sponge growth in the same areas can be extremely variable and is affected by food supply, currents and temperature. Smith (1973) calculated growth factors ranging from 0.24 to 1.31 for *S. tubulifera* in Card Sound, Florida and similar variability has been observed for cuttings of *H. lachne*, which exhibit a range of growth factors from 1.86 in the Florida Keys (Moore, 1910) to 2.94 in Belize (Crawshay, 1939).

The presence of a large percentage of small sponges within the commercial populations of Biscayne Bay may reflect successful reproductive events over the past several years, leading to an abundance of reproductively immature individuals recruited into the populations and contributing to the high densities observed within the bay. This may also result from larger sponges experiencing a higher mortality rate due to natural processes such as predation or physical damage from storms . A more likely explanation for the abundance of small sponges is that larger individuals have been selectively harvested. A decrease in the number of reproductively active individuals may affect reproductive success and lead to a decline in population numbers. In Biscayne Bay, mean size of *H. lachne* and *S. tubulifera* is slightly less than the minimum legal harvest size and the mean size of *S. barbara* and *S. graminea* is less than half the legal minimum size. Without more information on the age structure of sponge populations and on growth, recruitment and mortality rates, it is difficult to predict the affect of an unregulated commercial harvest of Biscayne Bay sponges.


NO. of COLONIES
NO. of SPECIES
COVER
Mean
400
300
200
100
15
10
5
8
7
6
5
4
3
2
1
(cm)
1
2
3
4
5
6
7
8
9
10
11
12
No. of Transects

The commercial sponging areas of Biscayne Bay are highly productive. The mean sponge density of the total study area is over 300 sponges/ha; when calculated only for suitable hard bottom area, the mean density is over 750 sponges/ha. This compares favorably with results of a study conducted over the same area in 1978, before the recent increase in sponge harvesting (Tilmant, 1978). In contrast, commercial sponge density in other sponging areas found in the Florida Keys is approximately 100/ha (Stevely, personal communication) and only slightly higher (125/ha) in the Gulf of Mexico (Storr, 1976).

Although there has been no dramatic change in commercial sponge density in Biscayne Bay since 1978 (see Table 7), there are some notable differences in sponge distribution. Of the 39 hard bottom sites surveyed in both studies, commercial sponges were present at 33 sites in 1978 and only 26 sites presently. Therefore, while the number of commercial sponges in the bay has not been significantly reduced since 1978 by continued commercial harvesting, there has been a net loss of 21% of the sponge habitat.

Commercial sponges reproduce both asexually and sexually and individual sponges produce both eggs and sperm but probably are unable to self-fertilize (Stevely, *et al.*, 1978; Storr, 1964). Sperm are released into the exhalent stream of one individual and taken in by the inhalent stream of another individual. The fertilized eggs undergo early stages of development within the maternal sponge and are then released into the water column as mature, ciliated larvae. The brooded larvae are competent to settle shortly after release, decreasing the time spent in the plankton and possibly contributing to high local recruitment rates. In *H. lachne*, larval production is affected by both sponge density and sponge size (Storr, 1964) with large, sponges (>14 cm diameter) in high density areas producing many more larvae than either small sponges in high density areas or large sponges in low density areas. In areas where sponge density was below 22/ha, Storr (1964) found that only 30% were reproductively active and at low rates. The similarity of reproductive processes in the Demosponges suggests that this pattern may hold true for the other commercial species.

These four reefs vary in length from 1 to 5 km. Therefore, an area on each reef, within which to contain the stations, was chosen. These decisions were made with reference to surface landmarks, such as Pacific Reef Light, and the navigational tower at Triumph Reef. Sites were then limited to one side of this landmark and an approximate distance not more than 1 km from it.

At any randomly chosen site in a depth-zone, the transects were positioned in the following way. A one-hundred meter tape was attached to the anchor and run out on a heading of 180° using a SCUBA diver's wrist compass. Since the reefs lie in a north-south direction all transects were horizontal to the reef, roughly parallel to contours of equal depth. The first 20 m of this baseline was one transect. The positions of subsequent transects were determined by selecting from a random numbers table a number between 20 and 80 (the starting point of the second transect on the baseline) and 2 sets of 5 digits (Fig. 5). The first two digits of each set designated a reference point on the baseline. The third digit, by being odd or even, determined whether the next transect was shallower or deeper than the baseline, and the final two digits gave the distance from the baseline reference-point in number of kicks (Av. Kick,s.d. = .49,.05 m). These transects were also run out 180° from this point off the baseline. No more than five transects were sampled at any site. Consequently, each station or depth-zone was sampled at 2 or 3 sites. Eight transects were used in each of the three depth-zones on each of the four reefs, for a total of 96 twenty meter transects.

The depth of each transect was measured with the same oil-filled, SCUBA-diver depth gauge. Depth profiles of each reef were obtained

DISCUSSION

The distribution of commercial sponges is limited by several environmental factors including water depth, sediment depth, turbidity, circulation, food availability, salinity and temperature (Storr, 1976). Commercial sponges typically occur in assemblages on hard bottoms with other noncommercial sponges and soft corals (de Laubenfels, 1953; Moore, 1910; Storr, 1957, 1964). In Biscayne Bay, sponges are limited to hard bottom areas that experience little sediment deposition and support only sparse growth of seagrasses and algae. The north portion of the bay is covered by extensive turtle grass (*Thalassia testudinum*) meadows over a relatively deep layer of sediment. The grassbeds cover nearly all the bottom (<75% vegetative cover) and exhibit a luxurient growth as indicated by blade height, width and density. Noncommercial sponges commonly found in this area are *Chondrilla nucula, Aplysina fistularis, Spheciospongia vesparia, Ircinia campana* and *Haliclona* spp. Adjacent to the mainland, the bay bottom is covered by a fine, silty sediment and sparse patches of shoal grass (*Halodule beaudettei*) and manatee grass (*Syringodium filiforme*). This shallow area experiences dramatic fluctuations in salinity due to freshwater runoff from the land and discharge from five major drainage canals. The shallow area is also subject to wide diurnal fluctuations in temperature. No commercial sponges, and only a few noncommercial sponges are found at sites near this shore.

Commercial sponge densities increase with distance from the shore and the extensive grass beds typical of the western side of the bay. The highest densities of sponges are found in the center of the hard bottom area (Figs. 3 and 4). Since sponge density is dependent on the availabilty of habitat for settlement of larvae, we estimate that less than 40% (163 km^2) of the bay is suitable for commercial sponges. Considering the low densities of sponges along the edges of the hard bottom, most of the sponge productivity is limited to a relatively small portion of the total area of the bay. The patchiness of sponge distribution is evident in the large variation in sponge densities in areas of suitable habitat.

Figure 5

Schematic representation of the method of locating transects at the sampling sites.

Sponge Abundance and Density

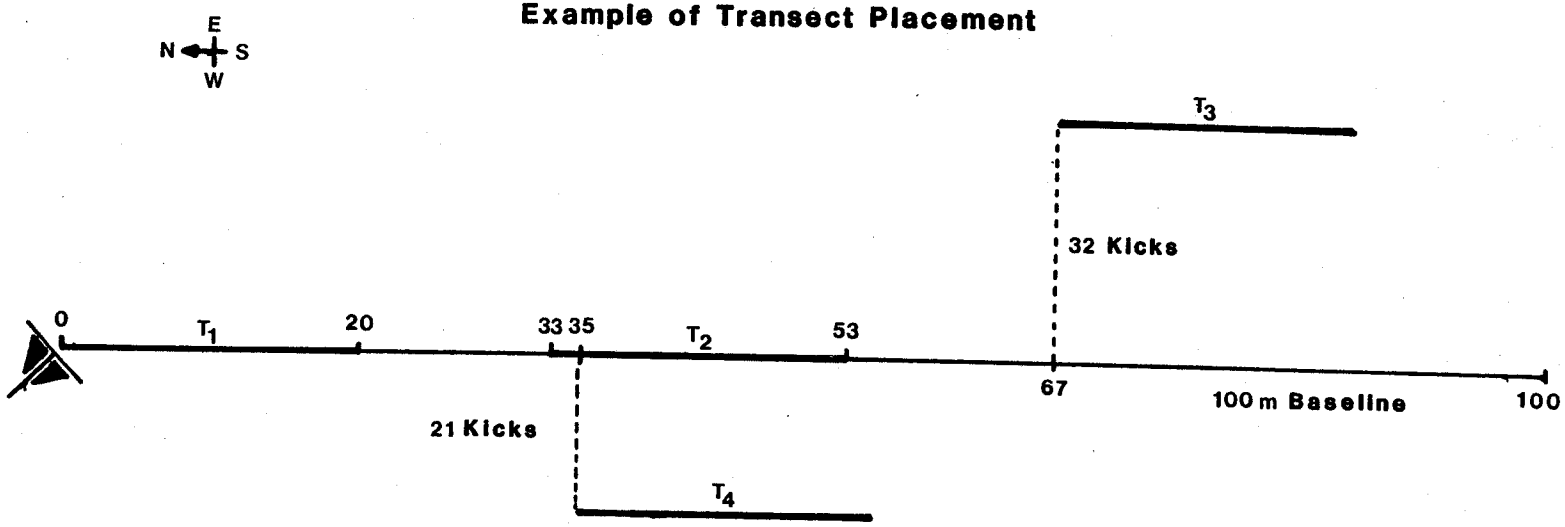
Commercial sponge density in the study area is highly variable, ranging from 0 to 3,285 sponges per hectare. Commercial sponge densities tend to be lowest in areas adjacent to grass beds, increasing with distance from the grass beds (i.e, along the gradient shown in Figure 3). The highest densities are found further away from the grass areas and are clustered in a pattern running from north to south following the central axis of the hard bottom area (Figure 4). The densities of the individual commercial species and the total commercial sponge density are presented in Table 4. The study area covers a total of 39,653 ha. The average density of commercial sponges within this study is 306.5/ha (coefficient of variation (c.v.) = 198.6%) with the individual species contributing the following: *H. lachne*, 58.6/ha; *S. graminea*, 61.2/ha; *S. barbara*, 77.0/ha; and, *S. tubulifera*, 109.7/ha.

Noncommercial sponges are widely distributed within the study area. Noncommercial sponge densities range from 63.7/ha to 44,563.3/ha (Table 5). Some of the variability may be attributed to extremely dense patches of *Chondrilla nucula*, a small, encrusting sponge found growing on grass blades. The mean density of noncommercial sponges in the study area is 6,622.4/ha (c.v. = 117.2%). Abundance patterns for noncommercial sponges are similar to those of commercial sponges, with highest densities found in hard bottom areas.

Commercial Sponge Size-Frequency Distribution

Size-frequency distributions for the four commercial sponge species are shown in Figures 5 - 8. The size measurements for all four species are significantly skewed to the left ($p < 0.001$) indicating that the populations consist mostly of smaller sponges with relatively few large individuals. Means, medians and ranges for each species are presented in Table 6. For both *H. lachne* and *S. tubulifera* , the mean size (11.4 cm and 11.1 cm, respectively) is slightly less than minimum legal harvest size (12.5 cm) and for *S. barbara* (6.2 cm) and *S. graminea* (6.3 cm) the mean is significantly less than legal size ($p < 0.001$). Assuming that sponge sizes are normally distributed in natural populations, the predominance of small sponges may be due to the selective harvesting of large individuals.

Example of Transect Placement



Random Numbers

33

67432

35921

RESULTS

Sponge Distribution

A total of 94 sites were sampled within southern Biscayne Bay. Location (latitude and longitude), bottom type, sediment thickness and water depth are presented in Table 1. Latitude and longitude coordinates correspond to the site locations on Figure 1. Commercial sponges are present at 38 of the 94 sites (40.4%) (Table 2). All four species were present at 16 of the 38 sites (42%), 3 species co-occur at 9 sites (24%), 2 species at 9 sites (24%) and at 4 sites (10%), only 1 one species is present. The grass sponge (*S. tubulifera*) has the widest distribution, occurring at 89% of the commercial sites and the glove sponge (*S. graminea*), which occurs at only 53% of the commercial sites, has the narrowest distribution.

Commercial sponges are limited in their distribution to areas of thin sediment cover and sparse vegetation (Table 3). Sediment thickness is significantly lower ($p < 0.0005$) at sites where commercial sponges are present (91.9 mm ± 107.3 mm, $n = 38$) than at sites where commercial sponges are absent (224.5 mm ± 184.2 mm, $n = 56$). Commercial sponges occurred most frequently at sites with less than 50% vegetative coverage (mean bottom type = 2.1 ± 1.2 at commercial sites *vs* 3.5 ± 1.1 at noncommercial sites, $p < 0.005$). Figure 2 shows the distribution of commercial sponges in Biscayne Bay. Approximately 233 km^2 of the study area are covered by seagrasses and other vegetation and 163 km^2 are hard bottom areas with sparse vegetative covering. Commercial sponge sites (crosses) are limited to hard bottom areas.

Noncommercial sponges occur at 79 of the 94 sites (84.0%) and are present at all of the commercial sites. *Spheciospongia vesparia* (loggerhead sponge) occurs at 37 sites (39.4%). No sponges were observed at 15 of the sites (16%). These sites are located adjacent to the mainland, an area subject to wide fluctuations in temperature and salinity due to the shallow contour of the bottom and influx of fresh water from canals and rainwater runoff.

using a Raytheon Precision Survey Depth Recorder (Model # DE-719B). The horizontal scale of the tracings was determined using a measured distance of 50 m .

Data analysis

Each sample consisted of the species identification and intercept length to the nearest centimeter for all hermatypic scleractinian corals crossed by the transect line. Identifications were made by the investigator. If any colony was of questionable identity, field notes were made and a small part of the colony was collected for later identification. From these data, species lists, the number of species sampled, and the relative abundance of these species were determined for all depth-zones.

The amount of surface area covered by a species is an important variable in benthic communities (Dahl,1973), especially when the organisms are sedentary and use sunlight in the production of food. Remembering that all transects were of equal length, cover is here defined as the sum of the intercept lengths and is used as such to compare depth-zones. Data is presented as percent cover (cover/total transect length). Comparisons of the relative abundance of species within a sample use the percent of total coral cover (cover of species A/cover all species).

Determining densities (#/m^2) from one-dimensional line-transects seems paradoxical, but MacIntyre (1953) and Strong (1966) have devised a method for doing so. The equation used in this study is that presented by Eberhardt (1978):

$$D = 1/nL \sum 1/w$$

separately. If no commercial sponges were found in the first two plots, a large scale visual survey of the area was conducted. If on further inspection, no commercial sponges were found in the area, that grid point was considered completed.

Water depth, sediment thickness and bottom type were recorded at each site. Water depth was measured using a weighted measuring tape lowered from the surface to the bottom. Depth was recorded to the nearest 0.1 m. For sediment thickness, an aluminum probe was pushed into the sediment until the underlying platform rock was reached. Sediment thickness was recorded to the nearest centimeter. Bottom types were categorized based on estimates of the percentage (in 25% units) of bottom area covered by either algae, seagrasses, or both. Bottom type 1 corresponds to a bottom with less than 25% of the area covered by vegetation; bottom type 2 has between 25%-50% coverage; bottom type 3, between 50-75%, and; bottom type 4, between 75%-100%.

Site location and habitat characteristics were analyzed on Grass Geographical Information System at the South Florida Research Center, Everglades National Park, FL. Density contours were plotted using Surfer v. 3.0 (Golden Software). Sponge densities (mean number of individuals of each species per hectare) were computed by averaging the density in each of the five random plots. All ststistical analyses were done using Systat software package (Systat Inc.).

Eberhardt's measure, w, for any intercepted colony, is the distance between the two tangents that are parallel to the transect line (Fig. 6). L is the transect length and n is the number of transects.

Size, in the two dimensions theoretically imposed on most benthic ecology studies, is inseparable from both cover and density. It is an expression of the age and growth rate of an individual and it is natural to think of it as distinct from the other two. In this study the greater of the two measures, intercept length and Eberhardt's measure, was taken as a measure of size.

Loya (1972) suggested that, in studies of diversity, several indices should be employed to take advantage of their sensitivities. Three popular indices were chosen for this study. The number of species, S, is one component of diversity. The widely used statistic, H', was developed in information theory (Shannon and Weaver,1948) and is used to measure the uncertainty of encountering a species due to the distribution of individuals or cover among the different species. With it one can compare the diversity of coral communities. Pielou (1977) has pointed out the assumptions inherent in the use of H', the difficulty of determining the bias of sample-size and the uncertainty of sampling an indefinitely large community. She proposed that if samples are regarded as a census of the complete community the Brouillon index of diversity, H, should be used. An alternative is to employ Simpson's Index of Dominance (Simpson, 1949) modified for diversity. This index is free of the above difficulties and is an index of the second component of diversity, that of the evenness of the distribution of individuals among the species. The modification chosen for this study is that presented by Loya (1972):

METHODS

Biscayne National Park is located southeast of Miami, Florida and includes the southern portion of Biscayne Bay. All work in the field took place between June, 1991 and September, 1991. The study area (Figure 1) was bound by the Arsenicker Keys to the south, Key Biscayne to the north, the shoreline of the mainland to the west and the broken line of the Florida Keys to the east . The sampling scheme was developed by Tilmant (1978) after consultation and approval by the Southeast Regional Office of the National Park Service .

Survey of Sponge Density, Sediment Depth and Bottom Type

The study area is located within southern Biscayne Bay within the boundaries of Biscayne National Park. A Micrologic Loran C was used to locate transect lines and specific study sites. Transect lines were selected to form a 2 km x 2 km grid covering the entire area of southern Biscayne Bay. The specific locations of the survey sites were determined by the intersections of perpendicular transect lines (Figure 1). Transect lines running east and west were labeled A through I starting with the northernmost line. Transect lines running north and south were numbered 1 through 16 starting at the western edge of the grid. Stations were identified by using the letter and the number of the intersecting transect lines. At each survey site, all sponges, commercial and noncommercial, occuring within five randomly selected circular plots (5 m radius, 78.5 m^2 area) were counted. The greatest horizontal dimension of every commercial sponge within each plot was measured with a set of calipers. Two divers using SCUBA recorded the data on underwater slates. Species identifications were made in the field based on the available literature (de Laubenfels, 1953a, 1953b; Van Soest, 1978; Weidenmeyer, 1976) and voucher specimens were collected for verification. Commercial sponges (*H. lachne*, *S. tubulifera*, *S. barbara* and *S. graminea*) were scored in individual species categories and all other sponge species were grouped as noncommercial sponges. Loggerhead sponges (*Sphecispongia vesparia*), the largest of the noncommercial species, were counted

Figure 6

Two examples of line-intercepts showing intercept length and Eberhardt's measure for each.

The project reported here was conducted by the Resource Management Section of Biscayne National Park. The primary objective of this project was to repeat an earlier National Park Service survey of commercial sponges in Biscayne Bay (Tilmant, 1978) to examine how the commercial sponge population and he distribution of sponges within the Park have changed. To accomplish this objective, the present survey of commercial sponges was designed to provide the following information:

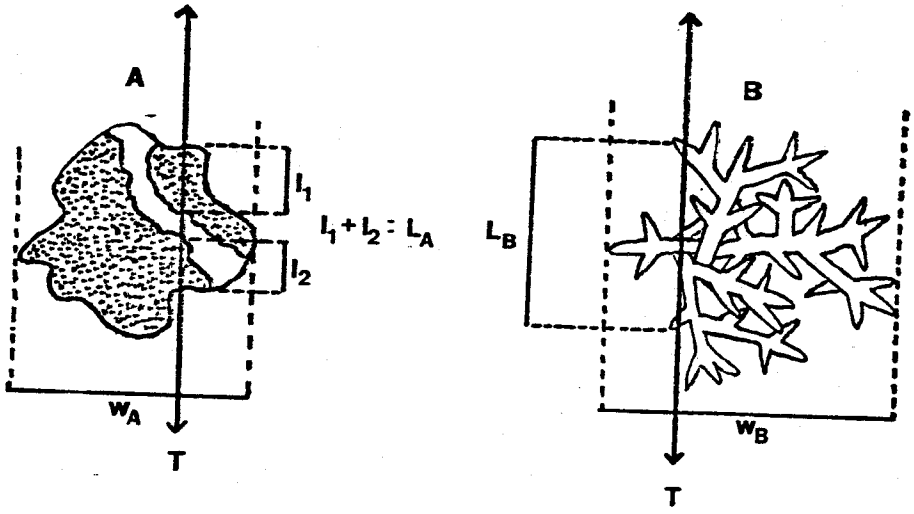
(a) an estimate of the abundance of commercial sponges within the boundaries of Biscayne National Park;

(b) an assessment of the correlation between habitat charactertistics and the occurrence of commercial sponges;

(c) a map of the distribution of suitable sponge habitat in the Park, and;

(d) an estimate of the size-frequency distribution of the individual commercial sponge species.

Comparing the results of this study with those of Tilmant (1978) provides an indication of changes in commercial sponge populations since 1978. Information on the abundance, habitat utilization and size-frequency distribution of commercial sponges in Biscayne Bay is essential for management of the sponge fishery and the ecological health of the bay.



L : Intercept length

W : Width measure for density (Eberhardt, 1978)

T : Transect Line

INTRODUCTION

The dramatic increase in sponge harvesting within the boundaries of Biscayne National Park between 1989 to 1991 led the National Park Service to request the Florida Marine Fisheries Commission to close the Park to commercial harvesting of sponges. The Florida Marine Fisheries Commission responded by closing the fishery on December 1, 1991. Except for one study conducted by the National Park Service over a decade ago (Tilmant, 1978) and one around the turn of the century (Smith, 1896), there is essentially no information available concerning either the commercial sponge population in Biscayne Bay or the effect of harvesting on this population.

Sponges are a major component of the benthic macrofauna of hard bottom communities in Biscayne Bay. They are most common in areas of substantial water circulation and low sedimentation, where they occur in characteristic assemblages with other benthic organisms. The abundance and diversity of sponges in these communities contribute to the overall biodiversity and water quality of this ecosystem. All of the sponges commercially harvested form Biscayne Bay are in the order Demospongia. The most common, although of least commercial value, is the grass sponge, *Spongia tubulifera.* The least common, yet most valued is the sheepswool sponge, *Hippospongia lachne.* Only two other sponges are of any commercial interest, the yellow sponge, *Spongia barbara* , and the glove sponge, *Spongia graminea.* Where present, these sponges are very conspicuous and account for most of the sponge biomass. The loggerhead sponge (*Spheciospongia vesperia*) and the stinker sponges (*Ircinia* spp.) are also very common and represent a significant component of the sponge biomass in this area. Because of their abundance and biological function, sponges are important to the ecology of the bay, and an understanding of population dynamics of the commercial sponges is important for effective management of the Biscayne Bay ecosystem.

$$D_N = 1 - \sum_1^s P^2_i \; : \; P = N_i/N$$

where s is the number of species and N is the number of colonies.

The statistical significance of differences in numbers of species, cover, number of colonies, size, and density among the stations were tested using the Kruskal-Wallis Analysis of Variance by Ranks Test (Nie, et al., 1975) on transect totals. This test is appropriate for the data (Sokal and Rohlf, 1981). The data does not have to fit a normal or bell-shaped distribution, nor must variances be equal. Siegel (1956) stated that the Kruskal-Wallis test is as powerful as the parametric equivalent in such situations. In all cases the null hypothesis was that there were no differences between zones. The probability values presented in the results are the probabilities of incorrectly rejecting the null hypothesis. Probabilities less than or equal to 0.05 were considered significant. A non-parametric multiple comparison test (Zar, 1974) was used to make a posteriori comparisons between depth-zones and reefs.

A Bray-Curtis similiarity index (Bray and Curtis, 1957) was determined for all pairs of zones using both cover and number of colonies. This index indicates the relative similiarity of two zones' community structure, i.e. the distribution of individuals or occupied space among the species. The twelve sample-areas were classified by successively clustering groups with the greatest similarity using the furthest-neighbor strategy. In this method the similarity index for a newly formed group and all others was taken to be the smaller of the two choices (Clifford and Stephenson, 1975). The similarity of the species composition of all pairs of stations were compared with the Jaccard coefficeint (Clifford and Stephenson, 1975).

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RESULTS

Triumph Reef

The twenty-four transects at Triumph Reef provided measures of 17 species of hermatypic corals. Eight species were recorded in the shallow station and eleven in each of the two deeper areas (Table 1). Four species were common to each of the three depth-zones.

Total coral cover in these zones increased slightly with depth from 1.3 to 2.1 percent of the sampled area. Only a few more coral colonies were encountered on transects in the 6 - 12 m station, but the density of coral colonies did vary ($P = .03$). Colonies were increasingly less crowded in the deeper reaches of this reef. Overall, relative coral abundance on Triumph Reef was very low (Table 2).

Differences in the abundance of individual species were observed between Triumph Reef's depth-zones. The mustard hill coral Porites astreoides showed significant differences among the three zones ($P < .05$). Cover ($P = .03$), number of colonies ($P = .01$), and density ($P = .003$) were significantly higher in the shallow zone than in the other two (Fig. 7). The cover and number of colonies were the largest of the shallow fore-reef station (Fig. 8), but this species only covered 0.6 percent of the sampled substrate. Although the clubbed finger coral Porites porites and the starlet coral Siderastrea siderea were relatively important with 8 colonies and 71 cm cover, respectively, differences between depth-zones were insignificant.

The elliptical star coral Dichocoenia stokesii and the lettuce coral Agaricia agaricites possessed a greater number of colonies and

A STUDY OF POPULATION DENSITY, HABITAT CHARACTERISTICS AND SIZE-FREQUENCY DISTRIBUTION OF COMMERCIAL SPONGES IN BISCAYNE NATIONAL PARK, FLORIDA

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Table 1. Species Totals: Triumph Reef

Depth-zone	Shallow			Mid			Deep		
Species	L	N	T	L	N	T	L	N	T
Acropora cervicornis						μ	5	1	1
Agaricia agaricites	8	3	3	56	12	6			μ
Colpophyllia natans							26	1	1
Dichocoenia stokesii			μ	74	14	7	46	8	4
Diploria clivosa	2	1	1						
Diploria labrynthiformis				10	1	1	12	1	1
Favia fragum	2	1	1						
Madracis decactis						μ	14	3	2
Meandrina meandrites	13	1	1	34	3	3	23	3	2
Montastrea cavernosa			μ	13	3	3	76	7	3
Porites astreoides	92	24	7	5	2	1	23	3	3
Porites branneri				3	1	1			μ
Porites porites	20	8	5	18	3	3	16	1	1
Siderastrea radians	3	2	1						
Siderastrea siderea	71	2	2	31	7	4	31	8	6
Stephanocoenia michelinii			μ	3	1	1	62	6	4
Solenastrea bournoni				15	1	1			μ
Zone Total =	211	42		262	48		334	42	

L = Sum of intercept lengths (cm)
N = Number of colonies intercepted
T = Number of transects on which species occurred
μ Species observed but not intercepted

Table 2. Total Coral Abundance and Size - Mean/(s.d.)

Reef: zone	S^1	Cover (cm)	N^2	D^3 (m^{-2})	Size (cm)
Triumph: shallow	2.6 (0.9)	26.4 (33.0)	5.3 (3.8)	9.8 (5.3) *	5.2 (4.6) **
: mid	3.9 (2.5)	32.8 (21.0)	6.0 (3.4)	6.4 (4.3)	7.9 (0.8)
: deep	3.6 (1.5)	41.8 (20.0)	5.3 (2.2)	4.6 (1.8)	11.4 (2.6)
Long: shallow	3.9 (2.2)	114.6 (121.9)	8.8 (4.7)	8.6 (5.7)	20.0 (16.1)
: mid	5.4 (1.7)	61.9 (34.1)	8.6 (3.3)	9.7 (4.4)	8.9 (2.7)
: deep	5.4 (2.4)	72.1 (54.0)	8.8 (4.1)	10.1 (5.1)	11.4 (6.6)
Ajax: shallow	5.0 (1.4)	84.8 (55.0) **	10.0 (4.6)	13.7 (9.5)	11.5 (5.6) *
: mid	4.9 (1.1)	43.6 (13.9)	8.3 (2.4)	12.2 (7.8)	8.0 (3.2)
: deep	6.4 (1.6)	157.9 (101.9)	13.6 (5.1)	7.9 (1.9)	15.6 (6.6)
Pacific: shallow	4.6 (1.5)	42.3 (30.2) **	9.3 (2.4)	17.6 (7.3) *	5.5 (3.5) **
: mid	5.9 (1.1)	64.5 (32.8)	12.0 (5.2)	16.7 (6.4)	7.7 (2.0)
: deep	5.8 (1.7)	112.5 (41.3)	12.5 (2.9)	10.1 (2.8)	14.5 (4.2)

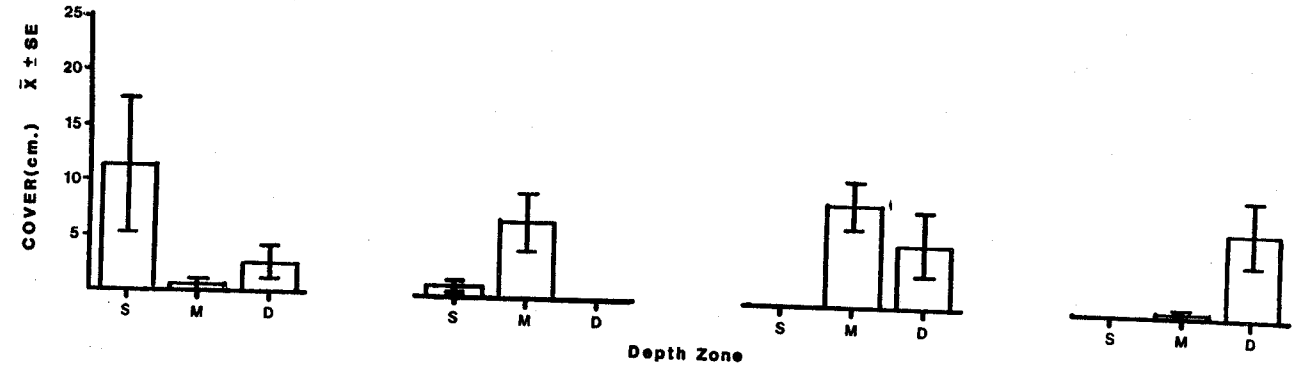
* Depth-zones significantly different by ranks ($P \leq .05$)
** $P \leq .01$
1. Number of species per transect
2. Number of colonies per transect
3. Density (Eberhardt, 1978)

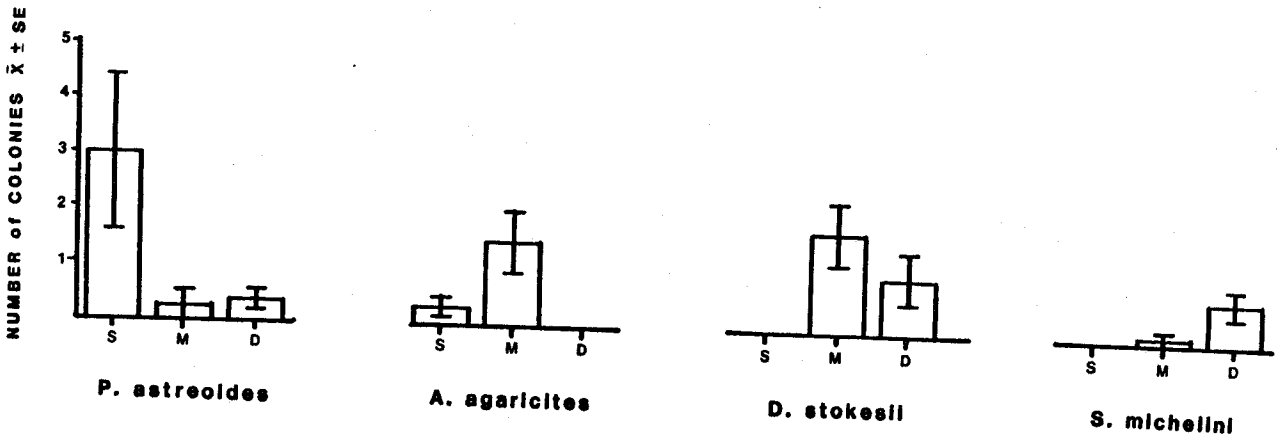
Figure 7

Mean coral cover and number of colonies per transect (n = 8) for selected species at Triumph Reef that showed significant differences among depth-zones by ranks.

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Original in
Museum Archives
BISC-118

TRIUMPH REEF





conducting nocturnal maneuvers over the Tortugas, spending their days at sea. Presumably, mating occurs during this time, for when they land on Bush Key in March, egg-laying begins immediately. Their nests are no more than depressions in the warm sand. The parents take turns shading their single egg from the sun. When the young are strong enough for continuous flight, the colony disperses. Unless hurricanes carry them farther north, most adult sooties spend the winter in the Gulf and northwest Caribbean. Juvenile sooties, however, leave their parents and follow an indirect, 14,500-km (9,000 mi) route to East Africa and do not return to the Tortugas until at least their fourth summer.

The presence of these tropical oceanic birds at Tortugas was recorded by Ponce de Leon in 1513, Captain John Hawkins in 1565, John James Audubon in 1832, and Louis Agassiz in 1858. Prior to the early 1900s, commercial egg raiding reduced the colony to a mere 4,000 individual birds. In 1903 and years immediately thereafter, a resident warden effectively protected the birds during the nesting season, and today the rookery contains an estimated 100,000 breeding adults. A colony of brown noddies, interspersed among the sooties, is composed of only about 2,500 birds, but the population is slowly increasing. The two species share the ability to capture fish and squid from the surface of the water while in flight, rather than diving into it as do most terns.

Large numbers of frigate birds also congregate at the Dry Tortugas in summer. With a wingspan of over 2 m (7 ft), the frigate bird is among the most graceful of soaring birds. Although it may occasionally indulge in aerial piracy, it usually captures its own fish from the water. A few blue-faced and brown boobies are observed occasionally. Roseate terns nest on Hospital, Bush, and Long Keys at the same time other terns are nesting. In season, a continuous procession of songbirds and other migrants fly over or rest at the islands, which lie across one of the principal flyways from the United States to Cuba and South America. Familiar gulls and terns of the north, as well as many migratory shore birds, spend the winter at the Tortugas.

Figure 8

Relative abundance of all species for the three depth-zones on Triumph Reef

Historical Aspects of the Dry Tortugas

Fort Jefferson, largest of the 19th-century American coastal forts, is the central feature of the seven Dry Tortugas islands and the surrounding shoals and waters of the Gulf of Mexico that compose Fort Jefferson National Monument. Although off the beaten track, the monument is famous for its bird and marine life, as well as for its legends of pirates and sunken gold.

Like a strand of beads hanging from the tip of Florida, reef islands trail westward into the Gulf of Mexico. Almost 120 km (75 mi) west of Key West is a cluster of coral keys called the Dry Tortugas. In 1513, Spanish explorer Ponce de Leon named them *las Tortugas*, the Turtles, because of "the great amount of turtles which there do breed." The later name, Dry Tortugas, warns the mariner that there is no fresh water there.

The treasure-laden ships of Spain, braving shipwreck and corsairs, sailed past the Tortugas. Not until Florida became part of the United States in 1821 were the pirates finally driven out. Then, as additional insurance to a growing United States commerce in the Gulf, a lighthouse was built at Tortugas, on Garden Key, in 1825. Thirty-one years later, the present 45-m-high (150 ft) light was erected on Loggerhead Key.

The strategic importance of the Tortugas was recognized early. In the words of the naval captain who surveyed the Keys in 1830, Tortugas could "control navigation of the Gulf." Commerce from the growing Mississippi Valley sailed the Gulf to reach the Atlantic. Enemy seizure of the Tortugas would cut off this vital traffic, and a fleet operating from this strategic base could be effective against even a superior force.

There were still keen memories of Jackson's fight with the British at New Orleans, and England was developing her West Indies possessions. Trouble in Cuba was near. Texas, a new republic, seemed about to form an alliance with France or England, thus providing the Europeans with a foothold on the Gulf coast. To guard against this possibility, Fort Jefferson was built on Garden Key.

During the first half of the 1800s, the United States began a chain of seacoast defenses from Maine to Texas. Fort Jefferson, 0.8 km (0.5 mi) in perimeter, was the largest link in the chain. From foundation to crown, its 2.5-m-thick (8 ft) walls stand 15 m (50 ft) high. Its three-gun tiers were designed for 450 guns, and it was large enough to garrison 1,500 men. Planned and supervised by the U. S. Army Corps of Engineers, the fort was started in 1846 and, although work continued for almost 30 years, it was never finished. Artisans imported from the north and slaves from Key West composed most of the labor force. After 1861, the slaves were partly replaced by military prisoners, but slave labor did not end completely until slaves were freed by Lincoln in 1863.

Federal troops occupied the half-completed, unarmed fort on January 19, 1861, to keep it from falling into the hands of Florida secessionists, but aside from a few warning shots at Confederate privateers, there was no action. The average garrison numbered 500 men, and building quarters for them accounted for most of the wartime construction.

Little important work was done after 1866, for the new rifled cannon had already made the fort obsolete. Furthermore, the engineers found that the foundations rested not upon a solid coral reef, but upon sand and coral boulders washed up by the sea. The huge structure settled, and the walls began to crack.

For almost 10 years after the war, Fort Jefferson remained a prison. Among the prisoners sent there in 1865 were several of the "Lincoln Conspirators," Michael O'Loughlin, Samuel Arnold, Edward Spangler, and Dr. Samuel A. Mudd. Dr. Mudd, knowing nothing of President Lincoln's assassination, had set the broken leg of the fugitive assassin, John Wilkes Booth. The physician was convicted of conspiracy and sentenced to life imprisonment at hard labor.

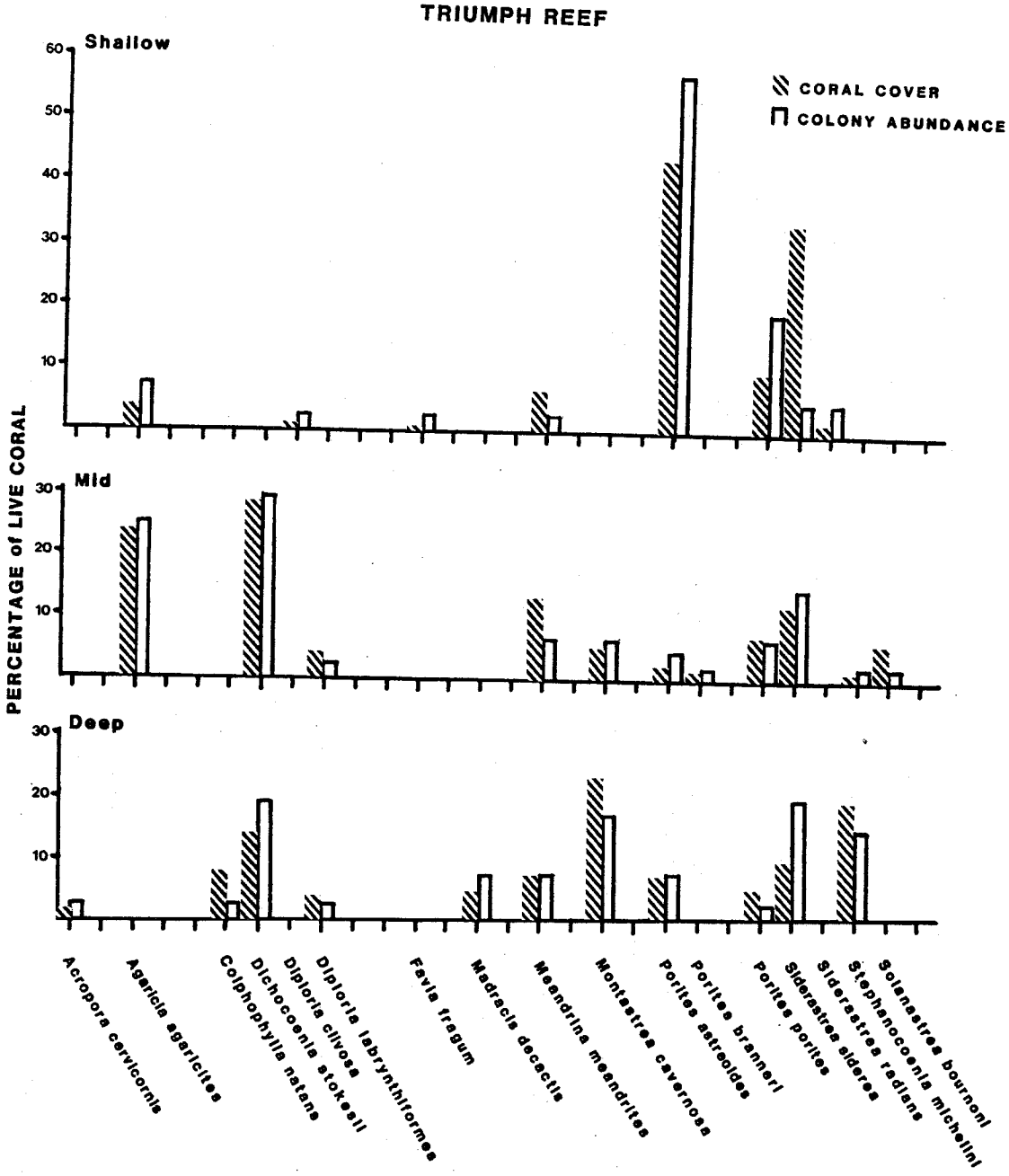
Normally, the Tortugas was a healthful post, but in 1867 yellow fever came. From August 18 to November 14, the epidemic raged, striking 270 of the 300 men at the fort. Among the first of the 38 fatalities was the post surgeon, Major Joseph Sim Smith. Dr. Mudd, together with Dr. Daniel Whitehurst from Key West, worked day and night to fight the scourge. Two years later, Dr. Mudd was pardoned.

Because of hurricane damage and another fever outbreak, Fort Jefferson was abandoned in 1874. During the 1880s, however, the United States began a naval building program, and Navy men looked at this outpost as a possible naval base. From Tortugas Harbor, the battleship ***Maine*** weighed anchor for Cuba, where she was blown up in Havana Harbor on February 15, 1898. Soon the Navy began a coaling station outside the fort walls, bringing the total cost of the fortification to some $3.5 million. The big sheds were hardly completed before a hurricane smashed the loading rigs.

One of the first naval wireless stations was built at the fort early in the 1900s and, during World War I, Tortugas was equipped to serve as a seaplane base. As the military moved out again, however, fire, storms, and salvagers took their toll, leaving the "Gibralter of the Gulf" a vast ruin.

Tortugas Birds

One of our great national wildlife spectacles occurs each year between April and September, when the sooty terns gather on Bush Key for their nesting season. The terns come by the thousands from the Caribbean Sea and west-central Atlantic Ocean. As early as mid-January. sooties begin


TRIUMPH REEF
Shallow
Mid
Deep
CORAL COVER
COLONY ABUNDANCE
PERCENTAGE of LIVE CORAL
60
50
40
30
20
10
Acropora cervicornis
Agaricia agaricites
Colphophyllia natans
Dichocoenia stokesii
Diploria clivosa
Diploria labyrinthiformes
Favia fragum
Madracis decactis
Meandrina meandrites
Montastrea cavernosa
Porites astreoides
Porites branneri
Porites porites
Siderastrea siderea
Siderastrea radians
Stephanocoenia michelini
Solenastrea bournoni

100
76
24
16
8

APPENDIX C
The Dry Tortugas

colony density in the mid fore-reef station than in the others ($P < .01$). A. agaricites also had a greater percent cover in this mid-zone ($P < .01$) (Fig. 7). These species were more abundant than the other species in the 6 - 12 m station. Their low percent cover, .5 and .35, provided 50 percent of the coral cover measured in this zone (Fig. 8)

Dichocoenia stokesii was also one of the more abundant species in the 12 - 18 m station on Triumph Reef (Fig. 8). The percent cover of D. stokesii in the two deep stations was significantly greater than the shallow fore-reef ($P = .006$). Montastrea cavernosa, the cavernous star coral, possessed the greatest cover in this deep station (Fig. 8), but differences between zones were not detected. Its percent cover (0.5%) was similar to abundant species in other zones, but fewer colonies were encountered on fewer transects (Table 1). Siderastrea siderea had a larger number of colonies, but was equally abundant in all three depth-zones. Only the blushing star coral Stephanocoenia michelinii showed significant differences between zones in cover ($P = .007$) and number of colonies ($P = .01$) (Fig. 7).

By comparing the three histograms of Figure 8, one can observe the differences between zones. Observable differences in the community structure are enumerated in the low values for the Bray-Curtis (B-C) Similarity index for both the distribution of cover and colonies (Tables 3,4) and the Jaccard index (Table 5). The greatest value at Triumph Reef was the B-C value from the Mid vs. Deep comparison of number of colonies (0.58).

The highest diversity was also found in the deep stations (Table 6). The number of species (S) and the Shannon-Wiener divesity

SPECIES LIST FOR FLORIDA KEYS AND DRY TORTUGAS

Species	Dry Tortugas	Long Key Reef	Key Largo	Carysfort Reef
Acropora palmata	*	-	*	*
Acropora cervicornis	*	*	*	*
Mycetophyllia lamarackan	*	*	*	*
Mycetophyllia ferox	*	*	*	*
Mycetophyllia danana	*	*	*	*
Mycetophyllia aliciae	*	*	*	*
Solenastrea hyades	*	*	*	*1
Agaricia agaricites	*	*	*	*
Agaricia lamarcki	*	*	*	*
Agaricia fragilis	*	*	*	*
Helioseris cucullata	*	*	*	*
Colpophyllia natans	*	*	*	*
Colpophyllia breviserialis	*	*	*	*
Scolymia cubensis	*	*	*	*
Scolymia lacera	*	*	*	*
Mussa angulosa	*	*	*	*
Montastraea annularis	*	*	*	*
Montastraea cavernosa	*	*	*	*
Dendrogyra cylindrus	-	-	*	-
Manicina areolata	*	*	*	*
Favia fragum	*	*	*	*
Favia conferta	*	-	-	-
Siderastrea radians	*	*	*	*
Siderastrea siderea	*	*	*	*
Dichocoenia stokesii	*	*	*	*
Dichocoenia stellaris	*	*	*	*
Stephanocoenia michelini	*	*	*	*
Diploria strigosa	*	-	*	-
Diploria clivosa	-	-	*	*
Diploria labyrinthiformis	*	-	*	*
Isophyllia sinuosa	*	*	*	*
Isophyllastraea rigida	*	*	*	-
Porites porites	*	*	*	*
Porites astreoides	*	*	*	*
Porites furcata	-	-	*	*
Madracis spp.	*	*	*	*
Madracis decactis	*	*	*	*
Millepora alcicornis	*	*	*	*
Millepora complanata	*	-	*	*
Eusmilia fastigiata	*	*	*	*
Oculina diffusa	*	*	*	-
Cladocora spp.	*	-	-	-
Meandrina meandrites	*	*	*	*

* = present

- = absent

1: outer terrace only

From Dustan, 1985

Table 3. Bray-Curtis Similarity of Reef-zones for Cover

Reef:zone	Percent Similarity										
Tri.:shallow	-										
Tri.:deep	.30	-									
Ajax:deep	.14	.31	-								
Pac.:deep	.21	.34	.65	-							
Long:deep	.28	.40	.48	.62	-						
Pac.:mid	.32	.35	.33	.41	.53	-					
Ajax:mid	.41	.44	.25	.34	.51	.64	-				
Long:mid	.36	.41	.50	.37	.52	.53	.76	-			
Pac.:shallow	.44	.40	.28	.26	.38	.44	.47	.67	-		
Tri.:mid	.32	.49	.19	.36	.43	.48	.54	.59	.56	-	
Ajax:shallow	.17	.29	.15	.16	.34	.40	.32	.49	.45	.45	-
Long:shallow	.22	.11	.08	.07	.15	.06	.09	.19	.23	.09	.52

Reef:zone	T:s	T:d	A:d	P:d	L:d	P:m	A:m	L:m	P:s	T:m	A:s	L:s

sediment producer.

29. *Colpophyllia natans* (Houttuyn). Valleys green, walls brown; large, light, convex mass; valleys more or less interconnected and winding, shallower than in *C. amaranthus* (Houttuyn); wall grooved. Depths: maximum 55 m, optimum 2-20 m. Geologic role: frame builder and sediment producer.

30. *Colpophyllia amaranthus* (Houttuyn). Valleys green, walls brown; small, light, slightly convex mass with short stock at base; valleys short, straight, not interconnected, grooved above with thin boundary ridges. Depths: maximum 15 m. Geologic role: frame builder and sediment producer.

31. *Montastraea cavernosa* (Linnaeus). Brown, olive, green-purplish, or blue; boulders 150 cm across; calices average 8 mm in diameter, usually projected above surface; septa prolonged into space between calices. Depths: maximum 95 m, optimum 10-60 m. Geologic role: frame builder and sediment producer.

32. *Isophyllastrea rigida* (Dana). Pink or purple with white oral discs; small boulders; calices polygonal and irregular in shape, 10 mm across; septa with 6 to 8 large teeth on edge extend over walls; wall 3 mm thick; 25 to 30 septa in single corallite, 5-8 meeting the columella. Depths: maximum 20 m, optimum 3 m. Geologic role: frame filler and sediment producer.

33. *Porites astreoides* Lamarck. Yellowish-brown; rounded, irregular masses, up to 50 cm in diameter; calices 1.25 to 1.5 mm in diameter; 12 septa; porous, small rough teeth. Depths: maximum 70 m, optimum 5-20 m. Geologic role: frame builder and sediment producer.

34. *Siderastrea siderea* (Ellis and Solander). Light reddish-brown; hemispherical mass up to 50 to 75 cm in diameter; 4 to 5 calices sometimes 6 mm in diameter, wall raised; 50 to 60 septa, five cycles, last incomplete. Depths: maximum 70 m, optimum 3-20 m. Geologic role: frame builder and sediment producer.

35. *Siderastrea radians* (Pallas). Grayish to brown; corals rounded, 30 cm or more in diameter, young colonies often encrusting; calices small (3 mm in diameter), angular, cavity of cup deep and narrow; 36 to 40 septa, four unequal cycles; distinguishable from *S. siderea* by smaller, deeper, and narrower cup. Depths: near surface to 33 m, optimum 2 m. Geologic role: frame filler and sediment producer.

36. *Stephanocoenia michelini* (Edwards and Haime). Polyps brown; forms rounded boulders under 30 cm in diameter; calices 213 mm in diameter, close together but not always touching; distinguished from *S. radians* by presence of lobes or pali at inner edges of septa; three cycles of septa, primaries and secondaries with well-developed pali, tertiaries thin and shorter, margin entirely or finely dentate. Depths: maximum 95 m plus, optimum 3-50 m. Geologic role: frame-builder, frame filler, and sediment producer.

37. *Montastraea annularis* (Ellis and Solander). Yellow-brown; large boulders 150 cm, often encrusting or irregular in shape; calices circular, 2.0 to 2.5 mm wide, average 1 mm apart; rims of calices slightly projecting; septa prolonged across space between cups. Depths: maximum 80 m, optimum 3-45 m. Geologic role: principal reef builder in Caribbean, also sediment producer.

38. *Solenastrea hyades* (Dana). Yellow-brown; lobed masses or irregular encrustations; calices 3 mm in diameter, rims slightly raised above surface; calices almost touching or 3 mm apart; septa do not extend across spaces between calices; 12 to 24 septa, 12 extend to columella; small paliform lobes. Depths: maximum 23 m, optimum 5-10 m. Geologic role: frame filler and sediment producer.

39. *Solenastrea bournoni* Edwards and Haime. Light brown; domes or rounded masses, 30 cm in diameter, often with irregular bumps or projections on surface; calices smaller than in *S. hyades* (2 mm in diameter), separated by 1 mm; low ridges extend from septa part way across space between calices that are somewhat blistered. Depths: more common below 10 m; below 20 m species more or less replaces *Montastraea annularis*. Geologic role: frame filler and sediment producer.

40. *Dichocoenia stokesii* Edwards and Haime. Yellow or brown with yellow polyps; heavy round colonies up to 30 cm in diameter; short valleys, separate from each other, walls projecting from general surface; septa thick, without teeth. Depths: maximum 40 m plus, optimum 3-20 m. Geologic role: frame builder, frame filler, and sediment producer.

41. *Favia fragum* (Esper). Light yellow to brown; forms small crusts on rocks; calices angular, circular, under 6.5 mm across; septa with irregular teeth on margins; 36 to 40 septa, three to four nearly complete cycles. Depths: maximum 30 m, optimum 2-8 m. Geologic role: frame filler and sediment producer.

Table 4. Bray-Curtis Similarity for Number of Colonies

Reef:zone	Percent Similarity										
Tri.:shallow	-										
Long:shallow	.52	-									
Ajax:shallow	.25	.43	-								
Tri.:deep	.17	.23	.43	-							
Tri.:mid	.24	.22	.62	.58	-						
Pac.:shallow	.29	.28	.62	.41	.66	-					
Long:mid	.32	.26	.62	.50	.60	.73	-				
Ajax:mid	.31	.21	.48	.57	.54	.60	.78	-			
Pac.:mid	.23	.12	.57	.32	.49	.58	.67	.64	-		
Long:deep	.20	.23	.53	.55	.54	.50	.70	.72	.63	-	
Pac.:deep	.20	.19	.29	.48	.36	.29	.45	.48	.43	.58	-
Ajax:deep	.12	.17	.33	.46	.36	.35	.47	.42	.47	.54	.66

Reef:zone	T:s	L:s	A:s	T:d	T:m	P:s	L:m	A:m	P:m	L:d	P:d	A:d

16. *Mussa angulosa* (Pallas). Pink, purple, or brown, living colony completely covered by flesh of polyps; heavy, short branches ending in cups up to 12 cm long and 4.5 cm wide; walls 6 to 8 mm thick; septa with strong teeth point obliquely upward. Depths: maximum 59 m, common between 10 and 25 m. Geologic role: frame filler and sand producer.

17. *Agaricia fragilis* Dana. Light brown; coral usually cup-shaped or saucer-shaped fronds, thin, delicate, up to 15 cm across; cups on upper surface only, 2 mm across; ridges between cups long and low. Depths: maximum 80 m, optimum 7-30 m. Geologic role: frame filler and sediment producer.

18. *Agaricia agaricites* (Linnaeus). Chocolate to purple-brown; short, white tentacles; coral usually foliaceous or frondous, massive or encrusting; fronds usually bifacial, irregular, 5 to 20 mm thick; calices arranged in groups more or less parallel, small and shallow, 2 to 3 mm; septa low, up to 36 in number, finely serrulate; var. *crassa* Verril - massive, slightly lobed form; var. *purpurea* Lesson - cups restricted to one face. Depths: maximum 60 m, optimum 10-40 m. Geologic role: frame filler and sediment producer.

19. *Mycetophyllia lamarckiana* (Edwards and Haime) Chocolate color but often with bright green, blue, or purplish in older colonies; flat growths either stalked or completely encrusting; valleys interconnected, walls tend to disappear on older corals; septa 8-10/cm, 4-5 extending farther into valleys, toothed. Depths: maximum 75 m, optimum 5-40 m. Geologic role: frame filler and sediment producer.

20. *Isophyllia sinuosa* (Ellis and Solander). Color varigated with patches of lavender, bright green, and white; medium size, massive with short stalk; valleys continuous, lobes radiating from center, average width 22 m widening toward rim to 35 mm, depth 8 to 10 mm, older colonies lose radial arrangement and valleys become discontinuous; 7-9 septa/cm, 6-10 slender coarse teeth, sides spinulose. Depths: maximum 10 m, optimum 2 m. Geologic role: frame filler and sediment producer.

21. *Isophyllia multiflora* Verril. Greener in color than *I. sinuosa*; smaller colonies, more singular cups, fewer and narrower valleys, walls thinner, and septa more crowded, thinner, and less protruding than in *I. sinuosa*. Depths: below 3 m. Geologic role: frame filler and sediment producer.

22. *Manicina areolata* (Linnaeus). Yellow to brown with greenish valley, tentacles transparent with white tentacles: oval shape with flat upper surface, narrow ends, short basal stock; 15 cm in length; valley branches out into side arms, up to 2.5 cm wide; septa thinner than in *M. mayori*. Depths: maximum 43 m, optimum 2-25 m. Geologic role: sediment producer.

23. *Manicina mayori* Wells. Yellow to brown with greenish valleys; larger and not narrow at ends as in *M. areolata*; no central stalk; valley not completely interconnected, long and winding; wall thinner, septa thicker, about 12/cm without holes or pores as in *M. areolata*. Depths: maximum 65 m, optimum 7-28 m. Geologic role: sediment producer.

24. *Dendrogyra cylindrus* Ehrenberg. Brownish-yellow, extended tentacles give colony a hairy appearance; heavy pillars up to 60 cm wide at base; winding, narrow valleys, not all interconnected; thick septa without teeth; narrow walls between valleys; sometimes reduced columella and septa meet across valley. Depths: maximum 20 m, optimum 3-8 m. Geologic role: frame builder and sediment producer.

25. *Meandrina meandrites* (Linnaeus). Yellow or brown, white tentacles; large boulders, flat or rounded, 30 cm plus in diameter; valleys long and twisting but not all interconnected, 10 mm wide, 8 mm deep; septa of adjacent valleys usually meet in sharp zigzag line on top of separating wall; 7 septa/cm, over 1 mm thick, no teeth on margins. Depths: maximum 70 m, optimum 8-30 m. Geologic role: frame builder, frame filler, and sediment producer.

26. *Diploria labyrinthiformis* (Linnaeus). Orange-yellow to brownish-yellow; large rounded boulders; valleys twisting, narrower and deeper than in *D. strigosa*, nearly all connected; walls thick with distinct groove; septa thicker, not as close as in *D. strigosa*. Depths: maximum 43 m, optimum 2-15 m. Geologic role: frame builder and sediment producer.

27. *Diploria clivosa* (Ellis and Solander). Greenish-brown in grooves, chocolate over walls, tentacles bright green with white tips; large, low growth with irregular knobs over surface; valleys not all connected together, shallow and narrow, very winding except near edge; walls never grooved; septa thin and close together. Depths: common to 25 m, optimum 1-3 m. Geologic role: frame builder, frame filler, and sediment producer.

28. *Diploria strigosa* (Dana). Dull yellow to greenish-brown; dome-shaped masses; valleys twisting, not all interconnecting, wider and deeper than in *D. clivosa*; walls between valleys wider than in *D. clivosa* but rarely grooved; if grooved, grooves small and narrow; septa continue over walls. Depths: maximum 40 m, optimum 3-10 m. Geologic role: frame builder and

Table 5. Jaccard Coefficeint of Similiarity

Reef-zone	Percent Similarity									
Tri.:shallow	-									
Pac.:mid	.46	-								
Ajax:shallow	.38	.50	-							
Long:shallow	.31	.25	.58	-						
Pac.:shallow	.31	.41	.53	.57	-					
Ajax:deep	.26	.42	.37	.32	.61	-				
Long:deep	.28	.53	.47	.33	.47	.55	-			
Pac.:deep	.24	.45	.33	.23	.41	.55	.65	-		
Ajax:mid	.29	.47	.33	.28	.50	.58	.61	.68	-	
Long:mid	.35	.44	.47	.41	.56	.55	.67	.65	.61	-
Tri.:mid	.36	.47	.50	.33	.33	.42	.63	.53	.47	.53
Tri.:deep	.27	.38	.50	.33	.41	.50	.53	.53	.47	.53

Reef:zone	T:s	P:m	A:s	L:s	P:s	A:d	L:d	P:d	A:m	L:m	T:m	T:d

Brief Descriptions of the Stony Corals of the Florida Keys and the Dry Tortugas

1. ***Millepora alcicornis*** **Linnaeus.** Light orange-yellow to dark brown with whitish rims; encrusting, branching, and flattened forms, lattermost frond-like, often referred to as *M. complanata*; entire surface covered with minute holes, arranged in patterns of five smaller ones around a central larger one; not a true coral but a hydroid. Depths: maximum 50 m, optimum 1-10 m. Geologic role: frame filler and sediment producer.

2. ***Scolymia lacera*** **(Pallas).** Dull brown, red, or green with dark patches or concentric rings; large, circular solitary cups up to 6 cm in diameter, single center to the valley; not branched; radiating septa have large teeth and extend beyond wall of cup or corallite. Depths: maximum 59 m, optimum 10-38 m. Geologic role: frame filler and sand producer.

3. ***Phyllangia americana*** **Edwards and Haime.** Encrusting, moderately large cups (10 mm in diameter), nearly circular and deep; septa usually prolonged beyond wall of cup. Depths: maximum 17 m, optimum 3 m. Geologic role: sediment producer.

4. ***Astrangia solitaria*** **(leSueur).** Cups single, growing attached to base of larger corals or rock, thin encrustations often connect several bases of cups; cups tabular, 6 mm tall, 4 mm in diameter; septa with toothed edges; septa prolonged as low ridge down side of cup. Depths: maximum 43 m, optimum 1.5-5.0 m. Geologic role: sediment producer.

5. ***Acropora palmata*** **(Lamarck).** Ramose or branching; brownish-yellow; branches broadly flattened, resembling moose antlers; corallites project from surface; calices cover entire surface. Depths: maximum 17 m, optimum 1-5 m. Geologic role: frame builder and sediment producer.

6. ***Acropora cervicornis*** **(Lamarck).** Ramose; brownish-yellow; branches cylindrical or nearly so; corallites protuberant, tubular, or paliform; calices along entire branch surface. Depths: maximum 50 m, optimum 15-30 m. Geologic role: frame filler and sediment producer.

7. ***Porites divaricata*** **leSueur.** Branches smaller than in *P. furcata*, under 6 mm in diameter, no tapering or dilation along length of branches; calices very shallow, 2 mm in diameter. Depths: maximum 47 m, optimum 1 m. Geologic role: frame filler and sediment producer.

8. ***Porites furcata*** **Lamarck.** Branching colonies, average 10 mm in diameter without swollen ends of *P. porites*; calices 1.5 mm in diameter: five pali usually present. Depths: maximum 50 m, optimum 1-20 m. Geologic role: frame builder, filler, and sediment producer.

9. ***Porites porites*** **(Pallas).** Yellowish-brown; branched with ends swollen and blunt (clubbed); calices shallow, deeper on ends of branches, 2 mm in diameter; columella and six pali usually present. Depths: maximum 25 m, optimum 2-3 m. Geologic role: frame builder, filler, and sediment producer.

10. ***Madracis decactis*** **(Lyman).** Polyps yellow to purple-brown with white tips; form thin, small (under 15 cm) encrustations, sometimes sparse branches or lobes; angular or circular cups; beaded boundaries 2 mm in diameter; septa usually 10, sometimes 8, smooth; columella styliform, well developed; peritheca extensive, nonporous. Depths: maximum 70 m, optimum 5-40 m; usually below 20 m, most common below 30 m. Geologic role: frame filler and sediment producer.

11. ***Madracis mirabilis*** **(Duchassaing and Michelotti).** Ten septa; intercalicular surface spinose to smooth; corallum ramose; branches thick (6-10 mm), blunt, long, slender; differs from *M. decactis* in having prickles or ridges between calices instead of rows of beads. Depths: maximum 60 m, optimum 3-40 m. Geologic role: frame filler and sediment producer.

12. ***Oculina varicosa*** **leSueur.** Colony up to 60 cm high; branches fewer and longer than in *O. diffusa* and wider calices swollen at base. Depths: not well known. Geologic role: probably frame filler and sediment producer.

13. ***Oculina diffusa*** **(Lamarck).** Colonies bushy and profusely branched, forming dense rounded clumps; calices with low walls projecting only slightly above surface of branch, never on prominent conical verrucae; branches less than 10 mm thick; 24 septa; columella well developed. Depths: maximum 15 m. Geologic role: frame filler and sediment producer.

14. ***Cladocora arbuscula*** **leSueur.** Small, densely branching colonies; branch terminates as a calice; calices 3.5 mm in diameter; branches with fine longitudinal ridges continuous with septa. Depths: maximum 15 m, optimum 2-4 m. Geologic role: frame filler and sediment producer.

15. ***Eusmilia fastigiata*** **(Pallas).** Deep brown with greenish cup ringed with whitish tentacles; branched with cups at ends of branches, oval, valleys up to 35 mm long, 8 to 13 mm wide with sharp rim; no teeth on septa; 15-18 septa/cm, 7-9 principals. Depths: maximum 65 m, optimum 3-30 m. Geologic role: frame filler and sediment producer.

Figure 5. Size distribution of all coral species assessed in campuses. Giant colonies of *Montastraea* that form clusters are not included as they were assessed separately. Note that there is a change in the scale of colony diameters above 100 cm.

Figure 6. Results of the campus census. Black bars show mean percentages of colony surface that are less than 1/3 dead; arrows show standard deviation. The numbers of colonies are indicated for each entry. Note that there is both regional and local variation in the data..

Figure 7. Tree diagrams of cluster analyses of 10 localities including the condition of 9 coral species and of all corals with less than 1/3 dead colony surface. Localities situated in the same areas do not group together, showing that there is no spatial pattern decipherable in the condition of corals in the campuses.

Figure 8. Histogram showing the condition of clusters of large *Montastraea* spp.

Figure 9. Results of observations on clusters. Black bars show mean percentages; arrows show standard deviations. (a) Percent dead colony surface. Note the local and regional variability of the data. (b) Percentage of rubble within clusters. Higher amounts of rubble off Elliot Key because of the effects of Hurricane Andrew and tropical storm Gordon.

Figure. 10. Graph showing the distance from shore of 65 *Montastraea* clusters plotted against percentage of dead surfaces.

nia michelinia (Edwards and Haime) (36)
Center of calices with group of small papillae at point where septa converge.....38

38. Thin, sharp costae corresponding with septa extend out of calices onto peritheca; columella distinct.....*Montastraea annularis* (Ellis and Solander) (37)
Costae absent or reduced; broad ridge on peritheca around calices; columella inconspicuous.....39

39. Third-cycle septa bend toward and join those of second cycle before reaching columella; 24 septa; paliform lobes indistinct.....*Solenastrea hyades* (Dana) (38)
Third-cycle septa short and free along inner edges, not joining septa of second cycle; 24 septa; 12 distinct paliform lobes.....*Solenastrea bournoni* Edwards and Haime (39)

40. Edges of septa finely granulated, wavy in projecting upper part, sides with fine sharp beads arranged in radiating rows; calices ovate to very elongate (up to 28 mm long but only 3 to 5 mm wide).....*Dichocoenia stokesii* Edwards and Haime (40)
Edges of septa distinctly toothed, sides spinulose; calices round, ovate, or bluntly polygonal.....*Favia fragum* (Esper) (41)

Figure captions

Figure 1. Study area off the coast of South Florida. The study area is divided into four zones based on variation in major natural impacts. Upper and lower Keys reefs are protected from unfavorable waters from Florida Bay and the Gulf of Mexico by a nearly continuous backstop of islands. Reefs of the middle Keys are not protected from these waters. Upper Keys are subdivided into two zones, the northern of which was passed by Hurricane Andrew (1992) and tropical storm Gordon (1994). Reefs, which were given names for this study, are indicated with asterisks.

Figure 2. Major reef-building elements, reef types, and reef type distribution in south Florida. Bank-barrier reefs can be divided into well-zoned *A. palmata* reefs and low relief hard-bottoms with scattered coral. Patch reefs consist predominately of massive corals either as cluster reefs of giant colonies of *Montastraea* spp. or as composite reefs composed of a campus of massive corals 0.2 to 0.5 m in diameter with localized clusters of giant *Montastraea* spp. The names of representative reefs for each reef type are given at bottom of each box and those that were examined in this study are listed in Table 1.

Figure 3. Patch reef belt off Elliot and Old Rhodes Keys traced from aerial photographs, scale 1: 48,000, National Geodetic Survey, NOAA. All the small black spots and dots indicate the locations of patch reefs, a total of some 3000. Triumph, Long, Ajax, and Pacific are bank-margin shoals composed predominantly of rubble and skeletal sands and or limestone pavements, with scattered corals (Burns, 1985). The only well-developed bank-barrier reef is Ball Buoy. Reefs, which were given names for this study, are indicated with asterisks.

Figure 4. Map of Bache Shoal (Fig 1) showing the distributions of campus, clusters, and other bottoms types. The distributions were based on transects within each of the areas identified on aerial photographs. Coral rubble in campus areas accumulated during Hurricane Andrew (pers. observations of the senior author).

21. Septa distinctly toothed or serrated throughout.....22
Uppermost edge of septa minutely dentate, septa smooth near columella.....26

22. Teeth coarse and irregular, large ones spinelike.....23
Teeth fine and regular.....27

23. Floor of valleys with several parallel septal plates connecting calicinal centers, weak columella.....*Mycetophyllia lamarckiana* (Edwards and Haime) (19)
Floor of valleys without parallel lamellae connecting centers.....24

24. Columella well developed, colony 30 cm in diameter, valleys 20 to 25 mm in width, septa 7 to 9/cm.....*Isophyllia sinuosa* (Ellis and Solander) (20)
Columella weak, colony 10 to 13 cm in diameter, valleys 12 to 25 mm wide.....
.....*Isophyllia multiflora* Verril (21)

25. Edges of septa distinctly serrated, columella of flattened, twisted trabeculae.....
.....*Manicina areolata* (Linnaeus) (22)
Edges of septa smooth, near columella, finely denticulated on upper surface, lamellar columella.....
.....*Manicina mayori* Wells (23)

26. Valleys without a lamellar columella, colonies large, ascending pillars.....
.....*Dendrogyra cylindrus* Ehrenberg (24)
Valleys with lamellar columella at bottom.....
....*Meandrina meandrites* (Linnaeus) (25)

27. Valleys with spongy or trabecular columella, continuous along bottom.....28
Bottom of valleys without spongy or trabecular columella, double wall conspicuous along top of collines.....30

28. Valleys separated by collines furrowed on top, forming ambulacra that may be deeper than valley.....
.*Diploria labyrinthiformis* (Linnaeus) (26)
Valleys separated by collines ridged or rounded on top, sometimes with narrow, shallow, but never wide, ambulacra.....29

29. Valleys are wider than 6 mm, usually 3.5 to 4.0 mm; narrow, sharply ridged collines.....
..*Diploria clivosa* (Ellis and Solander) (27)
Valleys between 6 and 9 mm in width, septa 15 to 20/cm, very few do not meet the columella.....*Diploria strigosa* (Dana) (28)

30. Colonies massive, hemispherical boulders; valleys sinuous, usually continuous, 10 to 12 mm wide, 8 to 9 septa/cm.....
.....*Colpophyllia natans* (Houttuyn) (29)
Colonies smaller, turbinate, with central attachment; valleys discontinous, 15 to 20 mm wide, 10 to 12 septa/cm.....
.*Colpophyllia amaranthus* (Houttuyn) (30)

31. Calices large, 5 mm in diameter or more.....32
Calices small, 5 mm in diameter or less.....33

32. Calices 5 to 8 mm in diameter, monocentric; septa with fine teeth; columella large and distinct.....
....*Montastraea cavernosa* (Linnaeus) (31)
Calices 10 mm in diameter or larger, septa with coarse teeth.....
.....*Isophyllastrea rigida* (Dana) (32)

33. Skeleton very porous, calices in close contact, with common porous walls.....34
Skeleton dense, calices distinctly separated by solid skeletal material.....36

34. Calices 2.5 to 5.0 mm in diameter, distinctly polygonal, 36 or more septa of laminar nature but perforated; beaded or dentate margin.....35
Calices less than 2 mm in diameter, indistinctly polygonal, 12 septa consisting of 1 to 4 united spirelike projections.....
.....*Porites astreoides* Lamarck (33)

35. Septa numerous (up to 64), gently sloping into calicular pit; calices 4 to 5 mm in diameter.....*Siderastrea siderea* (Ellis and Solander) (34)
Septa up to 40, steeply sloping into calicular pit, which is deep and narrow; calices 2 to 4 mm wide.....
.....Siderastrea *radians* (Pallas) (35)

36. Not more than 24 septa in fully developed calices.....37
Largest calices have more than 24 septa
.....40

37. Center of calices with solid, conical, or columnar columella standing up at point where septa converge.....*Stephanocoe-*

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Key to the Stony Corals of the Florida Keys and Dry Tortugas

1. Skeleton surface characterized by radiating patterns of septa or sinuous grooves and ridges.....2
   Skeleton surface smooth, characterized by barely visible pores .... *Millepora alcicornis* Linnaeus (1)

2. Coral consists of a single cup or calice.....3
   Coral forms colonies with many cups, may be branched, massive, or encrusting.....5

3. Cup with diameter up to 6 cm, numerous radiating septa with well-developed teeth.. ..... *Scolymia lacera* (Pallas) (2)
   Cups less than 10 mm in diameter, may occur in groups, growing on shells or other hard substrates.....4

4. Cup with diameter of 10 mm, poorly developed columella.....*Phyllangia americana* Edwards and Haime (3)
   Cups with diameter of 5 mm or less, distinct columella..... .....*Astrangia solitaria* (leSueur) (4)

5. Coral skeleton branched.....6
   Coral skeleton not branched, may have lobes.....17

6. Branches broadly flattened..... .....*Acropora palmata* (Lamarck) (5)
   Branches cylindrical or slightly flattened.....7

7. Cups distributed along entire length of branch.....8
   Branches with terminal cups only.....15

8. Skeleton porous.....9
   Exotheca between calices, solid, forming nonporous skeleton.....12

9. Corallites in close contact, walls not projecting above surface of branch.....10
   Corallites separated, walls project above surface of branch..... .....*Acropora cervicornis* (Lamarck) (6)

10. Branches less than 6 mm in diameter, bifurcating to form clumps..... .....*Porites divaricata* (leSueur) (7)
    Branches between 15 and 30 mm in diameter 11

11. Branches taper, often bifurcate near end... .....*Porites furcata* Lamarck (8)
    Branches with swollen or clubbed ends.... .....*Porites porites* (Pallas) (9)

12. Ten or fewer septa.....13
    Twelve or more septa.....14

13. Corallum elevate or nodular..... .....*Madracis decactis* (Lyman) (10)
    Corallum ramose, branches 6 to 10 mm thick.....*Madracis mirabilis* (Duchassaing and Michelotti) (11)

14. Colonies of few, long, tapered, ascending branches; calices usually on prominent conical projections..... .....*Oculina varicosa* leSueur (12)
    Colonies bushy and profusely branched, calices never on prominent conical verrucae.....*Oculina diffusa* (Lamarck) (13)

15. Corallite circular, usually less than 4 mm in diameter, paliform lobe indistinct..... .....*Cladocora arbuscula* leSueur (14)
    Corallites oblong, usually larger than 8 mm in width.....16

16. Corallites up to 35 mm long, 8 to 17 mm wide, septa smooth..... .....*Eusmilia fastigiata* (Pallas) (15)
    Corallites up to 12 cm long and 4.5 cm wide, septa with strong teeth..... .....*Mussa angulosa* (Pallas) (16)

17. Coral leafy or cup-shaped, upright from substrate, or spreading and platelike, free edge; columella present.....18
    Coral massive, rounded, or hemispherical, often with projections or thick encrustations over substrate.....19

18. Valleys continuous, corallum unifacial.... .....*Agaricia fragilis* (Dana) (17)
    Valleys discontinuous or reticulate, corallum unifacial or secondarily bifacial..... .....*Agaricia agaricites* (Linnaeus) (18)

19. Coral usually firmly attached to solid bottom.....20
    Coral lies unattached on sea floor.....25

20. Surface marked with pattern of sinuous grooves and ridges.....21
    Surface marked with pattern of starlike calices, usually with only one center (sometimes two or three).....31

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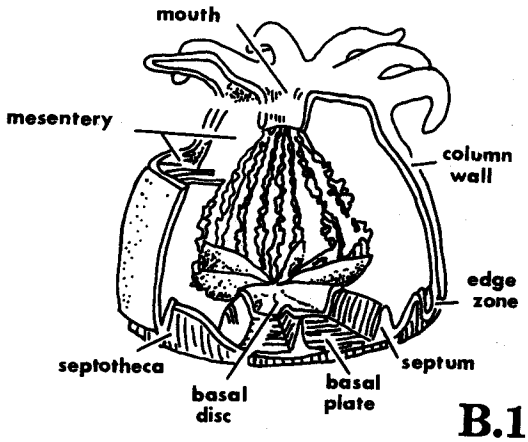
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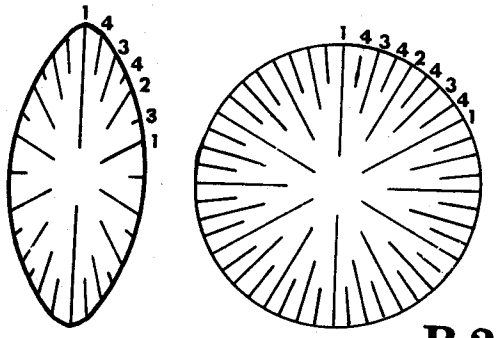
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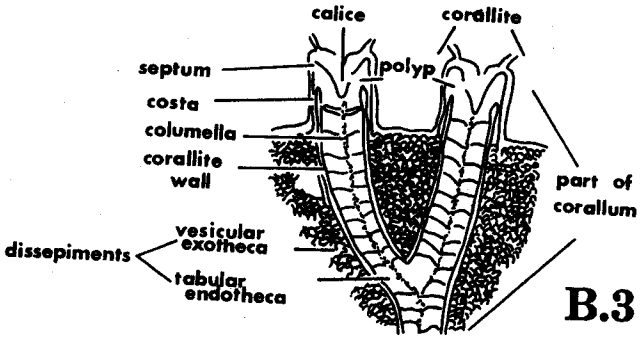
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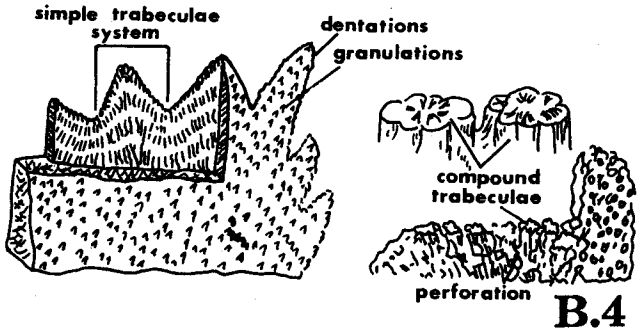
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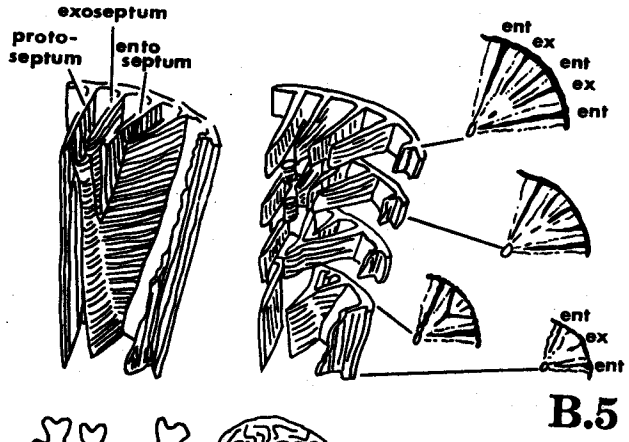
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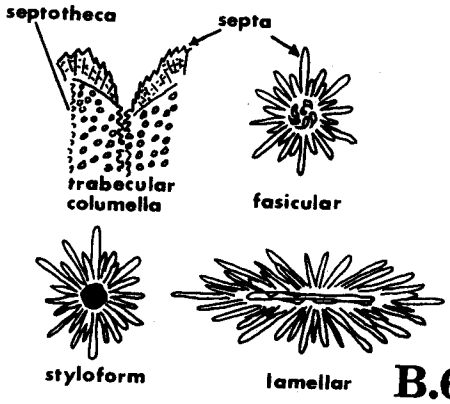
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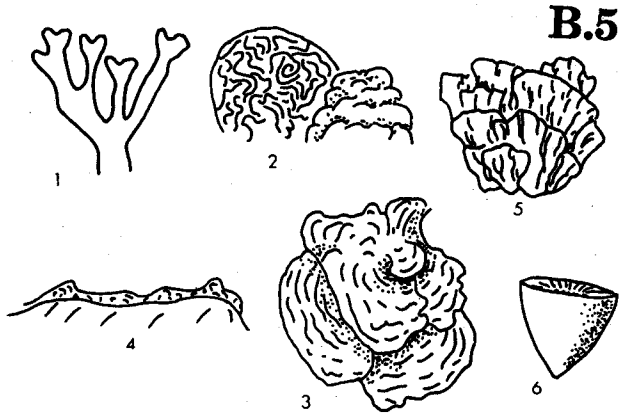
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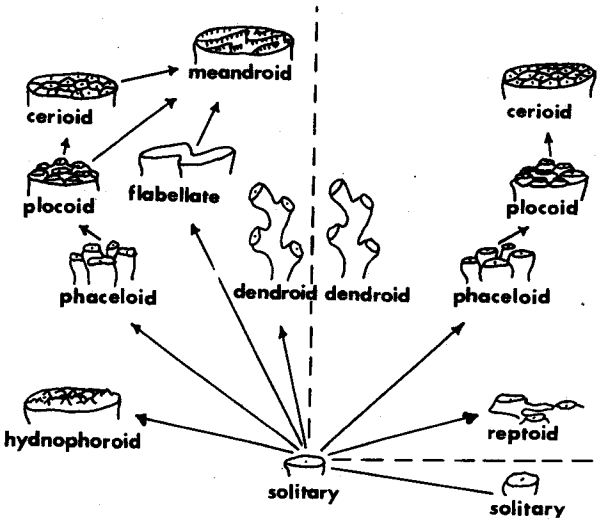
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Introduction to Coral Key

The coral key presented here is developed and borrows heavily from the keys presented by Smith (1948) and Bayer and Cairns (handout, Rosenstiel School of Marine and Atmospheric Science, University of Miami). A brief review of coral terminology with illustrations copied from Wells (1956) is presented to introduce and clarify all terms used in the key and subsequent descriptions.

Coral descriptions are listed in the order in which they appear in the Key to Stony Corals. The number of each species description corresponds to the number in parentheses following the species name in the key. The descriptions are based on the original author's description, found in Smith (1948), Roos (1964, 1971), Weisbord (1974), and Vaughan (1919). Good illustrations of most corals can be found in these references and in Vaughan (1916). Following the coral descriptions is an updated species list from Dustan (1985).

Outline of Coral Terms with Brief Descriptions and Sketches

Corals begin their lives as planula larvae, which remain planktonic until they find a suitable substrate upon which to settle. Shortly after the larva becomes sessile, a basal disc is deposited firmly on the substrate. As a polyp grows upward from the disc, the margins of the disc turn upward, forming a cup called the epitheca, or cup wall. The septa are the first skeletal structures to appear after deposition of the basal plate (Fig. B.1).

As the coral grows, secondary thickening of the epitheca and sometimes the septa occurs. As the coral polyp matures, additional cycles of septa may develop. The first cycle is always complete and consists of six septa that are usually the largest ("1" in Fig. B.2). Additional cycles of septa are added between the previously existing septa. The second cycle has a total of six septa ("2") and the third cycle twelve, if complete. The majority of reef corals exhibit three or four cycles of septa; often the third and fourth cycles will be incomplete (Fig. B.2).

A portion of the polyp overhangs the top of the epitheca and is called the edge zone (Fig. B.3). This is the area responsible for the addition of carbonate material between and within corallites as growth continues in colonial corals.

A great deal of variation occurs in the shape and development of the septa and columellae. Septa consist of trabeculae, which are spines or rods formed by the sclerodermites in the polyp. Sclerodermites are the centers of calcification. Basically, there are two types: simple trabeculae, which are composed of series of simple sclerodermites, and compound trabeculae, composed of bundles of single sclerodermites (Fig. B.4).

Associated with the septa are pali and paliform lobes. A palus is a vertical lamella or pillarlike structure developed along the inner edge of certain entosepta, composing the remnant part of a pair of exosepta joined at their inner margins. They are structurally identical with the septa and secondary to them. Entosepta are septa developed within the space between a pair of mesenteries. The second cycle of septa is generally developed within exocoeles if they form after full development of the primaries. If they form at the same time, both primaries and secondaries are entoseptal. Paliform lobes are structures resembling the palus, but are formed by detached trabeculae offset from the inner edge of the septa, appearing in vertical succession and differing from pali in not being formed as a result of substitution. Paliform lobes of primary and secondary septa may mingle axially to form a columella (Fig. B.5).

The columella is a solid or non-solid calcareous axial structure formed by various modifications of inner edges of septa and often projects into the calice in the form of a sharp-pointed protuberance in the central part of the calice in some corallites. There are three common types: laminar, spongy or trabecular, and styloform. Trabecular columellae are spongy axial structures formed of trabeculae loosely joined with paliform lobes. Styloform columellae are solidly fused and longitudinally projecting axial structures with entosepta fused to them by secondary dense calcareous skeletal deposits that generally cover or thicken various parts of the corallite (stereome). Lamellar columellae are platelike axial structures oriented parallel with the long axis of the calice (Fig. B.6).

Corallum or colony growth morphology is dependent upon environmental factors and type of coral. Common coral morphologies are: (1) ramose or branching; (2) hemispherical or massive; (3) platelike; (4) encrusting; (5) frond or lacelike; and (6) solitary (Fig. B.7).

In addition to variations in growth morphology, great variation exists in colony formation or the distribution pattern of individual polyps in a colony (Fig. B.8).

EPILOGUE

The results of this study were the foundation for the development of an expanded method to assess the condition of key reef elements. The new method includes a more precise estimate of partial mortality subdivided into recent and old mortality and the relative abundance of major algal communities. For reef fish the expanded method combines a roving diver census of fish species with belt transects to estimate sizes and abundance of target species. This new method has been applied throughout the Wider Caribbean and Gulf of Mexico under the Atlantic Gulf Rapid Reef Assessment Program (AGRRA). A full description of the method and preliminary results of assessments can be found at http://coral.aoml.noaa.gov/agra/

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APPENDIX B

Key to South Florida Corals

CONCLUSIONS

1. Shallow patch reefs of the Florida Reef Tract consist of combinations of two size populations of nine species of massive corals: a campus composed of colonies generally < 1m in diameter and/or clusters of larger colonies 1-5 m in diameter.

2. The more numerous colonies of the campus have diameters between 10-60 cm. The size distributions of all but one of the nine species examined are skewed toward the smaller sizes. The smaller number of larger colonies is believed to be the result of the cumulative effects of disease, bioerosion, and removal by storm waves.

3. Visual estimates of partial mortality of 3, 232 massive corals at 23 patch reefs off the Florida Keys found that 74% had <1/3 dead surfaces. Of 65 clusters of giant colonies of *Montastraea annularis and Montastrea faveolata,* 2-5 m in diameter, the line point intercept transect sampling method (Loya, 1978) showed that some 60% had between 40 to 70% dead surfaces. The amount of dead surfaces on massive corals of shallow patch reefs increases with size of colony.

4. In terms of relative amounts of dead surfaces, colonies of the three species of *Diploria* have the least, next are the two species of *Siderastrea, Colpopyhllia natans, M. cavernosa, M. franksi, and M. faveolata,* and those of *M. annularis* have the most dead surfaces.

5. As the conditions of the Florida Reef Tract are less than optimum for reef-building corals, we do not believe that the amount of dead tissue indicates a regional, anthropogenic impact, nor do the results reflect a significant effect of the large population or heavy use off Key Largo. The increased amount of dead tissue in clusters of the Middle Keys and Lower Keys is believed to be the result of unfavorable water quality. For the Middle Keys Section, it is likely that outflows from lagoonal Florida Bay are responsible; for the Lower Keys, both natural and anthropogenic impacts in the nearshore zone are the probable cause of increased colony mortality.

rubble (Fig. 10b), (see also Lirman and Fong 1995, 1997). The next zone south, the area off Key Largo, probably has large human impacts because of the relatively large population and the focus of fishing and diving. There is however, no clear increase in dead tissue/colony for those off Key Largo as compared with the same species off uninhabited Elliot Key.

The Middle Keys Zone has a perennial influence of unfavorable water quality resulting from out flows from Florida Bay and the Gulf of Mexico which is reflected in the limited number of reefs and in the condition of the corals (Ginsburg and Shinn, 1964, 1994; Smith, 1994). Episodes of cold water outflow from Florida Bay in the winters of 1969 and 1977 killed large amounts of coral including the near demise, in 1969-70, of those massive corals on one of the largest patch reefs of the area, Hen and Chickens Reef (Roberts et al., 1982). The fact that *Montastraea* clusters in this zone have more dead surface than those off Elliot Key and Key Largo (Fig. 9a) is believed to be a combination of those known episodes of cold water and other episodes of unfavorable water quality from Florida Bay, i.e., warmer, more saline, or unusually turbid (see references cited above).

In the Lower Keys, the clusters of *Montastraea* have more dead surfaces than in any of the other zones (Fig. 9a). However, the limited number of cluster reefs (4) is an inadequate sample; moreover the fact that there are so few patch reefs suggests that conditions for their occurrence are relatively unfavorable. Given the limited data base and the less favorable setting for patch reef development, there is no clear evidence to determine whether or not localized human impacts from divers, fishers, and runoff have contributed to the declines we observed.

Lewis (1997) used the same methods as we did to determine if variations in partial mortality of *S. siderea* are related to variations in eutrophication on fringing reefs of the West Coast of Barbados. He found no clear relationship, but he did find the same positive correlation between size and percent dead tissue reported above.

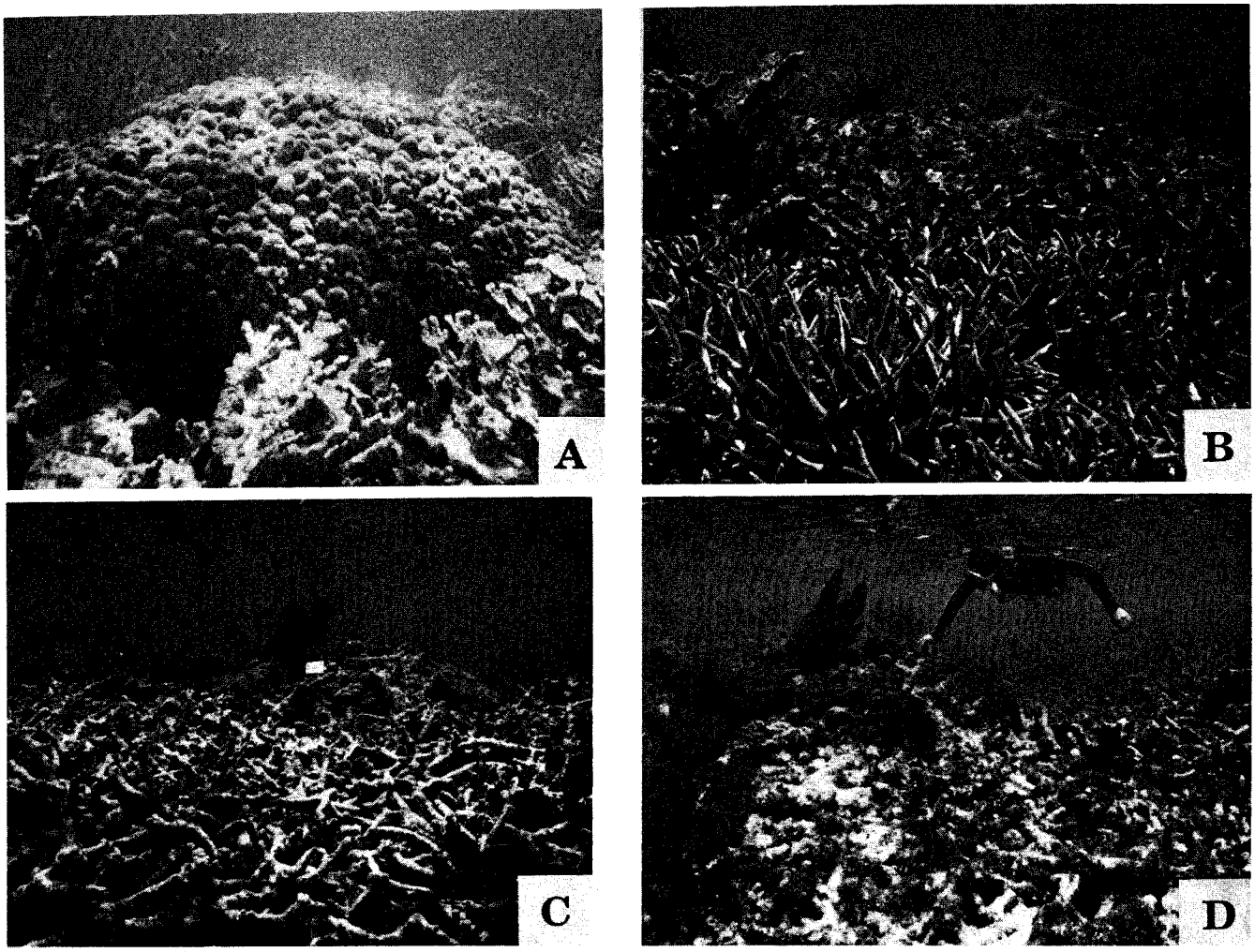


FIGURE A.6. Time series of an area 15 m (49 ft) from the series shown in Figure A.5. (A) Looking south, large *Montastraea annularis* head surrounded by *Acropora palmata* in May 1961. Note 10-cm-growth spike in top of head. (B) Same view taken in July 1971. Note lush *A. cervicornis* in foreground and *A. palmata* to left. (C) Same view taken in August 1980. *Acropora cervicornis* in foreground is dead and *A. palmata* is absent. (D) Same view taken in May 1988. *Acropora cervicornis* has degraded to rubble and become populated by fleshy algae.

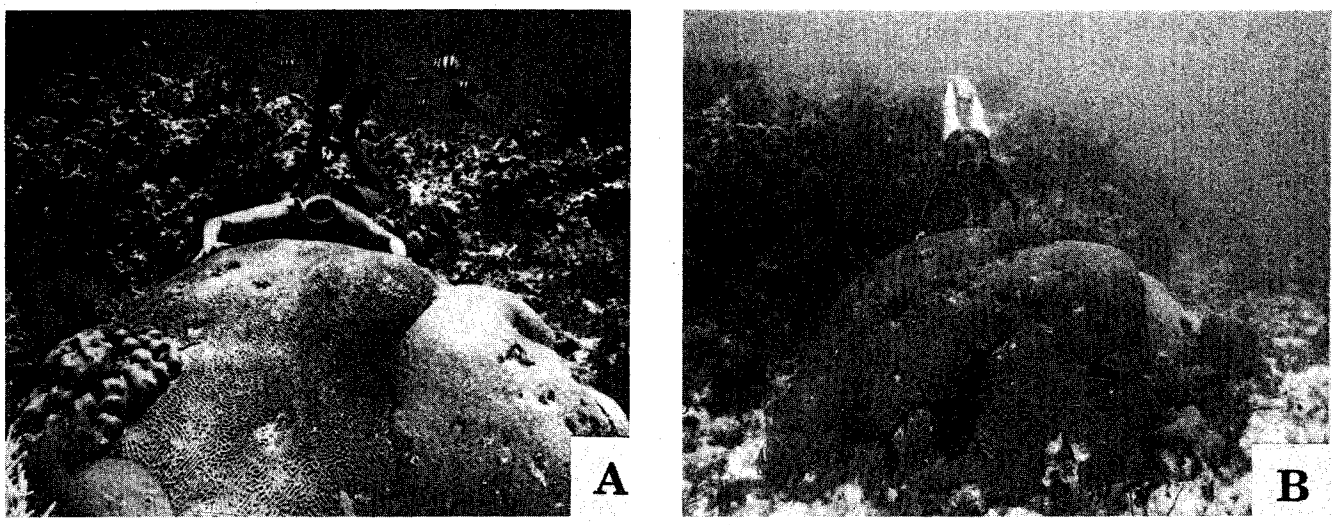


FIGURE A.7. (A) *Colpophyllia natans* head at Grecian Rocks with *Diploria strigosa* on right and *Montastraea annularis* on left, 1959. (B) Same coral May 1988 from slightly different angle.

could well be normal for part or the entire Florida Reef Tract. Confirmation of this inference must await data from comparable reefs in other areas of the Western Atlantic.

Species of *Diploria* have the least partial mortality, i.e., largest percentages of colonies with <1/3 dead surfaces. Comparable results were reported by Bythell et al. (1993) who compared chronic and storm-related, catastrophic mortality in *D. strigosa, M. annularis* and *P. astreoides.* They found that *D. strigosa* is generally unaffected by chronic factors such as grazing and tissue necrosis, but showed heavy damage by Hurricane Hugo. On the other hand, *M. annularis* showed only minor storm damage, but high chronic mortality from grazing and necrosis. *Siderastrea siderea is* known to withstand high turbidity as colonies thrive at distances less than 100 m from shore, e.g., in Florida (Hudson, 1981a) and in Belize (R.N. Ginsburg, E. Gischler, unpublished data). This species alone can form patch reefs of giant colonies in the restricted lagoon of Turneffe Islands, Belize, where extreme fluctuations of temperature (up to 32°C) and of salinity (up to 70‰) have been reported (Smith, 1941; Gischler, unpublished data) The fact that species of *Diploria* and *S. siderea* are tolerant forms can also be seen in the small variability of the data for these species (see Fig. 6).

Further and more detailed observations are needed to bolster our finding of the overall condition of massive corals. The category of <1/3 dead surface is too broad and distinctions must be made between recently dead with polyp surface still present (Diaz, 1995) and old dead. In addition, the nature of the dead surfaces need to be described and where possible the cause(s) identified (Dustan, 1994).

Natural and anthropogenic impacts.- On the basis of natural and human impact, the study area may be divided into four zones (Fig. 1). The northern zone includes the reefs off Elliot and Old Rhodes Keys, which are in the track of Hurricane Andrew of 1992, and the unusually severe tropical storm Gordon of 1994. As a consequence, reefs in this zone have large amounts of coral

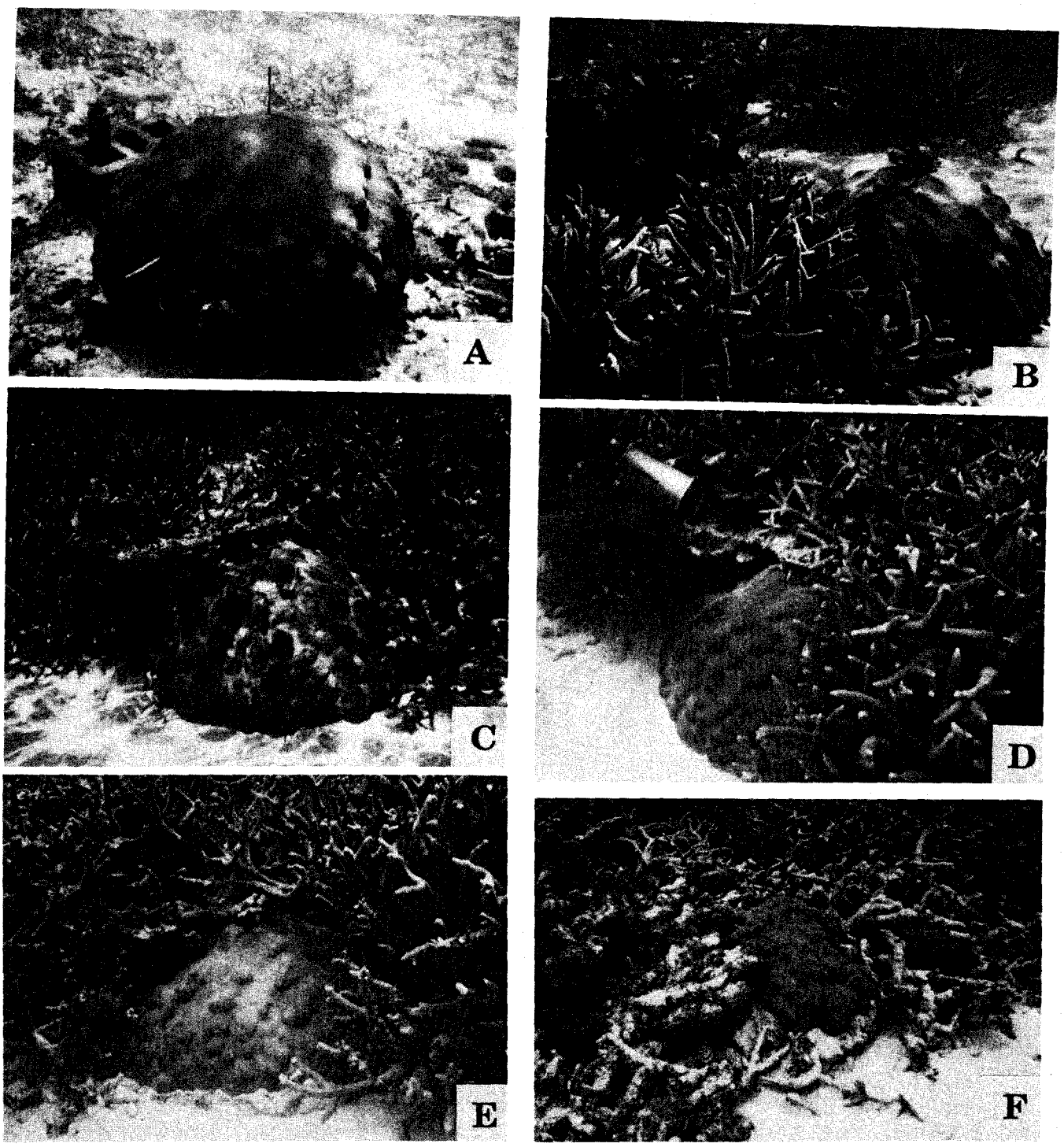


FIGURE A.5. A series of photographs showing 27 years of change at Grecian Rocks. (A) *Montastraea annularis* photographed in May 1961. Ten-cm-long stainless steel pins were part of growth-rate study. Cinder block holds tubular sediment trap. Coral head was located in center of a sand hole near south end of reef (see Fig. A.2). (B) Same colony photographed at 90° angle from (A) in January 1965. Note encroachment of *Acropora cervicornis* in foreground. (C) Same colony (photograph taken approximately 90° from B) in July 1971. Note *A. palmata*, which partially overhangs coral head, and lush nature of *A. cervicornis*. (D) Same head being overgrown by *A. cervicornis* in July 1976. Note that the colony of *A. palmata* is dead, except for small patch just below diver's light. (E) Same head (view same as in C) half engulfed in mostly dead *A. cervocornis*. *Montanstraea annularis* head is dead on side away from camera. (F) Same head coral (same angle of view as in B) engulfed in dead *Acropora cervicornis*. The *Montastreaea* head has a lumpy growth surface and only about one-fourth of the head is living. White sand in lower right corner is part of sand patch at point of arrow in Figure A.2.

regenerate from damages with increasing colony size (Meesters, 1995).

The continued development of new clusters of giant colonies of *Montastraea spp. is* of special concern as these clusters provide essential habitats for fish and invertebrates through the large cavities within and beneath them. To determine if the condition of clusters in Florida is unusual and is owing to some combination of natural and or anthropogenic impacts, comparative studies are needed of clusters in areas outside the storm zone and in areas with minimal populations. As a first step in that direction, measurements of the dead surfaces of a few clusters in the Dry Tortugas National Park, some 100 km west of Key West were found to be similar to those in the Reef Tract reported here. If further measurements of dead surfaces in this remote Park confirm these initial results, they would indicate that clusters with half their surfaces dead in the Reef Tract are not the result of local direct anthropogenic impacts, but instead reflect a widespread condition.

Condition of corals.- Our results for all massive corals we assessed (Fig. 6), indicate that 74% of the 3,232 colonies examined have less than 1/3 dead surfaces. In evaluating this finding as well as in evaluating all our results, several special conditions of the study area need to be considered. The Florida Reef Tract and especially the north half of our study area is near the northern limit of both well-developed patch and bank-barrier reefs. Reef-building corals extend farther north, but most of these communities do not produce significant sea-floor relief. A second aspect that bears on our results is the shallowness of all but three of the reefs we assessed as indicated above. Thirdly, the turbidity of the water is often high for prolonged periods during the winter when winds are often strong. The Middle Keys zone and perhaps part of the Lower Keys is under the influence of water issuing out of Florida Bay that is unfavorable for coral and reef development (see references cited above). Given these unfavorable conditions, the partial mortality we found



FIGURE A.2 Oblique aerial photograph of Grecian Rocks Reef showing location of cores used to construct cross section shown in Figure 11. Light area under the words "Grecian Rocks" is the reef flat composed of dead *in situ Acropora palmata*. Large heads of *Montastraea annularis* occupy backreef area between cores 5 and 6. *Acropora cervicornis* thickets are abundant on south end (left corner of reef). Arrow shows spot where photographs shown in Figures A.5 and A.6 were taken. Dark area behind reef is populated by turtle grass. White area in right corner is carbonate sand in 8 m (25 ft) of water.



FIGURE A.3. Aerial photograph of a portion of Hen and Chickens patch reef. Note lighthouse and 6-m (20 ft) boat for scale. Massive head corals are surrounded by sand halos.



FIGURE A.4. Sand Key Reef and lighthouse off Key West, Florida. Note well-developed spurs and grooves facing into the Straits of Florida.

estimates from line point intercept counts of dead surface are not subject to operator error. The test of variability related to the number of points (Table 2) indicates that the standard deviation for individual transects is between 1 and 15%.

Size distribution.- For demographic studies in colonial organisms such as corals, it is legitimate to use colony size rather than age, even though processes like partial mortality, fission, or fusion can severely distort size-age relationships (Hughes and Jackson, 1980). Variation in genetic or environmental influence can cause significant differences in growth rates, which, e.g., in the case of *M. annularis* is about 200% in shallow reefs of the Florida Keys (Hudson, 1981b; Hudson et al., 1994). Size correlates better with probabilities of mortality and natality of colonial organisms and is therefore more useful (Hughes, 1984). For example, larger corals are generally more fecund than smaller ones and smaller colonies have higher rates of mortality. In several large massive corals, reproductive ability is dependent on size, not on age (Connell, 1973; Szmant, 1986). Studies including both size and age of corals are very rare, but have shown that size effects on population dynamics are stronger than age effects (Hughes and Connell, 1987; Babcock, 1991).

The size distributions of all species are skewed and have maxima between 0.2 and 0.5 m. Lewis (1997) found similarly skewed size distributions of *S. siderea* at Barbados. One obvious reason for the decreased abundance of larger colonies is the observed increase in percent dead colony surface with increasing size (Fig.5). Evidently this relationship is a general one as it has been signaled by Hughes and Connell (1987) and by Lewis (1997). The longer a colony exists and the larger it grows, the higher the probability that diseases, bioerosion, and physical disturbance affect it. As a consequence, only few colonies reach large sizes. In *D. strigosa* and *D. labyrinthiformis* increasing mortality with increasing size is much less pronounced than in the other species investigated. This difference might be a result of the greater ability of *Diploria* to

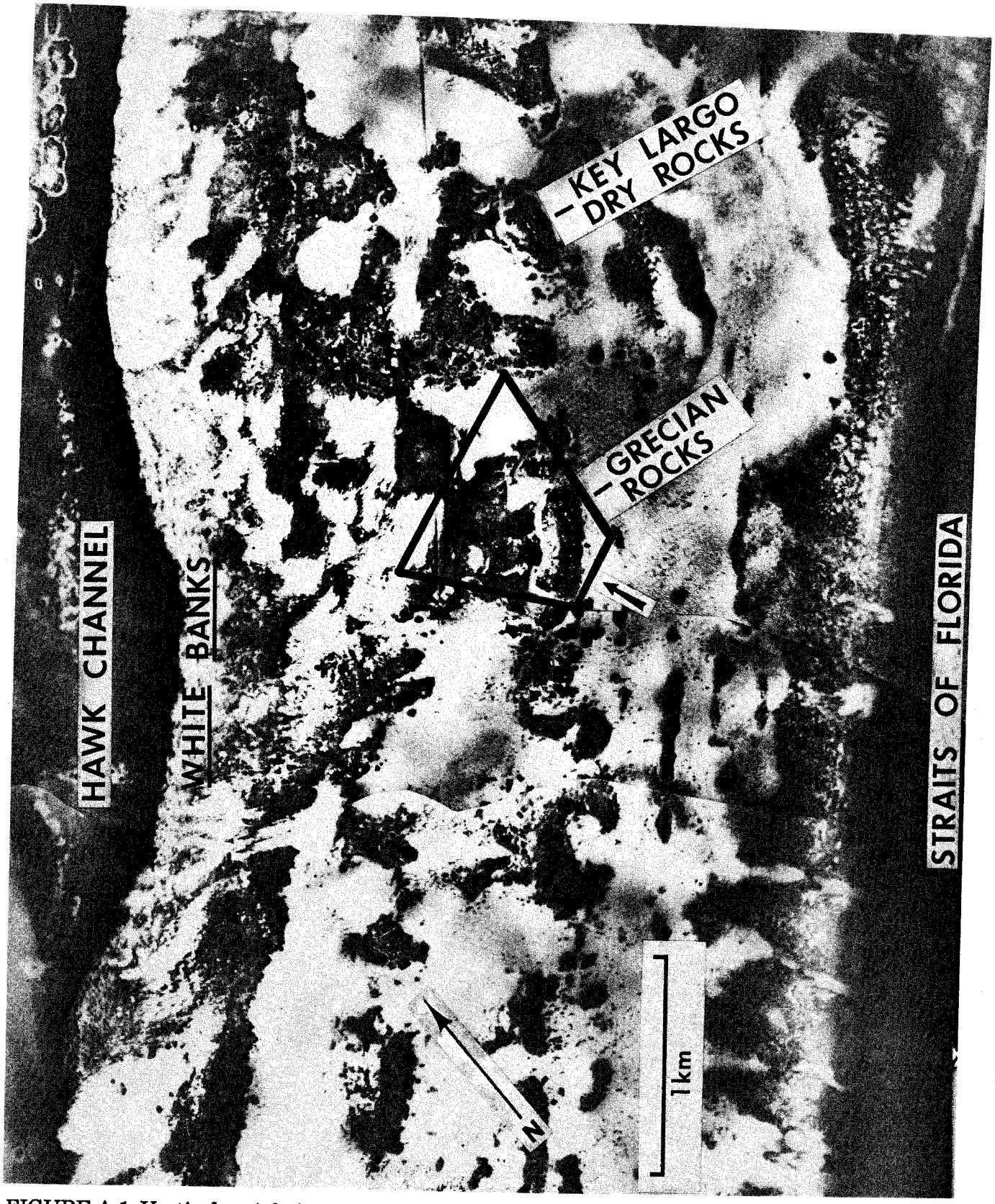


FIGURE A.1. Vertical aerial photograph of White Bank area in Key Largo National Marine Sanctuary off Key Largo. Grass-bottomed Hawk Channel is to left with a series of patch reefs at upper left. Grecian Rocks, part of a chain of discontinuous reefs that includes Key Largo Dry Rocks, is enclosed by border that shows view of reef in Figure A.2. White areas are carbonate sand. Most of the dark areas are populated by turtle grass.

rubble associated with clusters off Elliot Key (Fig. 9b) reflects the impact of Hurricane Andrew 1992 whose center passed over reefs off that island (Table 4), see also Lirman and Fong (1995, 1997).

Discussion

Data limitations.- There are several inherent limitations in our data set. All but three of the 22 patch reefs examined are shallow, with their tops within a few meters or less of sea level (Table 1). This shallowness means the corals are more likely to be affected by sea surface waves and water quality, small boat groundings and possibly by fishermen and recreational divers. There are limited numbers of colonies of certain species on individual reefs and limited number of patch reefs in two of the sub-areas of the Reef Tract. In figure 6, it is evident that the relatively large variability in the percentages for *M. franksi* and *C. natans* are related to small numbers of colonies. Similarly, the limited number of patch reefs off the Middle Keys could be responsible for the large variability in the data on clusters (Fig. 6). In the Lower Keys, two of the three patch reefs examined are within less than a kilometer of the shoreline (Table 1).

Another limitation of our results is the inherent variability in the type of patch reef and their distribution. As shown in Figure 1 patch reefs are much more numerous in the Upper Keys than elsewhere. Moreover, seven of the twelve patch reefs, which we assessed had both campus and cluster elements. In contrast only one of the seven reefs we studied in the Middle and Lower Keys had the campus element. These differences, which may well reflect succession (Jones, 1977), limit comparison of reefs to clusters.

A limitation of our data on dead surfaces for corals of the campus is that different observers collected it without inter-calibration. However, the categories of dead surface are so broad, that we believe the estimates of different observers are comparable. For the clusters, the

APPENDIX A

Selected Aerial and Underwater Photographs

between species are revealed by the Kruskal-Wallis test (Table 3). Species of *Diploria* have less dead surface than most other species and *M. annularis* has more dead surface than other species. All species show to varying degrees an increase in the amount of dead surfaces with increasing size (Fig. 5).

Figure 6 shows the variations in condition at various spatial scales by species. On an individual reef we found specimens of *M. annularis* without any dead surface, yet nearby colonies could have 1/3-2/3 dead surfaces. A further indication of the variability on an individual patch reef is evident in the data for Bache Shoal in figure 6. Similarly, for groups of reefs shown in figure 6, the data for some species shows large variation in condition, but for others it is much less. Some of the large variations are probably owing to the small number of colonies we examined, i.e., *M. franksi* and *C. natans.* A cluster analysis indicates no major spatial variations in condition for the entire study area (Fig. 7). However, there are differences in the condition of four species between two zones (see Fig. 6). Off Elliot Key, *S. siderea* has a significantly larger percentage of colonies with less than 1/3 dead surfaces than off Key Largo. (Kruskal-Wallis analysis of variance by ranks, $p=0.05$). Off Key Largo, *M. cavernosa* ($p=0.025$), *D. strigosa* ($p=0.004$), and *D. labyrinthiformis* ($p=0.005$) all have significantly fewer colonies with > 2/3 dead surfaces than off Elliot Key (Kruskal-Wallis analysis of variance by ranks).

For the clusters, the frequency distribution of dead colony surfaces is skewed and nearly 60% of those clusters measured have between 40-70% dead surface (Fig 8). There are significant variations in the amount of dead surfaces on individual reefs, within reef areas and for all clusters (Fig. 9a). We did not find as might be expected, a significant decrease in dead tissue/colony on the few patch reefs examined that occur on the bank barrier. A statistical comparison of the condition of the corals for the four areas studied shows that those off the Lower Keys have more dead surfaces than those off Key Largo and Elliot Key (Table 4) The greater amount of coral

tubing marked in 10-cm increments. The partial mortality of each colony was estimated visually as <1/3 dead, 1/3- 2/3 dead and > 2/3 dead surface (Endean et al., 1988; Ginsburg et al., 1996). For larger patch reefs such as Nirvana, Sting, and Higdon (Table 1), this census technique was applied at more than one location.

For the clusters of giant colonies of *M. annularis* and *M. faveolata,* we used the line point intercept transect sampling method (Loya, 1978) to determine partial mortality. Nylon lines 5 m long with marks at 25 cm and weights at each end were draped over the clusters diametrically or radially from the approximate center. Observers assigned what was under each mark to one of five categories: living, dead, rubble, corals other than *Montastraea,* substrate, i.e., neither coral nor coral rubble. At each cluster, a series of these transects were made by moving the line around the points of the compass. On some clusters, four transects 90° apart were made giving 100 points, at others 8 transects 45° apart were inspected to give 200 points, and at some, 16 transects some 20° degrees apart were examined to yield 400 points. A test of the variations in the results as a function of the number of points is shown in table 2.

RESULTS

Size distributions.- The size distributions of all corals by species, except those of the clusters, are shown on figure 5. The distributions for *M. cavernosa, D. strigosa, D. clivosa, D. labryinthiformis, and S. siderea* are similar, they are skewed toward the smaller sizes and most colonies are between 20 and 50 cm in diameter. The irregular size distributions for *M. franksi* and *C. natans* are probably owing to the small number of colonies available.

Condition of corals.- The results from the census of corals in the campus are shown in figures 5 and 6. Seventy-four percent of the 3,232 colonies examined have less than 1/3 dead surfaces with only a quite small standard deviation. Significant differences in the amounts of dead surfaces

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shoal fringe buildups built of the skeletons of *Porites furcata,* green and red algae (Fig. 2) were not examined.

To gain some idea of the relationships between campus and clusters, we made observations of belt transects for bottom types which could be identified from aerial photographs (1:1,200) of the patch reefs of Bache Shoal (Fig. 4) and another area we named Nirvana (Fig. 1). For each bottom type, we made 10-12 belt transects, each 1 m x 6 m, in which the massive corals and octocorals were counted independently by two persons. The abundance of areas of sea grass and of rubble was also estimated independently by two persons. The mean value of the two estimates was calculated to characterize the bottom types.

METHODS: ASSESSING CORAL CONDITION AND COLONY SIZE

The assessments were made between July 1995 and January 1996 by free diving from outboard-powered small boats 5-7 m long. In the Upper Keys (Fig. 1), reefs were selected to cover the geographic range of patch reefs and to include representatives of the major types. Off the Middle and Lower Keys where there are a limited number of patch reefs, all shallow examples were included. The location of each reef was determined with a GPS instrument whose uncertainty is approximately 60 m. At some reefs, more than one site was assessed either for corals of the campus or cluster, see Appendix.

The evaluation of corals in the campus areas was a census of massive corals only as listed above. We ignored the branched corals because they are not the major reef builders of these patch reefs, they are often transitory (Davis, 1982), and because estimates of their partial mortality is more uncertain than for massive corals. At each reef selected, observers swam four radial transects - north, east, south, west - from the approximate center of the reef, measuring and estimating partial mortality of the one to three species assigned to them that were in sight. The projection diameter of each colony was measured to 10 cm, with a section of small-diameter PVC

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building corals are largely massive species varying widely in abundance, diversity and colony sizes. Coral cover is the highest of all Florida reefs, ranging from 8-61%, and half of the examples had 20% or more cover.

In this study we considered only shallow patch reefs whose surfaces are within a few meters or less of the level of low tides. Using size and relief of the massive corals, two main types of patch reefs can be identified (Fig. 2). **Cluster reefs** consist almost entirely of giant colonies and coalesced colonies, 1-5 m in diameter, of *Montastraea annularis* and/or *M. faveolata* with only occasionally other massive corals - *Siderastrea siderea* and *Colpophyllia natans.* **Composite reefs** usually have two or three subdivisions: 1) a campus of massive corals with abundant octocorals; which were it not on a elevated reef would be termed a hard ground community; 2) areas in which coral rubble and skeletal sands predominate; and 3) one or more localized clusters of giant colonies of *M annularis or M. faveolata.* The corals of the campus are mostly less than 0.5 m in diameter and are distributed irregularly over the bottom in variable densities. They include most commonly *M. annularis, M faveolata, M. cavernosa, Diploria strigosa, D. clivosa, D. labyrinthiformis, Siderastrea siderea, S. radians, Porites porites, P. astreoides, Colpophyllia natans, Dichocoenia stokesii and species of Millepora.* Less common corals are *Acropora cervicornis, Stephanocoenia michelini, Solenastrea bournoni, Favia fragum, Manacina areolata, Meandrina meandrites and species of Mycetophyllia.* Among the most common octocorals are species of *Plexaura, Pseudoplexaura, Eunicea, Muricea, Pseudopterogorgia and Gorgonia* spp. The distinction between campus and cluster is comparable to the distinction between knob (cluster) and ledge (campus) for Bermuda patch reefs (Scoffin, 1972). Within each of the two types of patch reefs, there are further distinctions in size and depths (Table 1). We also assessed the massive corals of three bank-barrier reefs (Table 1). The

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The two major reef types are illustrated schematically in figure 2. There are only some ten to twelve, near-surface bank-barrier reefs with abundant living coral in the entire Florida Reef Tract (Shinn et al., 1989). They are separated by much larger areas of relict reefs or limestone pavement (Chiappone, 1996), here termed bank margin shoals. Patch reefs are found in the crescent-shaped zone, usually some 5-10 km wide, between the bank-margin and the Florida Keys; a few occur along the bank margin (Fig. 1). Figure 3 shows the area of most abundant shallow patch reefs off Elliot Key, where some 3,000 individual reefs can be identified on aerial photographs.

Patch reefs.- In Florida the term "patch reef" is used for localized, **elevated** accumulations of corals, octocorals, and associated benthos. Marszalek et al. (1977) mapped the distribution of all patch reefs from Miami to Key West using aerial photographs and diver observations. They found more than 6,000 dome- and linear-shaped examples ranging in size from a few meters to several hundred meters and with relief over the surrounding sea floor of generally less than 5 m. An overview of patch reefs was given by Jaap (1984) who focused on patch reefs, which rise to near the level of low tides from depths of 2-9 m. These shallow patch reefs vary widely in size (30-700 m according to Jaap 1984), in shape (sub-circular, linear, amoeboid), and in abundance and spacing. Shallow patches are most abundant and closely spaced off Elliot and Old Rhodes Keys (Fig. 3) where Marszalek et al. (1977) report almost 4,000 in number. Off Key Largo these authors found nearly 1,600 examples, but only 50 off the Middle Keys. In the Lower Keys, they report 420 patch reefs of which fewer than 20 are as shallow as those in the Middle and Upper Keys.

Jaap (1984), Chiappone and Sullivan (1997), and Chiappone (1996) have reported quantitative inventories of the composition of nearly 20 patch reefs in south Florida. The reef-

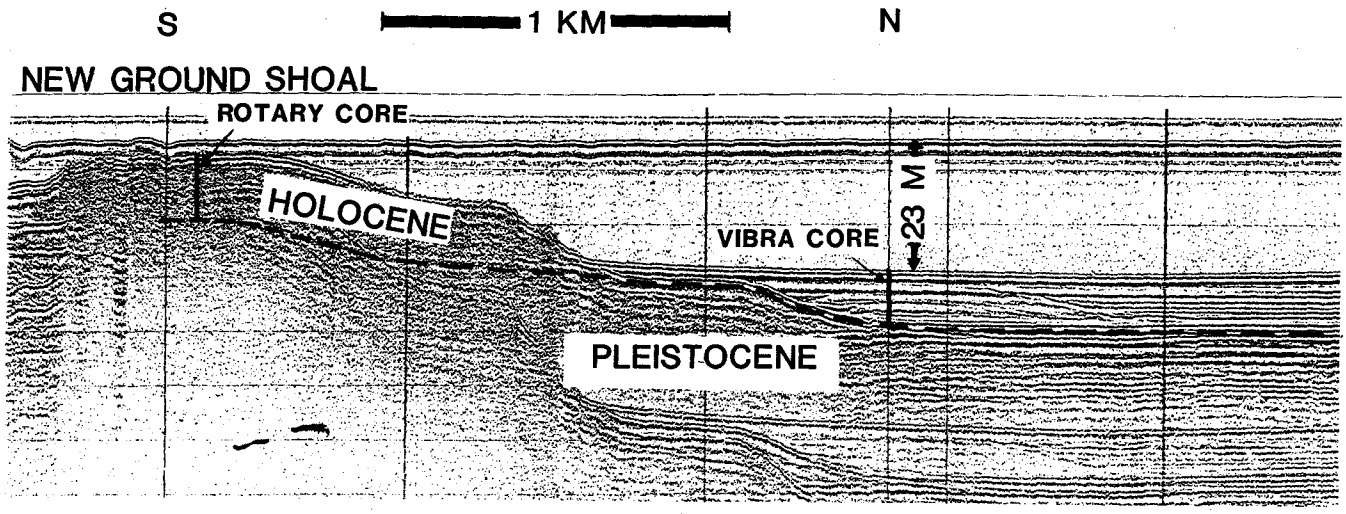


FIGURE 29 High-resolution seismic-reflection section extending northward across New Ground Shoal Reef (left) and into area of muddy carbonate sediment (right). Rotary core showed Pleistocene high beneath reef to be equivalent to Key Largo Limestone; fauna of 8-m-thick Holocene section was similar to that of the Pleistocene and lacked branching corals. Vibracore penetrated 8-m section of lime mud and fine carbonate sand lacking corals. Reflectors were possibly caused by concentrations of mollusc shells, probably deposited by storms.

be fringing reefs. If sea level drops to the same position it occupied in 15 to 20 ka (i.e., approximately -100 m or -328 ft), fringing reefs will grow at the base of a 100-m-high (328 ft) limestone terrace. Here and there, reef growth would be retarded by freshwater springs or possibly by runoff from streams or small rivers. It is likely that such lowering of sea level due to glacial growth would also result in lower seawater temperatures, possibly too low to support reef growth.

Whether sea level rises, falls, or remains stable, it is clear that reef growth is affected both directly and indirectly by the change, directly by exposure to air or drowning to great depths, indirectly by creation of bays and channels with their inimical waters.

It should be mentioned that there is an unstudied, laterally continuous, dead reef at depths ranging from 8 to 18 m (25 to 60 ft; average 12 m or 40 ft) that parallels the seaward side of the entire reef tract. The reef is usually separated from the shallower main reefs by a 100- to 300-m-wide (328-980 ft), 18- to 21-m-deep (60-70 ft), sand-filled trough. Because of its continuity, uniform depth, and closely spaced spur-and-groove system, it is thought to be a fringing reef drowned between 10 and 6 ka as sea level rose. Future core drilling will determine its age and composition and hopefully will provide more understanding as to how reef evolution will occur under variable sea-level conditions.

Acknowledgments

From 1974 to 1989, the U. S. Geological Survey supported a field station at Fisher Island off the south tip of Miami Beach. The small Fisher Island Station staff, ranging from three to five professionals during the 15 years of its existence, was charged with study of all modern and Pleistocene deposits in south Florida, including coral reefs. This guidebook is an attempt to summarize the results of the various reef studies that took place at Fisher Island Station during that time period. We thank the USGS for allowing us the time and freedom to pursue these studies.

Much of the research referred to here, especially that involving coral growth rates, was funded by the Marine Sanctuary Program of NOAA. Additional funding came from the Conservation Division of the USGS, now called the Minerals Management Service, and the National Park Service. Throughout this period, we have benefited greatly from our colleagues and neighbors, the Rosenstiel School of Marine and Atmospheric Science's School of Comparative Sedimentology, headed by Robert N. Ginsburg.

Drilling and other forms of sampling and observation required many hours under water and the ability to find and remain at work sites for days at a time. Little of this would have been accomplished without the aid of Captain Roy Gaensslen and his work-horse boat the ***Sea Angel.***

From time to time we have benefited greatly from the aid of technicians and part-time helpers, many of whom were funded by the National Association of Geology Teachers program. Technician/scientist/publisher Daniel M. Robbin not only did much of the nitty-gritty work, but also found time to publish several significant findings that are referenced herein. NAGT students who were especially productive and went on to lead their own professional careers were Lee Kump, Carol Kindle Lee, Van Mount, and Bill Zempolich. Our

would reveal variations in partial mortality related to variations in natural and anthropogenic impacts. From our examination of the numerous patch reefs we found that there are two types and they are not represented equally along the study area. Accordingly, we had to limit the comparisons to the reef type most widely distributed.

STUDY AREA AND SETTING

The Florida Reef Tract and its reef types. - In this Report, "Florida Reef Tract" is used as proposed by Vaughan (1914) to include the entire assemblage of reefs and intervening environments extending from the Florida Keys to the seaward limit of reef growth. Others (Chiappone and Sullivan, 1997; B. Causey, personal communication, 1997) would limit the use to the arc of bank barrier reefs (outer reefs, shelf-margin reefs).

The Reef Tract can be subdivided into three sections based on inferred water quality, continuity of the Keys and abundance of reefs. The Upper Keys section is characterized by an almost continuous backstop of islands of Pleistocene reef limestone (Elliot Key, Old Rhodes Key, Key Largo, and Plantation Key) and by the most numerous reefs, both patch reefs and the bank-barrier variety, of all three sections. In the Middle Keys, only about half of the backstop is composed of islands of Pleistocene limestone and Holocene sediments; the rest are shallow passes and channels that lead into Florida Bay and the Gulf of Mexico. Only a few patch reefs and no well developed bank-barrier reefs are present in this section, probably as result of the influence of poor water quality and frequent movement of the bottom sands (Ginsburg and Shinn, 1964, 1994; Smith, 1994). The Lower Keys, like the Upper, have a backstop of almost continuous islands of Pleistocene limestone with only extremely shallow channels separating them. Both bank-barrier and shallow patch reefs occur here, but they are less numerous than in the Upper Keys section.

small areas where no accumulation took place, and calcrete-coated Pleistocene bedrock can be observed with no sediment or coral cover. Such bare areas, however, support numerous sediment-producing organisms that are periodically swept away to accumulate elsewhere. Muddy sediment in Hawk Channel ranges from a few centimeters to several meters thick but averages about 3 m. Thus, if all the sediment and coral were spread evenly over the reef tract, the thickness would probably range between 3 and 5 m (10 to 15 ft). This represents an enormous amount of organic productivity, considering the short time.

For purposes of speculation, use the low figure of 3 m of accumulation in 6,000 years (a rate of 0.5 m/ka). In another 6,000 years, the accumulation would double to 6 m, and in 18,000 years, the thickness would be 9 m. This simple approach makes it apparent that if sea level remains constant, there will be very little water anywhere on the reef tract 18,000 years from now. Whether it actually takes 10,000, 100,000, or a million years, it is nevertheless apparent that, given stable sea level, the reef tract will fill and become land. During the shoaling-upward phase, the major facies belts would expand only slightly, while maintaining their present geometries. During the final stages of filling, however, reduced depth and wave energy, as well as reduced water circulation, would retard growth rates, and sediment would become finer grained as sedimentation slowed. Carbonate sediment would likely be replaced by peaty soils and vegetation. Because coral reefs could only grow at the platform margin, they would have to accrete seaward. Such seaward outstepping would undoubtedly produce the classic progradational sequences so common in the geologic record. Carried even further, such accretion, given millions of years, could fill the Straits of Florida. Similar filling of deep straits has been demonstrated in the Bahamas, where a 1,500-m-deep (5,000 ft) strait (the Straits of Andros) has filled since the Cretaceous (Eberli and Ginsburg, 1987). According to these authors, the west edge of the Great Bahama Bank accreted some 20 km (12 mi) into the Florida Straits during the same time period.

As the platform margin reefs accrete into the Florida Straits, coral rubble and sediment would be thrown up onto the accreting land behind the reefs to produce beaches and/or dunes. Laterally continuous beaches and dunes would tend to pond water behind them, thus maintaining swampy peat-forming conditions. A climatic change toward arid conditions could replace the swamp with an evaporitic tidal flat similar to the sabkhas presently accreting along the southern shore of the Persian Gulf.

The Future during a Rising Sea

If sea level continues to rise, as many believe, the reefs will continue to backstep and larger areas of the reef tract will be affected by inimical waters as larger tidal passes and estuaries form. Once drowned beyond the critical growth depth (the depth varies depending on water quality), reefs would no longer keep pace with rising sea level. They would become the drowned "give-up" reefs described by Neumann and Macintyre (1985). Sediment would continue to form and accumulate but at a reduced rate. With continued rise and eventual drowning of the Pleistocene Keys, greater wave energy would impact Florida Bay. Mud banks and mud islands would probably be eroded away. Lime sand would probably begin to accumulate where mud now exists. Florida Bay conditions would migrate inland across the Everglades and probably to Lake Okeechobee.

Once Key Largo was flooded, corals would commence growth on the high areas, and by analogy with the corals at Ellis Rock and New Ground Shoal (Fig. 29), Acroporids would be excluded. Unimpeded flow of cold Gulf of Mexico water in winter months would prevent their establishment. Whether the Miami and Key West Oolite areas would become coral reefs, or whether ooids would once again form there is unknown. We can be certain, however, that corals would become established on the upper and middle Keys, and they would attach directly to the calcrete-coated subaerial unconformity. Boreholes showed that reefs grew on subaerial unconformities at least five different times during the Pleistocene (Perkins, 1977). History may repeat itself with or without the greenhouse effect. This scenario would result in renewed upward growth of a more than 160-km-long (100 mi), porous and permeable reef deposit situated 6 to 8 km (4 to 5 mi) westward of the platform margin.

During the last interglacial at 125 ka, sea level was at least 6 m (20 ft) above present. Depth could have been as great as 18 m (60 ft; Stanley, 1966). Such a depth is reasonable, because the coral species that built the Key Largo Formation currently flourish at those depths at the Flower Gardens Reef in the northern Gulf of Mexico. Growth-rate measurements have shown that *Montastraea annularis* in 20 m (65 ft) of water at the Flower Gardens grows at the same rate as those growing off Key Largo in 3 m (10 ft) of water (Hudson and Robbin, 1980). The contemporaneous oolite shoals that formed the land under Miami and the lower Keys, however, suggest much shallower depths.

The Future and a Lowered Sea Level

Should sea level fall, the reef tract will become exposed and cemented by meteoric diagenesis, and soils and calcrete crusts will develop, such as those described by Multer and Hoffmeister (1968), Robbin and Stipp (1979), and Shinn and Lidz (1988). The only reefs that could grow then would

well-documented examples of declines in corals come from bank-barrier reefs. Dustan and Hallas (1987) found a decline in *Acropora palmata* between depths of 10-21m at Carysfort Reef (Fig. 1) over a period of 8 years. From repeated photographs of quadrats 4.5 m^2, Porter and Meier (1992) reported significant declines in coral cover over a period of 7 years at Carysfort Reef (7-33%) and at Looe Key Reef (13-44%), while for the same period at Ball Buoy reef, cover increased some 30%. Jaap and Sargent (1994) summarized the repeated loss of A. *palmata* at the Dry Tortugas since 1881. Chiappone and Sullivan (1997) found generally low coral cover, < 20%, of *A. palmata* in their assessment of 20 bank barrier reefs. Lirman and Fong (1995, 1997) documented the effects of storms on this same coral. Declines in *Acropora cervicornis* are more widespread than in *A. palmata* (Davis, 1982; Roberts et al., 1982; Jaap et al., 1988, pers. communication, 1998; Dustan 1994).

Of the several studies of massive corals, only a few provide information on condition of colonies, which is relevant to this study. The only well established example of a major decline in massive corals of patch reefs is the report of the nearly complete death of many of the giant colonies of *Montastraea annularis* at Hen and Chickens Reef off the Matecumbe Keys (Fig. 1), as a result of an episode of unusually cold water from Florida Bay in 1969-70 (Hudson et al., 1976; Walker et al., 1982; Roberts et al., (1982). Hudson (1981a) used the response of transplants of *M. annularis* to show that the absence of this species from nearshore areas is the result of natural aperiodic heating and chilling of the water.

Purposes of the study. - The primary purpose of this research was to explore the use of partial mortality of massive corals by species and colony size as a measure of condition and provide data that could be used for comparison with other areas. Initially, we assumed that, by examining the massive corals on shallow patch reefs along some 200-km of the Florida Reef Tract, our results

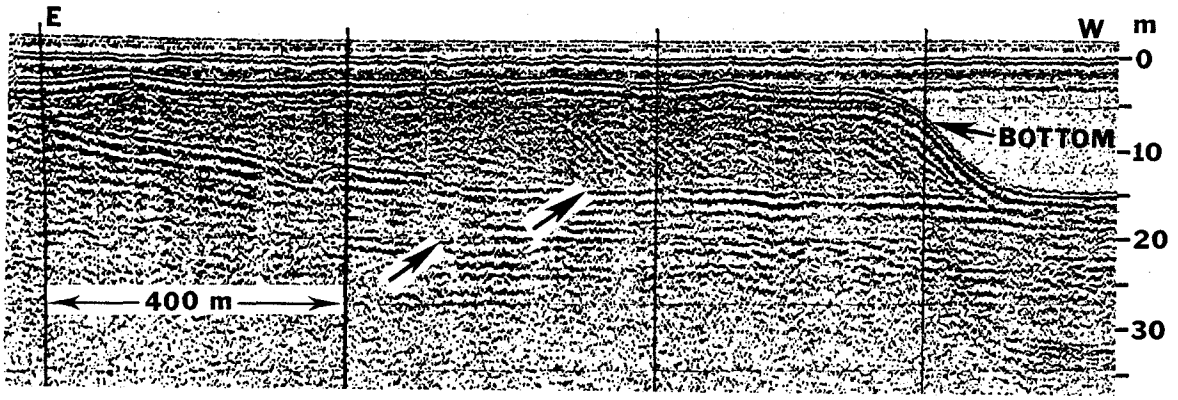


FIGURE 28 High-resolution seismic profile of thick-sediment area at Halfmoon Shoal. Note accretion of sediment to west. Pleistocene surface shown by arrow in center. Arrow to left shows a prominent reflector (Q3 Unit of Perkins, 1977) within the Pleistocene. Q4 Unit above Q3 is composed of oolite. Oolites are absent from overlying Holocene sands.

ticeable at Little Molasses Island and the Elbow. According to Ball et al. (1967), high-energy currents of large storms are influenced by the same local and regional topography that controls day-to-day tidal and surf action. Therefore, direction of sediment transport during storms is about the same as that of day-to-day tide and wave currents. Combination of depth, topography, fetch, and wind and wave direction is also responsible for the landward distribution of coral rubble at Looe Key, which is almost parallel to normal day-to-day winds.

Direction of sediment transport in the lower Keys is related to the east-west trend of the platform margin and to the angle at which day-to-day currents as well as hurricanes impinge on the platform in this area. Gentle winds and seas impinging on the Looe Key Reef area will cause the forereef sediments to move in the direction of flow, that is, to the west or parallel to the platform margin. Behind the reef, however, sediments lie protected within the shadow of the reef, where they become bound by heavy marine grass cover.

The primary direction of sediment movement during hurricanes is also to the west (Ball *et al.*, 1967). Landward and seaward movement, however, would also occur at specific times during the course of a storm. Most hurricanes have approached Florida from the southeast. Because hurricane winds rotate counterclockwise, the first winds to obtain landfall will blow offshore from the northeast in the middle and lower Keys but landward in the upper Keys. Therefore (and depending on the relative location of the eye), the first and strongest winds to hit the lower Keys will be from the northeast. Offshore and longshore currents caused by hurricanes account for the coral-rich sands seaward of Looe Key Reef. The same hurricane would have a different effect in the upper Keys, where the trend of the platform margin is essentially north-south. The ebb of the storm tide, however, together with offshore winds in the storm's southeast quadrant, will also cause offshore transport in the upper Keys as the hurricane progresses to the northwest. Florida Bay water, piled up on the shelf as much as 3 m (9 ft) above normal spring high tide by onshore winds during Hurricane Donna, was propelled offshore along the upper reef tract by southwest winds as the hurricane passed (Ball *et al.*, 1967).

In the lower Keys, winter-storm winds from the north-northeast that push Florida Bay water off shore transport sand to the south-southwest, particularly in the areas of aligned (north-south) spurs and grooves and elsewhere along the break in slope, where sediment is not anchored by sea grasses. Winter storms thus contribute significantly to the burial of the deep reef and formation of the sedimentary lobe in front of Looe Key Reef (Lidz *et al.*, 1985).

DISCUSSION AND SPECULATION

The Future under a Stable Sea

Ancient reefs, whether exposed or buried, are usually much more extensive and thicker than the Florida Keys reefs. However, with the knowledge we have learned about facies distribution and growth patterns, we can project what the size and facies of the Florida Keys reefs will be in the next few thousand years under different sea-level conditions. Models obtained from such projections could have more application to the understanding of ancient reefs than the thin Holocene reefs described thus far. The reef accumulations seen on this excursion are geologically very young. The oldest corals began growing only about 6 ka on an area that was land just 8 ka. Nevertheless, during this short period of flooding, several reefs accumulated 10 to 14 m (35-45 ft) of deposits (a rate near 4 m/ka). Vast areas of sediment, such as the 10 m (33 ft) of carbonate sand and wackestone beneath White Bank, also accumulated during this period. However, in this region there also exist numerous,

Most reports of declines in reef-building corals in Florida summarized below come from bank-barrier (shelf-margin) reefs. For the much more numerous patch reefs, which occur in the 5-10 km between the bank-barrier and the islands of the Florida Keys for some 200 km. (Fig. 1), there are thorough descriptions of the benthos including coral cover and species diversity, but little or no published information on the condition of the coral communities. These patch reefs are widely used by commercial and sport fishers, by recreational divers and snorklers and by teachers and their students. As most patch reefs are closer to the populated islands of the Florida Keys, they should show more of any effects of land-based impacts than the bank barrier reefs. This combination of nearly no information on coral condition of patch reefs and the chance to assess the responses of the same reef type to variations in natural and anthropogenic impacts led to the research whose results are reported here.

The most reliable indications of declines in coral communities come from repeated assessments or revisits to reefs previously surveyed (Davis, 1982; Dustan and Hallas, 1987; Porter and Meier, 1992; Hughes, 1994). The lack of significant previous data on the condition of the corals of Florida Keys patch reefs led us to develop a method of instantaneous assessment (Ginsburg et al., 1996). This field-oriented approach uses visual estimates of the amounts of dead surfaces of massive corals by species and size. Our use of partial mortality followed earlier works by Endean et al. (1988), Gomez et al. (1994), and Diaz (1995). Another approach by Dustan (1994) assessed the incidence of damage to colonies. They reported that 60% of the nearly 10,000 colonies examined showed signs of physical or biological stress. Recently, Lewis (1997) used this same method of estimating partial mortality of *Siderastrea siderea* along a gradient of eutrophication in Barbados.

Previous information on coral condition of Florida reefs. - Most, but not all, of the

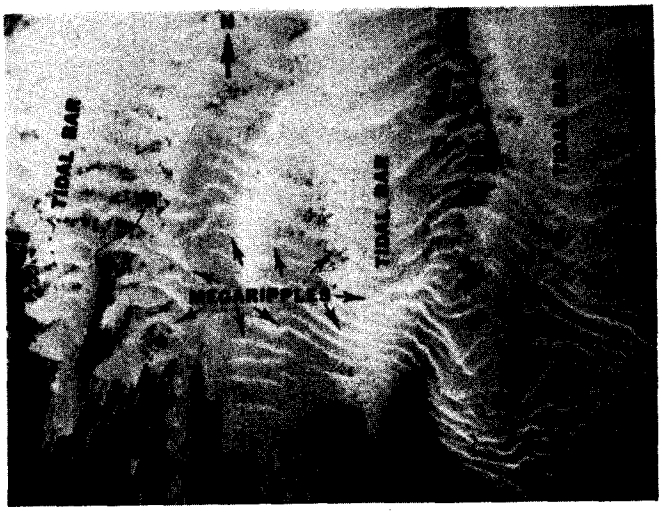


FIGURE 26 Vertical aerial photograph of *Halimeda* sand bars and megaripples in Quicksands area west of Marquesas Keys. Dark areas are populated by marine grasses and live *Halimeda*.

(Fig. 28).

The area west of the Quicksands, beginning at the west edge of Halfmoon Shoal, is deeper, between 18 and 24 m (60-80 ft), and is composed mostly of carbonate mud and silt. This area, from Halfmoon Shoal to the Dry Tortugas, has received little study. The deeper shelf areas have been studied by Holmes (1985), who has obtained seismic profiles that show a surprising amount of platform accretion at depths below 300 m (983 ft).

One large, shallow-water, reeflike area, Rebecca Shoal, occurs in this region and to our knowledge, it has not been studied. The reefs and islands of the Dry Tortugas, on the other hand, have been examined by many researchers, especially by biologists, during the period between 1910 and 1939.

Sediment Transport

Large, high-energy waves and storm tides produced by hurricanes are the most effective sediment transporters. Winds caused by northeasters produce smaller seas but nevertheless are also effective movers of sediment. Ball *et al.* (1967) reported that hurricane storm seas moving in a landward direction in the upper Keys transported enormous quantities of sand and boulder-size coral rubble. Such movement was especially no-

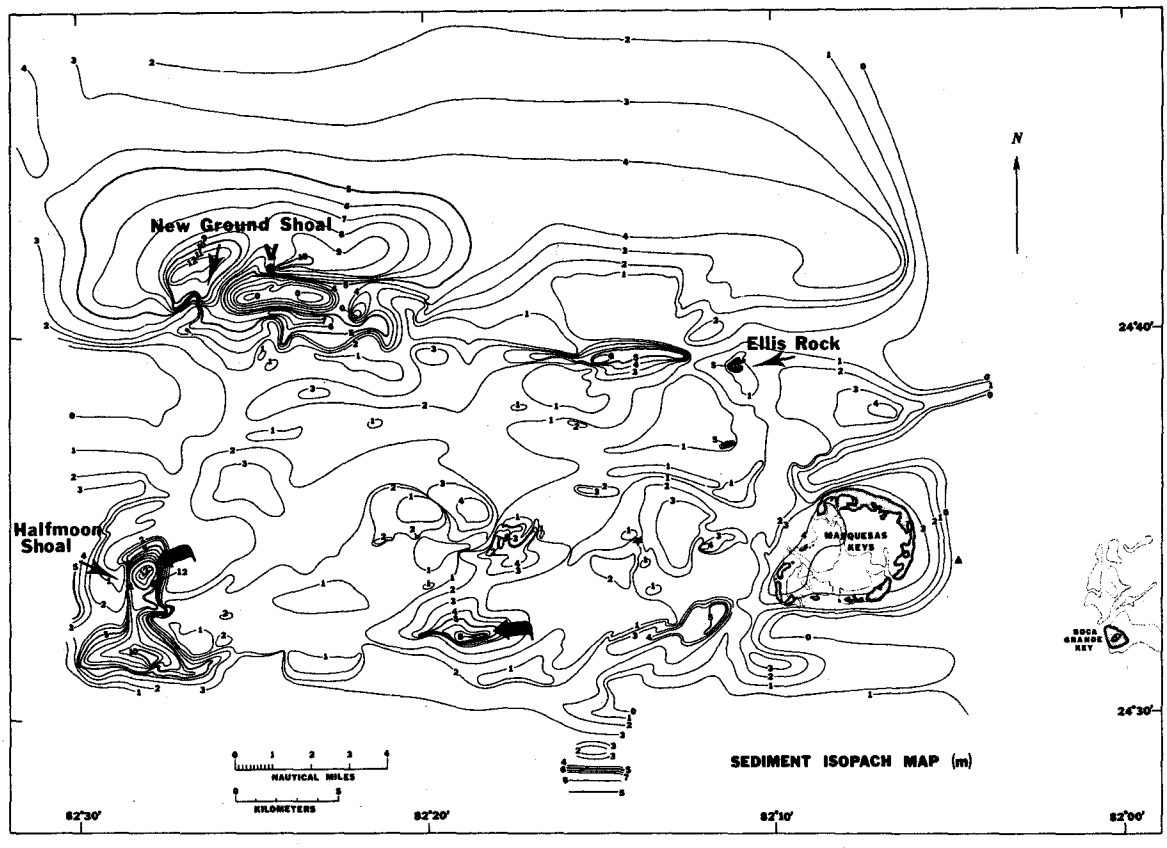


FIGURE 27 Isopach of sediments west of Marquesas Keys, based on high-resolution seismic profiles and vibracores. Area between Marquesas Keys and Halfmoon Shoal looks like area shown in Figure 23. Note thickness of sediment at Halfmoon Shoal. Newground Shoal and trend of thick-sediment areas extending to Ellis Rock are composed of massive corals. Branching corals *Acropora palmata* and *A. cervicornis* do not live on these reefs.

Diploria have less dead tissue than most other species and *M. annularis* generally has more than other species.

The amount of dead tissue on clusters of colonies >1 m was measured by monitoring along radial transect lines. It shows the same large variations within and between reefs as found for the smaller specimens. However, the amount of dead tissue on 60% of the 65 clusters measured is between 40-70%, much larger than on smaller colonies. The amount of dead tissue in the clusters in the Middle and Lower Keys is significantly higher than for clusters off the Upper Keys (Key Largo-Elliot Key) according to the Kruskal-Wallis analysis of variance.

Given the overall marginal conditions for reef corals in the Florida Reef Tract – periodic low or high temperatures; periodic high turbidity, locally unfavorable water quality – we believe that the condition of massive corals does not show clear evidence of direct anthropogenic impacts. Our results do indicate the negative impacts of storms and of locally unfavorable water quality either in the nearshore zone or from the effluent of shallow, lagoonal Florida Bay.

INTRODUCTION

Numerous reports of declines in the biota of coral reefs worldwide have prompted widespread concern about the future of these ecosystems (Brown, 1987; Grigg and Dollar, 1990; Glynn, 1991; Williams and Bunkley-Williams, 1990; Ginsburg, 1994; Hodgson, 1999). Of special concern to the United States and the State of Florida are the declines reported for Florida's reefs, as they are so valuable as a tourist attraction, an educational resource, and for recreational and commercial fishing. In addition to the direct impacts of users - divers, snorkelers, boaters, sport and commercial fishers - the wastes from the large and expanding population on the nearby Florida Keys and mainland are possible contributors to these declines (LaPointe and Clark, 1992; Porter and Meier, 1992; Hudson et al., 1994; Chiappone and Sullivan, 1997)

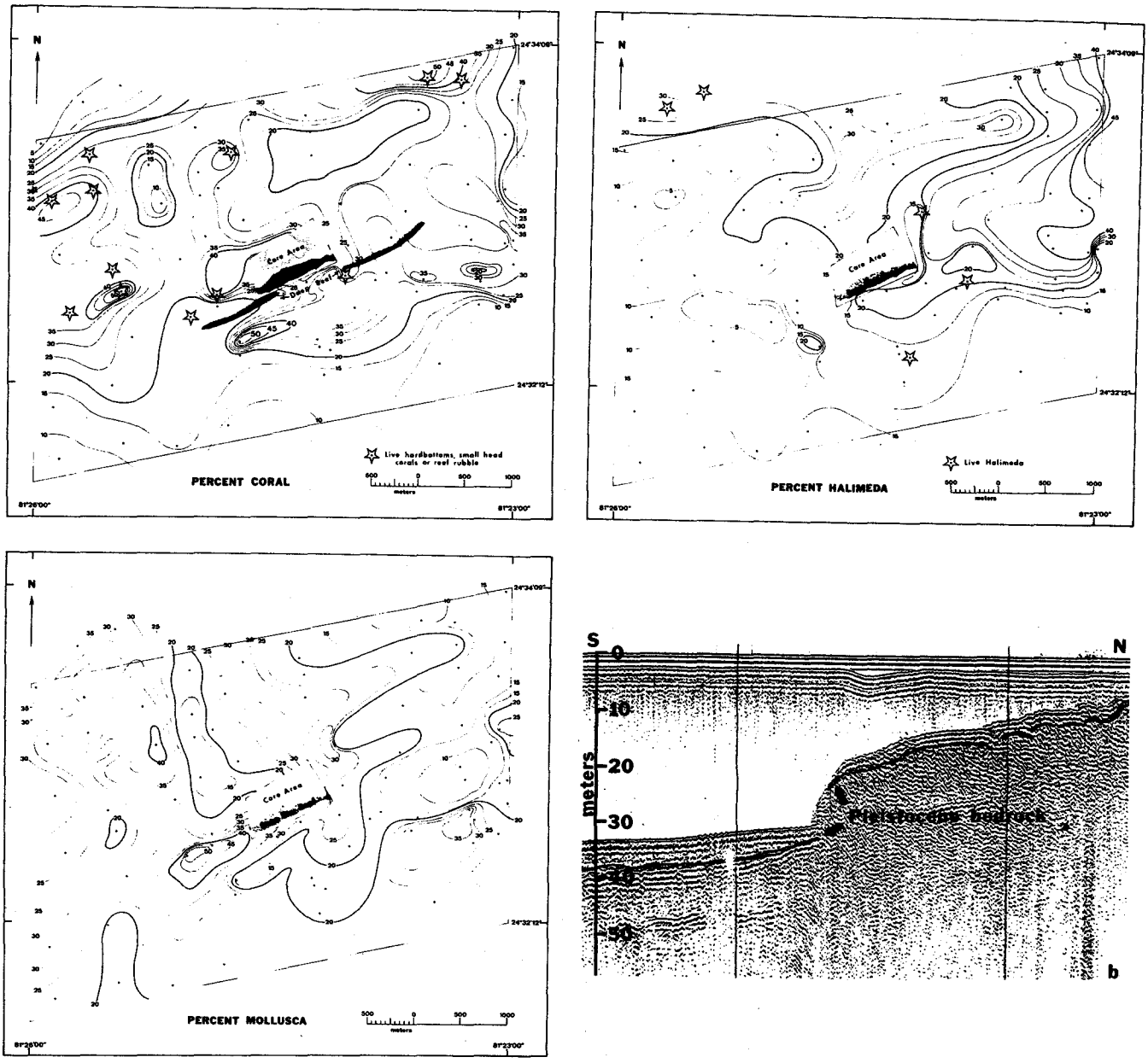


FIGURE 25 Major sediment constituents in Looe Key Sanctuary area. High-coral content in (A) closely corresponds to reef areas shown by stars. *Halimeda spp.* and mollusc compositions are shown in (B) and (C). (D) shows sediment above Pleistocene limestone at prominant dropoff seaward of Looe Key Reef. High-resolution seismic-reflection profile from Lidz *et al.* (1985).

(Hudson, 1985). In areas of dense *H. opuntia* growth, 1,250 g/m² were produced per year. The closest area of coral growth is at Ellis Rock and New Ground Shoal, north of and separated from the Quicksands by a 9-m-deep (30 ft) sediment-free zone more than 1 km (0.6 mi) wide. A hardground area and scattered patch reefs to the south are also separated from the Quicksands by deeper water. Thus, there are essentially no areas of coral production within the 28- by 47-km zone (17 by 29 mi) defining the Quicksands, where *Halimeda spp.*. the main sediment producer, grows in cushionlike clumps in turtlegrass-stabilized areas between migrating submarine dunes.

East-west-oriented carbonate-sand megaripples ornamenting the sediment surface of the Quicksands are commonly as high as 3 m (10 ft) and are perpendicular to north-south-reversing tidal currents (Fig. 26). The trend of the platform on which the Quicksands are located is east-west, however, and thus parallel to prevailing wind direction (Fig. 27). Increasing thickness of sediment to the west, as shown by high-resolution seismic-reflection profiling, led Shinn *et al.* (1982) to conclude that although tidal currents flow north-south, the net movement of sand is to the west

PARTIAL MORTALITY OF MASSIVE REEF-BUILDING CORALS: AN INDEX OF PATCH REEF CONDITION, FLORIDA REEF TRACT

Robert N. Ginsburg[1], *Eberhard Gischler*[2] *and William E. Kiene*[3]

ABSTRACT

Patch reefs are by far the most numerous reef type of the Florida Reef Tract. As they occur along the inner shelf, they are the nearest reefs to potential anthropogenic impacts from the islands of the Florida Keys – runoff of pollutants, fishing, boating, and diving. Massive corals of four genera (*Montastraea spp., Diploria spp., Siderastrea siderea,* and *Colpophyllia natans)* are the major reef builders of the patch reefs distributed discontinuously along some 200 km between the latitudes of Miami and Key West. To assess the condition of this coral community, we estimated and measured percent dead tissue of 3,232 colonies by species and size on 22 shallow patch reef sites.

Most colonies have diameters between 10-60 cm; those that are larger, to 300 cm, usually occur in clusters, which provide sheltered cavities for fishes and lobster. The size distributions of all but one of the nine species examined are skewed toward the smaller sizes. The smaller number of larger colonies is believed to be the result of the cumulative effects of disease, bioerosion, and removal by storm waves.

For colonies <1 m in diameter, we made visual estimates of percent dead tissue by thirds (< 1/3, 1/3-2/3, >2/3) of each colony. Large variations are the rule at most sites and between sites. However, of all colonies combined 74% have less than 1/3 dead tissue, with only a small standard deviation, and cluster analysis revealed no major spatial variations. Overall, species of

have been previously discussed. Additional effects are caused by hurricanes and storms. The devastating effects of Hurricane Donna in 1960 were described by Ball *et al.* (1967) and of Hurricane Betsy in 1965 by Perkins and Enos (1968). Ball *et al.* (1967) noted that hurricanes impact the area of reef growth on the average of once every 6 years; thus, during the last 8,000 years that the shelf was flooded, it should have been impacted by such natural events approximately 1,333 times. The devastation of a hurricane like Donna occurring 1,000 times, or only 500 times, helps explain why corals have not gained as much ground as their growth rates would predict.

Another factor that retards reef accumulation in the long term is disease. In Bermuda, Garrett and Ducklow (1975) reported that many nearshore colonies of *Diploria labyrinthiformis* and *D. strigosa*, the major reef builders there, are affected by the so-called black-band disease. Individual colonies of these species in Bermuda almost never attain a height much greater than 1 m, and their size and growth form may be controlled by the disease. The same disease occurs in Florida, where its most devastating effect is on *Montastraea annularis*. Many large 200-year-old colonies at Carysfort Reef, for example, died between 1978 and 1985. The disease has become rampant at Looe Key Reef in the past few years. The recent outbreaks may be related to the Caribbean-wide epidemic that decimated the population of the algae-eating urchin *Diadema spp.* (Lessios *et al.*, 1984). This species is known to ascend larger coral heads at night and feed on algae-infested diseased areas. Hallock and Schlager (1987) concluded recently that the flooding of land and creation of lagoons during rising sea level release nitrates and other nutrients not tolerated by most reef-building and reef-dwelling organisms. Reefs are usually associated with clear, nutrient-poor oceanic waters. Thus, increased sewage and other pollutants as well as natural factors may be causing increasing incidences of disease and algal infestation. *Acropora cervicornis* has been especially affected by disease in recent years. At this writing, most of the *A. cervicornis* thickets that thrived at Carysfort, Grecian Rocks, and Dry Tortugas 3 years ago is dead (see photographs in Appendix A).

These examples of factors affecting growth of individual corals help explain why a coral reef is not simply a mass of corals growing upward, one upon the other, at the average growth rate of the individual corals, and why corals do not grow everywhere. In light of the natural and man-induced changes over the past few thousand years, it seems surprising that many reefs have kept pace with rising sea level and have continued to flourish.

Sediments

The first comprehensive study of carbonate sediment composition and distribution off the upper Keys was by Ginsburg (1956). Similar research on surface sediments was later done in the middle Keys by Swinchatt (1965), followed by extensive surface- and subsurface-sediment studies in the upper, middle, and lower Keys by Enos (1977). The most recent such study, conducted in the vicinity of Looe Key Reef, was by Lidz *et al.* (1985).

The calcified codiacian alga *Halimeda spp.* has long been considered the dominant sand-size sediment producer throughout the Caribbean. The work of Lidz *et al.* (1985) showed, however, that the sands in the lower Keys adjacent to Looe Key Reef are composed predominantly of coral with subordinate particulate mollusc and *Halimeda* fragments (Fig. 25 A-C). Whereas *Halimeda spp.* compose more than 80 percent of the sand grains in the upper Keys, as shown by Ginsburg (1956), and around 50 percent in the middle Keys, as shown by Swinchatt (1965), these components average only about 20 percent at Looe Key (Lidz *et al.*, 1985). Farther west, in the sands west of the Marquesas Keys, *Halimeda spp.* content averages about 48 percent (Shinn *et al.*, 1982). These observations suggest a trend of decreasing *Halimeda*-sand content from north to southwest along the reef tract with increasing *Halimeda* components farther west. Much needs to be done to determine what controls this trend. Lidz *et al.* (1985) concluded that *Halimeda* particles are concentrated in the sediment in areas where reefs are healthy, whereas coralline particles are concentrated where reefs are in a state of decline. Dead corals are more readily attacked by boring organisms, such as sponges, molluscs, algae, and pholad clams, and by parrotfish, thus producing particulate coral, whereas live coral is less subject to bioerosion. Production of *Halimeda* particles is assumed to be more or less uniform, whereas particulate coral content fluctuates depending on reef health.

This explanation does not apply in the region of the Marquesas Keys and Quicksands, however, where both live and dead reefs are poorly represented and there is little source for coral particles. Reef growth there is prevented by cold winter-water temperatures, unimpeded flow of sediment-laden water from the Gulf of Mexico, and by shifting carbonate-sand megaripples (Shinn *et al.*, 1982). *Halimeda spp.* thrive, however.

In a year-long study of growth rate in *Halimeda opuntia* in the vicinity of the Marquesas, Hudson (1985) found growth was suspended during cold winter months when water temperature averaged 19°C but flourished during the summer when temperatures ranged between 28 and 31°C. For example, a single live *H. opuntia* plate proliferated to produce 3,000 individual plates in 125 days

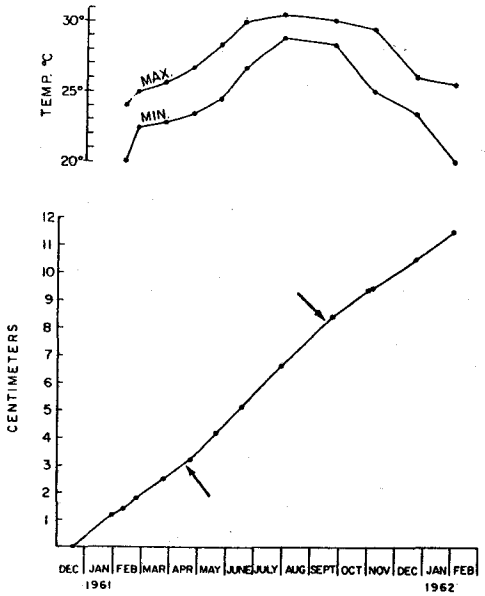


FIGURE 24 Graph of maximum and minimum temperatures and growth rate of the branching coral *Acropora cervicornis* at Grecian Rocks. Note inflection points (arrows), demonstrating effect of water temperature on growth rate. Colonies transplanted nearshore bleached due to loss of zooxanthellae when temperature exceeded 30°C and growth ceased. Growth resumed and became rapid when corals regained zooxanthellae as temperature fell to the 20 - 30°C range, but they died when it dropped below 13°C (Shinn, 1966).

new branch grows approximately 10 cm (4 in.) until the following year, when it branches into three; thus, this species produces branches at a phenomenal geometric rate. For example, a small colony with 10 branches has the potential to produce 65 km (35 mi) of branches in 10 years. This extraordinary potential for growth, combined with the susceptibility to breakage during storms and other causes, explains why its broken branches are so abundant in sediments hundreds of meters from reefs.

Diploria strigosa and ***D. labyrinthiformis.*** Of the various brain corals, only *Diploria strigosa* and *D. labyrinthiformis* have been studied using sclerochronology. Dodge and Vaisnys (1975) used the method on *D. strigosa* in Bermuda waters and determined an annual growth rate of approximately 3.3 mm/yr. Ghiold and Enos (1982) made extensive measurements of *D. labyrinthiformis* in the area of Key Largo and determined an annual rate of 3.5 mm/yr. None of the other massive brain corals has been analyzed, but it is likely their rate of growth is similar to that of *D. strigosa*.

Solenastrea bournoni. This massive coral, although uncommon on the reef tract, can grow to a height of a meter or more in the stressful environment of Florida Bay. Hudson *et al.* (1989) found a growth rate of 8.9 mm/yr. The rate is an average derived from a single colony over 100 years old.

Porites porites. Using the Alizarin Red-S stain method, Landon (1975) found that this branching form of *Porites* grew 16 mm/yr at Sambo Reef off Key West.

Dendrogyra cylindrus. In a preliminary unpublished experiment by Hudson using the Alizarin Red-S stain method, the pillar coral has been found to grow 5 mm/yr on patch reefs off Elliott Key in the upper Florida Keys. The species can be easily transplanted.

Siderastrea siderea. Resistant to cold and sedimentation, this hardy, massive coral is an important member of mid- and inshore patch reefs. A growth rate of 2.4 mm/yr for this species was determined by Landon (1975) at Sambo Reef.

Implications of Coral Growth

One implication of the various coral growth rates is that corals should easily keep pace with rise in sea level. Indeed, in many places corals, together with calcareous algae and other carbonate producers, have accumulated reefs 9 to 13 m (30-45 ft) thick that are awash at low tide. Consider the two main builders, *Montastraea annularis* and *Acropora palmata*. At approximately 1 cm/yr, *Montastraea annularis* can grow upward 1 m/100 yrs or 10 m/ka. Even at half that rate (about the minimum growth rate measured), this species could grow 5 m/ka. During the past 6,000 years (the oldest C^{14} date on coral growing on Pleistocene bedrock), the maximum rate of sea-level rise has been about 1 m/ka (Fig. 16).

Acropora palmata, whose growth rate is at least 10 times that of *Montastraea annularis*, theoretically could grow an astounding 100 m/ka. Because of its rapid growth, this species generally grows upward to sea level and dies for lack of space. The reef flats, such as those at Carysfort and Grecian Rocks Reefs, are good examples of *in situ Acropora palmata* that grew to low spring-tide level and died (Fig. 8). Once such reef flats form, growth is then restricted to expansion landward and seaward of the flats.

A consideration of the rapidity with which corals grow, compared to the rate of sea-level rise, indicates that coral reefs are complex and that upward accumulation of coral reefs is not continuous, but that it is frequently interrupted for long periods. As noted earlier, accumulation rates for Florida reefs fluctuate between 1.31 and 4.85 m/ka (see Shinn *et al.*, 1977; Lidz *et al.*, 1985). The fastest rates, based on C^{14} dating of corals from reef cores, are at St. Croix, where Ady (1975) measured rates as high as 15 m/ka.

Why have corals not continuously kept pace with rising sea level everywhere in Florida? The effects of lagoonal waters with their fluctuating temperatures and salinities and sediment content

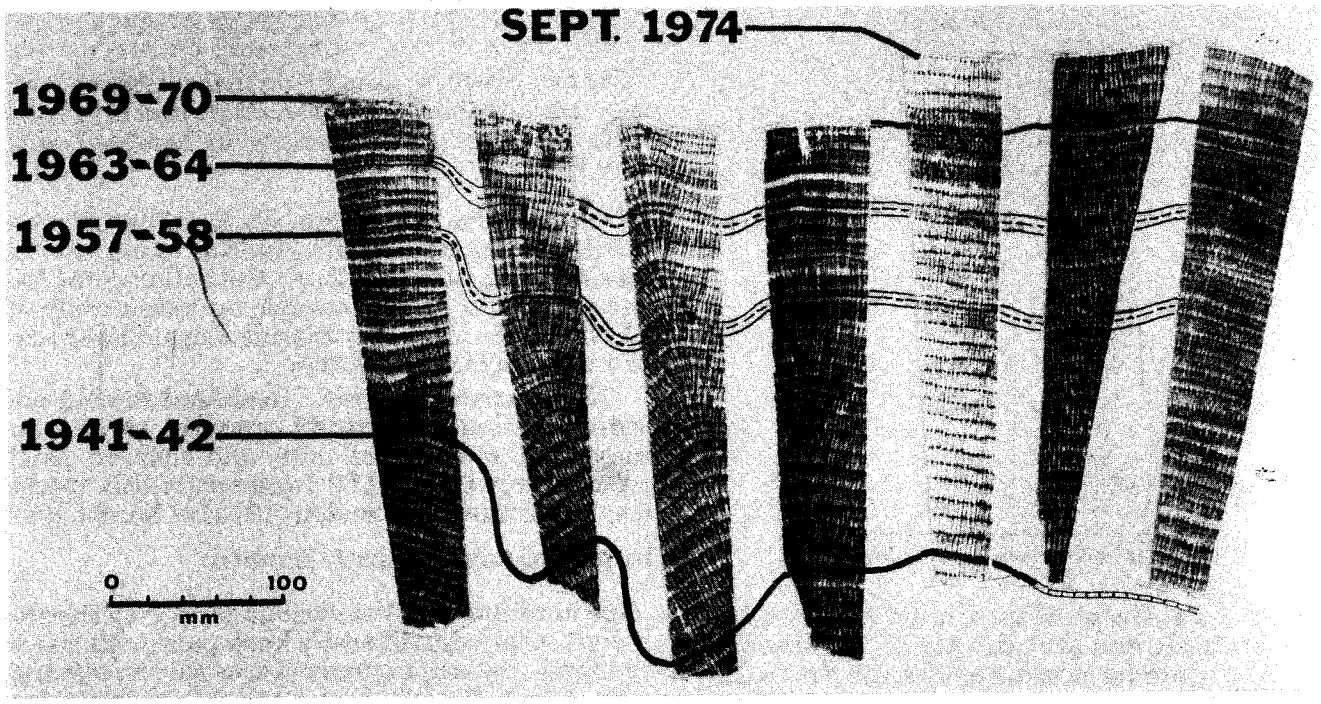


FIGURE 22 Correlation of annual bands in cores drilled in individual *Montastraea annularis* heads at Hen and Chickens patch reef (Hudson *et al.*, 1976). Four heads to left were killed during unusual cold-water outbreak in winter of 1969-1970, while three heads to right survived. A distinct stress band was deposited in survivors during the outbreak. All the corals survived previous cold-water outbreaks that caused stress bands in winters of 1941-1942, 1957-1958, and 1963-1964. A more recent and very severe outbreak of cold water occurred in the winter of 1977, which produced a stress band in many *M. annularis* heads in south Florida.

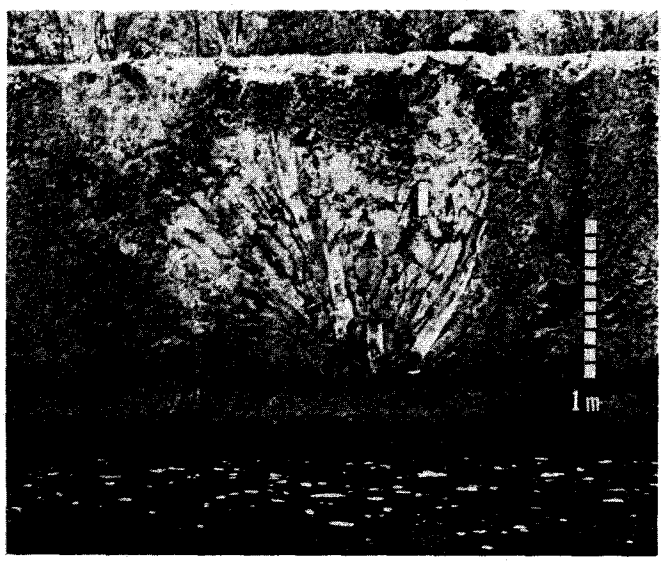


FIGURE 23 Pleistocene *Montastraea annularis* head exposed in Adams Waterway through Key Largo Formation. Counting of annual bands in X-ray photographs of material removed with power saw showed head is 360 years old; thus, section revealed above water in this area was deposited at 125 ka within a 300- to 400-year period.

curving branches, growth rates are difficult to measure. A definitive study of its growth rate in the Florida Keys has not been done. Studies elsewhere in the Caribbean, however, indicate linear growth rates on the order of 10-12 cm/yr (Lewis *et al.*, 1968). Although difficult to measure, its growth is fast enough to heal breaks by storm damage and boats in less than 5 years.

Acropora cervicornis is not a major reef-frame builder but dominates many areas immediately behind reef flats formed by *A. palmata*. *Acropora cervicornis* is a major contributor to sediments away from reefs. Sticklike fragments can be found in almost any excavation dug within 4 km (2.5 mi) of the platform margin. Fragments are especially abundant in sandy areas opposite the major tidal passes of the middle Keys, where very few living examples can be found today.

By transplanting and placing plastic bands on the rod-shaped branches, Shinn (1966) found that under ideal conditions, *A. cervicornis* at Grecian Rocks (called Key Largo Dry Rocks in Shinn, 1966) grew approximately 10 cm (4 in.) per year. Growth rate was found to be correlated with temperature, i.e., the species grows more slowly during winter and faster in the summer (Fig. 24). Later work (Shinn, 1976) showed that this species branches during winter months (January and February) and that each branch forks annually, forming two to five branches with an average of three. Each

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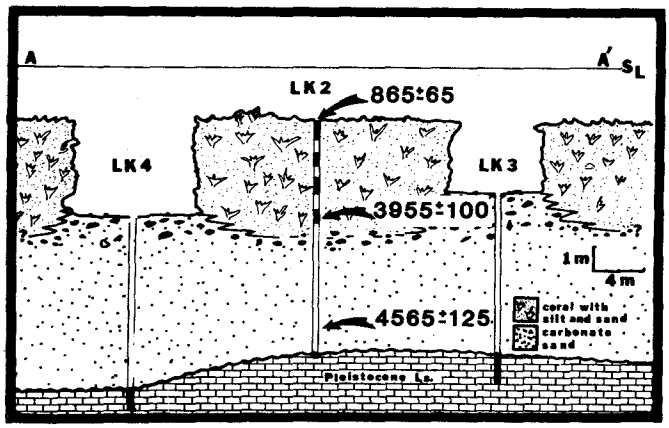


FIGURE 21 Cross section based on cores drilled across spur-and-groove system at Looe Key Reef. Spur is composed of *Acropora palmata* and is underlain by carbonate sand, demonstrating that spur is not controlled by Pleistocene topography.

grooves where carbonate sand accumulates.

Coral Growth Rates

The purpose of this section is to review growth rates of the major reef builders and to relate growth rate with rates of reef accumulation and reef distribution.

The first growth-rate experiments on corals from Florida were conducted in the early 1900s at the Carnegie Institution field station at Loggerhead Key in the Dry Tortugas. Principal among the coral investigators were Mayor (1914) and Vaughan (1915). Diving as we know it today had not yet developed, so experimentation was restricted to reef corals placed on tiles in shallow nearshore waters and in large laboratory aquaria. Temperature-tolerance experiments performed at the Loggerhead field station for the major reef builders still provide the most reliable data available (Mayor, 1914).

Later experiments on coral growth rates were performed at Carysfort Reef by J. E. Hoffmeister (1960, unpubl. data), who measured growth rates of *Acropora palmata*, *A. cervicornis*, *Dichocoenia spp.*, *Diploria spp.*, and *Montastraea annularis*. Measurements were made by weighing and measuring corals cemented to cement tiles, as had been done at the Tortugas laboratory. The presence of annual growth bands in *M. annularis* was not recognized at that time; thus, the more recent measurements, using the new method of sclerochronology pioneered by Knutson *et al.* (1972) and perfected for the Florida area by Hudson (1981b), provide much more accurate growth data (Fig. 22). Entirely subsurface methods employed by Shinn (1966) on *Acropora cervicornis* provided growth rates approximately double those of Vaughan (1915). These measurements and those of Hudson (1985) for transplanted *Montastraea annularis* have helped define how temperature and the inimical lagoonal waters control reef and coral distribution near shore and opposite major tidal passes.

Montastraea annularis. *Montastraea annularis* was one of the major reef builders during the Pleistocene and Holocene. The major constructor of the Pleistocene Key Largo Formation that forms the upper and middle Keys, this species of coral is the underpinning of Holocene reefs. In addition to being a component in outer linear reefs, it is the major component of Holocene patch reefs everywhere in Florida.

On the basis of more than 7,000 band measurements from 144 specimens of 50-year-old *Montastraea annularis* in different environments in the Key Largo Coral Reef Marine Sanctuary, Hudson (1981b) found that growth rates averaged 8.2 mm/yr in nearshore patch reef areas and 6.3 mm/yr in offshore waters deeper than 6 m (20 ft). Maximum rates of 11.2 mm/yr were found in shallow (less than 3 m or 10 ft deep) areas near the platform margin, such as at Grecian Rocks and Carysfort Reef. These studies also showed how growth rates have fluctuated through time, how they are a function of environmental conditions, and how extreme cold fronts produce characteristic stress bands. In one case, an unusually severe cold front in 1969-1970 killed 80 to 90 percent of the hundreds-of-years-old *M. annularis* at Hen and Chickens patch reef (Hudson *et al.*, 1976), and the chilling winter of 1957-1958 left its mark in every specimen examined thus far (Fig. 22). Surprisingly, major hurricanes do not appear to affect growth rates or to leave a recognizable signature in the coral skeleton. As a rule of thumb, *M. annularis* heads 1 m (3.3 ft) high are on the order of 100 years old.

The use of sclerochronology to study the health of coral reefs has also been applied to corals of the Pleistocene Key Largo Formation (Hudson, 1978, unpubl. data). A large (2.1 m or 7 ft high) Pleistocene *M. annularis* head exposed in the Key Largo Waterway (also called Adams Waterway) was sampled using a gasoline-driven circular saw (Fig. 23). The V-shaped samples were sawed and X-rayed to enhance annual banding for measurement and counting. Growth rate of this specimen averaged only 5 mm/yr. The same colony, depicted in Hoffmeister and Multer (1964), was estimated by them to be 230 years old by analogy with modern *M. annularis* growth rates of 10.7 mm/yr. Growth rate of this important reef builder during the last Pleistocene highstand, therefore, was only about half that of Holocene *M. annularis*. This finding has significant implications for temperature and environmental conditions during growth of the Key Largo Formation.

Acropora spp. *Acropora palmata* grows rapidly and dominates the surf zone where few other species can get a foothold. Because of its palmlike

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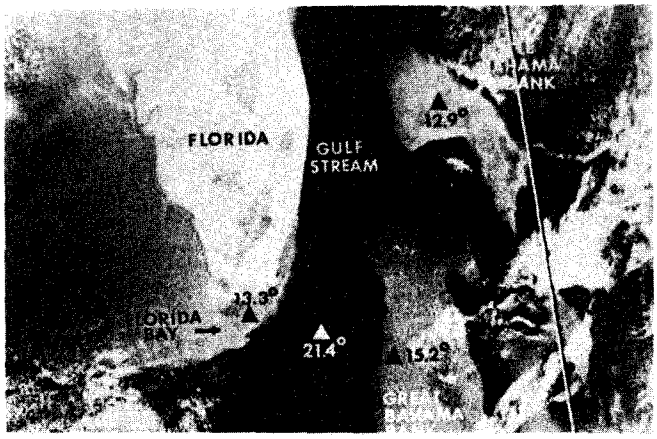


FIGURE 20 Infrared satellite image showing plumes of cold, murky water flowing onto reef tract in lower Keys following a severe cold front. Inshore waters were 13.3°C compared to 21.4°C in offshore Gulf Stream water. Also note temperatures on Bahama Banks. From Roberts *et al.* (1982).

around pre-existing topographic highs and along the platform margin. Sea level at 4 ka was approximately 3 m (10 ft) lower than today. Under such conditions, most of Florida Bay and many of the tidal passes through the Florida Keys did not exist, and water quality along the platform margin, where it was bathed by Gulf Stream water, was more favorable for coral growth than today. As sea level continued to rise to near-present conditions (see Fig. 17E, F), waters from Florida Bay in the vicinity of the middle Keys and from Biscayne Bay to the north slowly killed the principal, faster growing reef builders. Thus, today, only the more hardy, slower growing species of massive corals and non-reef-building gorgonians, sea fans, and *Millepora spp.* survive off the middle Keys.

Earlier, between 6 and 4 ka (see Fig. 17C-F), the flooding and creation of Hawk Channel probably had ecologic effects on certain coral reefs similar to those caused by the creation of Florida and Biscayne Bays. The deleterious effect of backreef lagoonal waters created by rising sea level has been demonstrated in many parts of the world (Neumann and Macintyre, 1985).

REEF FEATURES

Spurs and Grooves

A universal characteristic of reef flanks is the alternation of fingerlike projections, called buttresses or spurs, and channels, called grooves. Spurs and grooves are almost always oriented into the sea, normal to the reef front. They occur on fringing, bank, and barrier reefs, and are poorly developed or absent on patch reefs. Munk and Sargent (1948) showed that their spacing is controlled by wave energy. The larger the waves, the better developed and narrower the spacing. The spacing of spurs and grooves is usually closer and more uniform on fringing reefs than on bank or barrier reefs where there are no shallow reefs or shoals offshore.

Spurs may be erosional, such as those described by Cloud (1959), or constructional, as described by Goreau (1959), Shinn (1963), and Shinn *et al.* (1981). Erosional spurs and grooves are characterized by V-shaped to overhanging profiles, smooth, uncolonized walls, small circular potholes similar to those formed in stream beds, and smooth, circular coral boulders that roll back and forth during heavy seas. Such features have been described from numerous Pacific atolls (Cloud, 1959; Shinn *et al.*, 1986). Some grooves in the Bahamas are cut into cross-bedded Pleistocene eolianite (Newell *et al.*, 1951).

Constructional spurs have overhanging, rough, deeply pitted walls with labyrinthian passages and abundant secondary growth of encrusters such as the lettuce coral *Agaricia spp.*, small solitary corals, and bryozoans. The grooves are usually lined with sand and seldom contain rounded boulders. Spurs may be constructed by species of *Agaricia*, as in Belize (Shinn *et al.*, 1982), or they may be constructed by the head coral *Montastraea annularis*, such as in Jamaica (Goreau, 1959). Most spurs in the Caribbean and Florida, however, are constructed mainly by oriented fronds of *Acropora palmata*, a species that thrives in and just below the surf zone. The fronds are usually oriented away from the sea, but in other areas of the Caribbean, they point into the sea as well. Those that grow laterally into the grooves are periodically broken off by storms (Shinn, 1963).

Core drilling at Looe Key Reef revealed that spurs of *Acropora spp.* formed over a thick section of carbonate sand that overlies the Pleistocene bedrock (Shinn *et al.*, 1981). This observation, shown schematically in Figure 21, demonstrates conclusively that these spurs and grooves were not caused by erosion or inherited bedrock topography. There is little live *A. palmata* at either Looe Key or Molasses Reefs, and at both locations, the spurs are encrusted by a thin coating of the stinging coral *Millepora spp.* or the fleshy zoanthid *Palythoa spp.* (Fig. 9). Only a few reefs off Key Largo, such as Grecian Rocks and Key Largo Dry Rocks, have spurs formed of living *Acropora palmata* (Fig. 11), and they are poorly developed by Caribbean standards.

Whether spurs and grooves are erosional or constructional, they serve as breakwaters to dampen the energy of onrushing waves. They are probably vital to the survival of the reef and provide additional surface area and habitat for a multitude of fish and other marine life. The origin of their spacing is still not understood; however, they perpetuate, because storm seas tend to clear out any corals that may become attached in the

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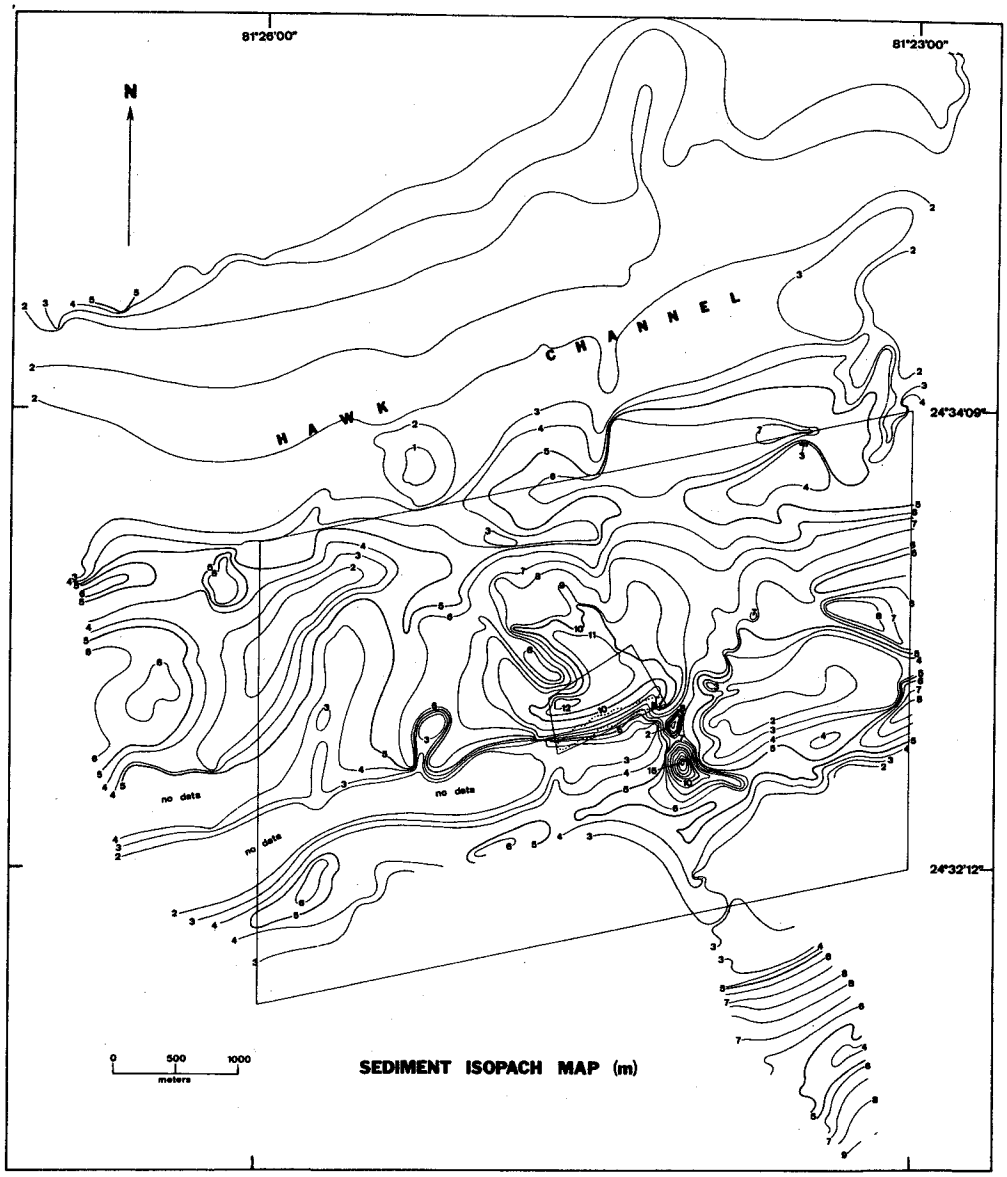


FIGURE 19 Sediment isopach of the Looe Key Sanctuary area, based on high-resolution seismic-reflection profiles. Note 12-m-thick sediment accumulation landward of reef. Reef is outlined by dotted lines within trapezoidal "core" area near center of Sanctuary (from Lidz *et al.,* 1985).

stressed nearshore environment, was also killed in 1977, when water temperature off the middle Keys dropped to 9°C for 4 hours (Hudson, 1981a). Unusually cold water killed 80 percent of the head corals at Hen and Chickens Reef (seaward of Snake Creek) in the winter of 1969-1970 (Hudson *et al.*, 1976).

Elevated water temperature can be equally detrimental to corals, causing loss of zooxanthellae and bleaching (Shinn, 1966), and if elevated temperature above 30°C is prolonged, many species die (Jaap, 1979; Glynn, 1988). These and other observations support the contention that waters of both high and low temperatures, variable salinity, and high-sediment content emanating from Florida Bay and the Gulf of Mexico are the cause of morbid reefs off the tidal passes of the middle Keys.

It should be noted, however, that there are several large, albeit dead, Holocene reefs off the middle Keys, proving that reefs flourished there before sea level rose to its present position. Exposures created recently by ship groundings and core drilling (Shinn, 1963; Shinn*et al.*, 1981) show that the major constructor of these senescent reefs was *Acropora palmata*, the species presently building reefs throughout the Caribbean and off the upper and lower Keys. C^{14} dating of *A. palmata* from the upper and lower Keys, i.e., Molasses, Alligator, and Looe Key Reefs, indicates they flourished from 4 to 2 ka (Robbin, 1981; Shinn *et al.*, 1981). These data suggest that before 4 ka, and before Florida Bay reached its present state of development, coral reefs were growing over and

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the exception of the well-developed spurs and grooves on the seaward side of Looe Key Reef, the east-west relief of the underlying bedrock in this area clearly controlled the formation and shape of Hawk Channel, the formation and shape of islands through time, the development of Holocene coral reefs, and the accumulation of sediment. Note in Figure 18A that the area of the Sanctuary, which was land in 15 ka, is located on the seaward edge of a broad east-west ridge that parallels a bedrock low to the north.

The first incursion of water into a topographic low behind the ridge edge occurred at about 14 ka. Sea level was 17.3 m (57 ft) below present. At 13 ka, the pond of water immediately behind the bedrock high broadened, and the landward east-west bedrock low was flooded. The shoreline at the deep seaward edge changed little during this 2,000-year period, a reflection of the abruptness of the coral-encrusted dropoff, which is more pronounced here than at anywhere else of similar depth along the reef tract (Enos, 1977). At 12 ka (Fig. 18B), the east part of the high that would become Looe Key Reef had become submerged, more ponds had appeared, the broad channel to the north had enlarged, and a small island had formed. Sea level was 14.3 m (47 ft) or more below present. Major flooding of this area off the lower Keys took place between 12 and 11 ka, and numerous islands oriented in an east-west direction were formed, then drowned, as the main shoreline continued to retreat north. By 11 ka, the area of the deep reef in front of Looe Key Reef (between the 12.8- and 14.3-m contours) had become submerged, as had the west part of the area of Looe Key Reef. Sediments and coral rubble began to fill the flooded bedrock trough behind the high that became Looe Key Reef. Very little land was left by 10 ka (Fig. 18C), and that exposed to the north had become an island on the seaward edge of the now drowned south part of Hawk Channel (Fig. 17A). By 9 ka, only three small islands remained within the area of the Sanctuary (Fig. 18D), among them a part of the Looe Key Reef bedrock high. Sea level was 10 m (33 ft) below present. According to measurements of bedrock topography, this area of the reef tract was completely inundated by 8 ka. It should be pointed out once more that the position of sea level before 8 ka (more realistically, before 6 ka) is not clearly recognized. The shorelines shown, however, did exist, even though the exact time may be different than shown here. From 8 ka to the present, the timing of shoreline positions is much more precisely known.

Today, the deep reef in front of Looe Key Reef is buried beneath a westward-moving lobe of carbonate sand. East and west of the sand-covered portion. the exposed parts of this older reef are ornamented with closely spaced spurs and grooves. These spurs have not been core drilled to determine the age or species of corals that formed them. Core drilling at Looe Key Reef, however, has revealed that coral growth was initiated at approximately 6.6 ka on the Pleistocene coralline limestone ridge at the edge of the abrupt seaward dropoff (Fig. 13; Shinn *et al.*, 1981). The reef, composed primarily of *Acropora palmata*, transgressed (backstepped) landward with rising sea level until it reached its present position overlying a sand- and coral rubble-filled depression (Fig. 19). Using an average sediment thickness in the area of 5.7 m (19 ft) and radiocarbon dates of Shinn *et al.* (1981) from material near the base of a rock core from Looe Key Reef, Lidz *et al.* (1985) calculated an average rate of reef accumulation of 1 m/ka since the beginning of coral growth. This rate, together with those calculated elsewhere in the Florida reef tract, shows the variability of reef growth, ranging from 1.36 m/ka to 4.85 m/ka (Shinn *et al.*, 1977). There are large areas throughout the reef tract, however, where there has been no reef accumulation, i.e., 0 m/ka. Within the sediment-filled bedrock depression immediately landward of Looe Key Reef, the average rate of lime-sand sedimentation has been on the order of 2 m/ka (Lidz *et al.*, 1985).

Corals versus Inimical Water

Florida Bay is well known for its numerous lime-mud banks and mud islands. The water is usually turbid from suspended sediment, and salinity fluctuates from 30 to 40 ppt in the region west of Key Largo and from 10 to 60 ppt in northern Florida Bay near the mainland (McCallum and Stockman, 1964). Water temperature ranges from 15 to 37°C and has been measured as low as 9°C in a tidal pass (Snake Creek) through the Keys (Hudson, 1981a). Ginsburg and Shinn (1964) noted the sparsity of thriving reefs opposite the large tidal passes of the middle Keys and suggested that quality of water emitted through those passes was detrimental to coral gowth. Ball *et al.* (1967) noted that, following passage of Hurricane Donna in 1960, soupy, sediment-laden water poured from the passes and inundated offshore reefs for several days. More recently, using satellite infrared spectral data, Roberts *et al.* (1982) mapped plumes of cold, sediment-laden bay water that passed for 8 days in 1977 over reefs opposite major tidal passes in the middle Keys (Fig. 20).

Coral transplanting experiments using the temperature- and sediment-sensitive reef coral *Acropora cervicornis* showed the coral was killed when water temperature dropped to 13°C (Shinn, 1966). *Acropora palmata,* the principal reef builder, is equally temperature sensitive. When transplanted to a 2-m-deep (6.5 ft) coral patch at Dry Tortugas (Hudson and Shinn, 1976, unpubl. data), *A. palmata* was killed along with hundreds of acres of *A. cervicornis* thickets during passage of an unusually severe cold front in 1977 (Porter *et al.*, 1982). The much hardier *Montastraea annularis*, whose growth rate was monitored in a

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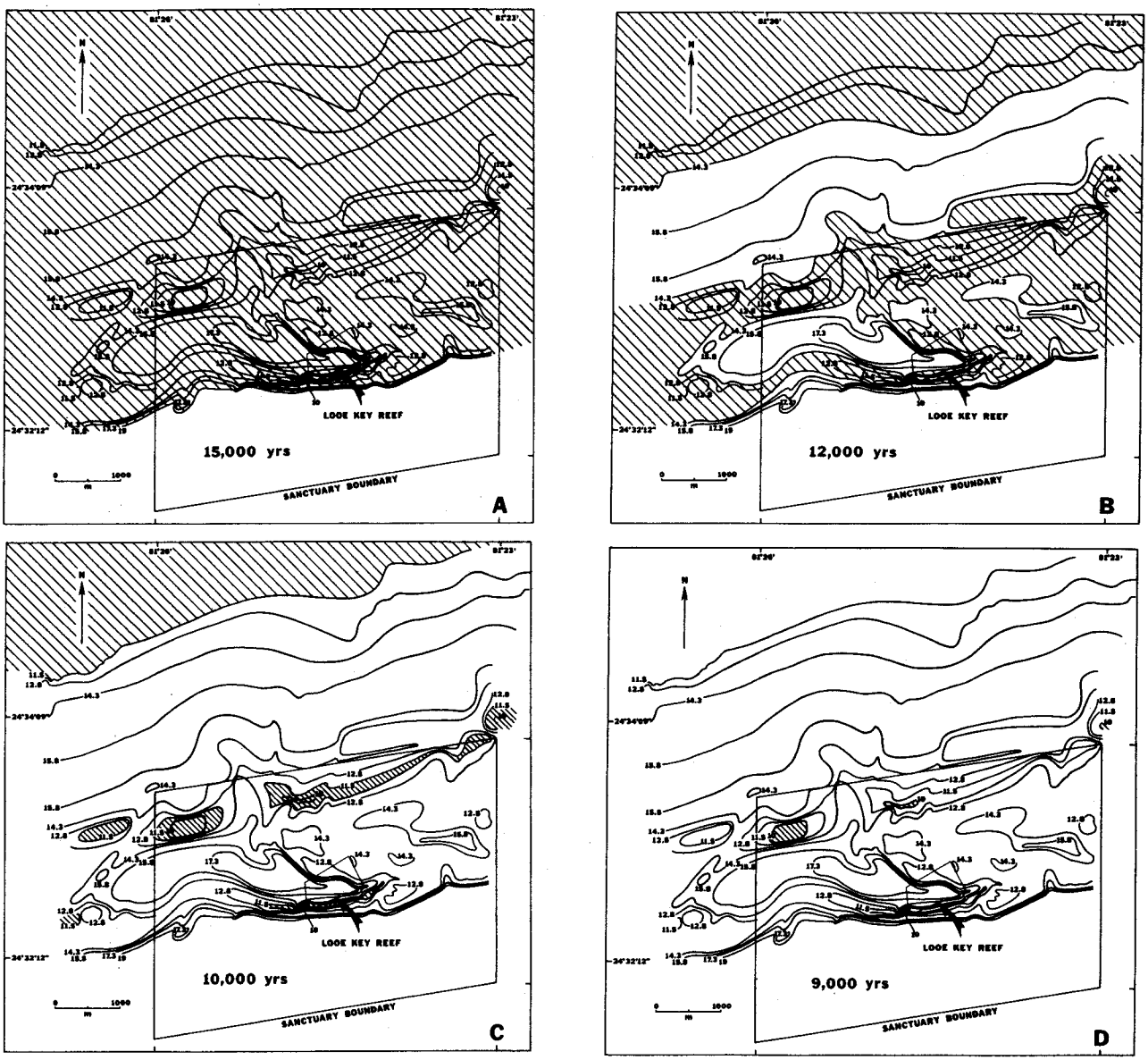


FIGURE 18 The shoreline and land (shaded area) in the Looe Key Sanctuary between 15 and 9 ka. Shoreline at 15 ka (A) is approximate. By 12 ka (B), Hawk Channel and a rock floor depression behind Looe Key Reef were flooded. By 10 ka (C), the high beneath Looe Key Reef and a chain of three high areas on the south side of Hawk Channel were islands. Today, a trend of patch reefs is located over these topographic highs. By 9 ka (D), only two of the three islands remained, and the main shoreline had migrated northward. Between 9 and 6 ka, the entire area became submerged. Carbonate sediments presently fill the topographic lows, whereas coral reefs occupy the highs.

of and between Vaca and Bahia Honda Keys; and Biscayne Bay had flooded. At 2.8 m (9 ft) below present sea level, the seaward edge of the shoreline ranged from 1 to 4 km (0.6-2.5 mi) from the present shoreline.

By 2 ka, the shoreline of the Florida Keys looked very similar to that of today (Fig. 17E, F). Virtually all the topographic lows had been flooded, as had areas of both Florida and Biscayne Bays. Sea level was just 0.5 m (1.6 ft) lower than today.

Looe Key Reef Shorelines

Interpretation by Lidz *et al.* (1985) of 114 km (70 mi) of closely spaced high-resolution seismic-reflection profiles collected in Looe Key National Marine Sanctuary permitted fine-scale mapping of bathymetry, bedrock topography, and sediment thickness in this area. The series of maps shown in Figure 18A-D is based on more detailed Pleistocene bedrock topography than the regional maps and shows the relatively rapid retreat of the shoreline and submergence from 15 to 9 ka. With

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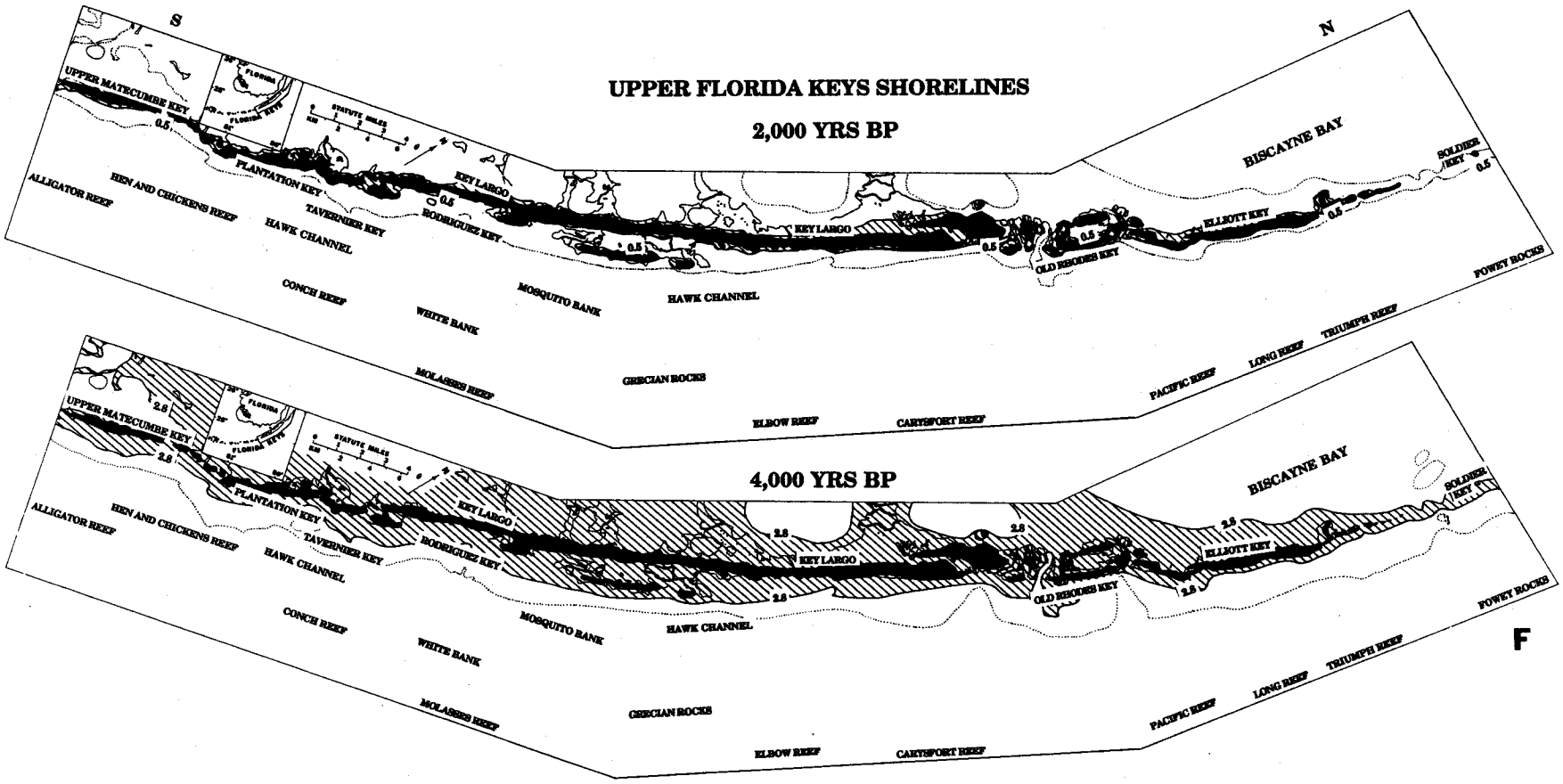
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UPPER FLORIDA KEYS SHORELINES
2,000 YRS BP
S
N
UPPER MATECUMBE KEY
FLORIDA KEYS
STATUTE MILES
PLANTATION KEY
KEY LARGO
BISCAYNE BAY
SOLDIER KEY
ALLIGATOR REEF
HEN AND CHICKENS REEF
TAVERNIER KEY
RODRIGUEZ KEY
HAWK CHANNEL
ELLIOTT KEY
OLD RHODES KEY
FOWEY ROCKS
CONCH REEF
WHITE BANK
MOSQUITO BANK
MOLASSES REEF
GRECIAN ROCKS
ELBOW REEF
CARYSFORT REEF
PACIFIC REEF
LONG REEF
TRIUMPH REEF
4,000 YRS BP
F

T176: 17

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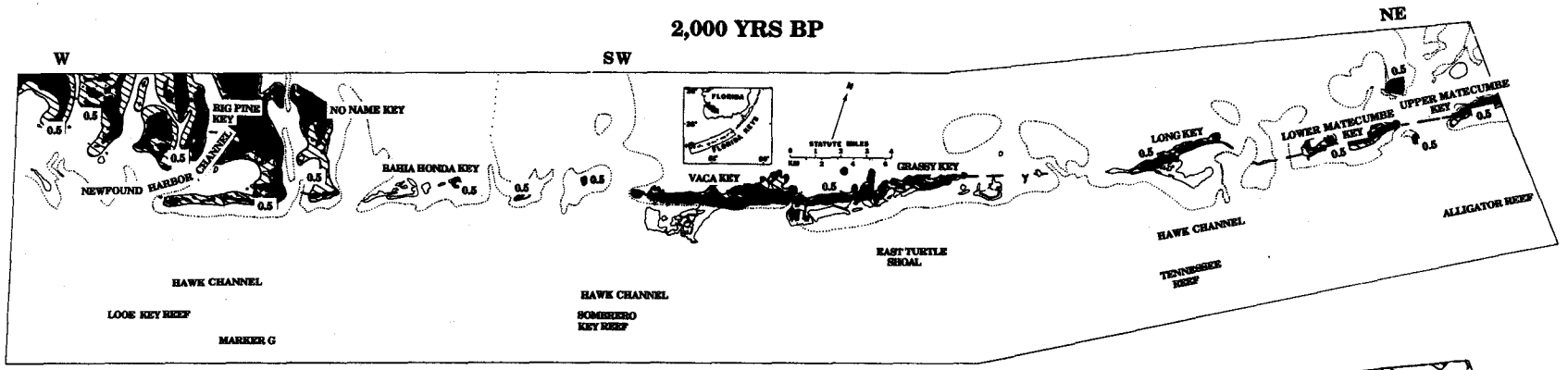
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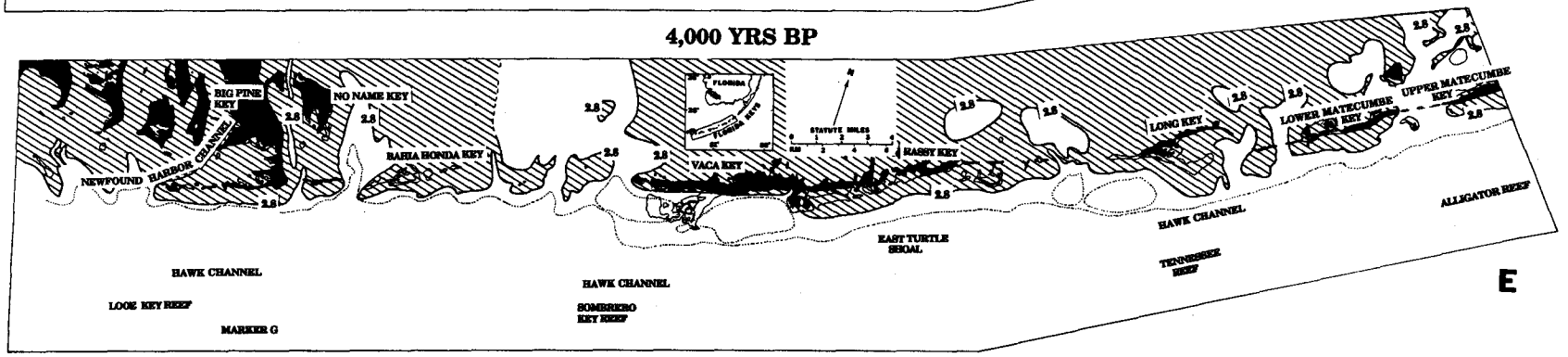
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LOWER AND MIDDLE KEYS SHORELINES

2,000 YRS BP



4,000 YRS BP



T176: 16

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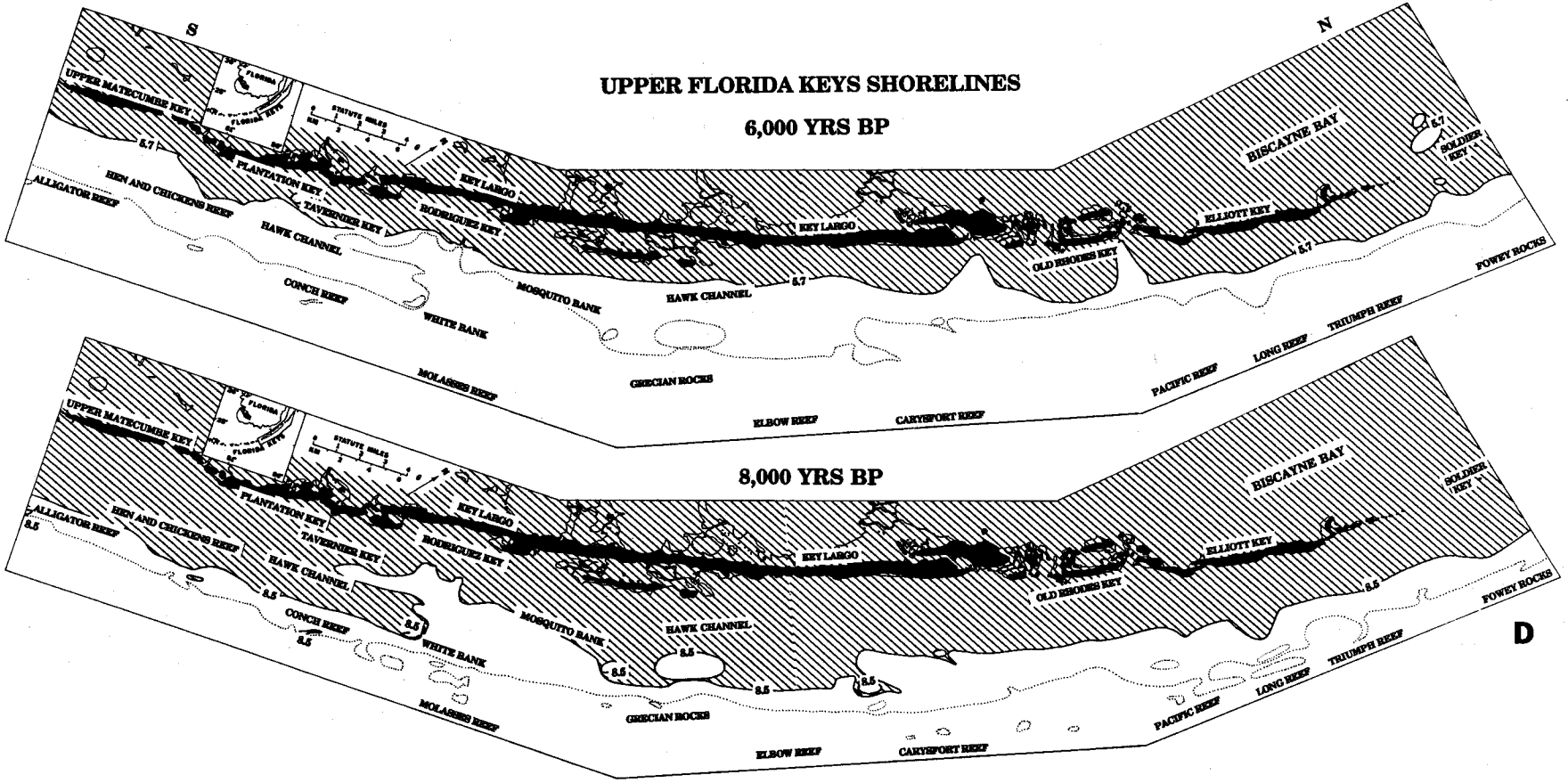
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UPPER FLORIDA KEYS SHORELINES
6,000 YRS BP
S
N
UPPER MATECUMBE KEY
FLORIDA KEYS
STATUTE MILES
PLANTATION KEY
TAVERNIER KEY
HEN AND CHICKENS REEF
ALLIGATOR REEF
HAWK CHANNEL
CONCH REEF
WHITE BANK
MOLASSES REEF
RODRIGUEZ KEY
KEY LARGO
MOSQUITO BANK
GRECIAN ROCKS
ELBOW REEF
CARYSFORT REEF
BISCAYNE BAY
SOLDIER KEY
ELLIOTT KEY
OLD RHODES KEY
PACIFIC REEF
LONG REEF
THUMPS REEF
FOWEY ROCKS
8,000 YRS BP
D

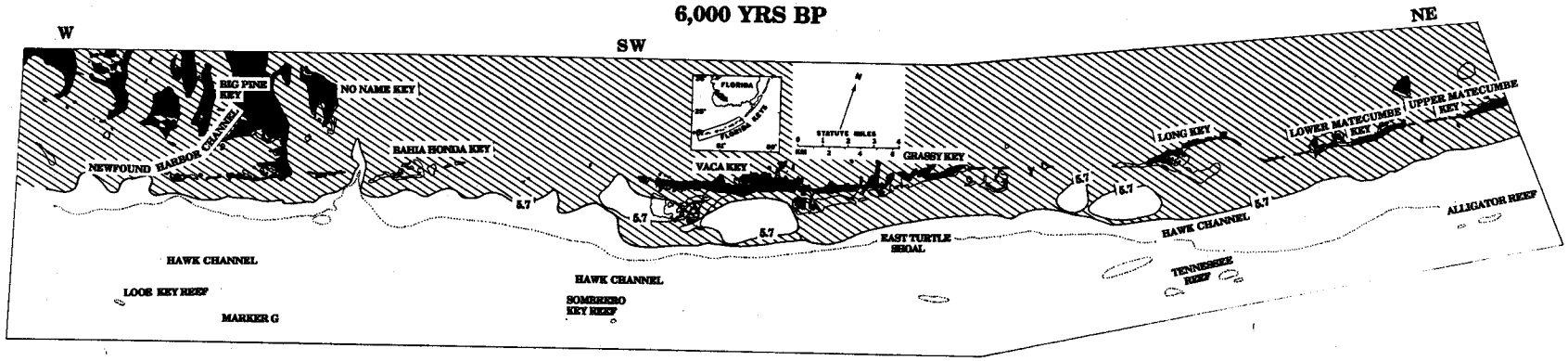
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Summary

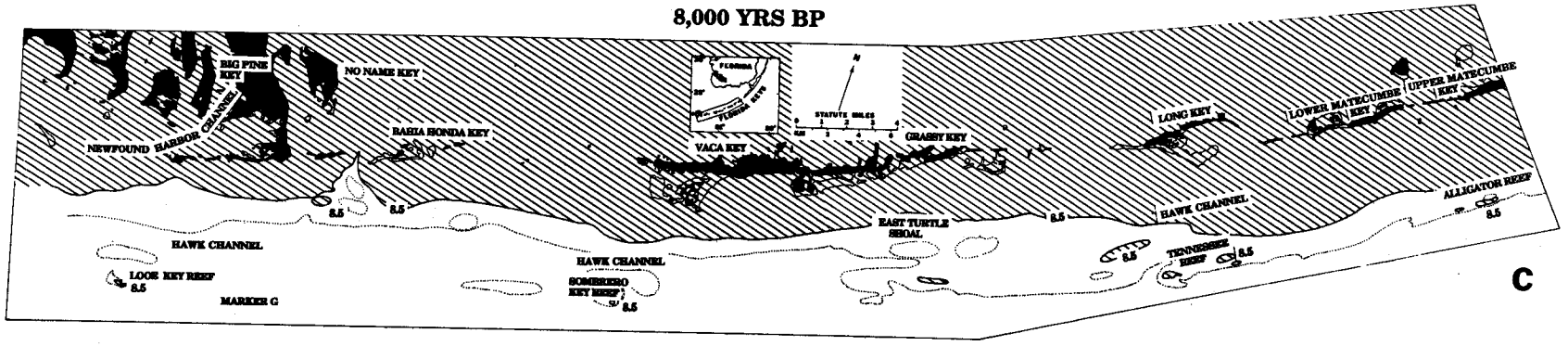
The low diversity and abundance of corals on four of the northernmost shelf-edge reefs in South Florida suggest that this area is a sub-optimum habitat for hermatypic corals. Community structure, diversity, and colony size vary among three depth-zones and among the four reefs. Diversity, percent cover, and size are greatest in the deep fore-reef stations and on the southernmost reefs. Variations in wave-energy, light, and sedimentation with depth cannot completely explain the observed distributions. Seasonal cold temperatures and occassional tropical storms most likely control and limit the distribution and survival of hermatypic corals on these reefs.

LOWER AND MIDDLE KEYS SHORELINES

6,000 YRS BP



8,000 YRS BP



C

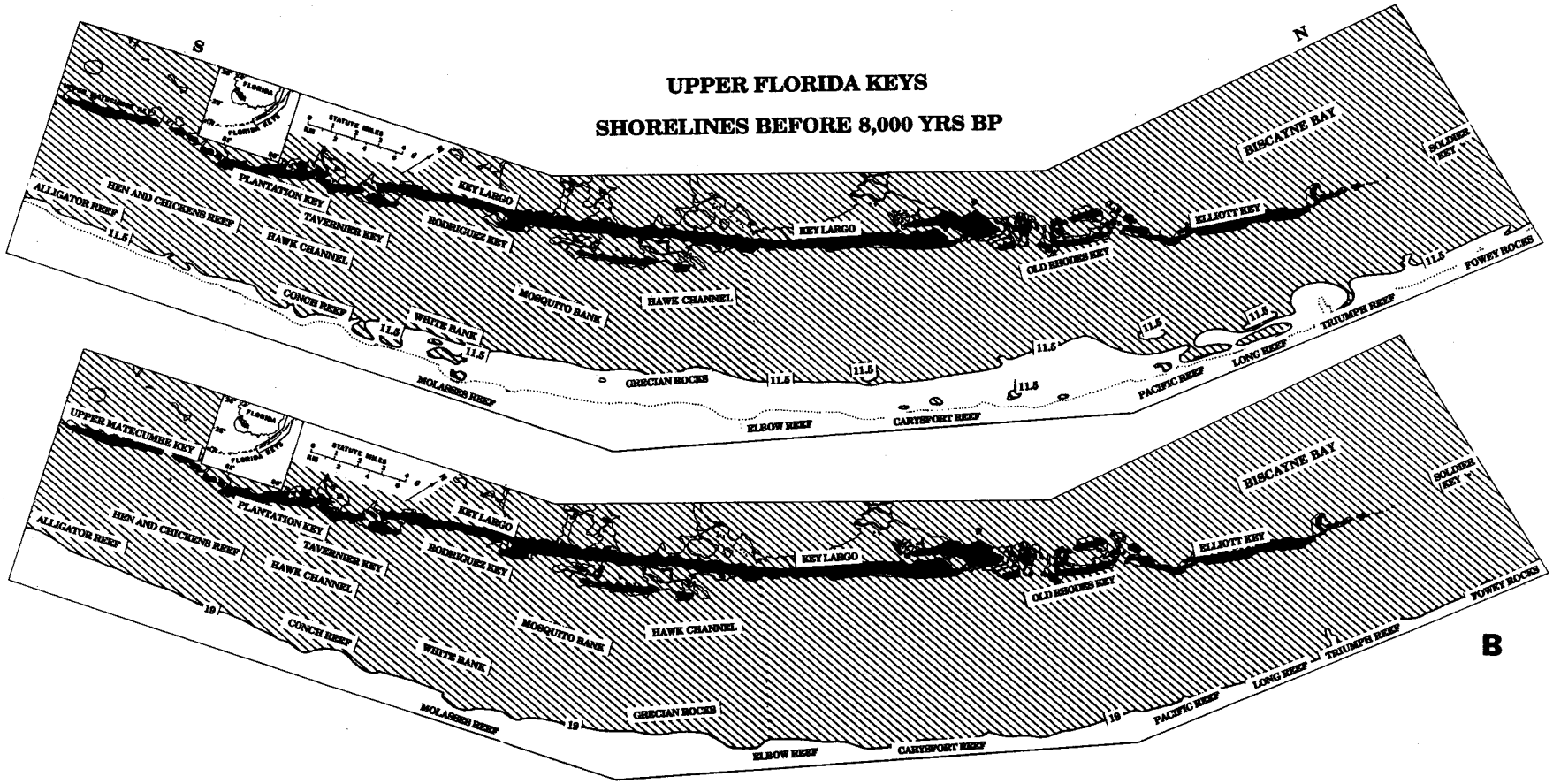
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Conclusions

1. Community structure and diversity of hermatypic scleractinian coral communities vary between 0 and 18 m on four shelf-edge reefs in Biscayne National Park. It is hypothesized that cold temperatures and tropical storms are the most important environmental variables on these reefs and best explain the greater diversities, percent cover, and colony-size of hermatypic corals in the deeper reef-zones.

2. Differences and similarities between the four reefs suggest that seasonal environmental conditions vary over the short distances between these reefs. The evidence supports the hypothesis that water flowing out of this area's shallow bays stress the shallow reef-zones more on those reefs closest to tidal-passes. Other causes must be invoked to adequately explain the patterns of distribution in deeper zones. One possible hypothesis is that there is a reduced frequency or magnitude of cooling of water over the reefs by winter cold fronts with decreasing latitude.

3. In contrast with other Caribbean coral reefs, these reefs are physically-controlled systems with low diversity and coral abundance due to frequent and severe disturbances. The size-frequency distribution of the most abundant colonies suggests that recruitment is high, but survivorship is low. Coral-coral interactions, predation, and competition are of secondary importance on these reefs.


UPPER FLORIDA KEYS
SHORELINES BEFORE 8,000 YRS BP
S
N
STATUTE MILES
FLORIDA
FLORIDA KEYS
UPPER MATECUMBE KEY
ALLIGATOR REEF
HEN AND CHICKENS REEF
PLANTATION KEY
TAVERNIER KEY
HAWK CHANNEL
CONCH REEF
WHITE BANK
MOLASSES REEF
KEY LARGO
RODRIGUEZ KEY
MOSQUITO BANK
GRECIAN ROCKS
ELBOW REEF
CARYSFORT REEF
PACIFIC REEF
LONG REEF
TRIUMPH REEF
OLD RHODES KEY
ELLIOTT KEY
BISCAYNE BAY
SOLDIER KEY
FOWEY ROCKS
11.5
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B

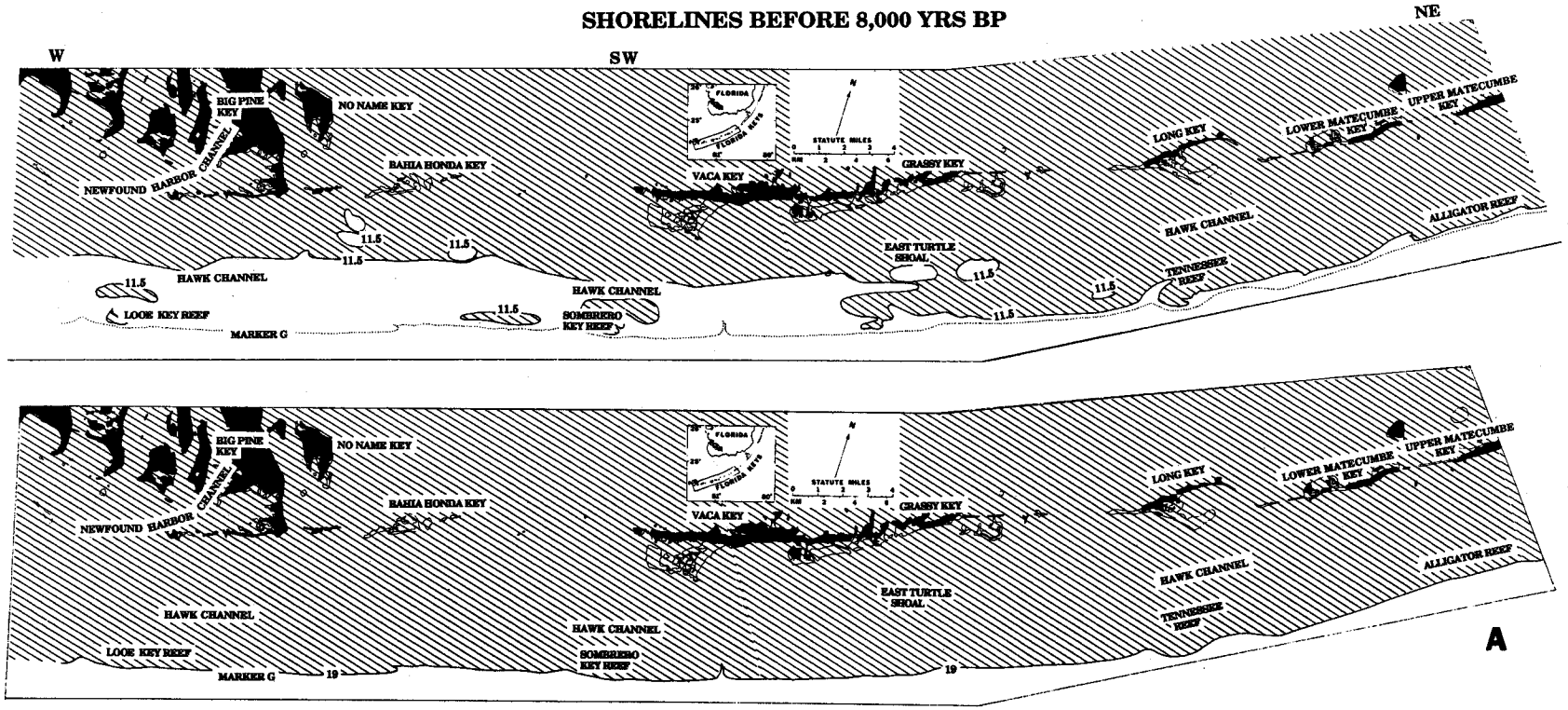
T176: 13

Differences in the diversity of cover (H'c) are more indicative of the poor development on the study reefs. H'c ($\log_{10}$) ranged from 1.0 to 3.5 on Panama's Atlantic reefs (Porter, 1972) and from 0.6 to 0.99 in BNP. It would be useful to compare the diversity of these study reefs to other Caribbean reefs that are exposed to different levels of disturbance. Until comparable methods are employed and quantitative data on tolerances and environmental variability are collected the coral community on the study reefs must be considered to be under stress from the physical environment.

Frequent and severe disturbances on these reefs, superimposed upon a background climate near the limit of coral tolerance to low temperatures, can explain the differences in the coral community with depth, its retarded development, and the observed size-frequency distribution. The deeper parts of these reefs more clearly approach the coral community one would expect to find. Normal development of a shallow reef-coral community, one capable of rebounding from storm damage, may be stifled by frequent cold-water disturbances. This unstable or nonequilibrium condition is consistent with communities controlled by physical, rather than biological processes (Sanders, 1968). The increased diversity and changes in species composition and the size-distributions from north to south point to a variation in these detrimental physical factors over a short distance. Even greater differences are evident among these reefs and reefs further south in Florida and the Caribbean.

LOWER AND MIDDLE KEYS

SHORELINES BEFORE 8,000 YRS BP



T176: 12

Caribbean reef-zonation. Acropora palmata is conspicuously absent from the shallow fore-reef stations of the study reefs, even though it is a distinct feature on the shallow shelf-break (6 - 9 m) in Pennekamp (Voss, pers. comm.). There is no development of spur and groove on the study reefs, although buttresses are present on Carysfort Reef and are well formed further south at Looe Key Reef (Pers. obs.). The outer belt of massive corals on these reefs was restricted to a narrow range of depth on the steep slopes below 12 m . Greater abundances of Siderastrea siderea, Montastrea annularis, M. cavernosa, and Colpophyllia natans in the deep fore-reefs match the increase in these populations' densities with depth in Panama (Dana, 1976). Between these two zones, the mid fore-reefs in BNP are characterized by large areas of bare substrate scattered with small colonies of coral. The ''inner rocky shoal'' or reef-flat was not sampled in this study, but was mostly coral rubble, the sea fan Gorgonia ventalina, and the stony-hydrozoan Millepora complanata (Pers. Obs.).

These reefs have not developed the robust coral communities typical of Caribbean reefs. The deep fore-reef station of Ajax Reef had the greatest percent cover (7.9), but does not approach the lowest measured by Loya (1976) at sediment-stressed West Reef,P.R. (30.3%). There, diversity (H'n) ranged from 1.83 to 2.20, with 20 species encountered. This is similar to the range (1.38 - 2.28) and the number of species (27) encountered in this study. It appears that both of these areas are stressed, but that the abundance of sediment-tolerant Montastrea cavernosa in Puerto Rico increases the coral cover. M. cavernosa is also very abundant on patch-reefs on the flat, sandy fore-reef below 18 m in BNP (pers. obs.).

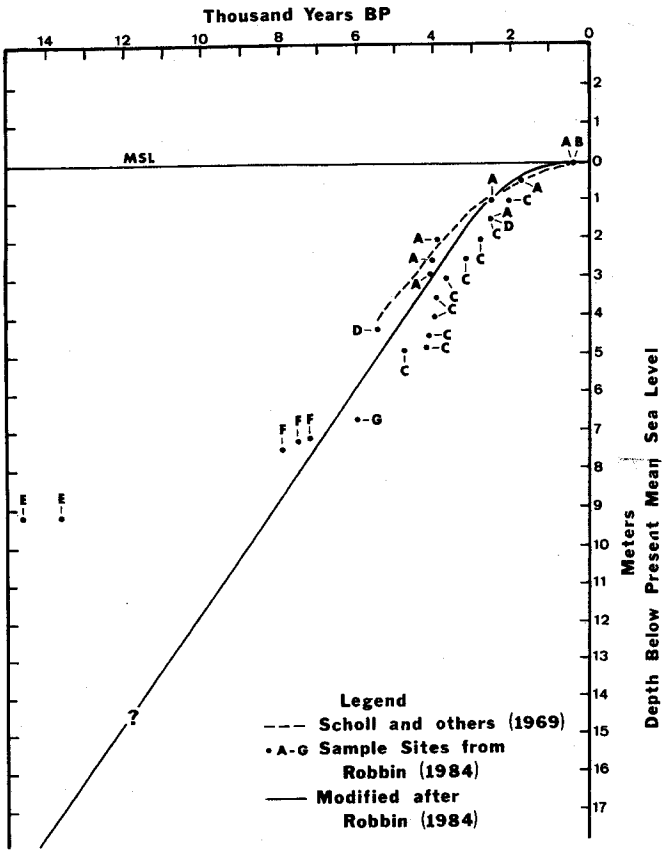


FIGURE 16 Sea-level curve modified after Robbin (1984). Data for 6 ka to present are considered reliable, but curve from 15 to 6 ka is speculative.

the sea-level curve (Fig. 16) allows approximation of the shoreline 15, 10, 8, 6, 4, and 2 ka. Lack of C^{14} data from this area before 8 ka makes the shoreline locations from 15 and 10 ka less reliable than those for 8, 6, 4, and 2 ka. To prepare the sea-level curve in Figure 16, the curve of Robbin (1984) was modified by simply projecting it downward. This projection places sea level between -9.2 and -7.5 m (-30 and -25 ft) for the period between 15 and 8 ka. Data from elsewhere indicate eustatic sea level was more than 100 m (328 ft) below present level 15 ka (Curray, 1965; Milliman and Emery, 1968). Although the discrepancy is considerable, it does not significantly change our maps because, due to uniformity and steepness of the limestone shelf below -15 m (-50 ft), the shoreline trend would not be significantly different if sea level were actually 100 m (328 ft) deeper than shown. The younger levels, where the data are more constrained (namely, those dated between 8 and 2 ka), are most significant to understanding the distribution of reefs.

It is assumed that there was little, if any, sediment on the limestone surface prior to flooding. Sediment and soil are usually absent on Pleistocene rock highs throughout the Caribbean; thus, there was probably little cover on topographic highs in this region in the past. There may have been 1 to 2 m (3-6 ft) of sediment and peats in topographic lows, as there are in the Florida Everglades today. In fact, peat in a bedrock low at Alligator Reef provided a critical data point for the sea-level curve shown in Figure 16.

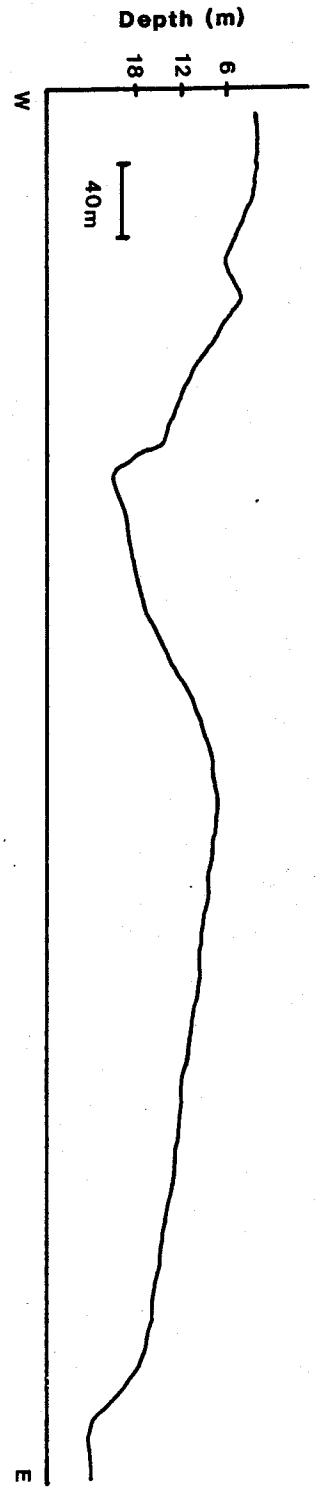
Whether or not the paleoshorelines are accurately dated, they nevertheless show that (1) a series of islands existed along the outer platform margin between 10 and 8 ka (these islands became locations of the major platform margin reefs); (2) a distinct trough existed behind the islands (the trough became what is known today as Hawk Channel); (3) flooding of the islands and Hawk Channel occurred earlier and probably faster in the lower Keys than in the upper Keys; and (4) creation of Florida Bay and the tidal passes into the bay and the middle Keys occurred during the last 3,000 years. This final phase has had the most pronounced effect on the distribution of living and dead reefs on the Florida reef tract.

As sea level rose between 15 and 8 ka, the relatively smooth coastline along the Florida Keys became more irregular (Figs. 17A, B). Bedrock highs formed islands at Sombrero Key off the middle Keys and at Molasses, Carysfort, Pacific, and Long Reefs off the upper Keys. Ponds of sea water appeared on land as sea level rose. The south-southwest and deepest part of Hawk Channel in the Florida Keys, in the vicinity of Looe Key, was submerged.

By 8 ka, islands still existed at Tennessee Reef and Alligator Reef off the middle Keys and at Conch Reef off the upper Keys (Fig. 17C, D). Only a vestige of land was left exposed at Looe and Sombrero Keys. A large tongue of water had begun to encroach landward into the north part of Hawk Channel in the area of Tavernier and Rodriguez Keys in the upper Keys, and a small inlet had formed south and west of Bahia Honda Key in the lower Keys. Sea level was 8.5 m (28 ft) below present, and the shoreline ranged from approximately 3 to 7 km (2-4 mi) offshore from what are now the Florida Keys.

By 6 ka, lagoons had begun to form on the mainland. Hawk Channel was fully formed, and in it water flowed freely along the length of the reef tract (Fig. 17C-D). All previously exposed islands had been submerged. The first breach of water through what would become the chain of islands that is now the Florida Keys occurred to the west of Bahia Honda Key. In the upper Keys, inlets of water approached the area on either side of Old Rhodes Key, and ponds formed west of Soldier Key. Sea level was 5.7 m (19 ft) lower than today.

By 4 ka, irregularity of the south Florida coastline increased dramatically as water spread from Hawk Channel through the numerous depressions between the topographic highs that would become the Florida Keys and covered the low-lying areas to the north and west (Fig. 17E-E'). A few islands formed in the lower and middle Keys; Florida Bay had begun to form in the area north



Carysfort Reef

died during the freeze of 1977. Cold water from the Gulf of Mexico during winter months has probably prevented Acroporids from becoming major reef builders since the Tortugas area was first flooded. The sediment in deeper areas (18 m or 60 ft) within the atoll lagoon is composed of muddy carbonate. There is an extensive, shallow (less than 2 m), grass-covered flat to the west of Southeast Reef. The sediment there is 12 to 15 m (40-50 ft) thick.



FIGURE 14 Beachrock fractured to form rectangular blocks on west side of Loggerhead Key at Dry Tortugas.

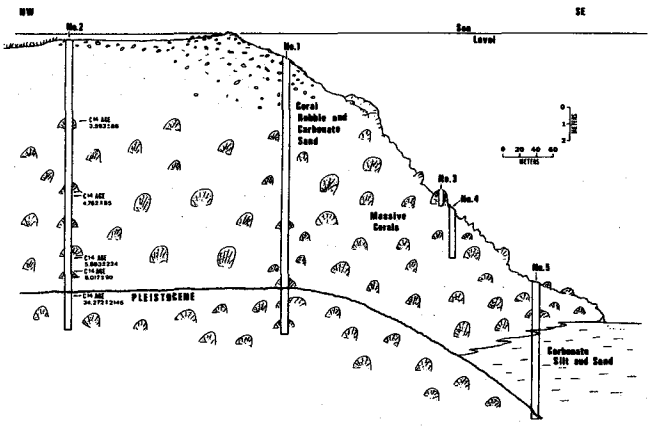


FIGURE 15 Cross section based on cores across Southeast Reef, the most continuous and best developed reef at Dry Tortugas. The reef was built by massive corals, and core 5 suggests some seaward accretion over carbonate sand and silt. *Acropora palmata* was not encountered in any core, but fragments are present within the rubble ridge between cores 1 and 2; this species of coral was also absent from underlying Pleistocene limestone.

Sea-Level Fluctuations and the Changing Shoreline

In this section, the guide considers important factors that have controlled reef distribution during the past 8,000 years and attempts to explain why so many reefs are now senescent.

The timing and rate of relative sea-level rise are vital to understanding the distribution of reefs and sediment facies. These data make it possible to locate and track shorelines as the sea flooded the irregular Pleistocene limestone surface. Since corals become established most easily on rocky, sediment-free topographic highs and only with great difficulty in sediment-filled topographic lows, a map of the underlying bedrock provides a way to understand reef distribution and development. Correlating former sea levels with bedrock contours provides a rough way to determine the location of paleoshorelines as sea level rose and flooded the reef tract.

The last major fall occurred at approximately 120 ka, while the reefs of the Key Largo Formation were growing and oolite facies were accumulating. Similar eustatic fluctuations occurred earlier during the Tertiary.

Perkins (1977) described a record of five major sea-level falls along the south Florida reef tract during the Pleistocene. Each fall of sea level led to the development of calcrete crusts and other features diagnostic of subaerial exposure. In core borings on the Great Bahama Bank, Beach and Ginsburg (1980) identified at least 18 exposure horizons within the Pleistocene section, many of which probably represented only minor fluctuations.

At approximately 16 to 15 ka, sea level began rising rapidly (Milliman and Emery, 1968) and at about 7 or 6 ka began flooding the south Florida shelf (Robbin, 1984). Information for the period 15 to 8 ka is scant for south Florida; reliable sea-level data cover only the period 8 ka to the present.

The first Holocene sea-level curve for south Florida was constructed by Scholl (1964) and Scholl *et al.* (1969). The curve was based on C^{14} dating of terrestrial and/or mangrove peats now below sea level in Florida Bay. More recently, Robbin (1984) constructed a curve on the basis of C^{14} dates of closely spaced samples of continuous peat sections exposed in the banks of tidal passes through the Florida Keys and of peats beneath coral reefs . Because this curve is based on data closer to and, in some cases, beneath the reefs, it is considered the most relevant curve for our purposes. Additional data come from C^{14} dates of corals recovered from cores and excavations in Holocene reefs (Lighty, 1977; Shinn *et al.*, 1977; Shinn, 1980; Shinn *et al.*, 1981). A revised version of the curve of Robbin (1984) is shown in Figure 16.

Figure 17 A-F is a series of maps roughly approximating the locations of paleo-shorelines off the Florida Keys during the past 15,000 years. The base map is from Enos (1977), who used a high-resolution subbottom profiler to map and contour the underlying Pleistocene bedrock surface. Interpolating the position of shorelines from

Figure 21

Profile of Carysfort Reef.

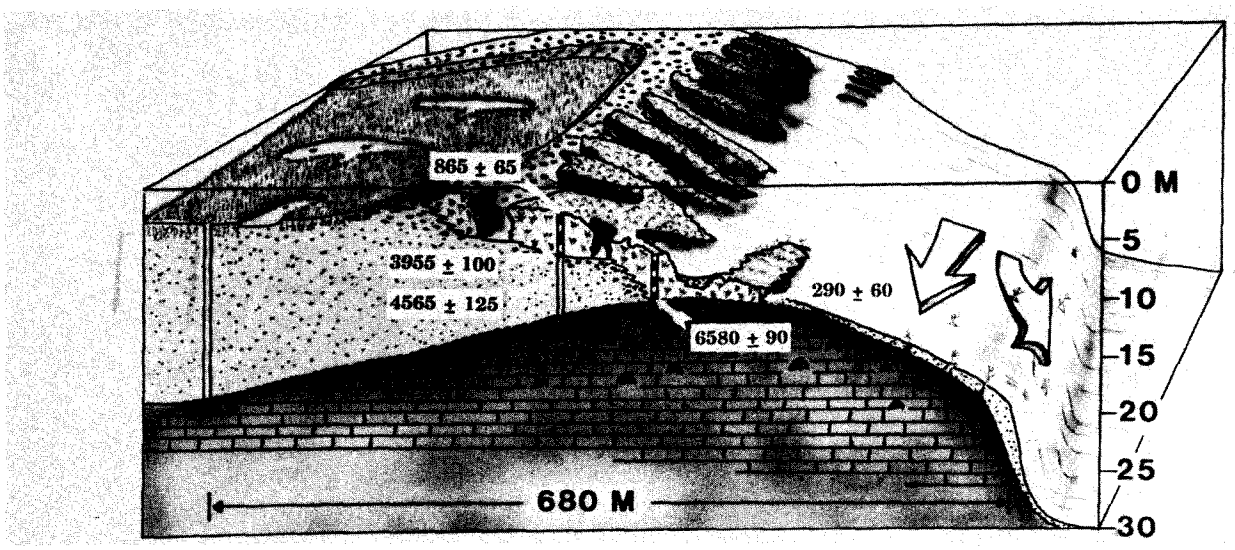


FIGURE 13 Schematic block diagram showing relation between Pleistocene topographic feature and spurs and grooves that form Looe Key Reef. Note reef began on crest of high and backstepped over coral sand and rubble as sea level rose. Carbonate sand has smothered portion of reef and covered steep slope seaward of reef, as shown by large arrows. Turtlegrass meadows with sand holes (blowouts) occupy area immediately landward of reef crest.

there are abundant patch reefs which, to date, have not been studied. There are also many well-developed shallow patches and small coral heads located less than 1 km (0.6 mi) offshore throughout the lower Keys, especially off the Newfound Harbor Keys, the southern termination of Key Largo Formation exposures.

A series of unnamed linear reefs, oriented east-west and composed of patch reef fauna, extends between Ellis Rock, north of the Marquesas Keys, and New Ground Shoal. Two core borings and numerous seismic-reflection profiles show that these reefs are 7.6 m (25 ft) thick and are located on top of Pleistocene topographic highs composed of coralline facies of the Key Largo Formation. No *A. palmata* or *A. cervicornis* grow on or are present in the 7.6-m (25 ft) section at either reef. Cold Gulf of Mexico water, which flows unimpeded over these reefs during winter months, is thought to prevent growth of these corals (Shinn, 1984).

The area between the Marquesas Keys, a circular accumulation of *Halimeda*-sand spits and beaches, and Halfmoon Shoal, 32 km (20 mi) to the west, is dominated by shifting, mostly grass-free, *Halimeda* sands. East-west-oriented megaripples as high as 3 m (10 ft) shift back and forth daily in response to north-south-shifting tidal currents. The area is appropriately named the Quicksands because of rapid sand movement and rapid burial of shipwrecks.

Patch reefs in the deep waters of Hawk Channel occur between the Quicksands and the platform margin hardbottoms that extend westward from Cosgrove Shoal. The Spanish treasure ship ***Atocha*** sank on a topographic feature a few kilometers west of Cosgrove Shoal in 1622 during a violent hurricane.

Dry Tortugas reefs. Beyond the reefless deeper waters west of Rebecca Shoal lie the Dry Tortugas, called an atoll by Vaughan (1914b). The atoll has a discontinuous elevated rim of Holocene coral and several small sandy islands, the most prominant of which are Loggerhead Key, site of the Carnegie Institution marine laboratory from 1910 to 1939, and Garden Key. Bush Key, adjacent to Garden Key, is famous for its colony of sooty terns. Hospital Key, which once supported a small hospital for treating yellow-fever patients, was destroyed during a hurricane. The most extensive beachrock in south Florida is located at Loggerhead Key (Ginsburg, 1953; Fig. 14). Shoals within the atoll, such as White Shoal and Middle Ground, had thriving thickets of *Acropora cervicornis* (Davis, 1982), which were mostly killed by the freeze of 1977 (Porter *et al.*, 1982). Although the corals recovered, they have recently been devastated by a coral disease. The largest reef is Southeast Reef, where a transect of cores was drilled in 1976 (Fig. 15; Shinn *et al.*, 1977). Coring showed the reef beneath the reef crest is 14 m (45 ft) thick, and the underlying Pleistocene rock is Key Largo Limestone (Shinn *et al.*, 1977). *Acropora palmata* was not encountered in any core holes, and only a few living colonies could be found on the reef in 1976. *Acropora palmata* transplanted there from Sand Key Reef by Hudson and Shinn (1976, unpubl. data) grew for a year but

increase in diversity with depth was due more to increasing species richness than to increasing evenness. This is the response one might expect if conditions improved allowing more sensitive species to survive. Conditions at Pacific Reef's deep zone may have been stable enough to allow the overwhelming predominance of two species and the greatest species richness of any zone. Local differences may be effected by location with respect to urban centers, structural variations in the reef-tract, and the major tidal pass to the north, the Safety Valve. We can observe differences among these closely spaced reefs, but only after detailed data collection will we know with certainty how temperature varies on these reefs, or if these changes are a result of random fluctuations in populations or unknown processes on a smaller scale.

Subtle differences in topography between these four reefs may provide different conditions for waves, currents, and ultimately the distribution of hermatypic corals. Carysfort Reef is considered one of the best examples of normal Caribbean reefs in the Florida Keys. Coincidentally, seaward of Carysfort's lush Acropora palmata-zone and highly developed fore-reef, a second reef-structure rises from below 15 m to within 7 m of the surface (Fig. 21). This difference in morphology between these four reefs and Carysfort Reef, 13 km south of Pacific Reef, may be one more reason the reef-coral communities are so different. This rise may shield the coral community on Carysfort Reef from the full destructive force of storms and hurricanes that effect this area.

The four study reefs are unlike coral reefs in other areas of the Caribbean. They only loosely fit Newell's (1958) description of

nis are absent.

Middle Keys reefs. Reefs of the middle Keys area (Molasses to Looe Key) are poorly developed, and none has living *A. plamata*-reef flats. Some, such as the south end of Davis and Alligator Reefs, have abrupt linear dropoffs of 2 to 3 m (6.5-10 ft) on the landward side. The top of the terrace lies in 4.5 to 6 m (15-20 ft) of water, and underwater observations along the dropoff show the terrace was constructed of *in situ A. palmata*. Since level surfaces are usually caused by corals growing upward to low spring-tide level, this terrace and others like it are thought to represent a drowned reef flat that flourished when sea level was 4.5 to 6 m (15-20 ft) lower than present. Pleistocene bedrock and peat have been found beneath a few centimeters of carbonate sand that cover the bottom beneath and landward of the dropoff (Robbin, 1984). For the most part, outer reefs in the middle Keys region have 1- to 2-m-deep (3-6.5 ft) boulder- and sand-strewn crests with *Millepora*-encrusted spurs and grooves in deeper water on the seaward side. These reefs once flourished. The cause of their demise is discussed elsewhere in this guide. It should be noted that those reefs that have "key" in their names, such as Sombrero Key Reef and Looe Key Reef, in historical times had sandy islands that supported vegetation (Romans, 1775). A dwelling and small lighthouse existed on Sand Key for many years before the island was destroyed by the hurricane of 1846 (Dean, 1982).

The long ledge south of Alligator Reef lighthouse was core drilled and found to have been built by *A. palmata* (Robbin, 1984); however, the most significant finding was a layer of peat on the landward side of a drowned reef flat. The peat actually extends beneath the reef (Fig. 12). The C^{14} age of the peat provided a significant point on the sea-level curve, discussed later.

Looe Key Reef has also been core drilled (Shinn *et al.*, 1981), and an extensive subsurface study of the area was conducted using high-resolution seismic-reflection profiling (Lidz *et al.*, 1985). Although there is more *A. palmata* at Looe Key Reef than at Alligator Reef, the amount is probably less than that which built Looe Key Reef a few thousand years ago. The most notable feature at Looe Key is the *Acropora*-built spur-and-groove system now encrusted with *Millepora spp.* and occasional large heads of *Montastraea annularis*. Drilling showed that the spurs rest on several meters of carbonate sand (Shinn *et al.*, 1981; Fig. 13).

A notable feature of the middle Keys area is the extensive accumulation of carbonate sand and relatively less turtlegrass cover compared to the northern Keys area. Another significant feature is the greater width of the tidal passes through the Keys relative to that in the upper and lower Keys, and patch reefs are relatively less abundant than elsewhere, although there are several well-developed ones. The most fully developed is at Hen and

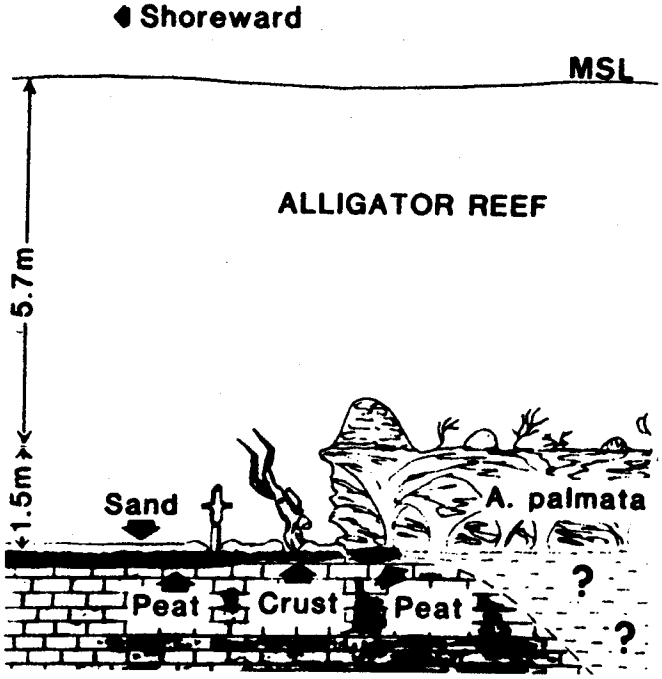
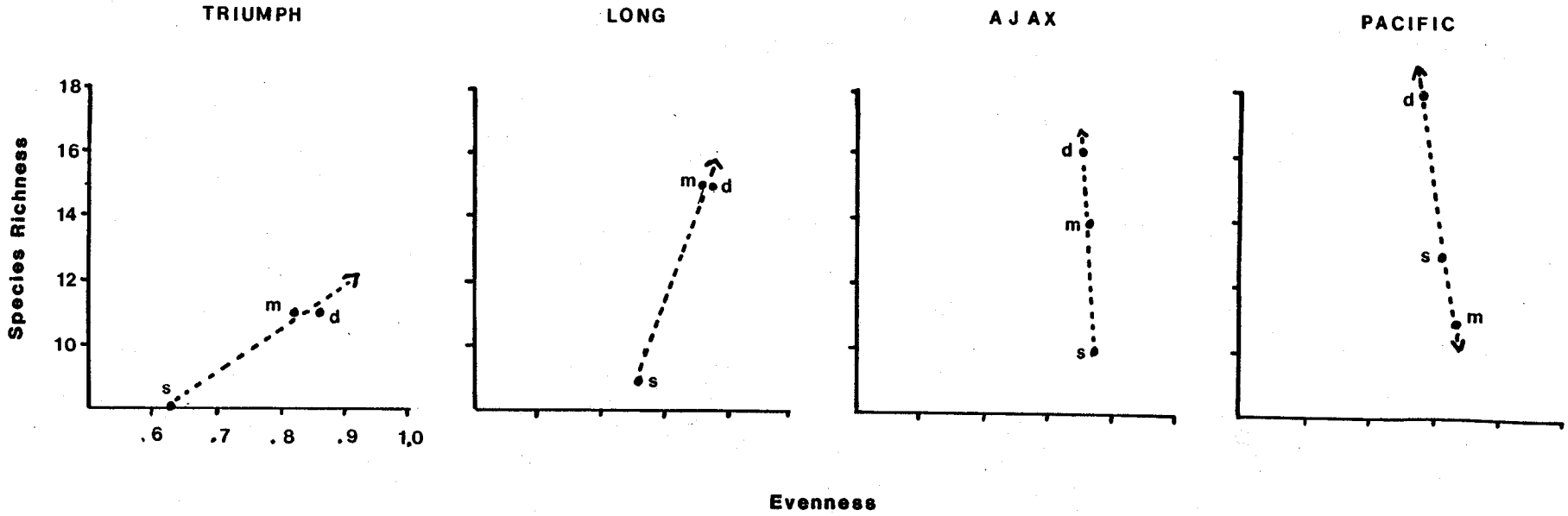


FIGURE 12 Peat beneath carbonate sand and back edge of reef at Alligator Reef in middle Keys region. Reef was built of *Acropora palmata*, which is no longer living. Flat surface of reef here and at Davis Reef site shown in Figure 10 suggests it was a "reef flat" formed when sea level was 5.7 m below present.

Chickens Reef. Although the corals there suffered about 80 to 90 percent mortality during the winter of 1969-1970 (Hudson *et al.*, 1976), the reef still has living *Montastraea annularis* heads 3 m (10 ft) high.

Lower Keys reefs. The lower Keys reefs include those reefs extending from Looe Key Reef to Cosgrove Shoal south of the Marquesas Keys. The best reef growth in this area, however, is restricted to those reefs between Looe Key and Sambo Reefs. This part of the lower Keys is protected from runoff from the Gulf of Mexico by the oolite islands that extend from Big Pine Key to Key West. The amount of live coral relative to dead coral from Sand Key to Cosgrove Shoal and farther west is much reduced. Sand Key has well-developed *Millepora*-encrusted spurs and grooves and a few living *Acropora palmata*. Practically no living *A. palmata* exists at Cosgrove Shoal. The reef line to the west of Cosgrove Shoal can best be described as a hardbottom with scattered live head corals and abundant alcyonarians. Until recent times, many of the reefs between Looe Key and Sambo Reefs had abundant *A. cervicornis* and *A. palmata* growth (Landon, 1975).

Noticeable is the deepening of Hawk Channel in the lower Keys relative to its depth in the middle and upper Keys. In places in the channel


TRIUMPH
LONG
AJAX
PACIFIC
Species Richness
18
16
14
12
10
.6
.7
.8
.9
1.0
s
m
d
Evenness

ft; Enos, 1977). The rubble slope accreted landward several meters during Hurricane Donna in 1960 (Ball *et al.*, 1967).

The remainder of the outer linear reefs extending southward to Molasses Reef also lack *in situ A. palmata*-reef flats. The crests of these reefs are composed of coral rubble. All of these reefs have well-developed *Millepora*-encrusted spurs and grooves. Colonies of *Acropora palmata* occur sporadically on the spurs, as do some large heads of *Montastraea annularis* and brain coral. The best known of these reefs, having spectacular spur-and-groove development, is Molasses Reef (Shinn, 1963). The grooves at Molasses were built by *Acropora palmata* that lived about 2 ka. Although there are some scattered colonies of living *A. palmata* and some large, massive corals, the spurs are essentially non-growing features encrusted with a thin coating of *Millepora spp.* (Fig. 9). By comparison, the amount of live coral at Molasses is much less than that at Carysfort Reef.



FIGURE 9. Artificial exposure showing internal composition of spur at MolassesReef. Spur was built entirely by *Acropora palmata*. The upper surface is coated by *Millepora spp.* and sea fans. Water depth 5 m.

Most of the outer linear reef area between Carysfort and Molasses Reefs is greater than 8 m (26 ft) deep and consists of bioeroded dead coral or exposed Pleistocene bedrock. Just landward of this old line of poorly developed reefs are several large patch reefs, many of which are populated by *A. palmata* along their seaward sides. The rock exposed at French Reef (just north of Molasses Reef, but not shown on Fig. 1) between spurs in 10 m (35 ft) of water is calcrete-coated Pleistocene Key Largo Formation (Fig. 10).

About 1.6 km (1 mi) landward of the belt of these mostly dead outer reefs is a linear chain of living *Acropora* reefs that includes Key Largo Dry Rocks, Grecian Rocks and several informally named reefs, such as North Dry Rocks, Little Dry

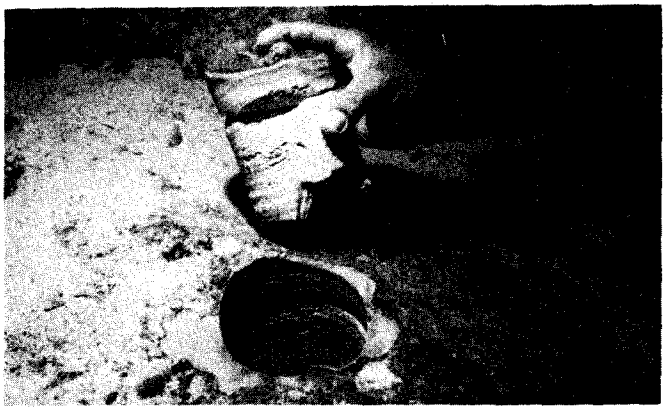


FIGURE 10 Pleistocene Key Largo Formation with calcrete- (soilstone crust) coated surface at Davis Reef. Holocene reef overlies this surface approximately 1 m behind diver's hand.

Rocks, and Little Grecian Reef. These reefs also have *A. palmata*-reef flats and distinct coral zonation of species and growth forms. The zonation of the best known reef, Grecian Rocks (formerly known as Key Largo Dry Rocks), has been described by Shinn (1963, 1980). A cross section of Grecian Rocks, based on core drilling, is shown in Figure 11. The distinct coral zonation is a result of these reefs receiving relatively large and constant waves. Deeper water and poorly developed reefs seaward of this reef chain allow waves to reach the area.

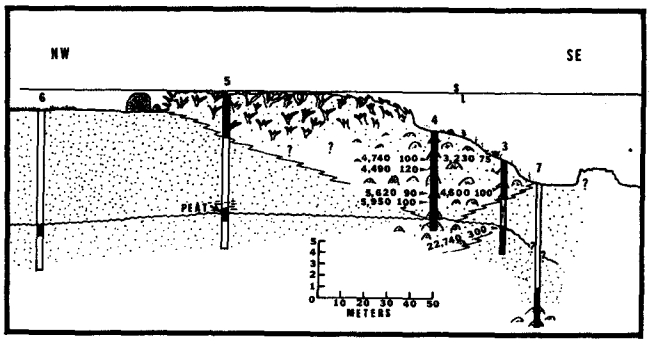


FIGURE 11 Cross section of Grecian Rocks, based on cores across center of reef perpendicular to reef trend. Note how reef has backstepped landward over backreef sands. Peat overlies calcrete-coated Pleistocene surface in core 5. Oldest corals in core 4 are approximately 6 ka.

Numerous patch reefs occur on White Bank landward of the Grecian Rocks reef line and along the seaward side of Hawk Channel. A large cluster of patch reefs occurs at Basin Hill Shoal inshore from Carysfort Reef and at Mosquito Bank inshore from French and Molasses Reefs. The patches are surrounded by relatively muddy carbonate sediment and are composed mainly of massive head and brain corals and abundant alcyonarians. *Acropora palmata* and *A. cervicor-*

Figure 20

Percent of Total Species Richness vs. Evenness (Simpson's Dn, see text) for the three reef-zones on each of the four reefs.

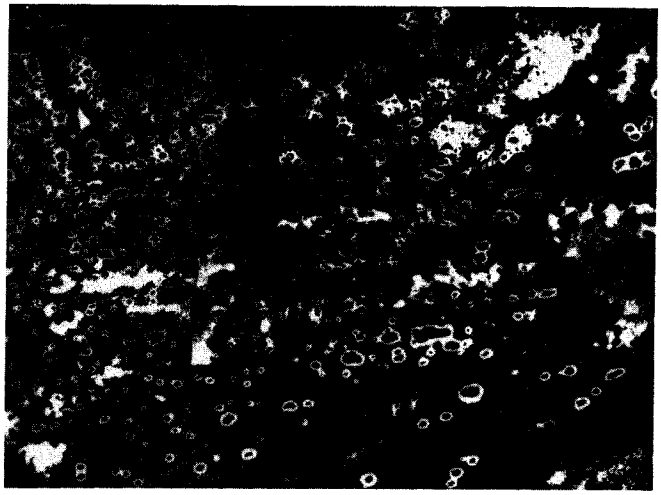


FIGURE 5 Vertical aerial photograph landward of Long Reef showing abundance of sand-rimmed patch reefs. Patches range from 6 to 18 m (20- 60 ft) in diameter.

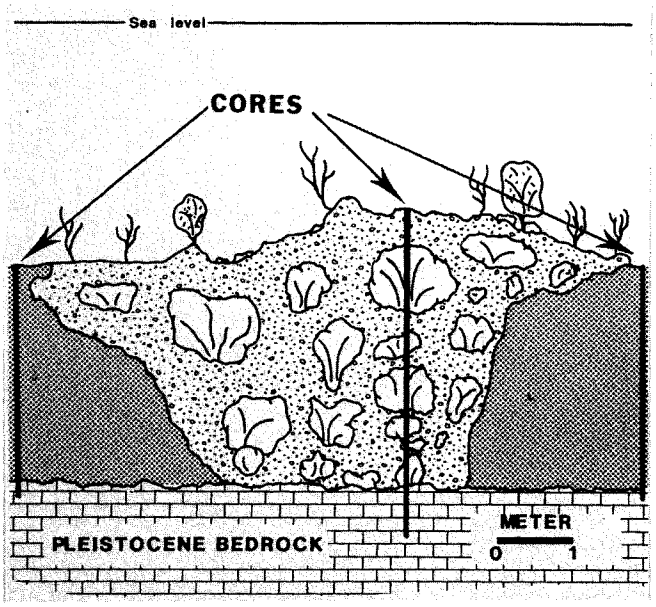


FIGURE 6 Cross section of a typical shallow patch reef of the upper Keys area (based on 5 cores, not all shown). Core in patch encountered large, massive coral heads (*Montastraea annularis* and *Diploria strigosa*) not presently living on patch. Vertical and horizontal scales are the same. Heavy lines show core locations.

to 9 m (15-30 ft) of water and on the landward side in 1.5 to 3.6 m (5-12 ft) of water. A core drilled 50 m (160 ft) seaward of the lighthouse revealed 13 m (43 ft) of Holocene coral accumulation. There are several smaller unnamed reefs just south of Carysfort with similar coral growth and reef flats composed of *in situ A. palmata*.

Patch reefs landward of Carysfort are in a better state of health than those to the north; however, they are considerably fewer in number.

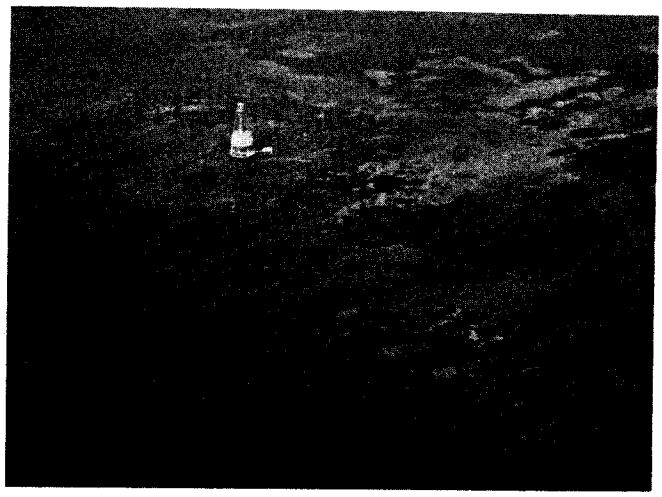


FIGURE 7 Aerial view of Carysfort Reef looking southwest. Lighthouse sits on reef flat composed of *in situ Acropora palmata*. Dark area to right is turtle grass with bare sand holes. Straits of Florida is to the left.

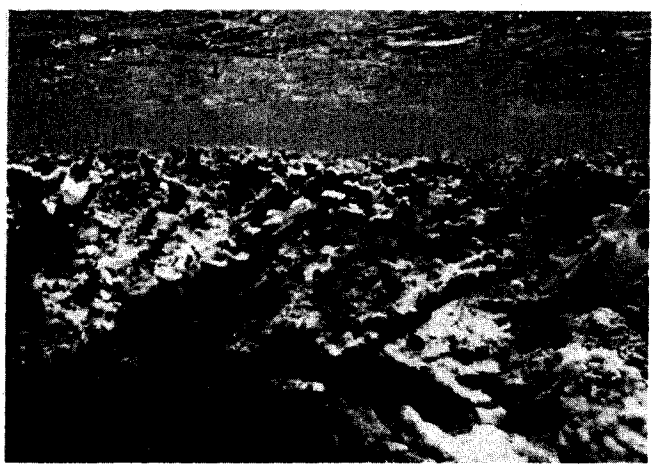
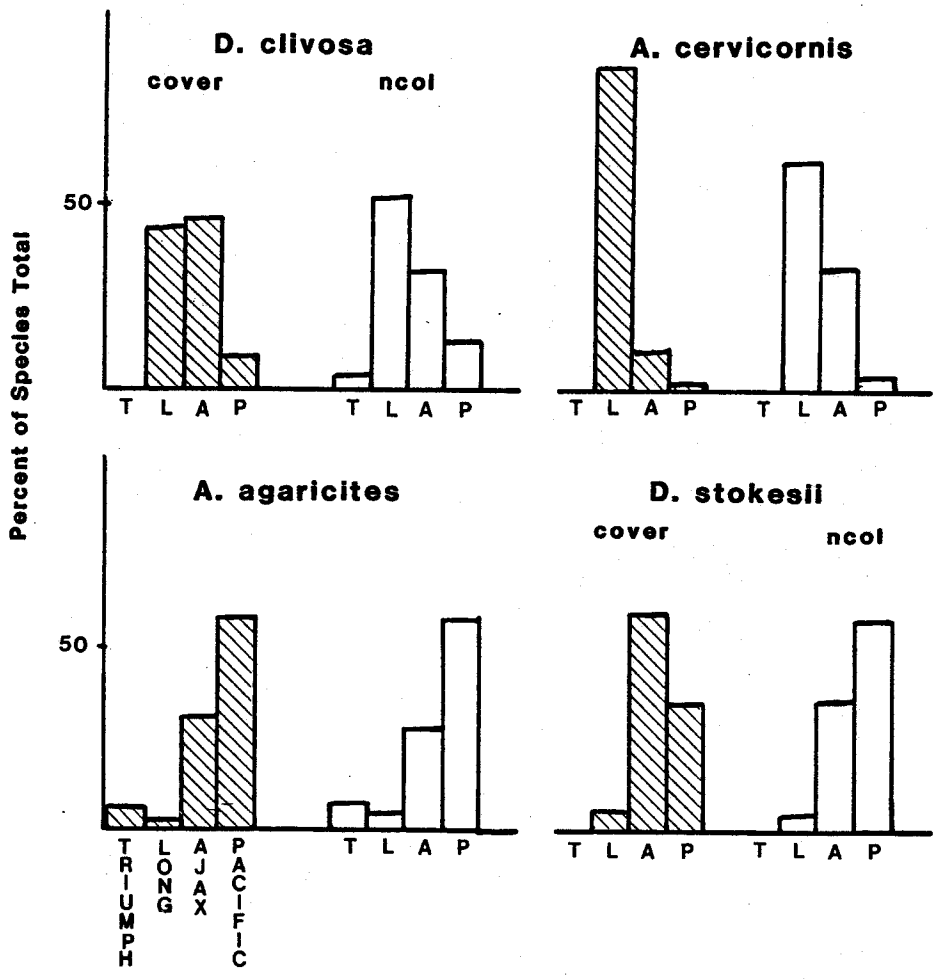


FIGURE 8 Underwater photograph of *in situ Acropora palmata* forming reef flat. Flat upper surface is controlled by spring low-tide level.

Much of the patch reef zone to the north is replaced in this area by a shallow sediment bank, the northern extension of White Bank. Water depths range from 1 to 2 m (3-6.5 ft) over northern White Bank. Landward of this bank is the deep channel called Hawk Channel, which is lined with muddy carbonate sediment and extensively covered with turtle grass. A few patch reefs are scattered in Hawk Channel, but for the most part it is navigatable.

The next major linear reef to the south is the Elbow, which lacks a reef flat composed of *in situ A. palmata*. Elbow Reef has spectacular *Millepora*-encrusted spurs and grooves in depths ranging from 3 to 15 m (10-49 ft). Water depth immediately landward of the Elbow is 12 m (40 ft). A steep (30°) slope of coral rubble extends down the landward side of the reef from 4.5 to 12 m (15-40

Relative Abundance in Shallow Zones



One facies found in the Miami area and not readily identifiable in the lower Keys is the bryozoan facies (Hoffmeister *et al.*, 1967). Typically, no bryozoan facies is evident in the lower Keys. The fence diagram and cross section shown in Figure 3 (from Kindinger, 1986) show the relation between the Key Largo Formation, whose surface exposure ends at the west tip of the Newfound Harbor Keys, and the adjacent oolite facies. It is thought that the barrier provided by the growing Key Largo Formation concentrated tidal currents between the Atlantic and Gulf at each end, thereby allowing the precipitation and shaping of cross-bedded oolitic tidal bars.

West of Key West, the oolite facies submerges and continues westward, forming the bedrock underlying the Holocene Marquesas Keys and the region known as the Quicksands (Fig. 1). Coring also revealed Pleistocene coralline facies (i.e., Key Largo Formation) beneath two Holocene reefs, Ellis Rock and New Ground Shoal, located in the Gulf of Mexico north and west of the Marquesas Keys. The location of these 8-m-thick (26 ft) Holocene reefs is controlled by underlying topographic highs.

There is no information on the bedrock in the area between the Quicksands and the Dry Tortugas. At Dry Tortugas, however, coring by the USGS Fisher Island Station has shown that Holocene reefs and sediments rest on coralline Pleistocene limestone, presumably the Key Largo Formation.

Platform Tilting

Higher topography in the east part of Florida led Parker and Cooke (1944) and Parker *et al.* (1955) to suggest westward tilting during the Pliocene and Early Pleistocene. Lower elevation of the Key West Oolite, believed to have been deposited at the same sea level as the topographically higher Miami Oolite, and a linear Pleistocene beach deposit that dips along strike to the west suggest westward tilting during the Late Pleistocene. In addition, thickening of the Pleistocene section to the west is compatible with westward tilting (Perkins, 1977). Slight tilting may be occurring today.

General Distribution of Reefs

Upper Keys reefs. The northern extent of modern reef growth is in the vicinity of Fowey Rocks (Fig. 1), as noted by Vaughan (1914a); however, at 7 to 4 ka, growth of Holocene *Acropora* reefs extended at least 40 km (25 mi) farther north (Lighty, 1977; Shinn *et al.*, 1977). Linear platform margin reefs in the northern part of the upper Keys region consist of alcyonarian- and *Millepora*-coated surfaces with scattered small head corals, mainly *Montastraea annularis*, *Colpophyllia natans*, *Diploria spp.*, and a few colonies of *Acropora cervicornis* and stunted *A. palmata*. Landward of the linear reef area is a slightly deeper carbonate sand area with scattered areas of turtlegrass cover. Grass cover becomes more continuous farther landward, where there are scattered patch reefs. The patches consist of either individual, large, massive heads of *Montastraea annularis* or *Siderastrea spp.*, or aggregations of head corals covering areas as large as 100 m (328 ft) in diameter. The corals are not flourishing, and most are dead. Alcyonarians are also abundant on patches. As is common in most places, there is a grass-free sand halo several meters wide surrounding each patch reef.

Farther south is Long Reef (Fig. 1), one of the longest unbroken reefs in the Florida reef tract. Long Reef is composed mainly of boulders and cobbles of dead coral with live heads of massive corals scattered here and there. Some fairly large heads of branching *Acropora palmata* are located on the north and south ends of this reef. A core drilled in 1.5 m (5 ft) of water at the reef crest showed an accumulation (mostly carbonate sand) 9 m (30 ft) thick, whereas a core drilled on the seaward side in 5 m (16 ft) of water revealed almost continuous coral (Shinn *et al.*, 1977). Other reefs in this chain, Ajax, Pacific, Star, and Brewster, have a similar appearance (Fig. 4).

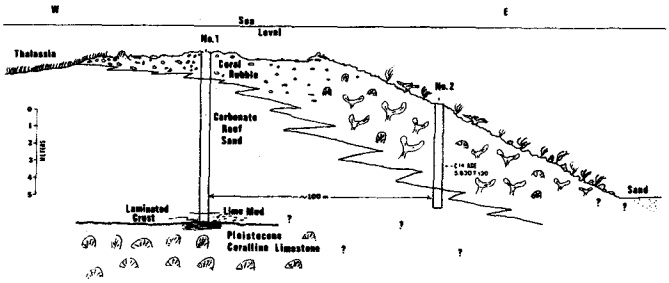


FIGURE 4 Cross section of Long Reef showing reef located over topographic high. C ^{14} age of coral 8 m below sea level in core 2 is approximately 5.5 ka.

At least 3,000 patch reefs in water depths from 1-12 m (3-39 ft) occupy the sea floor landward of the reefs south of Fowey Reef and especially Long Reef (Fig. 5). Some patches have as much as 4.5 m (15 ft) of vertical relief and range from a few meters to 100 m (328 ft) in diameter. Most are approximately 20 m (65 ft) across. Recently drilled core holes indicate those in 9 m (30 ft) of water are 4.5 to 6 m (15-20 ft) thick and were built by large, massive coral heads (Fig. 6). There are few large living corals on them today .

Farther south at Carysfort Reef, the zone of best coral growth in the Florida Keys begins (Fig. 7). The reef flat at Carysfort is composed of *in situ* *Acropora palmata*, whereas the tops of all reefs to the north are predominantly coral rubble and sediment (Fig. 8). Carysfort also has abundant thickets of *A. cervicornis* on the seaward side in 4.5

Figure 19

Relative abundance of a) Acropora cervicornis, b) Diploria clivosa, c) Agaricia agaricites, and d) Dichocoenia stokesii in the shallow zones of the four study reefs.

(the northernmost exposure of the Key Largo is at Soldier Key) has not been adequately studied. In the oolitic lower Keys, however, numerous recent core borings (Kindinger, 1986) have confirmed that the Key Largo Formation and the Miami Oolite equivalent, called the Key West Oolite by Sanford (1909), were deposited contemporaneously. There is no unconformity separating the two Pleistocene facies. The oolite facies of the lower Keys has many of the same characteristics as the Miami Oolite of the mainland, but it is thinner. There are basically four facies with a maximum total thickness of 12 m (39 ft) found in the lower Keys: (1) ooid grainstone; (2) ooid grainstone to packstone; (3) peloidal packstone, and (4) peloid-bioclast packstone to grainstone (Fig. 3).

The two ooid-rich facies can be generally divided on the basis of sedimentary structures: a cross-bedded unit and a mottled, abundantly burrowed unit. The islands of the lower Keys are basically composed of ooid-rich grainstone with subordinate amounts of uncoated fecal pellets, peloids, and bioclasts. Also found in this unit are relatively thin, moderately well-sorted, bioclast-rich zones containing molluscs and fragments of *Halimeda spp*. Characteristically, the ooid grainstone is seen as steeply dipping cross-laminations composed of well-sorted, medium-to-coarse grainstone with few burrows.

In contrast, the ooid grainstone-to-packstone facies is abundantly mottled and has a high degree of vertical and lateral variability. The ooid grainstone to packstone consists of fine-to-medium sand-size ooids with varying quantities of fecal pellets, peloids, and bioclasts. Burrows are common and many are mud-lined, suggesting that they were made by Callianassid shrimp. Also present are more randomly shaped, unlined burrows made by other organisms. Characterized by moderate sorting and obvious burrowing, this facies was deposited in a less agitated environment than the cross-bedded ooid grainstone.

The peloid-bioclast packstone to grainstone also has burrows with and without mud linings and is typically more mottled than the ooid grainstone to packstone. It has an extremely variable composition and consists of poorly sorted peloids, fecal pellets, bioclasts, especially *Halimeda spp.*, molluscs, and encrusting coralline algae. This packstone-to-grainstone facies, which contains occasional ooids, represents a low-energy deposit.

The lower Keys oolite is assumed to be the same age as the Miami Oolite; however, its maximum elevation is about half that of the Miami Oolite. The Miami Oolite is in places as much as 6.5 m (20 ft) above sea level, and the base of the cross-bedded unit is either at or slightly above sea level. At Big Pine Key, the base of the cross-bedded facies extends as much as 1 m (3 ft) below sea level (Kindinger, 1986).

Contour maps of the Miami Oolite reveal distinct tidal-bar morphology similar to that which is so obvious in the lower Keys (Fig. 1; Halley *et al.*, 1977). Flooding of the interbar lows in the lower Keys makes the tidal-bar morphology more obvious than in the higher unflooded area of Miami.

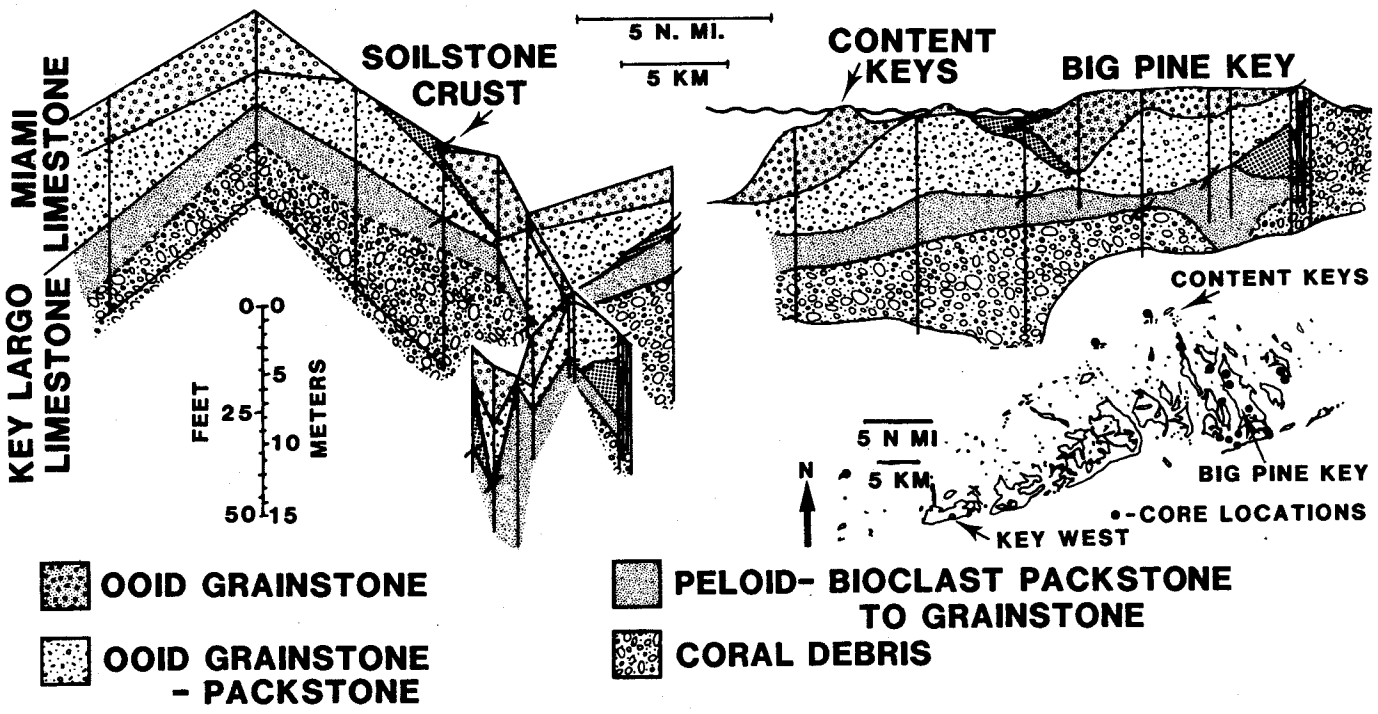


FIGURE 3 (A) Fence diagram based on cores shown in (B). (B) North-south cross section showing relation between Key Largo Limestone and Key West Oolite. No subaerial unconformity separates Key Largo coral facies from oolite facies.

a increased survival of M. annularis below six meters and on the more southern reefs.

Changes in the environment along a north-south axis may explain differences in the community structure among the four reefs. The detrimental effects of Biscayne Bay water should decrease with increasing distance from tidal passes. Triumph Reef, the most depauperate of the reefs, is the closest to the passes north of Elliott Key that connect the bay and the reef-tract. South of Triumph Reef, the abundance of Acropora cervicornis and Diploria clivosa in the shallow zones was greatest on the reefs furthest from Caesar's Creek (Fig. 19). In contrast, Agaricia agaricites was most abundant on the reef closest to this pass. The mean size of A. agaricites colonies on Pacific Reef's shallow zone was only 3.7 cm . This pattern of numerous small colonies is what one would expect if this species has a high rate of recruitment and is an early invader of disturbed areas (Bak and Engel, 1979, Dustan, 1977). As Dichocoenia stokesii and Porites porites had similar distributions they may also follow this pattern.

The hierarchical classification (Fig. 17) suggested that a third trend was superimposed upon the differences with depth and the differences among the shallow fore-reefs. Species diversity, the abundance and size of Montastrea annularis, and the similarity of reef-zones to their closest neighbors increased from a minimum at Triumph and Long Reef's shallow fore-reefs to a maximum on the deeper stations of Ajax and Pacific. One can hypothesize that the intensity and frequency of coral kills due to cold fronts decreases with latitude, as well as depth. Figure 20 depicts how each reef showed a different pattern of increasing diversity with depth. From north to south the

Rifting and faulting during formation of the Atlantic Ocean in the Early Mesozoic likely created topographic structural units upon which post-Mesozoic limestones began to form. It is this long depositional history that paved the way for development of the Holocene reefs of Florida.

THE PLEISTOCENE FOUNDATION

Holocene reefs and sediment deposits rest directly on Pleistocene bedrock throughout the area; thus, topography of the underlying rock has a great influence on reef distribution. Core drilling in scattered locations indicates that reefs off the upper, middle, and many of the lower Keys are underlain by Upper Pleistocene coralline limestone, the submerged extension of the Key Largo Formation that forms the upper and middle Keys. The exposed Key Largo Formation, named by Sanford (1909), is the Q5 Unit of Perkins (1977) that formed during the last interglacial stage 100 to 125 ka (Fig. 2).

The Pleistocene section is of variable composition and consists of as many as five separate units (Brooks, 1968; Perkins, 1977). Total thickness of these five units ranges from 18 m (60 ft) near Miami to more than 61 m (200 ft) in the lower Keys at Big Pine Key (Fig. 1). Total thickness of the Pleistocene Key Largo Formation, which is beneath the offshore Holocene reefs, is not known. Only three deep borings have been drilled, one each at Carysfort, Little Molasses, and at Looe Key Reef (Hoffmeister and Multer, 1968). Perkins (1977) found more than 45 m (150 ft) of Pleistocene reef deposit at Little Molasses Reef. All other core borings (those recently drilled by the USGS Fisher Island Station) only penetrated a few meters, enough, however, to confirm age (Pleistocene) and composition (Shinn *et al.*, 1977). These shallow penetrations reveal considerable compositional variation. In general, a Pleistocene coral facies, dominated by *Montastraea annularis*, underlies Holocene reefs, whereas a Pleistocene carbonate-sand facies composed of species of *Halimeda* underlies Holocene carbonate sands, also composed principally of *Halimeda spp.* This relation suggests that environmental conditions today are similar to those 125 ka. Although the areas west of the upper Florida Keys are not an essential part of this guide, it should be noted that recent coring has shown numerous abrupt facies changes within the Pleistocene section there.

Florida Bay to the west of Key Largo is underlain by a burrowed-pellet facies (the bryozoan facies of Hoffmeister *et al.*, 1967), which is the Q5 Unit (Quaternary) of Perkins (1977). Beneath the Q5 Unit are four Pleistocene units, each capped by a calcrete-coated unconformity indicative of subaerial exposure. These units have recently been identified in numerous 12- to 15-m-deep (40-50 ft) core borings drilled by the USGS and Wichita State University. The lowermost units have a high-quartz sand content. Quartz-free facies of these units were also identified in the deep boring beneath the Holocene reef at Little Molasses Island (Perkins, 1977).

The southeastern portion of the Florida mainland, i.e., the rock beneath the city of Miami, is composed of Upper Pleistocene oolite named the Miami Oolite (Sanford, 1909) and later called the Miami Limestone (Hoffmeister *et al.*, 1967; Halley and Evans, 1983). Those portions above sea level are mostly cross-bedded, whereas below sea level and beneath Biscayne Bay, Card Sound, and Florida Bay, the unit is composed of burrowed oolite and/or pellets and bryozoans. It is what Hoffmeister *et al.* (1967) called the bryozoan facies.

The exact relation between the Miami Oolite and the Key Largo Formation of the upper Keys

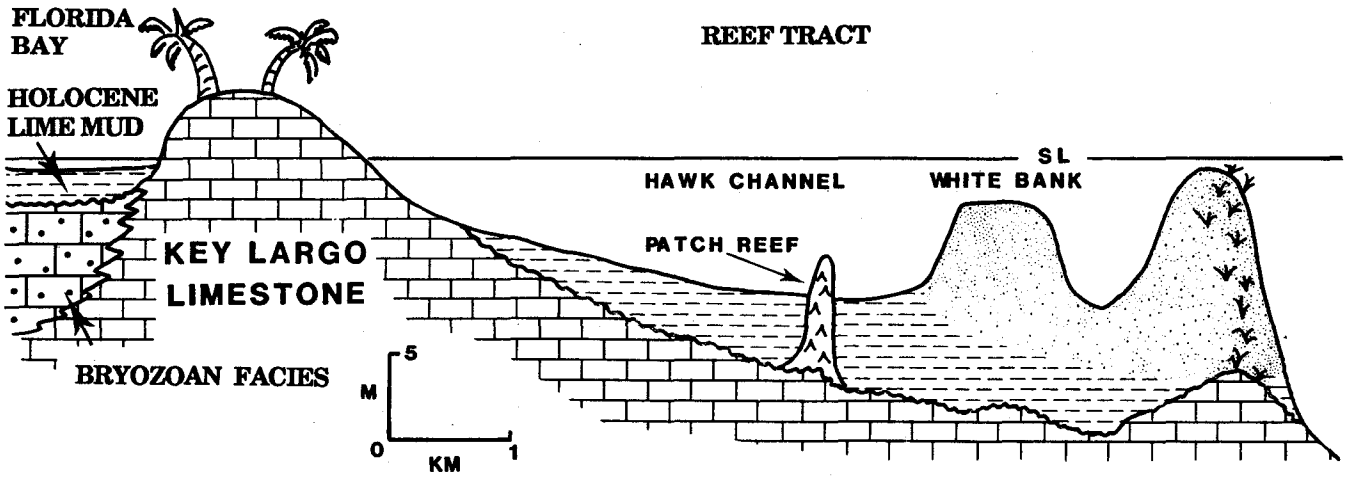


FIGURE 2 Generalized cross section showing relation of Key Largo Limestone and bryozoan facies of Hoffmeister and Multer (1964), which underlies Florida Bay to the west. Both facies compose the Q5 Unit of Perkins (1977). Key Largo facies underlies offshore reefs to the east. Patch reefs occur in the muddy wackestone facies of Hawk Channel and the carbonate sand facies of White Bank. Modified after Enos (1977).

the line. A low number of interspecific interactions is consistent with the low abundances and densities of coral on these reefs and suggests that coral competition is not increasing the diversity. There is also no evidence that there are differences in predation on coral or competition with other benthic organisms in those depth-zones with different diversities. This study indicates that physical factors are controlling the coral community on these shallow shelf-edge reefs.

This study has documented the small size of coral colonies on these reefs. As the probability of intercepting any colony increased with width (Eberhardt, 1978) and the measure of size was the larger of two dimensions, intercept and width, we expected the distribution to be biased toward larger size-classes. The greatest number of colonies, however, were from the smallest (1 - 5 cm) size class (Fig. 15). From Fig. 16 we can see that the size-distribution of several abundant species changed with depth. Shallow stations contained a greater percentage of smaller colonies. Studies suggested that coral growth-rates decreased with depth (Barnes, 1973, Hudson, 1981) and with increased age (Connell, 1973). If this were the case, then the majority of corals on these four reefs were very young or grew very slowly. This suggests that there is a high mortality of corals on these reefs and more so in shallower reef-zones.

Deeper stations contained a greater percentage of larger colonies. This is most notable for Montastrea annularis, an important reef builder. Hughes and Jackson (1980) concluded that partial mortality of corals would cause ages to be underestimated. The greater number of large colonies in the deep fore-reefs and its absence from Triumph Reef and the shallow fore-reefs of Long and Ajax Reefs suggests that there is

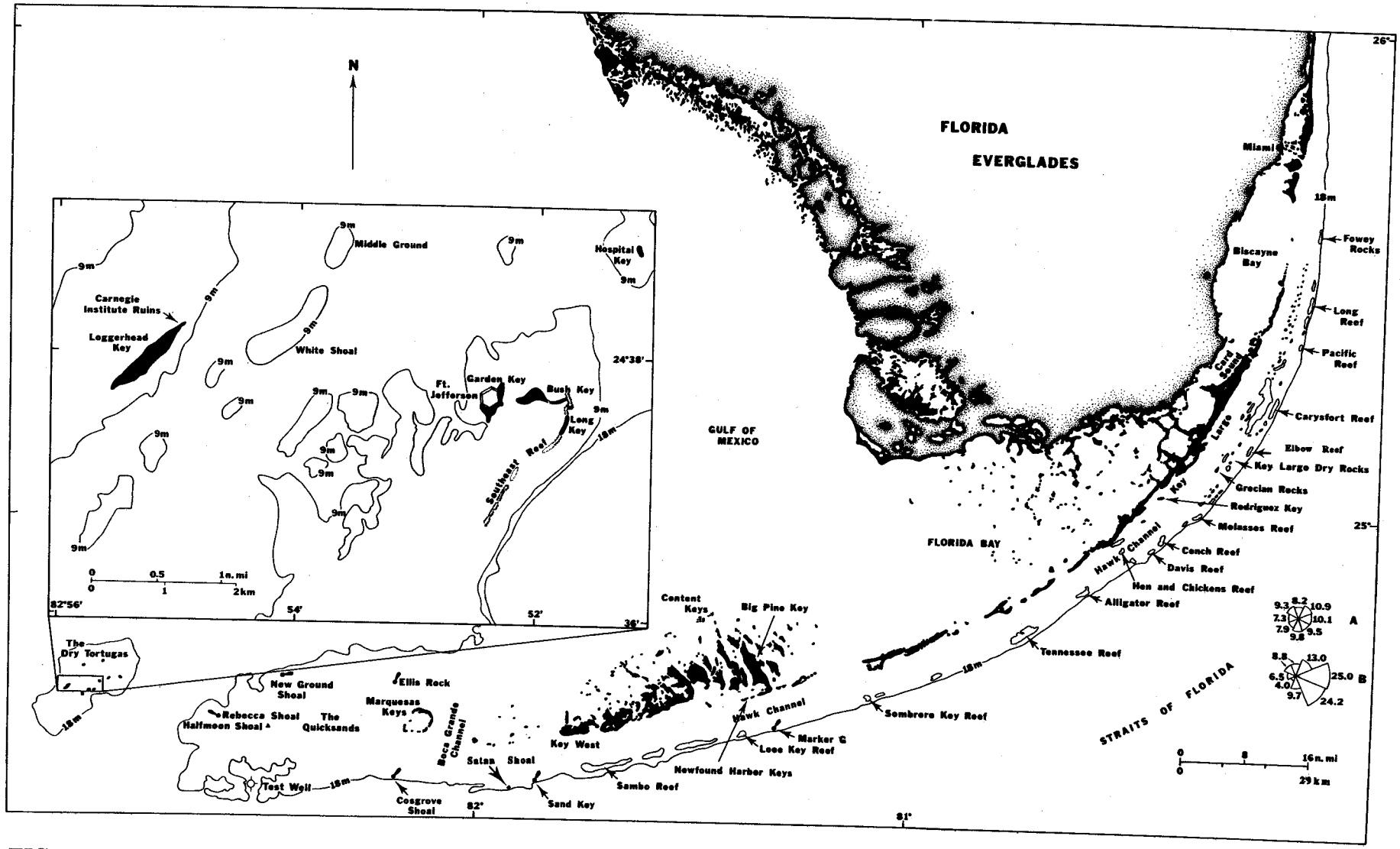


FIGURE 1 Index map of Florida reef tract showing upper Keys (Miami to Molasses Reef), middle Keys (Molasses to Marker G) and lower Keys and the Dry Tortugas (Marker G to Dry Tortugas). Note width of tidal passes between middle Keys and large areas without Keys between Key West and Dry Tortugas. Lower Keys are composed of Pleistocene oolitic tidal bars; upper and middle Keys are Pleistocene coral reefs. Surface exposure of Key Largo Formation ends at Newfound Harbor Keys in the south and at Soldier Key to the north (northeast of "e" in the word "Biscayne"). Stratigraphic relation of Key Largo Formation to Key West Oolite near Newfound Harbor Keys and Big Pine Key is shown in Figure 3. Rose diagram (A) shows mean of average hourly wind velocities; (B) shows percentage of total hours wind blows from each direction.

assume that an event of sufficiently cold water and upward movement could not occur. The existence and frequency of such events needs to be established through long-term monitoring of these reefs, especially temperature measurements at various depths on the reef substrate.

Control of the coral community on the study reefs by this phenomenon is inconsistent with the results of this study. If upwelling is detrimental to the coral community, one would expect the development, diversity, and abundance of corals in the community to decrease with depth. The high species diversity, the abundance of massive corals, and the greater coral cover on the deep fore-reefs suggest that upwelling may only temporarily stress corals. It may even be of some benefit. Lee et al. (1981) have documented an annual input of 55,000 tons of nutrient nitrogen onto the Georgia shelf by spin-off eddies. This is one more way the deep fore-reef may benefit from its greater depth and proximity to the Florida Current.

Species diversity increased with depth on all four reefs. Diversity should be lower on the shallow fore-reef if unpredictable, aperiodic disturbances, such as severe cooling or hurricanes, are extreme on the scales of frequency, magnitude, or space (Connell, 1978). Porter (1972) and Loya (1972) found that diversity (H'n) initially increased with depth. Even deeper, where reefs are subject to less disturbance, competition and predation can reduce diversity (Slobodkin and Sanders, 1969). Lang (1973) and Sheppard (1979) have proposed that some slow-growing species prevent overgrowth by attacking faster-growing species with their tentacles and extruded digestive organs, and that this process could increase diversity. On these reefs there were only 8 instances in 1,920 m of transect where two species made contact under

IGC FIELD GUIDE T176:
A FIELD GUIDE: REEFS OF FLORIDA AND THE DRY TORTUGAS

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INTRODUCTION AND SETTING

This guide for the 28th International Geological Congress field trip to the modern coral reefs and sediments of southeast Florida and the Dry Tortugas is focused toward explaining (1) the distribution of Holocene coral reefs, (2) the relation between topography and Holocene sea-level rise, and (3) the compositional and thickness variations of sediments produced in and adjacent to the reefs. This excursion will visit and examine representative reefs and sediments throughout the area and will relate differences to environmental conditions.

The excursion begins at Miami and makes numerous swimming stops to examine reef-building processes and sediment distribution en route to the Dry Tortugas. Because this is a boat trip, there is no rigid stop-by-stop plan with measured distances, as is common in guidebooks for land-based excursions. This guide provides geologic and biologic background and discussion relating to reef distribution throughout the field trip area. Day-by-day trip plans will be provided on the first day. A coral identification key and historical information are included in Appendices A-C. Under ideal weather conditions, all the sites listed can be visited in the order presented.

Because of environmental conditions, the region is divided into three major areas: (1) the upper Keys, where the trip begins, (2) the middle Keys, and (3) the lower Keys, including the Marquesas-Quicksands area and the Dry Tortugas. Notice in Figure 1 how the island chain forms an arc. The upper Keys are oriented nearly north-south and face almost directly into the prevailing east-southeast winds. The middle Keys are oriented more or less northeast-southwest and, for the most part, face directly into the east-southeast winds. The lower Keys, however, are situated essentially parallel to the east-southeast winds. The major differences along the reef tract occur in the middle Keys, where reefs are sparse, carbonate sands abundant, the water slightly deeper, and where large tidal passes separate the Pleistocene islands (Fig. 1). These changes in trend relative to winds and waves have a pronounced effect on the distribution of reefs and movement of carbonate sands. In addition, the lagoonal area landward of the lower Keys reefs is deeper by several meters than off the upper and middle Keys, and the shape and composition of the Pleistocene islands differ dramatically from those of the upper and middle Keys.

The Pleistocene islands in the lower Keys are oriented perpendicular to those in the middle Keys and are composed of oolite rather than coralline limestone. The lower Keys have been interpreted as preserved tidal-bar deposits (Hoffmeister *et al.*, 1967). Although there are numerous tidal passes between these keys, the water is shallow and water exchange is much less than in the middle Keys. Reefs off both the lower and upper Keys are thicker and better developed than those off the middle Keys. The reefs from Satan Shoal off Key West and continuing westward approximately 120 km (75 mi) to the reefs of the Dry Tortugas are poorly developed; however, reef growth is much improved at the Dry Tortugas. Between Key West and the Dry Tortugas is an area of extensive current-swept sand that forms sand waves as high as 3 m (9 ft). This extensive sand deposit, known as the Quicksands, is as thick as 12 m (40 ft). The shifting nature of these sands prevents reef growth but, at the same time, the lack of reefs allows extensive carbonate-sand production by algae, chiefly by *Halimeda spp.*

Except for Rebecca Shoal, the deep-water areas (25 m or 80 ft) that extend from the Quicksands to Dry Tortugas lack reef accumulations. The Tortugas reefs are luxuriant, have an elevated atoll-like rim, and are as thick as 17 m (55 ft). Several sand islands are located around the atoll, including Loggerhead Key, which is 14 m (45 ft) thick. Fort Jefferson, the largest brick fort ever built by the United States, rests on a similar, uncemented Holocene buildup at Garden Key in the Tortugas.

South Florida has been predominantly an area of limestone accumulation since the Mesozoic, and a test well drilled near the platform margin southwest of the Marquesas Keys (Fig. 1) penetrated 4,500 m (15,000 ft) and bottomed out in Cretaceous limestone and dolomite. A well drilled in north Key Largo bottomed in the Lower Cretaceous at 3,675 m (12,053 ft). Depositional thickening to the south and west apparently has been occurring from Mesozoic time to near the present.

experience sub-optimum temperatures. This can explain the lack of Acropora palmata, the low diversity and abundance of coral colonies, and their small size on the shallow and mid fore-reefs. The two most abundant species in these zones, Diploria clivosa and Dichocoenia stokesii, respectively, are tolerant to low temperatures. They made up 25.6 percent of the coral colonies between 16 and 20 m. off Boca Raton,Fl. (26°30'N) (Goldberg, 1973). Siderastrea siderea, the most widespread and abundant coral in this study, has been reported living off North Carolina (MacIntyre and Pilkey, 1969) and was one of the species that was predicted (Mayor, 1914) and reported (Porter et al., 1982) to survive severe cooling at the Tortugas. The deep reef stations on all but Triumph Reef show less indication of disturbance. Montastrea annularis was considered one of the most sensitive reef corals (Mayor, 1914) and it is absent from the shallow stations. Deeper parts of the reefs are hundreds of meters closer to the warmer waters of the Florida Current and may be protected from the cooling of near-shore waters.

Hudson (1981) hypothesized that unusual high-density skeletal bands in Montastrea annularis from deep fore-reefs in Pennekamp were caused by the stress of cold water from a different source. Lee and Mooers (1977) present evidence that cold water from deep in the Florida Current upwells into surface-waters in association with eddies sheared off the current's western edge. The shelf-edge reefs of BNP definitely experience periods of strong southerly currents and increased visibility, which suggest the passage of a spin-off eddy (Pers. obs.). There is no direct evidence that water, 16°C or colder, has upwelled far enough to affect coral communities. There is, however, no reason to

Table 11. Low Water Temperatures on South Florida Reef-tract

Location	Temp °C	Z (m)	Date mo/year	Source
Caesar's Creek (BNP)	13.9	2	1/1978	Tilmant, et al.
(80 14'W,25 23'N)	16.3	2	1/1979	(pers. comm.)
	14.8	2	2/1980	
	13.8	2	3/1980	
	15.6	2	1/1981	
	16.0	2	2/1981	
Elkorn Co. Reef(BNP)	16.7	3	2/1978	
(80 10'W,25 22'N)				
Key West,Fla.	17.9	?	1/1886	Vaughan, T.W.(1918)
(81 48'W,24 33'N)				
Carysfort Lgt(KLNMS)	20.1	?	1/1879	
(80 13'W,25 13'N)	18.2	?	1/1893	
Fowey Rocks, Fla.	15.8	?	12/1898	
(80 06'W,25 36'N)	15.8	?	1/1902	
	19.8	?	2/1904	

Z = Depth

Madracis mirabilis (Duchassaing and Michelotti) 47
Oculina varicosa leSueur 47
Oculina diffusa (Lamarck) 47
Cladocora arbuscula leSueur 47
Eusmilia fastigiata (Pallas) 47
Mussa angulosa (Pallas) 48
Agaricia fragilis Dana 48
Agaricia agaricites (Linnaeus) 48
Mycetophyllia lamarckiana (Edwards and Haime) 48
Isophyllia sinuosa (Ellis and Solander) 48
Isophyllia multiflora Verril 48
Manicina areolata (Linnaeus) 48
Manicina mayori Wells 48
Dendrogyra cylindrus Ehrenberg 48
Meandrina meandrites (Linnaeus) 48
Diploria labyrinthiformis (Linnaeus) 48
Diploria clivosa (Ellis and Solander) 48
Diploria strigosa (Dana) 48
Colpophyllia natans (Houttuyn) 49
Colpophyllia amaranthus (Houttuyn) 49
Montastraea cavernosa (Linnaeus) 49
Isophyllastrea rigida (Dana) 49
Porites astreoides Lamarck 49
Siderastrea siderea (Ellis and Solander) 49
Siderastrea radians (Pallas) 49
Stephanocoenia michelini (Edwards and Haime) 49
Montastraea annularis (Ellis and Solander) 49
Solenastrea hyades (Dana) 49
Solenastrea bournoni Edwards and Haime 49
Dichocoenia stokesii Edwards and Haime 49
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fore-reefs suggest that other disturbances have occurred locally in the 17 years since Hurricane Betsy.

We must look at a different aspect of the biology of hermatypic corals to understand the lack of acroporids in the shallow stations and the low abundance of corals above 12 m . Vaughan (1918) suggested that cold weather limited the coral community in this area. Water temperatures below 16°C are potentially lethal to most reef-corals and branching corals even more so than head corals (Mayor, 1914,1915). Since 1957, air temperatures in Homestead, Fl.(25°30'N) have dropped below 10°C (50°F) for two or more consecutive days an average of twice a month from December to March. The cold air and strong winds (> 4.5 m/sec) of these cold fronts or ''Northers'' cool surface waters (Table 11). A series of cold fronts in January 1977 lowered water temperatures in the Dry Tortugas (24°60'N) to 14°C (Davis, 1982). Porter, et al. (1982) describe the extensive death of Acropora cervicornis in the shallow reefs there.

Ginsburg (1972) hypothesized that the flow of water out of Florida Bay stifled reef development offshore of tidal passes. Roberts et al. (1982) document the severe cooling of Florida Bay and, subsequently, the waters of the back-reef to temperatures below 16°C. Water flowing through Caesar's Creek (BNP) from Biscayne Bay has been recorded as low as 13.9°C twice between 1978 and 1981 (Tilmant et al., pers. comm.). Detailed mapping of the flow of cooled water is needed to determine if patch-reefs in the park, with their large coral heads, lie in the path of this cold water.

If water over the reefs is cooled or cold water from shallower areas flows over and then down these reefs, the coral community will

growth-form to the wave-environment (Shinn, 1963) and has a stronger skeleton than head corals (Chamberlain, 1978). A. palmata and A. cervicornis propagate and disperse through the fragmentation of their branches (Highsmith et al., 1980, Tunnicliffe, 1981). Porites asteroides and Diploria clivosa on these reefs form low heads or encrustations that present little cross-sectional area to moving water (pers. obs.). Massive corals, despite their size, have more porous skeletons (Chamberlain, 1978) and cannot remain upright under the combined effects of the erosion of their bases and the force of breaking waves. We would expect and do find greater abundances of large head-forming species in the deep fore-reef stations.

Hurricanes and tropical storms are frequent in the South Florida area. At least eighteen storms with winds 80 km/hr (50 mph) or greater have passed over these reefs since 1886. Storm waves breaking upon the reef can devastate shallow-water coral communities (Stoddart, 1962), but coral colonies in deeper water are more protected. In 1980, Hurricane Allen pounded Jamaica with winds up to 110 km/hr. Damage was observed as deep as 50 m, but destruction decreased with increased depth (Woodley et al., 1981). Differential destruction with depth could explain the increased abundance of corals in the deeper areas on the study reefs and the lack of Acropora palmata in shallow water.

Hurricane Betsy in 1965 was the last major storm to cross South Florida. There is little doubt that recovery-time is dependent on the extent of damage (Highsmith et al., 1980), but Shinn (1976) did report extensive recovery of acroporids in 3 to 5 years following hurricanes Donna (1960) and Betsy. Even if recovery is on the order of 20 years (Stoddart, 1974), the abundance and size of corals on the shallow

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sediments away from corals. Loya (1976) found the highest coral diversity on the steepest reef-slopes. The greater abundunce of corals less capable of removing sediments, e.g. Montastrea annularis and Siderastrea siderea, suggests that sedimentation does not limit their distribution and abundance in the deep fore-reef.

Physical forces do play a role in the distribution of species in shallow water. Munk and Sargeant (1954) calculated that reefs in the belt of the Pacific trade winds dissipate up to 500,000 horsepower from the waves breaking upon them. Coral reefs, however, flourish in exposed areas. Shallow-reef organisms have evolved structural, morphological, and behavioral adaptations to these tremendous levels of mechanical energy.

Acropora palmata, growing outstretched into the breaking waves, dominates shallow, wave-stressed reef-zones in the Caribbean. Its predominance has been documented in Jamaica (Goreau, 1959), Abaco Is. Bahamas (Storr, 1964), the Netherlands Antilles (Roos, 1964), Mexico (Milliman, 1969), Cuba (Kuhlmann, 1974), the Grenadines (Lewis, 1975), Anageda, B.V.I. (Dunne and Brown, 1979), and Belize (Ruetzler and MacIntyre, 1982) to name a few. According to a generalized zonation of Caribbean reefs (Geister, 1977), species of Diploria and Porites astreoides coexist with Acropora palmata in high energy wave-zones. Seaward, with reduced wave force, the thinner branched A. cervicornis and massive corals reach a greater abundance. Massive head-corals are also found in shallow water surrounding dense, energy-absorbing thickets of A. palmata (Goreau, 1959).

These general, yet widespread, trends are consistent with our knowledge of the biology of these species. A. palmata modifies its

Particulate matter suspended in seawater also decreases the intensity and quality of light. Turbidity and sedimentation rates, in turn, are a function of the physical properties of waves and currents. Waves provide energy for particle-transport to a depth of one-half the wave's length (Sverdrup et al., 1942). Winds over these reefs are predominately from the east and southeast at an average velocity of 4.2 m/sec (9 mph) (NOAA, 1982) and are capable of producing waves with lengths of 7 m and heights of 2 m . These wind-driven waves and longer wave-length ocean swell work upon the shallow fore-reef and transport all but the largest sediment grains to calmer back-reef locations (Barber and Tucker, 1962). Ginsburg (1956) found little sediment less than 0.125 mm in diameter on Triumph Reef. Constant turbidity and high sedimentation rates are rare in the well-flushed shallow fore-reef.

Decreased wave action with increased depth and the gradual slope of the mid fore-reef make sedimentation and turbidity more important factors. Dichocoenia stokesii, Porites porites, and Agaricia agaricites are the most abundant corals in this zone and are competent sediment rejectors (Hubbard and Pocock, 1972). The amount of fine sediment may be less here than on patch-reefs in back-reef areas where heads of Montastrea annularis are common. The poor coral community in the mid fore-reef suggests that other variables are limiting the growth and survival of species adapted to the amounts of sediment and light experienced at these depths. More data on sedimentation rates and turbidity levels are needed to compare these reefs to better developed reefs.

In the deep fore-reef only the finest particles remain suspended. The more complex topography and greater slope more efficeintly channel

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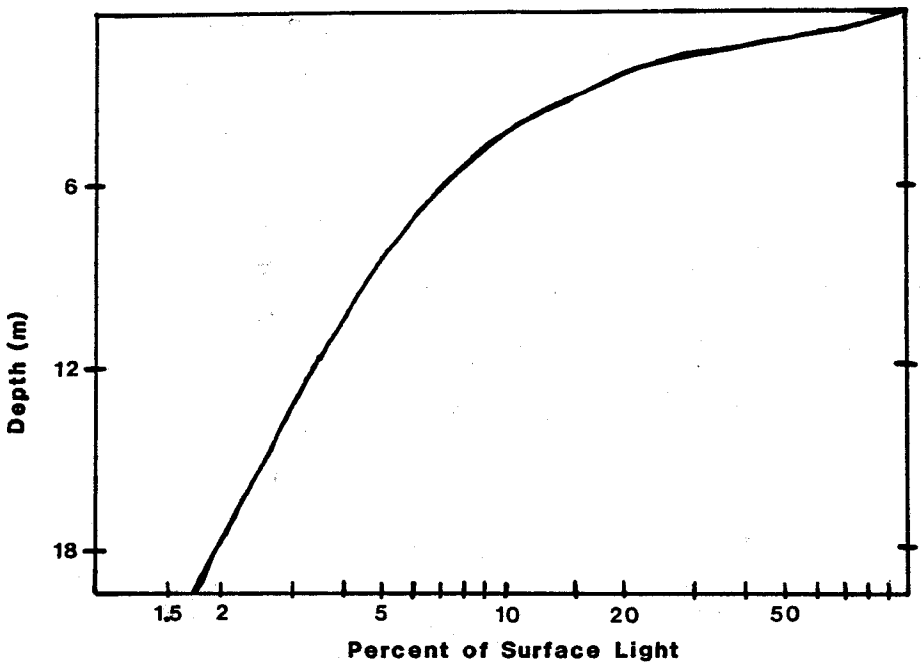

Depth (m)
6
12
18
1.5
2
5
10
20
50
Percent of Surface Light

Figure 18

Percent of surface light at bottom of reef vs. depth for Abaco Is., Bahamas (adapted from Storr,1964).



COVER U.S.G.S. diving geologists coring reef off the Florida Keys using an underwater drilling device perfected at the U.S.G.S. Fisher Island Station.

DISCUSSION

One would expect to find differences in species composition and community structure in different environments. Environmental conditions on reefs change with depth. Light, important to the nutrition and skeletal growth of corals, is at a maximum in the shallow fore-reef and decreases with increasing depth. Storr (1964) presented a curve of light penetration for the Abaco Is. (Bahamas) reef-tract at 26°30'N, 110 km north of Triumph Reef. This curve shows that light penetration decreases from 8 percent of surface illumination at 6 m to 2 percent at 20 m (Fig. 18).

Decreasing intensity, the concurrent change in the color of light with depth, and the inhibition of calcification (Roth et al., 1982) or photosynthesis (Steeman-Nielsen, 1971) by long-wave ultraviolet light cannot fully explain the distribution of corals in this area. Montastrea annularis and Colpophyllia natans are just two of the species that were not abundant in the shallow fore-reef stations, but are common and massive corals on shallow patch-reefs in South Florida (Jones, 1977). Despite sub-tropical light levels sufficient for luxuriant coral growth on patch-reefs, the shallow fore-reefs at similar depths possessed lower species diversity, diversity of cover, and percent coral cover than did deeper areas. Species that may be restricted to shallow-water, i.e. Siderastrea radians, and Acropora palmata, were only encountered in the shallow zone, but were rare. The scarcity of these characteristic species in the sufficiently illuminated, shallow fore-reef forces us to question the importance of light as a control on coral distribution with depth on these reefs.

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unique. Triumph's deep fore-reef was also unlike the other reef-zones. These six groups are separated at the .50 similarity level.

Reefs of Florida and the Dry Tortugas

Miami to Key West, Florida
July 2–7, 1989

Field Trip Guidebook T176

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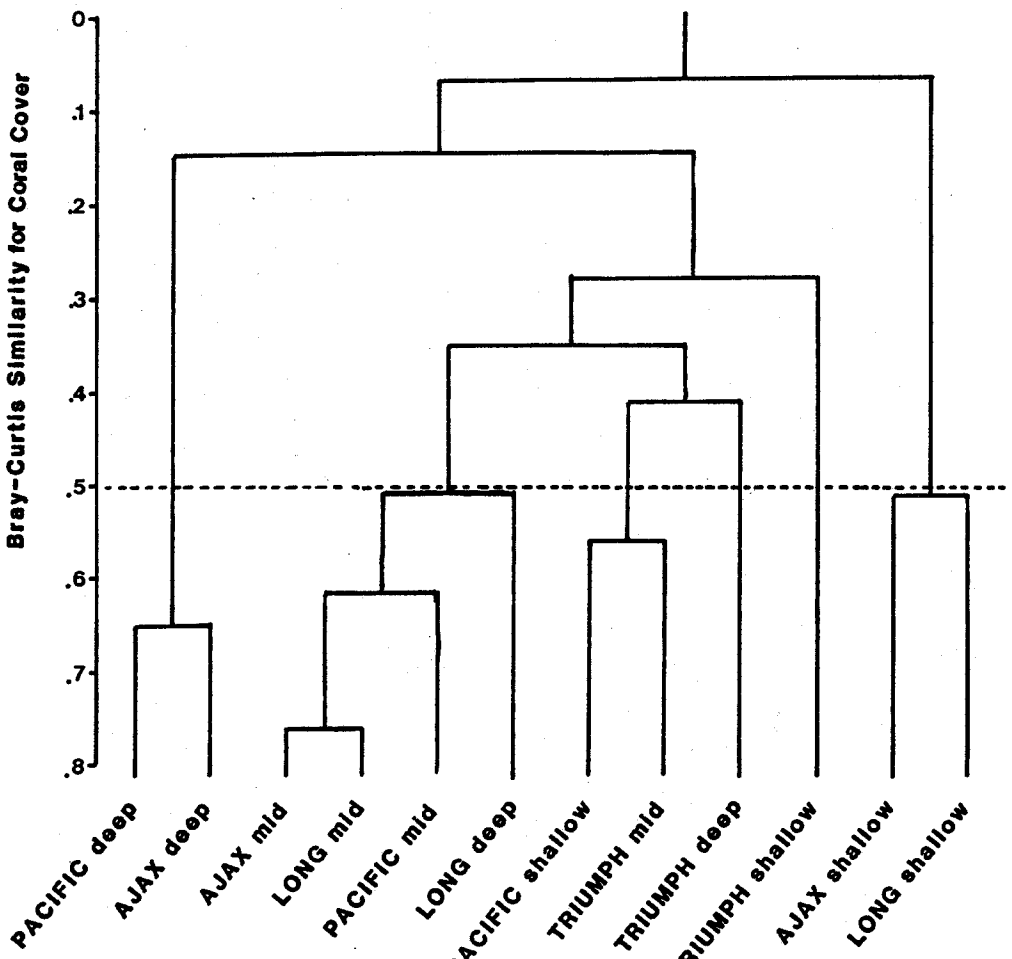

Bray-Curtis Similarity for Coral Cover
0
.1
.2
.3
.4
.5
.6
.7
.8
PACIFIC deep
AJAX deep
AJAX mid
LONG mid
PACIFIC mid
LONG deep
PACIFIC shallow
TRIUMPH mid
TRIUMPH deep
TRIUMPH shallow
AJAX shallow
LONG shallow

Figure 17

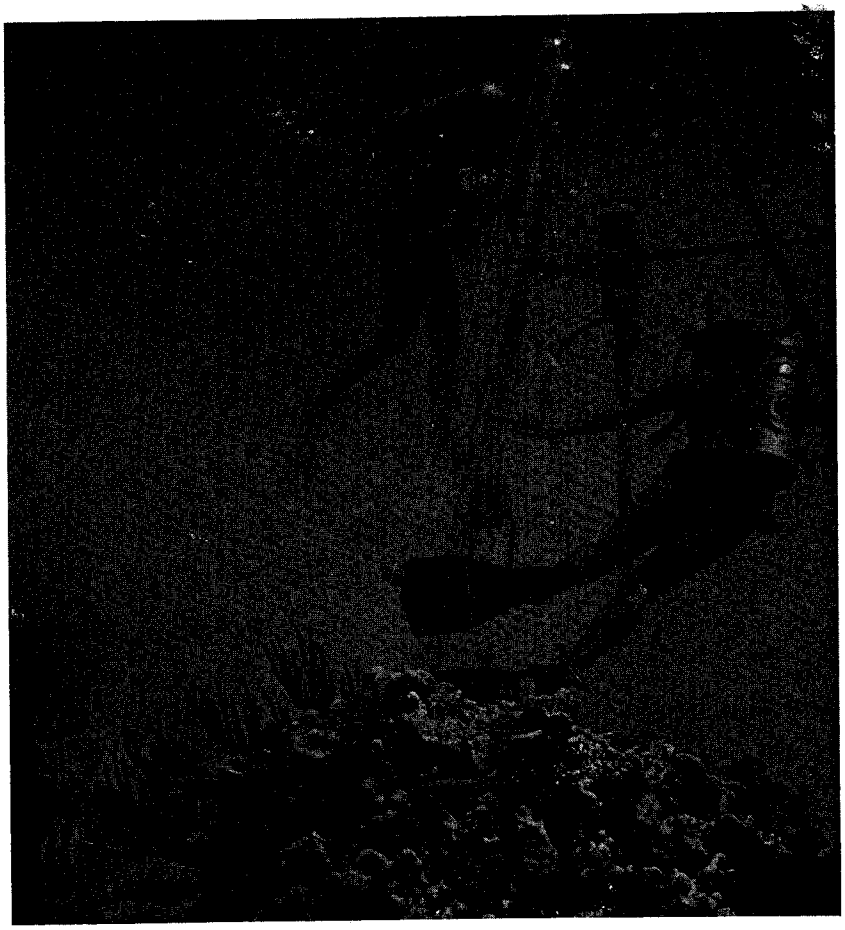
Dendrogram showing furthest-neighbor clustering of reef-zones for Bray-Curtis values of the similarity of coral cover.

28th International Geological Congress

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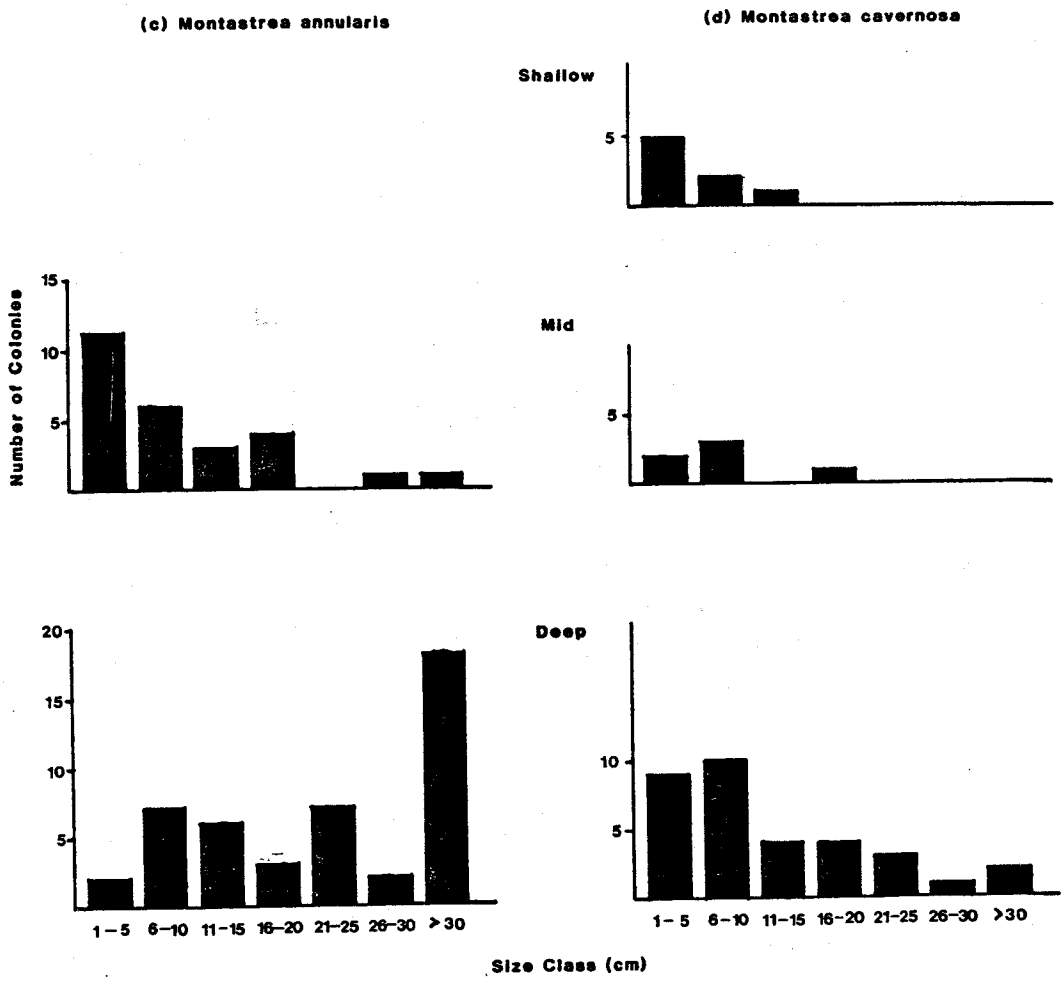
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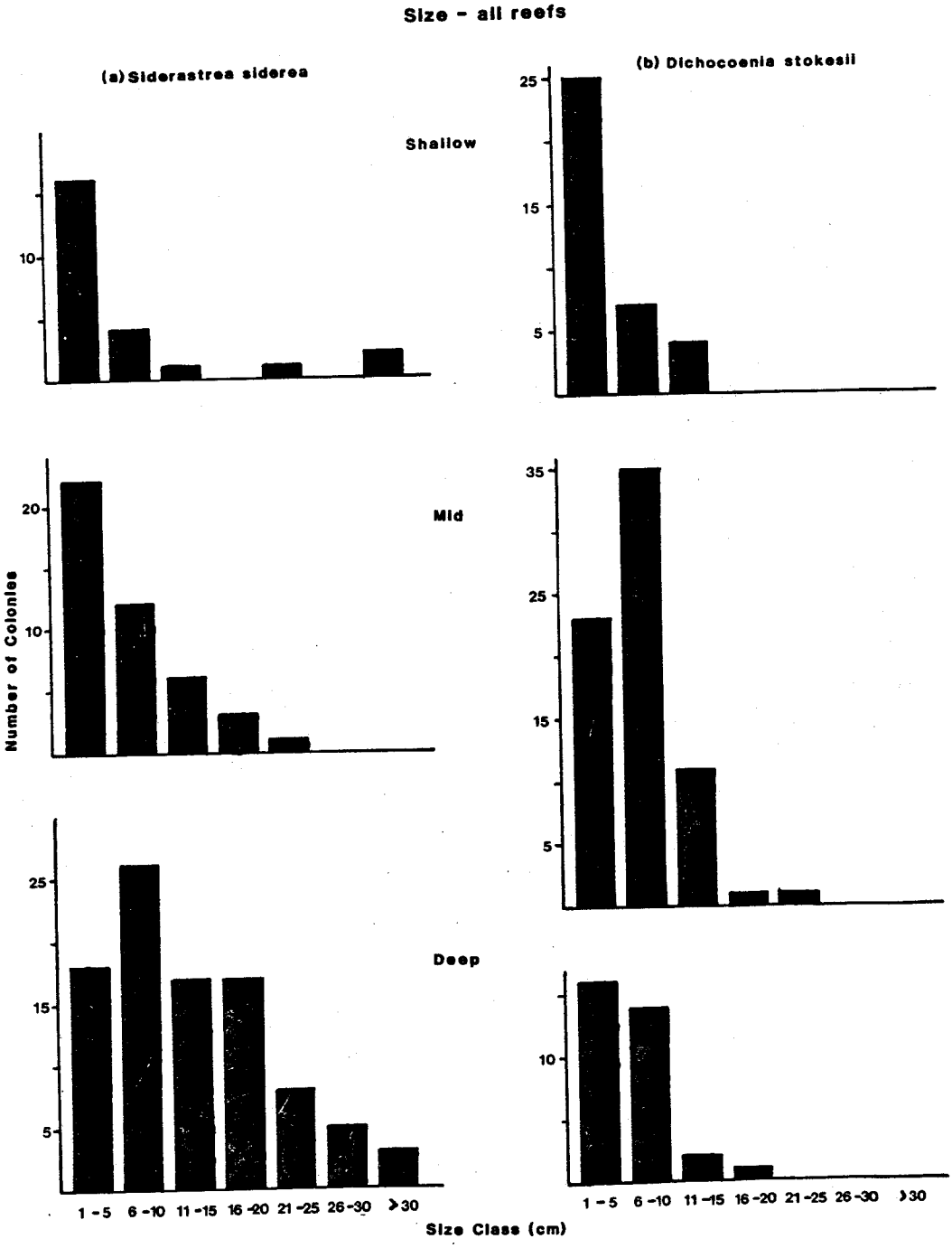
(P = .006) density of colonies (Table 2) and number of colonies of Porites porites and Montastrea annularis (P < .01). Species diversity, H'n, and Dn were lowest at Triumph. H'c was lowest at Ajax's mid fore-reef.

For the deep fore-reefs, Triumph Reef was ranked significantly lower than the other reefs in coral cover (P = .008), number of colonies (P = .002), density (P = .003), and number of species per transect (P = .04). Pacific Reef had a significantly greater cover and number of colonies of Siderastrea siderea than Long or Triumph Reefs. Triumph Reef had the lowest number of species but the greatest H'c. Pacific Reef had the lowest H'c, H'n, and Dn. H'n and Dn ranged from 2.11 to 2.28 and .867 to .780, respectively, for all four reefs.

Jaccard values were greatest for the mid and deep stations at Long, Ajax, and Pacific reefs, where values ranged from .68 to .55. Only Pacific Reef's mid fore-reef was less similar than this to these stations. The shallow zones of these three reefs were all relatively similar with Jaccard values from .58 to .53. Triumph Reef's mid and deep zones were most similar to each other, but the species composition of the shallow station was most like the mid fore-reef station at Pacific Reef (.46).

The B-C similarity matrices for all stations are presented in Tables 3 and 4, and the dendrogram of a furthest-neighbor classification by percent cover in Figure 17. From the matrix we can see that the four mid-depth stations were the most similar. The dendrogram indicates that Long Reef's deep station was most similar to the mid-depth stations. The deep fore-reef stations of Pacific and Ajax form a distinct group, as do Pacific-shallow and Triumph-mid. The other shallow stations were


(c) Montastrea annularis
(d) Montastrea cavernosa
Shallow
Mid
Deep
Number of Colonies
15
10
5
20
15
10
5
5
10
5
1-5
6-10
11-15
16-20
21-25
26-30
>30
Size Class (cm)


Size - all reefs
(a) Siderastrea siderea
(b) Dichocoenia stokesii
Shallow
Mid
Deep
Number of Colonies
Size Class (cm)
1 - 5
6 - 10
11 - 15
16 - 20
21 - 25
26 - 30
> 30

DUPLICATE:
Original in
Museum Archives
BISC-118

Figure 16

Size-frequency distributions for four species by zone for all reefs combined: a) Siderastrea siderea, b) Dichocoenia stokesii, c) Montastrea annularis, d) Montastrea cavernosa.

loading by sewage outfalls and septic tanks in the Keys, deterioration of the water quality of Florida Bay must be assessed and reversed. This will require integrated studies of the entire South Florida assemblage of ecosystems.

The level and impact of human usage of the Reef Tract needs to be studied. Information is needed on the number of users, the resources they are utilizing, the effects they are having on water quality, and the amount of physical damage to reef resources that is attributable to human activities.

As the result of growing scientific and public concern for the deteriorating health of the Florida Reef Tract, the Florida Keys Coral Reef Research and Management Workshop was convened in June 1988, bringing together over 50 experts on coral reefs and their management. The recommendations and conclusions of that workshop (Miller 1988) are summarized below:

"A. The Florida Reef Tract is in serious trouble because of a combination of events including:

1. Excessive nutrients and other waste products in the water originating from nearby land masses and Florida Bay.
2. Physical damage to corals caused by boaters, divers, and fishermen.
3. Natural causes such as storms, thermal shock from cold water in periodic storm events, warm water events....
4. The lack of consistent management policies....
5. The lack of sufficient data to make effective long range management decisions.
6. Insufficient education of the public....

B. A series of definitive steps can be taken now to reduce the rate of deterioration of the Florida Reef Tract and to aid in its recovery.

1. Establish permanent monitoring sites....
2. Initiate the following research studies, using standardized instrumentation, at each of the permanent monitoring sites:
   (a) animal and plant inventories
   (b) nutrient transport and loading
   (c) installation of oceanographic 'weather' stations
   (d) satellite, aerial, and underwater photography
   (e) coral physiology, population dynamics, and biotic processes.
3. Initiate a series of education and management programs aimed at immediately reducing the adverse human impact on reefs...."

There are initiatives at the Federal and State level to designate the Florida Reef Tract as a National Marine Sanctuary and to designate a shipping avoidance zone offshore of the Florida Keys. These efforts, should they succeed, will provide significantly improved management of reef resources. However, the threat of urbanization and nutrient runoff from uplands would not be addressed by these management programs. The reef system must be managed in the context of the drainage basin patterns and the anthropogenic processes that threaten environmental quality.

Ajax Reef. The mean colony size of Dichocoenia stokesii in Pacific's deep fore-reef was 5 cm greater than the mid-depth station and 8 cm greater than the shallow station.

Due to the overall low abundance of coral colonies, the size distributions from the four reefs were combined to further compare differences with depth for selected species. S. siderea was the most abundant colony in the study area, and a greater percentage of its colonies were larger in the deep fore-reefs (Fig. 16). This trend was equally noticeable for the two massive, head-forming species Montastrea annularis and M. cavernosa.

The population of Dichocoenia stokesii in the mid fore-reef stations had a greater percentage of colonies in the larger size-classes, despite the larger colonies present in Pacific's deep fore-reef station.

Reef Comparison

Triumph Reef ranked lower than all other stations for most of the parameters of interest to this study (Tables 2,6). In the shallow fore-reef stations, Triumph had a significantly lower number of species and total coral cover ($P < .05$) and a lower number of colonies per transect. Species diversity, H'n, and Dn were also the lowest of the four reefs. Long Reef had the lowest colony density and H'c. Porites porites, Agaricia agaricites, and Dichocoenia stokesii had significantly different cover, colony abundance, and density among the shallow fore-reefs and were always more abundant on Ajax and Pacific Reefs.

Triumph Reef also ranked lower than the others for the mid fore-reef zones. Pacific Reef had the greatest abundance ($P = .03$) and

The Florida Keys are economically dependent on the coastal ecosystem that includes coral reefs. The subtropical climate and clear, warm, azure waters provide an ambience that attracts millions of visitors from all over the world. Tourists come to snorkel, scuba dive, and view the reefs from glass-bottom boats. Reef-related recreational fishing and pleasure boating also support the economy of Monroe County. Commercial fishing, which includes the harvest of spiny lobster, grouper, and snapper from coral reef habitat, is second only to tourism in economic importance. Much of this harvest is consumed by the tourists in local restaurants. Coral reefs are a refuge and breeding habitat for lobster, grouper, and snapper, which are being utilized at or near maximum sustainable yield.

Unfortunately, the geographic setting of Florida's reefs exposes them to less-than-optimal environmental conditions. Because they are among the northernmost coral reefs in the Caribbean/western Atlantic, extreme winter cold fronts periodically stress the reefs, causing fish and coral kills. Summer doldrums that create abnormally warm water also stress the reefs, as do frequent hurricanes.

In addition to natural stresses, urbanization of the Florida Keys and increased tourism have reduced coral reef vitality. During the last decade, environmental quality in the Florida Keys has deteriorated. Problems include declining water quality (due to nutrient enrichment and turbidity); boat and ship groundings; loss of coastal mangroves, which serve as a natural buffer-filter between inhabited areas and the more sensitive seagrasses and reefs; contamination of the habitat by pesticides and trace metals; and physical damage by anchors, divers, and fishing gear. The synergistic effect of these human actions threatens the continued survival of these sensitive marine communities.

The possibility of a major oil spill from existing tanker traffic or future oil exploration and development is further cause for concern. The Bahia las Minas spill in Panama, which occurred in a similar environmental setting, caused significant, long-term damage to coastal communities (see Chapter 15). Because South Florida coral reefs are precariously located near the ecological limits for reef growth, their ability to recover from such damage is doubtful.

From an ecological viewpoint, the diversity observed in the Florida Keys coral reef ecosystem has evolved through natural selection with little or no human interference. If this process is to continue, human effects on the reefs must be minimized, or a unique and precious National heritage will be lost.

There are numerous ongoing research programs in the Florida Keys area, including programs sponsored by the National Oceanic and Atmospheric Administration, the National Park Service, the U.S. Geological Survey, the State of Florida, private foundations, and others. Some critical research needs are outlined below.

In general, details of biology and life history are poorly known for the vast majority of coral reef biota. Population dynamics and interspecific interactions among reef organisms must be more thoroughly investigated. In particular, because diseases and algal overgrowth are rapidly eliminating living corals in the Florida Keys (e.g., Shinn et al. 1989; Porter unpubl. data as reported in Miller 1988 and Shinn 1988), research is immediately needed on pathogens of coral and other reef organisms. The extent of coral pathogen distribution in the Reef Tract should be studied. Information is needed on the types of pathogenic conditions present and the net annual loss of coral cover due to disease. Further research is also needed on coral-algal and coral-bioeroder interactions. Because growth of algae, bioeroders, and possibly disease pathogens seem to be promoted by nutrient loading, research must include determining sources of anthropogenic nutrients and determining ways to reduce nutrient loading. In addition to nutrient

Table 10. Mean Colony Size (± SE).

Species - Location	Shallow	Mid	Deep
Agaricia agaricites			
Ajax Reef	4.7(0.7)	3.0(0.0)	9.8(2.7)
Dichocoenia stokesii			
Pacific Reef	4.3(1.0)	7.1(0.7)	12.6(1.4)
Diploria clivosa			
Pacific Reef	23.3(9.2)	3.0(0.0)	--
Montastrea annularis			
* * Long Reef	--	11.3(2.7)	42.5(10.6)
* Ajax Reef	--	12.4(5.6)	31.2(6.1)
* Pacific Reef	5.0(0.0)	8.8(1.6)	34.5(7.6)
Porites astreoides			
Ajax Reef	--	3.2(0.5)	10.5(0.5)
Siderastrea siderea			
* * Ajax Reef	4.4(0.6)	6.6(1.5)	15.3(1.4)

* Significant differences between zones by ranks ($P \leq .05$)

* * $P \leq .01$

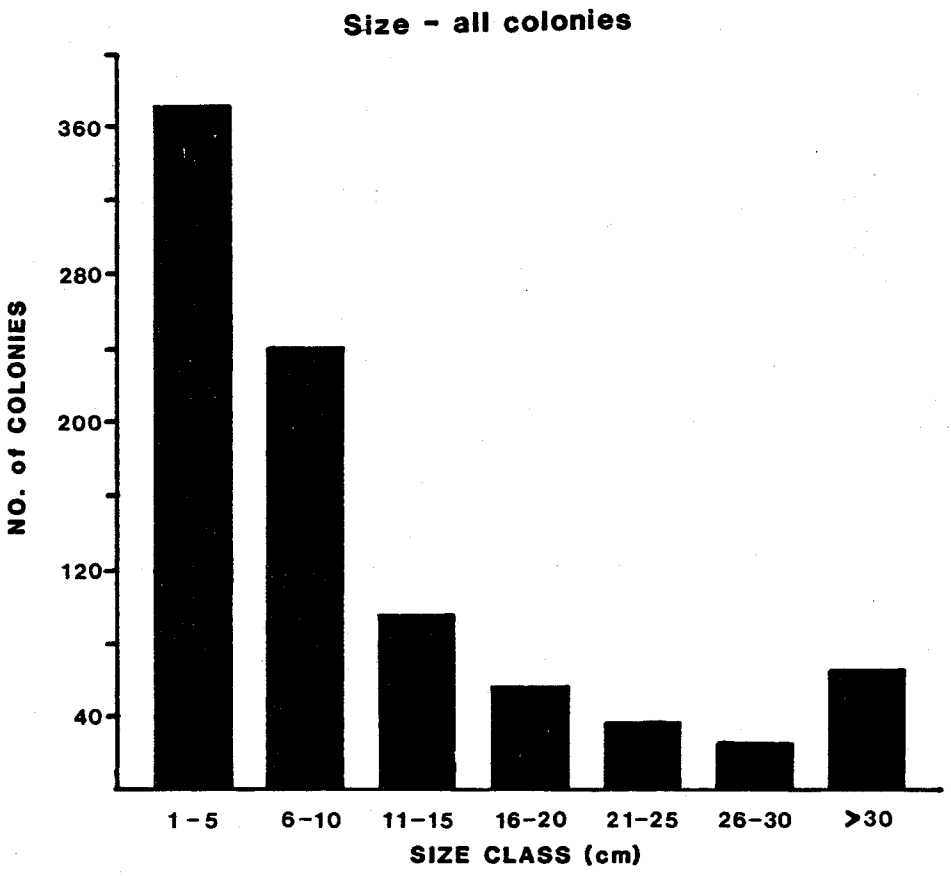
Federal administration. In the Lower Keys off Key West, the islets of Sand Key and Pelican Shoal extend State jurisdiction to the outer bank reefs from Maryland Shoal to Satan Shoal. This complexity of boundaries makes enforcement difficult. The State of Florida and the Federal government have statutes protecting stony corals and the sea fan *Gorgonia* from harvest, sale, or damage on the seafloor. Permits from the Florida Department of Natural Resources (State waters) or the National Marine Fisheries Service (Federal zone) are required for all coral collections. Parks, sanctuaries, and National monuments receive special management. Fragmentation of responsibility makes it very difficult for an agency to react quickly to information on destructive human activities.

As previously noted, many vessels have grounded on Florida reefs. Such impacts not only damage or destroy the vessels, but also damage reef, seagrass, and mangrove habitats. Coral reef communities require at least several decades to recover from major natural disturbances; recovery following human disturbance is less predictable, especially if the habitat has been permanently altered (Pearson 1981). Large vessels, such as the freighter *Wellwood* which grounded in August 1984, devastate extensive areas of the reef (Gittings 1988; Hanisak et al. 1988; Hudson and Diaz, 1989). Large ships are a menace to Florida's coral reefs. In a span of 18 days three large ships ran aground on reefs off the Florida Keys during 1989. All of these accidents were caused by human error. The 47-m-long offshore oil supply vessel *Alec Owen Maitland* grounded on south Carysfort Reef on 25 October. The 145-m-long bulk carrier *Mavro Vetranic* grounded on Pulaski Shoal, Dry Tortugas on 30 October. The 143-m-long bulk carrier *Elpsis* grounded on a reef in the Key Largo National Marine Sanctuary on 11 November. It is difficult to understand these accidents; none occurred during severe weather conditions and none of the ships reported mechanical difficulties. All of these accidents caused massive damage to the coral reefs where the ships had grounded. Even small boats can drive antifouling paint or fiberglass into coral surfaces, cut deep gashes into coral heads, shatter stands of elkhorn coral, or split large head corals that are hundreds of years old. In addition to overt physical damage, these accidents seem to make corals more susceptible to disease. The large number of boats operating in waters around the Florida Keys results in numerous groundings every year. Most are caused by navigational errors or poor knowledge of local water hazards. Shallow patch reefs, such as Mosquito Bank off Key Largo, are particularly prone to damage by pleasure boats; boaters seeking shortcuts to offshore reefs commonly run aground on the patch reefs. Anchors (Halas 1985) and lobster and fish traps, when deployed on a reef, can crush and scar corals and other biota. Even during coral recovery, traps may be pulled across the reef until they clear the bottom, often abrading or dislodging algae, corals, and sponges.

Conclusions

While the majority of the continental U.S. lies in the temperate climatic zone, the Florida Keys border the subtropics. The Florida Keys possess a unique coastal ecosystem that is Caribbean-West Indian in its biogeographic affinity. This ecosystem is characterized by an onshore-to-offshore gradient of communities: a mangrove coastal fringe, and a mosaic of seagrass, sedimentary, and coral reef communities seaward of the coast. The coral reefs are a National heritage of an aesthetic value equal to the Grand Canyon or Yellowstone National Park. Nowhere else in the continental U.S. can a citizen experience coral formations, schools of tropical fish, and the bountiful variety of life found on a coral reef.

Coral reefs provide complex three-dimensional structure on an otherwise featureless continental shelf. The heterogeneity provides habitat that is occupied by many sessile and mobile species. These reefs are analogous to the tropical rain forest in ecological characteristics: high gross primary productivity, low net primary productivity, rapid recycling of limited chemical resources, extreme spatial complexity, high species diversity, and species interdependence (symbiosis).


Size - all colonies
NO. of COLONIES
360
280
200
120
40
1-5
6-10
11-15
16-20
21-25
26-30
>30
SIZE CLASS (cm)

and Palm Beach Counties has damaged reefs. Increased sedimentation rates, burial, and physical damage by dredge cables and anchors have all occurred there (Courtenay et al. 1974; Jaap 1984; Goldberg et al. 1985; Blair and Flynn 1988).

Although specific studies of the effects of excess nutrients on Florida's coral reefs have not yet been carried out, other research has shown how sensitive reef growth is to nutrient loading. Successful coral recruitment is inversely correlated with nutrient availability (Birkeland 1977). Smith et al. (1981) found that strong eutrophication can eliminate corals from a benthic community. Although mild eutrophication does not eliminate adult corals, an event such as excessive storm runoff can kill them, leaving the habitat to be taken over by benthic algae due to sparse juvenile coral recruitment. Tomascik and Sander (1985) found that coral growth was inversely proportional to particulate organic carbon concentrations in waters over the reefs of Barbados. Birkeland (1987) classified the coral reefs of the western Atlantic and Caribbean as "continental" because nutrients are readily available from nearby land sources. Hallock et al. (1988) observed nutrient suppression of coral reef development in an area remote from anthropogenic influence (the Nicaraguan Rise of the western Caribbean). Because the Florida Reef Tract is on the climatic boundary of reef development and is occasionally stressed by exceptionally strong winter cold fronts, Florida reefs can only survive if human activities that directly or indirectly affect coral reef communities are minimized.

Value of Florida Coral Reef Communities

Florida's reef system is a unique resource in the continental U.S. Coral reefs are vital to Florida's economy. Commercial and recreational fishing industries depend on numerous species that inhabit reefs during all or parts of their life cycles. Additionally, non-consumptive uses, such as boating, scuba diving, snorkeling, and educational and natural history activities, are major producers of local revenue. Considering lodging, meals, transportation, equipment rental, and boat charters, there are strong economic incentives for effective reef management and preservation involving the sustained vitality of the commercial and recreational fishing and diving industries. These industries contribute not only to Florida's economy but also to the quality of life for Florida residents and visitors. The very existence of the Florida Keys is the result of millions of years of coral and algal limestone deposition. The reefs serve as living breakwaters, dissipating storm and hurricane wave energies before they reach the coast, protecting low-elevation human settlements. The importance of Florida's shallow-water reefs as offshore breakwaters is often taken for granted. Sea level is rising several centimeters per decade (Scholl et al. 1969); healthy coral reefs can build at that rate and thus continue to function as self-tending breakwaters. However, pollution not only kills most corals but also increases the rate of bioerosion of reef framework (e.g., Smith et al. 1981; Hallock 1988), compounding the problem of rising sea level.

Finally, there is the ethical responsibility of society to conserve unique natural resources for future generations. From an ecological perspective, rational management must seek to maintain the organic evolutionary process that is responsible for the diversity of life found in the biosphere (Bradbury and Reichelt 1981). The U.S. has only one Florida Reef Tract and one Everglades. Society has the responsibility to preserve them.

Coral Reef Management

Several government agencies are responsible for specific areas of reef management. The State boundary is 5.6 km (3 nmi) seaward of the coast on the Atlantic (Ocean) side and 16.7 km (9 nmi) on the Gulf (Bay) side, except around islands and bays where there are special considerations. The area between the State boundary to the 370 km (200 nmi) National conservation boundary is under Federal jurisdiction. Thus, most patch reefs in the Upper Keys are under State jurisdiction, whereas bank reefs are under

Figure 15

Size-frequency distribution of all colonies from all reefs.

Massive coral bleaching events (zooxanthellae expulsions) occur once or twice a decade; bleachings occurred during 1973, 1983, and 1987 (Jaap 1979, 1985, 1988). The cause in South Florida is believed to be hyperthermia brought on by long-lasting doldrums during late summer (Jaap 1985), in conjunction with El Nino - Southern Oscillation (ENSO) meteorology (Glynn 1988). Bleached Florida reefs usually recover in six to eight weeks following cessation of the doldrum. However, when the weather pattern continues for six weeks or longer, corals may not regain their color for several months. Rejuvenation is accomplished by cell division in remnant populations of zooxanthellae that remain in the coral tissues. Bleached corals have low tissue biomass, tissue carbon, and tissue nitrogen; reproduction (oocyte development) was disrupted in severely bleached specimens (Gassman and Szmant 1989). Weakened corals may be prone to algal overgrowth or disease (Shinn 1988).

Hurricanes play a significant role in coral reef development in the western Atlantic (Stoddard 1962, 1969; Woodley et al. 1981). The Florida Keys have a greater probability of hurricane impact than any other Florida coastal area (Florida Department of Natural Resources 1974). Violent hurricanes pass through the reef system (Sugg et al. 1970; Jindrich 1972; Shinn 1976), dislodging and fragmenting corals, moving fish away from their resident reefs, scouring and abrading the sessile organisms with sediments, and significantly reducing water transparency (Springer and McErlean 1962a; Ball et al. 1967; Shinn 1976). After Hurricane *Donna* in 1960 redistributed much of the coral at Grecian Rocks and Key Largo Dry Rocks, recovery took about 5 to 10 years (Shinn 1976). Such recovery indicates the resilience of a reef to mechanical destruction (Shinn 1988), although recovery depends on the scale of destruction.

Review of Human Interaction with Coral Reef Communities

As the human population has increased in South Florida and the Florida Keys, coral reefs of the Florida Reef Tract have suffered. Coral reefs are adapted to environments where nutrients are scarce and terrigenous sediment influx is limited; human activities inevitably increase inputs of both into nearshore waters. Clearing forest and mangroves, dredging, and boat operations all increase sedimentation stress. They also indirectly increase nutrient loading by reducing natural nutrient traps, including vegetation and soils, and by mixing nutrients into the water column that would otherwise be trapped in sediments. A workshop on coral reef research and management in the Florida Keys, held in Key Largo in June 1988 (Miller 1988), concluded that "The Florida Reef Tract is in serious trouble" and the first problem listed is "excessive nutrients and other waste products in the water originating from nearby land masses and Florida Bay" (Miller 1988). Lapointe and O'Connell (1988) demonstrated that the use of septic tanks and shallow injection wells in the porous limestones of the Florida Keys is accelerating eutrophication of surface waters. Mean concentrations of ammonium and nitrate were 350-fold higher in groundwaters of developed Keys as compared with pristine groundwaters; phosphate was 60-fold higher in groundwaters of developed Keys. During summer months, there is a greatly increased discharge of contaminated groundwater into sea-surface waters, raising nutrient concentrations and increasing phytoplankton stocks.

Terrestrial vegetation and mangroves are crucial to the survival of seagrass and coral reef communities because they act as filters, absorbing runoff, which carries sediments, organic debris, and nutrients, before it reaches the seagrass beds and reefs. Coastal urbanization threatens seagrass and reef habitats by removing these natural filters. At the same time, urban activities such as landscaping, dredging, and domestic waste disposal increase the need for the filters. Turbidity caused by sediments and plankton blooms reduces the depths to which seagrass and coral reefs can live. Eutrophication also stimulates benthic algal growth (which can prevent recruitment of larval corals) and increases microbial use of oxygen, reducing its availability in the environment. To the north, beach renourishment to counter erosion on the barrier islands of Dade, Broward,

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species and H'n.

Size

Figure 15 shows the distribution of colony-size for all stations. Coral colonies on these reefs were small, the mean size was 11.6 cm. Exceptions were limited to several species, most notably Diploria clivosa, Siderastrea siderea, and Montastrea annularis. The bushy growth-form and patchy distribution of Acropora cervicornis provided a few large measurements.

Differences in the size of colonies between depth-zones were easier to discern in those species that occurred in more than one zone, provided a large sample size, and were larger. Differences by ranks of transect means were often significant despite differences in means of only a few centimeters.

Siderastrea siderea was the only species at Triumph Reef that showed a large difference in the mean colony size between depth-zones (Table 10). This difference was not considered significant because only two colonies, one 80 cm and one 1 cm, were encountered.

Colony size of Montastrea annularis differed between depth-zones on Long, Ajax, and Pacific Reefs by ranks of transect means ($P < .05$) and average colony size. This species did not occur on the shallow transects at Long or Ajax, and only one colony was sampled on Pacific's shallow fore-reef. Mean colony size on the deep fore-reef stations were between two and four times larger than on the mid fore-reef (Table 10). The deep fore-reef at Ajax was one of memorably large colonies and scattered areas of luxuriant cover. Siderastrea siderea and Porites astreoides possessed a greater mean colony size in the deeper station at

including hard substrata, vigorous currents, and temperatures ranging from 5 to 10°C (Cairns and Stanley 1983). Habitat depths indicate dependence upon planktonic and detrital food sources. Because these reefs are so inaccessible, little else is known of their ecology.

The banks serve as refuge, feeding, and breeding grounds, as well as nursery shelters for other species. Large, commercially exploited deep-sea crabs (*Geryon quinquedens* and *G. fennerí*) are found associated with deepwater coral banks in the Gulf of Mexico and off Southeast Florida (Neumann and Ball 1970). Corals provide both food and shelter for fish (Squires 1964). Isopods and other crustaceans are also associated with these banks. Other publications that deal with Florida deep coral banks include Teichert (1958), Moore and Bullis (1960), and Neumann et al. (1977).

Interactions of Coral Reef Biota with Associated Communities

Coral reefs are interdependent with other marine and terrestrial communities that constitute the coastal ecosystem. Energy, chemical constituents, and mobile species move between the reefs and other communities, including pelagic, mangrove, seagrass, sedimentary, and hardground. This interdependence is exemplified by the life cycle of the spiny lobster (*Panulirus argus*) in the Florida Keys. Mature spiny lobsters live, breed, and spawn on coral reefs. The planktonic larvae live for several months in the oceanic water column. Juveniles settle near shore in *Laurencia* algae associated with seagrass communities (Marx and Herrnkind 1985). Larger juveniles live in live bottom habitats or mangroves before moving offshore to patch reefs and finally to reef margins as mature adults (Lyons et al. 1981). Adult lobsters also use different ecosystem components on a diurnal cycle, seeking refuge in reef dens during the day and moving into seagrass beds and sedimentary environments to forage for small molluscs, crustaceans, and other prey at night.

Understanding that coral reefs are adapted to nutrient-deficient waters (Muscatine and Porter 1977; Smith et al. 1981; Hallock and Schlager 1986) helps explain why reefs near terrestrial nutrient sources are so dependent upon associated ecosystems, particularly mangroves and seagrasses (Jaap and Hallock in press). Nutrients and sediments shed from terrestrial environments are intercepted by mangrove and seagrass communities, protecting the reef margin from their detrimental effects. With their more plentiful supplies of nutrients, mangrove and seagrass communities also provide nursery areas for juveniles, and foraging areas for adult animals that inhabit the reef.

Environmental Phenomena

In general, natural environmental stresses on coral reefs include extreme temperature fluctuations and hurricanes and other storms that produce high volumes of terrestrial runoff of low salinity and high-sediment load. Most of Florida's reefs are sufficiently distant from the relatively small keys that salinity and sedimentation generally do not produce serious environmental stress.

Because South Florida occurs in the transition between temperate and subtropical climatic zones, the Florida Keys are frequently exposed to winter, polar frontal systems that drastically cool the water (Walker 1981; Roberts et al. 1982). Thermal tolerance is species specific (Mayer 1914); however, most species display adverse affects below 15°C. Fish kills, coral bleaching, and mortality are often associated with hypothermic meteorological phenomena (Hudson et al. 1976; Jaap et al. 1989). Reefs adjacent to channels connecting the Atlantic to Florida Bay and at Dry Tortugas are more susceptible to this stress. Reefs offshore the northern Keys are closer to the Florida Current and are protected by the warmer waters.

the deep station was greater (1.5 vs. 0.64), but percentage of total coral cover was only slightly greater (Fig. 13). The mid fore-reef ranked higher with a mean density of $1.5/m^{-2}$ and was significantly greater than the deep station ($P = .01$). Differences in cover of M. annularis were notable between these two stations (Fig. 14), but were not significant. These two had greater cover and numbers than the shallow fore-reef ($P < .05$), where only one 5 cm colony was encountered.

Montastrea cavernosa and Solenastrea bournoni increased in abundance with depth (Fig. 14). Both species showed differences between depth-zones for cover and numbers of colonies ($P < .05$). M. cavernosa was also more dense in this deep station than in the shallower zones ($P = .01$).

Siderastrea siderea was the most abundant coral in the 12 - 18 m station on Pacific Reef (Fig. 13). Percent cover (2.3) and the average number of colonies per transect (1.1) were greater than the two shallower stations ($P < .05$) (Fig. 14). Significant differences in the density of colonies were not detected.

B-C indices for Pacific Reef were greatest for the shallow vs. mid comparison (Tables 3,4). This confirms the apparent similarities observable in figure 13. The shallow and deep stations were the least similar. The species composition of the mid and deep zones were only slightly more similar than when either were compared with the shallow zone (Table 5).

The four diversity indices gave conflicting results (Table 6). H'c of the shallow and mid stations (2.03) were greater than the deep station. The mid fore-reef possessed the most even distribution of colonies (Dn = .83), but the deep fore-reef had the greatest number of

Dry Tortugas Reefs. Dry Tortugas is composed of islands, shoals, and reefs located about 120 km (65 nmi) west of Key West (**Figure 4.4**) (Davis 1982; Jaap et al. 1989). While Dry Tortugas reefs have many characteristics in common with other South Florida reefs, they are notable for their thickets of branching staghorn coral (*Acropora cervicornis*) that occur west and north of Loggerhead Key. Early work in the region (Agassiz 1883) documented wide distribution of staghorn corals at Dry Tortugas, despite an environmental perturbation that nearly eliminated those corals in 1878 (Mayer 1902). Vaughan (1911) also reported staghorn corals west of Loggerhead Key. Cold temperatures have dramatically reduced staghorn populations at least twice during this century. Populations were reduced by roughly 95% during the winter of 1962-63 and again in 1976-77 when cold fronts lowered temperatures to 14 °C. Mayer (1914) reported the lethal lower thermal tolerance of *A. cervicornis* to be 13.5 to 15 °C. Staghorn coral proliferates during favorable periods by rapid growth and by fragmentation, which propagates new colonies (Tunnicliffe 1981). Populations recovered to form massive thickets of a least 0.5-m relief by 1981 and over 1-m high by 1984.

Live Bottom Communities

Live bottom communities are among the most widely distributed marine communities in Florida waters. They occur from subtidal areas to the continental shelf edge, virtually anywhere that there is solid substratum upon which members of this epibiotic community attach. Attached biota occupy everything from reef limestones to rocky outcrops on the seafloor to artificial reefs, seawalls, buoys, bridge pilings, and boat bottoms. Flora and fauna naturally vary throughout this range of depths and substrata, but algae, sponges, octocorals, hardy stony corals, and bryozoans are often visually dominant. In general, shallow-water (<6 m), live bottom biota throughout Florida show temperate, Carolinian affinities, with tropical West Indian affinities becoming increasingly important to the south (Collard and D'Asaro 1973).

In a remote area northwest of Dry Tortugas (24 °47.25' to 25 °16.75'N and 83 °37.75' to 83 °51.00'W) in depths of 64 to 76 m, a zone of highly irregular relief supports an unusual biological assemblage visually dominated by frondose green algae, *Anadyomene menziesii*, and large plates of lettuce coral, *Agaricia* spp. This assemblage was discovered during surveys sponsored by the Minerals Management Service in 1982 (Woodward-Clyde Consultants and Continental Shelf Associates, Inc. 1985) and may be similar to those found on vertical escarpment habitats of the Bahamas and central Caribbean basin (Ginsburg and James 1973; Goreau and Land 1974; Lang 1974; Reed 1985). This assemblage is discussed further in **Chapter 5.**

The distribution and species composition of live bottom communities offshore Southwest Florida is discussed in reports by Continental Shelf Associates, Inc. (1987, 1989) and Environmental Science and Engineering, Inc. et al. (1987). For further information, see **Chapter 5.**

Deep Coral Banks

Deepwater coral banks occur on the continental slope margins of Florida at depths of 400 to 800 m, but knowledge of their distribution is incomplete. *Lophelia prolifera* and *Enallopsammia profunda* are the primary framework builders (Cairns and Stanley 1983), with minor contributions by *Madrepora carolina* and *Solenosmilia variabilis* (Cairns 1979). *Enallopsammia profunda* dominates the banks, while *L. prolifera* is typically limited to upper portions (Stetson et al. 1962). In some places, these fragile, branching corals coalesce to form dense thickets; in other areas, they produce isolated ridges and mounds of their own debris.

Coral growth on the deepwater banks is relatively slow, 5 to 7 mm/year (Wilson 1979). Several environmental characteristics seem necessary for these banks to develop,

the shallow station (Table 9), but an equal number were intercepted in the mid fore-reef. The twenty-one colonies of D. stokesii in each of these two stations were significantly greater than the three colonies in the deep station (P = .007) (Fig. 14). Agaricia agaricites was relatively abundant in both numbers (28.4%) and cover (18.6%) in the shallow station and showed significant differences among depth-zones. More colonies and cover were recorded in this station (P = .02) (Fig. 14). Its density in the shallow fore-reef ($6.4/m^2$) was highest and was significantly greater than the density in the deep fore-reef ($0.82/m^2$) (P = .01).

The mid fore-reef station is graphically portrayed in Figure 13. Porites porites and Dichocoenia stokesii were again the most abundant for number of colonies (24) and percent cover (0.66%), respectively. Both had significantly different numbers of colonies ($P < .01$), cover ($P < .05$) and density (P = .003) in the three depth-zones. Figure 14 depicts the transect means for cover and colony abundance of these two species. In all four cases the mid fore-reef had significantly greater cover and colony abundance than the deep zone ($P < .05$). The density of these two species (2.5 and $6.4/m^2$) was also higher in this station. The human brain coral Diploria labrynthiformis was relatively abundant in the mid fore-reef station (Fig. 13), but only four colonies and 62 cm were measured. Differences between stations in the number of colonies intercepted were detected (P = .04), but differences in cover may be considered insignificant (P = .054).

Montastrea annularis proved to be abundant in both of the deeper stations on Pacific Reef. A slightly greater percentage of colonies was intercepted in the mid fore-reef station (Fig. 13). Percent cover in

The deepest portions of Florida bank reefs are in 37- to 40-m depths (Jaap 1981) and occur as isolated outcrops surrounded by sediments. Species that appear more abundant in this habitat include *Agaricia fragilis*, *Agaricia lamarcki*, *Leptoseris cucullata*, *Madracis decactis*, *Meandrina meandrites* forma *brasiliensis*, *Mycetophyllia aliciae*, and *Mycetophyllia lamarckiana*.

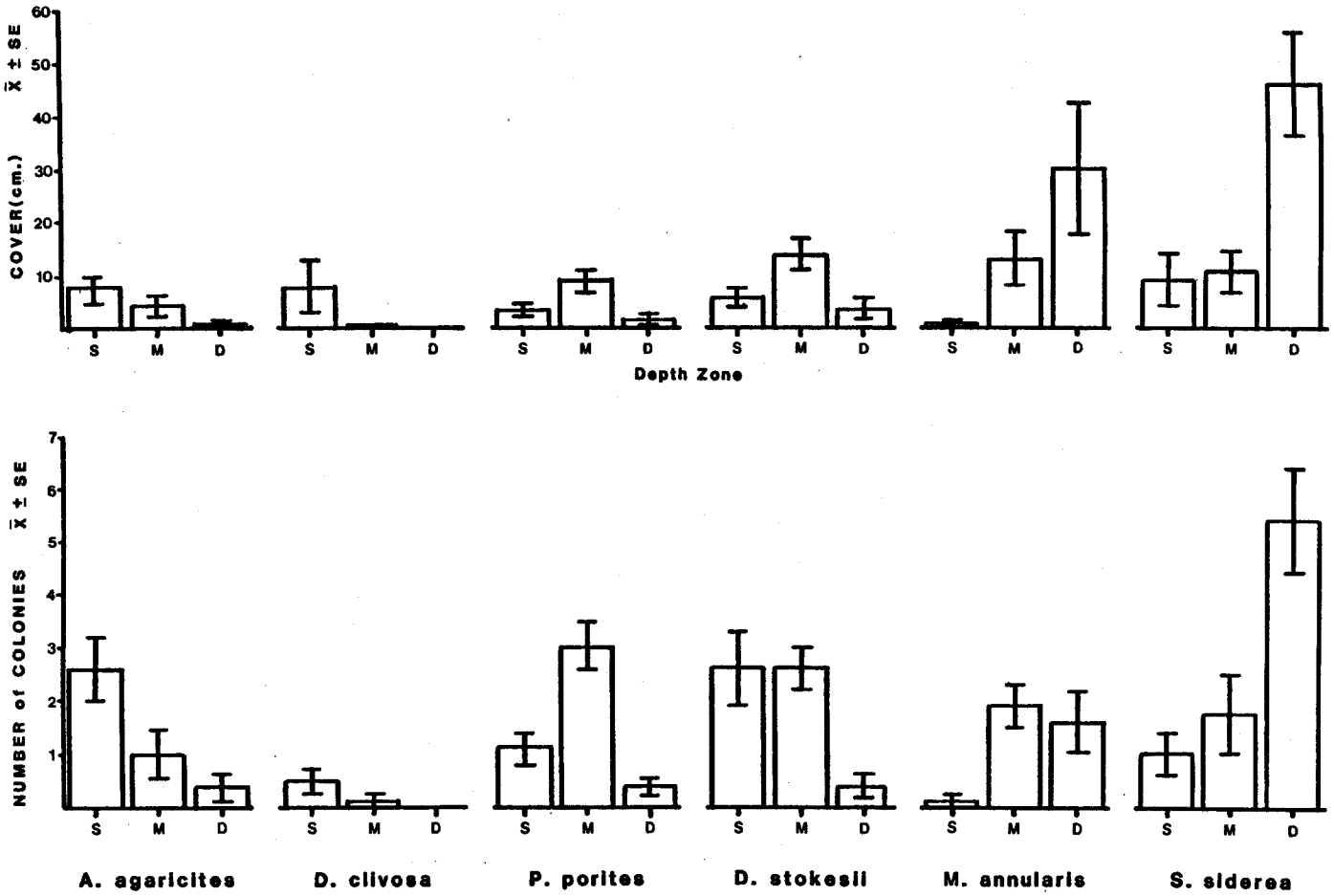
Stony corals were surveyed on several bank reefs in the Florida Keys (Jaap 1984). With the exception of shallow spur-and-groove habitats, there is considerable variability among samples from similar habitats. Intra-reef similarity is usually greater than inter-reef similarity. Temporal change in shallow reefs is high, particularly for small branching or poorly attached species (Shinn 1976; Jaap 1984, 1985; Dustan and Halas 1987; Jaap et al. 1989), because these corals typically recruit by fragmentation (Tunnicliffe 1981).

Patch Reefs. Patch reefs occur throughout most of the Florida Reef Tract (Jones 1977; Marszalek et al. 1977; Davis 1979, 1982). They are the principal reef form between northern Elliott Key and northern Key Largo (Figure 4.4) where approximately 5,000 patch reefs occur (Marszalek et al. 1977). Most patch reefs are situated seaward of Hawk Channel and inshore of the outer reef line; exceptions occur between Plantation Key and Newfound Harbor Keys where patch reefs occur close to the coast. Patch reefs, which typically occur in water depths of about 2 to 9 m, are usually roughly circular in outline, and range from 30 to 700 m in diameter.

Patch reefs provide topographic relief and biotic diversity in seagrass and sedimentary habitats. The region directly adjacent to the reef is usually barren because reef-dwelling herbivores venture from the reef to graze algae and seagrasses (Randall et al. 1964; Randall 1965; Sammarco et al. 1974). Local environmental conditions (Jones 1963), physical characteristics, and reef age determine physiography. Smith and Tyler (1975) and Jones (1977) proposed a model that considers the patch reef a superorganism with distinctive life stages. In the initial stage, pioneer corals settle on available hard substrata (rocky outcrops, conch shells, etc.). These pioneers, *Cladocora arbuscula*, *Favia fragum*, *Manicina areolata*, *Porites porites*, and *Siderastrea radians*, are short-lived; however, their skeletal remains provide a foundation upon which the primary framework-building species can settle. Following establishment of these framework builders (which include *Colpophyllia natans*, *Diploria labyrinthiformis*, *Diploria strigosa*, *Montastraea annularis*, and *Siderastrea siderea*), other corals, sponges, algae, and bryozoans begin to settle and occupy the newly created habitats. As the framework corals grow upward, they add to the heterogeneity of the environment, thereby creating additional niches for other plants and animals. The creation of caverns and tunnels by merging of the coral canopy and bioerosion provides habitat for shade-dwelling organisms and shelter for fish and larger mobile invertebrates. Carbonate production on patch reefs was studied by Ghiold and Enos (1982), who estimated potential vertical accretion at 2.2 to 6.6 m per thousand years.

As the reef approaches sea level, growth is limited to lateral expansion. The upper, central portions of older patch reefs are often hardgrounds occupied by dense populations of octocorals. The reef margins are dominated by stony corals. This pattern can be seen in the coral community of Dome Reef patch reef in Biscayne National Park (Jaap 1983, 1984). At the reef periphery, star coral *Montastraea annularis* was the most abundant stony coral, accounting for 17% of all coral colonies and 87% of stony coral cover. In the reef interior, octocorals were the dominant element, while star coral accounted for 7% of all individuals and 55% of stony coral cover.

PACIFIC REEF



astreoides). Waves, intensive solar radiation, and frequent tidal exposure severely limit the reef-flat community. Shoreward, the reef flat grades into a mosaic of sedimentary or seagrass habitats (Shinn et al. 1989).

Spur-and-groove formations are a principal characteristic of bank reefs. Spurs are elongate reefal limestone formations covered with living corals. Grooves are valleys containing carbonate sand and rubble that separate the spurs. Spur tops are <1 m deep at shoreward ends and as deep as 10 m at seaward margins; spurs may extend a linear distance of a hundred meters or more. Grooves may be <1 to 4 m deep. Most spur-and-groove formations extend laterally 1 to 2 km (0.5 to 1 nmi) along reefs within the 1- to 10-m depth contours. Spur formations are usually aligned perpendicular to the coast and continental shelf margin. In particular, they face into the predominant wind-sea direction. Where the groove system is present, sediments and water pass through the reef with minimal damage to attached biota.

Spurs are constructional features in Florida reefs (Shinn 1963, 1980; Shinn et al. 1981). The major spur builder is *Acropora palmata* (elkhorn coral) (Shinn 1966). Other corals, algae, and limestone debris fill spaces between *A. palmata* colonies. This species, under optimum environmental conditions, can monopolize large areas (Glynn 1973; Adey 1977). As the population grows upward to low tide level and increases in density, localized reduction in water circulation reduces planktonic food supply and may also influence oxygen and carbon dioxide exchange and sediment removal. When coral growth reaches low tide level, corals die back from environmental stress when exposed. Dead corals are encrusted with coralline algae, producing a pavement upon which other organisms can live. Meanwhile, the *A. palmata* population continues to colonize seaward, building upon the skeletons of deeper-dwelling corals that grew upward into the *A. palmata* zone or upon debris from its own population.

Communities occupying and constructing spurs are zoned by depth; the major controlling parameters are wave energy and water transparency. A guild of 15 to 19 specialized coral and zooanthid species occupies the shallow (<2 m) spur habitats [known as the *Millepora/Palythoa* zone for its dominant species, *Palythoa caribbae* (golden sea mat) and *Millepora complanata* (bladed fire coral)]. Other common members include *Zoanthus sociatus* (green sea mat) and *Ricordea florida* (false coral) (Wheaton and Jaap 1988). These species are adapted to intense solar radiation and high wave energy. Benthic cover can exceed 100% (canopy and understory), and the density of stony corals, principally *Millepora complanata*, ranges from 7.6 to 9.6 colonies/m^2 (Wheaton and Jaap 1988; Jaap et al. 1989).

Acropora palmata dominates between 2 and 5 m depths. *Agaricia agaricites* is abundant on vertical surfaces (spur sides). Diversity increases and dominance of species diminishes with increasing depth. Below 6 m, large heads of *Montastraea annularis* are major contributors to coral cover. Eighteen to 22 stony corals and 7 to 15 octocorals populate deeper spur-and-groove habitats; density of stony corals averages between 9 and 15 colonies/m^2 (Wheaton and Jaap 1988; Dustan 1985; Jaap et. al. 1989).

Some reefs show little or no development seaward of the spur-and-groove zone, whereas others have a well-developed fore-reef that slopes to 30 to 40 m (e.g., Eastern Sambo Reef off Boca Chica). Local topography and reef age may influence fore-reef development. Where fore-reefs are developed, they may be characterized by low relief, spur-and-groove complexes running seaward downslope. Corals are often diverse and abundant, averaging about 8 colonies/m^2 (Wheaton and Jaap 1988; Jaap et al. 1989). Algae, octocorals, and sponges are also common.

Figure 14

Mean coral cover and number of colonies per transect (n = 8) for selected species at Pacific Reef that showed significant differences among depth-zones by ranks.

heterogeneity, depth, age of the reef, frequency and magnitude of physical disturbance (environmental predictability), and organismal life histories (Grassle 1973).

To date, no one has completed an intensive investigation of floral and faunal diversity of a single Florida reef. Voss (1983) reported 62 algal species, 3 seagrasses, 55 sponges, 73 cnidarians, 22 polychaete worms, 67 molluscs, 37 crustaceans, 7 tunicates, and 224 fish species from the Key Largo area, including sedimentary, seagrass, live bottom, and coral reef habitats. Those numbers represent only a small fraction of the species that actually live there. Kissling (1977) reported 420 invertebrates from nine reefs off the Lower Florida Keys. Longley and Hildebrand (1941) listed 442 species of fish from Dry Tortugas and Starck (1968) reported 517 fish species from Alligator Reef.

Spatial heterogeneity is an obvious factor controlling reef diversity; more kinds of microhabitats support more species (Wells 1957; Grassle 1973). Depth, water transparency, and age of the reef influence spatial heterogeneity. Coral species show depth zonation: branching species thrive in relatively shallow water where at least 60% of surface light is available; star and brain corals flourish down to 20% of surface light (Huston 1985a); and plate corals can occur at depths with as little as 0.15% of surface light (Reed 1985). On a Florida Keys reef, the depths to which those light levels are available are approximately 5, 15, and more than 43 m, respectively (calculated from values reported by Jaap 1984). On a mature reef, three-dimensional spatial heterogeneity is well developed in the massive head-coral zone, possibly declining somewhat upward into the branching-coral zone and declining substantially with increasing depth as massive head corals give way to low-lying plate corals. Topography of the original substratum upon which the reef grew can also influence spatial heterogeneity.

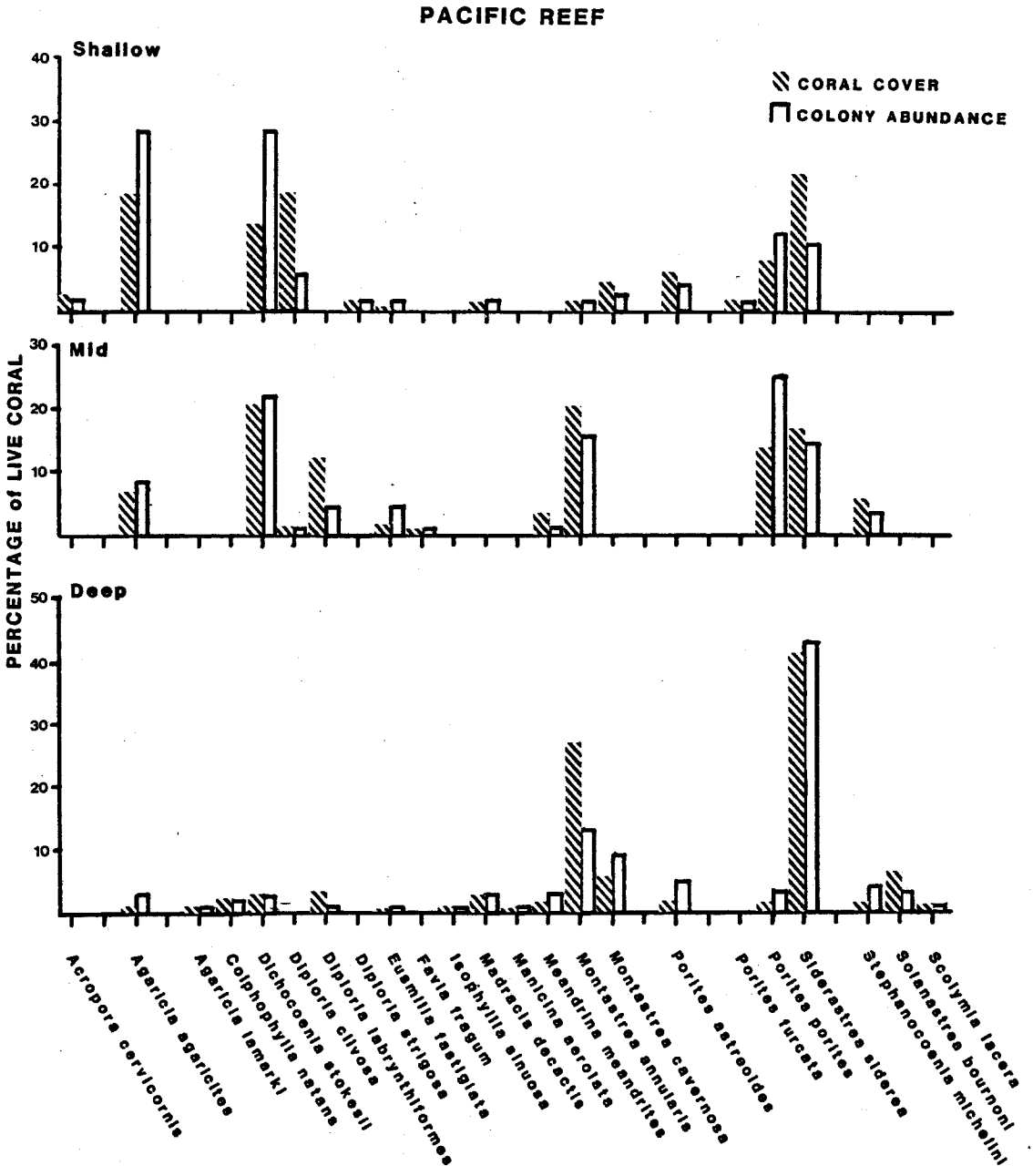
Environmental predictability is also a major factor creating depth-related diversity gradients. Though spatial heterogeneity on a shallow, reef margin may be comparable to that of the deeper head-coral zone, lack of environmental predictability limits diversity on the shallow margin. Ultraviolet radiation, thermal extremes, desiccation during extremely low spring tides, high wave energy, and abrasion by sediments carried by storm waves all act to reduce diversity. Connell's (1978) intermediate magnitude and frequency disturbance model, when applied to Florida's reefs, indicates that disturbance occurs at such magnitude and frequency to prevent development of highly diverse reef communities at depths <2 m.

For the Caribbean in general, coral and algal species diversity increases from the reef crest to maxima at depths of 20 to 30 m (Huston 1985b). Because light penetrates only about half as deeply on Florida's reefs as on many other Caribbean reefs, maximum diversity is expected at about 8 to 15 m.

Major Reef Types

The region of reef development seaward of the Florida Keys is 270 km (146 nmi) long (Fowey Rocks to Marquesas Keys). There are 96 km (52 nmi) of bank reef habitat and 6,000 individual patch reefs (Marszalek et al. 1977). The Upper and Lower Keys have greater reef development than the Middle Keys area (Marszalek et al. 1977; Shinn et al. 1989).

Bank Reefs. Bank reefs occur 7.4 to 13 km (4 to 7 nmi) seaward of the Florida Keys, paralleling the coast and continental shelf margin. Major bank reefs are shown in Figure 4.4. Most occur off Key Largo and from Big Pine Key to Key West where major islands protect the reefs from the detrimental influence of Florida Bay waters. A reef flat is located on the inshore side of the reefs. This relatively barren area is characterized by coral rubble encrusted by coralline algae and mustard hill coral (*Porites*


PACIFIC REEF
Shallow
Mid
Deep
CORAL COVER
COLONY ABUNDANCE
PERCENTAGE of LIVE CORAL
Acropora cervicornis
Agaricia agaricites
Agaricia lamarki
Colphophyllia natans
Dichocoenia stokesii
Diploria clivosa
Diploria labyrinthiformes
Eusmilia fastigiata
Favia fragum
Isophyllia sinuosa
Madracis decactis
Manicina areolata
Meandrina meandrites
Montastrea annularis
Montastrea cavernosa
Porites astreoides
Porites porites
Porites furcata
Siderastrea siderea
Stephanocoenia michelini
Solenastrea bournoni
Scolymia lacera

Reef Communities

Community Structure

Coral reefs are often compared to tropical rain forests in the way space and resources are stratified: canopy, understory, and substory. As the principal builders of the reef system, corals are the principal source of spatial complexity and shelter. Literally hundreds of species of protists, macrophytes, invertebrates, and fish are known to live in the Florida Reef Tract. Complexity is further enhanced by transitory animals such as fish, birds, and turtles that feed, breed, or seek temporary shelter on coral reefs. Floating algae, with associated organisms, are also transitory constituents.

Stony corals, together with some octocorals and larger sponges, form the canopy. Branching corals, as well as the reef framework, provide shelter for fish that feed upon the plankton in the overlying water column. Fish are analogous to the small birds and bats that dwell in the forest canopy and venture out to feed on insects. The coral canopy provides shelter from larger predators, such as sharks and barracuda, that prowl the reef margins. The reef also provides shelter for organisms, such as lobsters, that hunt in seagrasses behind the reef. There is mutual benefit to the reef and the organisms that seek refuge in the reef. Fish and crustaceans transfer nutrients and organic matter, via their excreta, from the water column or seagrass flat to the reef (Faulkner and Chesher 1979; Meyer et al. 1983). These nutrients and organic matter are therefore available to corals and algae living in the understory, but do not promote phytoplankton growth in the overlying water column--growth that would reduce light reaching the benthos.

Understory biota, including photosynthetic organisms such as algae, sponges, ascidians, and foraminifera that harbor algal symbionts, all contribute to the organic productivity of the reef while benefiting from the nutrients brought in by mobile organisms. These and other epibenthic organisms, such as polychaetes and bryozoans, dwell upon the dead portions of the coral surface.

Substory biota (cryptofauna) live within the coral framework. Smaller caves are occupied by crustaceans, molluscs, ophiuroid echinoderms (brittle stars), fish, and polychaete and sipunculid worms. Larger, deeper excavations, often found at the reef base, provide shelter for fish, crabs, and lobsters. The excavations also provide surfaces on and within the reef for sessile organisms, such as bryozoans, ascidians, and serpulid worms. Cryptic biota inhabiting coral rubble interstices in Biscayne National Park includes at least 80 species (bryozoa, coralline algae, foraminifera, molluscs, polychaetes, sipunculids, sponges, and tunicates); maximum species diversity occurs between 20 and 30 m in the fore-reef slope; water motion and sediment texture are important factors influencing species distributions (Choi and Ginsburg 1983).

Diversity

Biogeographic and environmental factors determine how many and which species occur on a particular reef. The diversity of organisms on a healthy Florida reef is not as high as that of a comparable western Pacific reef simply because West Indian reef biotas have declined in diversity more during the past 15 million years than have Indo-West Pacific biotas (Frost 1977). Because Florida's reefs are located near the northern limit of West Indian biotas, their diversities are further diminished relative to comparable central Caribbean reefs, e.g., those of the Cayman Islands. The actual number of plant and animal species on a particular reef at a point in time is primarily controlled by local environmental factors, such as water transparency, spatial

Figure 13

Relative abundance of all species for the three depth-zones on Pacific Reef.

bioeroders and other fauna are apparently limited by the normally scarce food supplies, but where nutrients and food are more readily available, their abundances increase sharply (e.g., Smith et al. 1981; Rose and Risk 1985). Hein and Risk (1975) reported that, in mature coral heads in the Florida Keys, rate of bioerosion approximately equals the rate of skeletogenesis. Hudson (1977) estimated that rates of bioerosion in dead *M. annularis* heads were sufficient to reduce a solid, 1-m-high head to rubble in 150 years.

Competitive interactions include overgrowth of understory species by species with rapid growth rates (e.g., the stony coral *Acropora cervicornis*) (Shinn 1976; Jaap et al. 1989). Birkeland (1977) demonstrated experimentally that coral recruitment is inversely related to nutrient supply; when nutrients are plentiful, filamentous algae, barnacles and bryozoans outcompete coral larvae for space. Some bryozoa can overgrow other sessile reef organisms (Buss 1980). Under low light conditions, sponges are very successful competitors for space (Bryan 1973; Vicente 1978; Jackson and Winston 1982). Fire corals are successful in colonizing living octocoral branches (Whale 1980). Scleractinian corals expand and defend territory by digestion of adjacent coral tissues through use of mesenterial filaments (Lang 1971, 1973). Other coral species defend themselves from such attack with specialized sweeper tentacles (den Hartog 1977; Richardson et al. 1979; Wellington 1980; Bak et al. 1982; Chornesky and Williams 1983). Allelopathy, or chemical defense and offense, is another mechanism used by some organisms, particularly octocorals, to prevent overgrowth and gain living space (Cameron 1974; Glynn 1980; Bak et al. 1981; Tursch 1982; Sullivan et al. 1983).

Grazing organisms also play important roles in coral reef communities. For example, damselfish (*Pomacentrus planifrons*) destroy coral tissue and farm algae on dead coral (Kaufman 1977; Brawley and Adey 1981; De Ruytor 1984). Black sea urchins graze algae from the reef, as well as from areas adjacent to the reef (Sammarco et al. 1974; Bak and Van Eys 1975; Ogden and Lobel 1978), providing settlement habitat for coral larvae by exposing clean limestone substrate (Sammarco 1980).

Coral predators are also numerous and diverse. The marine worm *Hermodice carunculata* feeds on numerous coral species, including staghorn coral (Marsden 1960, 1962; Glynn 1962; Ebbs 1966; Antonius 1974; Lizama and Blanquet 1975). Gastropod molluscs known to feed on corals include *Coralliophila abbreviata*, *Calliostoma javanicum*, and *Cyphoma gibbosum* (Glynn 1964, 1973; Robertson 1970; Ott and Lewis 1972). Fish that feed on corals include parrotfish (Scaridae), spadefish (Ephippidae), damselfish (Pomacentridae), and butterflyfish (Chaetodontidae) (Glynn 1973).

Sponges also interact with the coral reef in ways other than bioerosion and competition for space (e.g., Goreau and Hartman 1963; Schmahl 1984). Some sponges bind coral skeletons to the reef substrate (Wulff and Buss 1979; Wulff 1984); some sponges protect the coral undersurface from attacks by boring organisms (Goreau and Hartman 1966).

Numerous organisms are highly specialized to live in close association with corals, gaining shelter and food, and often devouring mucus that is prevalent on the coral tissue surface. Examples include copepods with worm-like bodies (Patton 1976), and the crab *Domecia acanthophora* and some pyrogomatid barnacles that induce coral skeletons to grow around them, forming a shelter for the symbiont (Patton 1967).

Table 9. Species Totals: Pacific Reef

Depth-zone	Shallow			Mid			Deep		
Species	L	N	T	L	N	T	L	N	T
Acropora cervicornis	8	1	1						
Agaricia agaricites	63	21	7	34	8	5	8	3	2
Agaricia lamarcki							8	1	1
Colpophyllia natans							20	2	1
Dichocoenia stokesii	45	21	6	106	21	8	26	3	2
Diploria clivosa	63	4	3	3	1	1			
Diploria labrynthiformis				62	4	4	29	1	1
Diploria strigosa	6	1	1						
Eusmilia fastigiata	2	1	1	7	4	3	1	1	1
Favia fragum				2	1	1			
Isophyllia sinuosa							8	1	1
Madracis decactis	4	1	1				24	3	2
Manicina aerolata							2	1	1
Meandrina meandrites				16	1	1	14	3	3
Montastrea annularis	5	1	1	103	15	7	242	13	5
Montastrea cavernosa	15	2	1						
Porites astreoides	20	3	3				14	5	3
Porites furcata	6	1	1						
Porites porites	27	9	6	70	24	8	13	3	3
Siderastrea siderea	74	8	5	84	14	6	370	43	8
Stephanocoenia michelinii				29	3	3	14	4	3
Solanastrea bournoni							56	3	3
Scolymia lacera							2	1	1
Zone Total =	338	74		516	96		900	100	

L = Sum of intercept lengths (cm)
N = Number of colonies intercepted
T = Number of transects on which species occurred

tip; (2) radial growth or increase in diameter of the branch; and (3) internal calcification or infilling of space within a branch (Gladfelter 1982). The first phase occurs in the dark, the other phases occur in the light and at rates two to three times greater than the first phase (Barnes and Crossland 1980). Mass calcium accretion is correlated with number of sun hours (Gladfelter 1984). Coral growth is independent of plankton supply and is significantly reduced by shade (Wellington 1982). Zooxanthellae may also prevent phosphate poisoning of coral calcification by removing phosphatic wastes and any phosphates in the microenvironment; phosphate inhibits precipitation of aragonite crystals (Simkiss 1964; Mucci 1986), the skeletal building blocks of corals.

Biological Interactions

Complex biological interactions are particularly characteristic of coral reef communities. In addition to such common processes as grazing and predation, typical interactions on coral reefs include disease, bioerosion, competition, chemical "warfare," and symbioses.

A variety of disease pathogens may injure or kill corals (Antonius 1974, 1976, 1981a,b; Mitchell and Chet 1975; Ducklow and Mitchell 1979) and other reef-associated organisms. Shinn (1988) has argued that, in the Florida Keys, destruction by diseases is far more devastating and long lasting than mechanical damage. Shinn contends that the disease outbreaks may be associated with nutrient loading and other anthropogenic and natural stresses.

The most common coral pathogen is "black band" disease (*Phormidium corallyticum*: Cyanobacterium: Oscillatoriaceae), which was originally described by Antonius (1974) and subsequently studied by Dustan (1977b), Rützler and Santavy (1983), Rützler et al. (1983), and Taylor (1983). The cyanobacterium often invades massive corals following structural damage to tissues. This disease killed many large, old colonies of *Montastraea annularis* at Carysfort Reef between 1978 and 1985, and is now rampant at Looe Key Reef (Shinn et al. 1989). Other coral pathogens include bacterial infections such as "white band" disease (Peters et al. 1983; Peters 1984) and fungi (Ramos 1983; Jaap 1985; Te Strake et al. 1988). Neoplasms (calicoblastic epithelioma) were found in populations of elkhorn coral (*Acropora palmata*) at Carysfort Reef and Grecian Rocks (Peters et al. 1986). Overcrowding may increase incidence of disease (Gladfelter 1982; Peters et al. 1983). *Entociadia*, a microalga, infects the octocoral *Pseudoplexaura*, producing galls that weaken the skeletal structure (Goldberg et al. 1985). An epidemic bacterial disease decimated black sea urchin (*Diadema antillarum*) populations throughout the Caribbean and Florida Keys during 1983 to 1984 (Bak et al. 1984; Lessios et al. 1984a,b; Bauer and Agerter 1987).

Florida reefs, which exist at the climatic threshold for western Atlantic reef environments, also live a marginal existence in the interplay between limestone production by corals and coralline algae, and destruction by biological and physical processes. Some organisms chemically or mechanically break down reef limestone, a process known as bioerosion (Neumann 1966). Bioeroders include such diverse groups as parrotfish that bite off bits of coral and coralline algae, *Diadema* echinoids that erode the limestone as they graze algae, and boring organisms such as endolithic bivalves, clionid sponges, a variety of polychaete and sipunculid worms (Bromley 1978; Risk and MacGeachy 1978), and microorganisms (Golubic et al. 1975). Bioeroders sculpt reef morphology, providing holes and spaces for a diverse array of organisms (Warme 1975). Many of these organisms, particularly the sponges, echinoids, and bivalves, are capable of erosion rates that equal or exceed rates of reef growth (Bromley 1978; Risk and MacGeachy 1978; James and Macintyre 1985). In a healthy reef system, abundances of

S. michelinii was measured at a higher density ($P < .001$).

Similarity indices for Ajax Reef are presented in Tables 3,4 and 5. The shallow and mid fore-reef stations when compared had the highest B-C index values. Values for the abundance of colonies were greater than those for cover. The mid and deep stations had the most similar species composition. The Jaccard value of 0.67 was the second highest of all comparisons.

The mid fore-reef station at Ajax was slightly more diverse (H'n). Species diversity (S) and H'c increased with depth. Dn, in contrast, decreased with the depth of the sample-area (Table 6).

Pacific Reef

Pacific Reef had the most species of hermatypic corals in its samples. The deep fore-reef had 18 species, and the shallow and intermediate depth-zones possessed 13 and 11, respectively (Table 9).

The estimate of total percent cover increased significantly with depth of the sample-area, from 2.1 to 5.6 ($P = .004$). The density of all coral colonies also varied ($P = .03$). Samples showed no difference in the number of species or colonies per transect (Table 2).

Four species of coral dominated the shallow fore-reef at Pacific (Fig. 13). The species with the greatest cover, Siderastrea siderea, had less cover ($P = .02$) and colonies ($P = .007$) than in the deep station (Fig. 14). Diploria clivosa had 18.6 percent of the coral cover in the shallow station. Significant differences between zones were not detected because its total percent cover (0.4%) was attained from four colonies.

Dichocoenia stokesii provided the greatest number of colonies to

Nutrient levels in surface waters of the Florida Reef Tract can vary from barely detectable to more than 1 μM inorganic phosphorus and 3 μM inorganic fixed nitrogen (Skinner and Corcoran 1989). There is disagreement over which nutrient, fixed nitrogen or phosphate, limits coral growth (Gladfelter 1985). In Skinner and Corcoran's data, the lowest nitrogen values are often accompanied by relatively high phosphate levels and *vice versa*, indicating that either may be limiting under certain circumstances. Studies at Looe Key showed that ambient phosphate and nitrate in the reef areas ranged from 0.1 to 0.2 μM and 0.5 to 1.0 μM, respectively (Littler et al. 1986). Unusual upwelling events during late spring and early summer stratify the water column with respect to nutrients and temperature at Looe Key and elevate phosphate and nitrate concentrations in the water column (Lapointe and Smith 1987). Crossland (1983) noted that subtropical sea-surface waters typically contain <0.3 μM inorganic phosphorus and <1 μM inorganic fixed nitrogen.

Thus, while nutrient concentrations in the waters of the Florida Reef Tract are similar to those typical of subtropical waters, Florida waters are prone to nutrient pulses that can be detrimental to reef growth (Margalef 1968). Hallock (1988) suggested that the near-threshold position of the Florida Keys reefs is as much a factor of excess nutrients as of winter temperatures. As human populations have increased in South Florida, nutrient loading has inevitably increased in waters of the Florida Reef Tract. Both Voss (1973) and Dustan (1977a), in non-technical papers, suggested that sewage pollution was damaging the reefs of the Florida Keys. The classic study of how nutrient pollution can damage a coral reef was reported by Smith et al. (1981) for Kaneohe Bay, Hawaii. Tomascik and Sander (1985) reported similar decline of Barbados reefs as a result of sewage pollution. Shinn (1988) identified excess nutrients as the most probable underlying cause of the serious decline in living corals in recent years. Following Lapointe and O'Connell's (1988) report that use of septic tanks and shallow injection wells in the porous limestones of the Florida Keys is accelerating eutrophication of surface waters, a workshop on coral reef research and management in the Florida Keys in June 1988 concluded that excessive nutrients from nearby land masses and Florida Bay are seriously threatening the Florida Reef Tract (Miller 1988).

Although corals are animals, they function as primary producers in the reef system via their zooxanthellae. Most corals are also highly specialized predators (Yonge 1930) and capture zooplankton from the water column. Some species ingest bacteria from seawater (Di Salvo 1971); some can feed on dissolved organics in seawater (Stephens 1962); and some feed on detritus (Goreau and Goreau 1960). Many species even digest the tissues of other coral species using mesenterial filaments (Lang 1971, 1973), although this is primarily a form of competition, not predation. Despite the variety of sources, direct feeding may supply $<10\%$ of the corals' energy needs (Muscatine and Porter 1977). In such cases, most energy comes from photosynthesis by zooxanthellae (Kanwisher and Wainwright 1967; Lewis 1977; Gladfelter 1983, 1985; Chalker et al. 1984; Kinsey 1985). Zooxanthellae, in turn, get nutrients from metabolic waste products of the coral host as well as from seawater or detritus. Thus, the coral-symbiont system is specialized to concentrate scarce and dispersed nutrients from a variety of sources and to use them for maintenance, growth, and reproduction.

Photosynthesis by zooxanthellae also promotes production of skeletal limestones that make up the reef framework (Kawaguti and Sakumoto 1948; Goreau 1959). Zooxanthellae provide coral with energy for calcification. Reef corals calcify at significantly higher rates in light than in dark, and carbon produced by the zooxanthellae is translocated to growth areas which lack zooxanthellae (Goreau and Goreau 1959a,b). Calcium ion transport is enhanced by the enzyme carbonic anhydrase, which requires expenditure of energy (Isa and Yamazato 1984). Growth in branching *Acropora* spp. is the integration of three processes: (1) linear extension of an axial corallite at the branch

the shallow station (16). It had a greater abundance of colonies, cover, and density in this shallow zone than in either of the deeper stations ($P < .05$) (Fig. 12).

Figure 11 shows the relative abundance of the species sampled in the shallow fore-reef. Dichocoenia stokesii, Agaricia agaricites, Acropora cervicornis, Siderastrea siderea, and Meandrina meandrites all provided 10 percent or more of the coral cover or colonies in this station. None were significantly more abundant in this zone than in the others.

Dichocoenia stokesii possessed significantly different amounts of cover on Ajax Reef ($P = .05$). This species was most abundant in the mid fore-reef with 0.8 percent cover. The number of colonies and density were not significantly different, although they were greater in the 6 - 12 m depth-zone. Two other abundant species, Siderastrea siderea and Montastrea annularis were found at even higher abundances in the deeper stations (Fig. 12).

In the deep fore-reef, three of the four species with significant differences between depth-zones were relatively abundant. The fourth was scarce. Madracis decactis, the Cactus Coral, occurred only in the deep station with a low percent cover (0.4%) and percent coral cover (4.6%).

Montastrea annularis, Siderastrea siderea, and Stephanocoenia michelinii dominated this zone (Fig. 11). The former had the greatest percent cover of any species in any station (3.0) and provided more cover and colonies in the deep station than in shallower zones ($P = .02$) (Fig. 12). The latter two species possessed greater cover and more colonies in this 12 - 18 m station than in shallower zones ($P < .05$).

columns, *encrusting*, and *fronds*. Stony coral generation times vary greatly, ranging from a few years in small, finger corals to hundreds of years in massive star and brain corals. In these larger corals, multiple generations of polyps coexist. Sexual maturity seems to depend upon both size and age of a colony. Large, sexually mature colonies, if broken into small fragments, cease gamete production until they grow to a minimum size (Kojis and Quinn 1984; Szmant-Froelich 1985).

Among stony coral species, internal fertilization, external fertilization, broadcasting of gametes, and larval brooding all have been reported (Fadlallah 1983). After fertilization and embryonic development, free-living planula larvae are formed, which can be either planktonic or benthic. After periods that vary from species to species and also with environmental conditions, the larvae settle and metamorphose into juvenile corals. A larva attaches itself to the substratum by secreting a basal plate, the initial skeletal structure. Walls and axial structures are secreted next (Wells 1956). Growth involves a harmonious integrated increase in coral tissue, zooxanthellae, and skeleton (Barnes 1973). When the larva is fully transformed into a polyp, growth proceeds with the budding of daughter polyps by asexual division.

Growth rates of Florida's reef-building corals have not been studied extensively (e.g., Landon 1975). Almost all growth rate evaluations focus on a very few species (*Acropora cervicornis*, *Diploria strigosa*, and *Montastraea annularis*). Growth rates of the 40 or more other species are poorly known. X-ray photographs of *M. annularis* reveal annual growth rings which can be used to determine growth and environmental conditions (Hudson et al. 1976; Hudson 1981). Growth rate in this massive, head-forming species is relatively slow; growth rates averaged 8.2 mm/year on nearshore patch reefs, and 6.3 mm/year in offshore waters deeper than 6 m. Maximum growth rates of <11 mm/year occurred in waters <3 m deep. For other head corals, Ghiold and Enos (1982) found that the brain coral *D. labyrinthiformis* in the Key Largo area grow at a rate of about 3.5 mm/year and Landon (1975) reported a growth rate of 2.4 mm/year for *Siderastrea siderea*. Thus, head corals grow so slowly that 1-m-high heads are approximately 100 years old (Shinn et al. 1989). In contrast, growth rates of the branching coral *A. cervicornis* (staghorn coral) can exceed 100 mm/year (Shinn 1966). Shinn (1976) found that branches form annually during winter months, and that each branch may grow as much as 10 cm during the following year. However, because branching corals do not produce the dense accumulations of limestone, apparent differences in growth rate are primarily the result of growth form and geometry. Other available growth data include *Porites porites* at Sambo Reef, 16 mm/year (Landon 1975); *Dendrogyra cylindrus* at Elliott Key, 5 mm/year (Hudson unpubl. data as reported by Shinn et al. 1989); and *Solenastrea bournoni*, 8.9 mm/year (Hudson et al. 1989).

Productivity and Calcification

Healthy, well-developed reefs thrive in clear, nutrient-depleted waters (Birkeland 1987). The symbiotic relationship between corals and their zooxanthellae allows efficient recycling of nutrients between host and symbiont (Muscatine and Porter 1977), providing corals with a competitive advantage over algae and animals lacking symbionts when nutrients are scarce (Hallock 1981). More abundant nutrients stimulate benthic algal growth; overgrowth by benthic algae is harmful to living corals (e.g., Smith et al. 1981) and inhibits coral recruitment (Birkeland 1977). Abundant nutrients also enhance plankton growth, which diminishes water transparency. The fewer nutrients in seawater, the clearer it is and the deeper corals can live. Furthermore, increased plankton abundances favor larval survival, recruitment, and growth of coral predators, competitors, and bioeroders (Hallock and Schlager 1986).

AJAX REEF

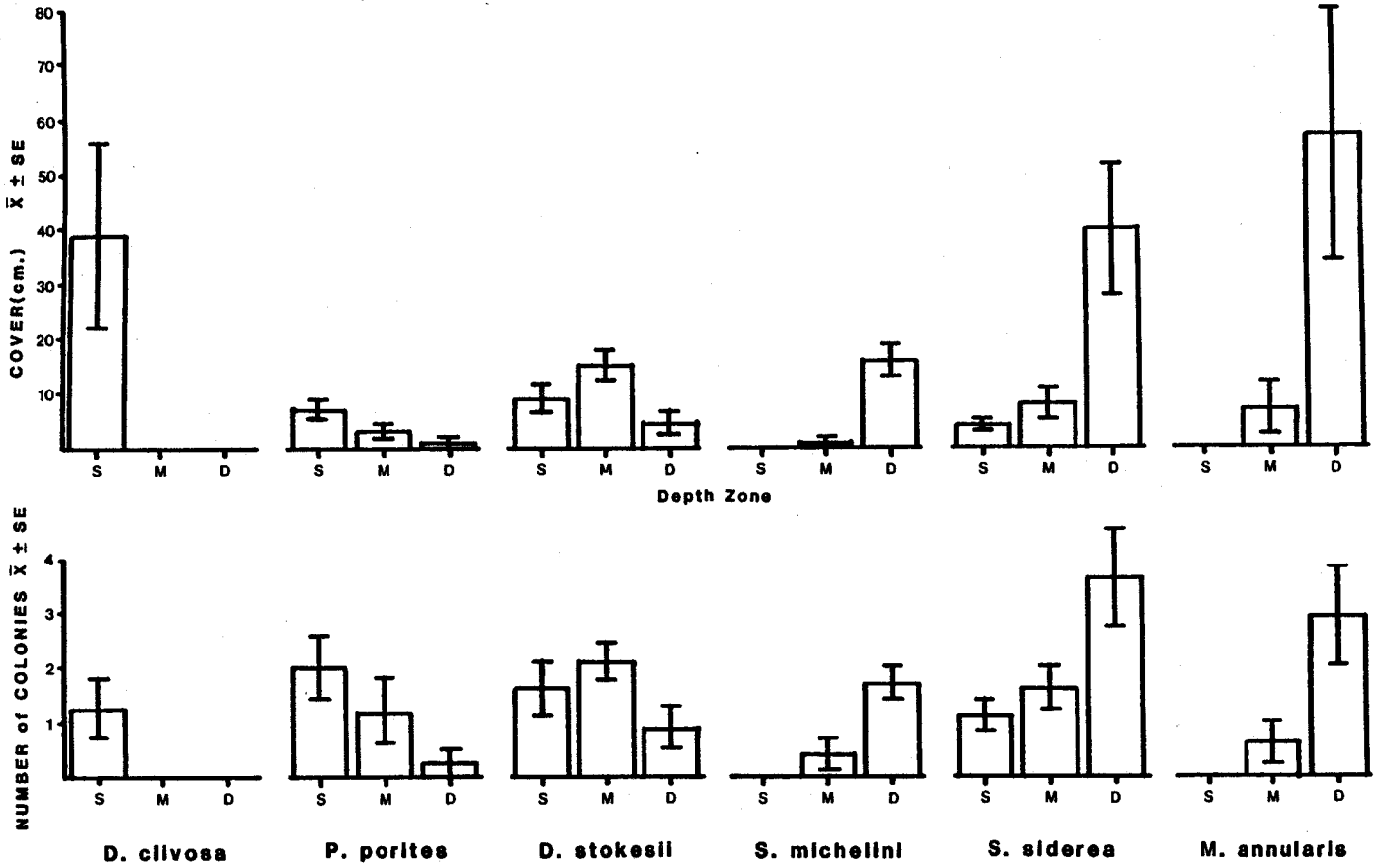

COVER(cm.) X̄ ± SE
80
70
60
50
40
30
20
10
S M D
Depth Zone
NUMBER of COLONIES X̄ ± SE
4
3
2
1
D. clivosa
P. porites
D. stokesii
S. michelini
S. siderea
M. annularis

Table 4.3. Scleractinian corals of the Florida Reef Tract.

Suborder Astrocoeniina Vaughan and Wells

Family Astrocoeniidae Koby
Stephanocoenia michelinii (Milne Edwards and Haime)

Family Pocilloporidae Gray
Madracis decactis (Lyman)
M. formosa Wells
M. mirabilis (*sensu* Wells)

Family Acroporidae Verrill
Acropora palmata (Lamarck)
A. cervicornis (Lamarck)
A. prolifera (Lamarck)

Suborder Funglina (Verrill)

Family Agariciidae Gray
Agaricia agaricites (Linne)
A. agaricites danai Milne Edwards and Haime
A. agaricites carinata Wells
A. agaricites purpurea (LeSueur)
A. lamarcki Milne Edwards and Haime
A. undata (Ellis and Solander)
A. fragilis (Dana)
Leptoseris cucullata (Ellis and Solander)

Family Siderastreidae Vaughan and Wells
Siderastrea radians (Pallas)
S. siderea (Ellis and Solander)

Family Poritidae Gray
Porites astreoides (Lamarck)
P. porites (Pallas)
P. porites divaricata LeSueur
P. porites furcata Lamarck
P. porites clavaria Lamarck
P. branneri Rathbun

Suborder Faviina Vaughan and Wells

Family Faviidae Gregory
Favia fragum (Esper)
F. gravida (Verrill)
Diploria labyrinthiformis (Linne)
D. clivosa (Ellis and Solander)
D. strigosa (Dana)
Manicina areolata (Linne)
M. areolata mayori Wells
Colpophyllia natans (Houttyn)
C. amaranthus (Muller)
C. breviseralis Milne Edwards and Haime
Cladocora arbuscula (LeSueur)
Montastraea annularis (Ellis and Solander)
Solenastrea hyades (Dana)
S. bournoni Milne Edwards and Haime

Suborder Faviina (Continued)

Family Rhizangiidae d'Orbigny
Astrangia astreiformis (Milne Edwards and Haime)
A. solitaria (LeSueur)
Phyllangia americana Milne Edwards and Haime

Family Oculinidae Gray
Oculina diffusa Lamarck
O. varicosa LeSueur
O. robusta Pourtales

Family Meandrinidae Gray
Meandrina meandrites (Linne)
M. meandrites brasiliensis (Milne Edwards and Haime)
Dichocoenia stellaris Milne Edwards and Haime
D. stokesii Milne Edwards and Haime
Dendrogyra cylindrus Ehrenberg

Family Mussidae Ortman
Mussa angulosa (Pallas)
Scolymia lacera (Pallas)
S. cubensis (Milne Edwards and Haime)
Isophyllia sinuosa (Ellis and Solander)
I. multiflora Verrill
Isophyllastraea rigida (Dana)
Mycetophyllia lamarckiana Milne Edwards and Haime
M. danaana Milne Edwards and Haime
M. ferox Wells
M. aliciae Wells

Suborder Caryophylliina Vaughan and Wells

Family Caryophylliidae Gray
Eusmilia fastigiata (Pallas)
Paracyathus pulchellus (Philippi)

Suborder Dendrophylliina Vaughan and Wells

Family Dendrophylliidae Gray
Balanophyllia floridana Pourtales

Figure 12

Mean coral cover and number of colonies per transect (n = 8) for selected species at Ajax Reef that showed significant differences among depth-zones by ranks.

Coral Biology

Taxonomy and Life Histories

Reef corals belong to two classes of the Phylum Cnidaria (Coelenterata): Hydrozoa and Anthozoa. Most reef-dwelling members of both classes host zooxanthellae, endosymbiotic dinoflagellate algae of the genus *Symbiodinium* (Blank and Trench 1985) and are therefore dependent upon ample light for photosynthesis. In the Florida Keys, *Millepora* (fire coral) is the only hydrozoan coral on shallow reefs (<30 m); *Stylaster* and *Distichopora* occur in deep reef habitats. Anthozoans include octocorals and stony corals (discussed below), as well as zoanthids, corallimorpharians (false corals), and anemones. Most reef corals are colonial organisms, each made up of thousands of genetically identical members or polyps.

Fire Corals. Two species of fire corals occur on Florida reefs. *Millepora complanata*, the bladed fire coral, is a keel-shaped species restricted to shallow windward reef tops. Mergner (1977) found that this species is restricted to turbulent and highly illuminated reef habitats. Crenulated fire coral (*M. alcicornis*) is a branching species found in a much wider range of reef habitats. The name "fire" coral comes from the burning sensation inflicted by nematocysts (microscopic stinging organs) within the organism's tissues. The animal secretes a limestone skeleton with microscopic pores in which the individuals (zooids) live. A porous skeleton contains tissues with dense concentrations of zooxanthellae that provide most of the energy needed by the colony. The golden-yellow color of the fire coral comes from these microscopic algae.

Octocorals. Octocorals, which include sea whips, sea plumes, sea fans, gorgonians, and soft corals, are a conspicuous and diverse faunal element on most Florida Keys reefs; 42 species have been recorded (Jaap 1984). Octocorals, which have polyps bearing eight tentacles, vary in form from irregular mats to large sea fans; polyps are distributed along the branches, fan surfaces, or mats. Organic skeletons are commonly reinforced by calcareous spicules, which are secreted by the polyps. Taxonomy of octocorals is based upon the microscopic morphology of the spicules (Bayer 1961). After death and organic decay of a colony, the spicules become part of the sand-sized sediments of the reef.

Life histories of most octocoral species are poorly known. One species, *Plexaura homomalla*, has been intensively studied in the Cayman Islands (Kinzie 1974). Colonies become sexually mature at 25 to 35 mm in height. Male individuals release sperm into the water, and fertilization occurs within the female polyps. Larvae spend a brief time in the plankton before settling on appropriate substrata and starting new colonies. Growth rates vary from 10 to 40 mm/year.

Octocorals are extremely abundant in some Florida reef habitats, occurring in densities up to 50 colonies/m^2 (Opresko 1973; Wheaton and Jaap 1988). Many octocoral species inhabit shallow patch reef and bank reef habitats in areas with substantial turbulence and high light intensities. Highest rates of mortality occur during larval and juvenile life stages. Mortality is also high among adult colonies dislodged by storms. Invertebrate predators include the snails *Cyphoma gibbosum* and *Coralliophila caribaea* and the fire worm *Hermodice carunculata*. Black band disease is a pathogen in some octocorals (Feingold 1988).

Stony Corals. The Scleractinia, or stony corals, include common reef-building species. Sixty-three taxa (species and subspecies or forma), living at depths of <1 to 45 m, have been recognized in the Florida Keys (Table 4.3). Taxonomy is based on external skeletal morphology and calyx characteristics (Vaughan and Wells 1943; Wells 1956; Zlatarski and Estalella 1982). Growth forms include *branching, hemispherical, plates,*

Figure 11

Relative abundance of all species for the three depth-zones on Ajax Reef.

Clear waters are crucial to reef-building corals because their microscopic symbiotic algae (zooxanthellae) require sunlight. The clearer the water, the deeper corals can live (Wells 1956, 1957). Water transparency over Florida reefs can vary considerably, from nearly opaque following storms, to exceptional clarity during prolonged calm (Jaap 1984). Plankton, suspended organic matter, and suspended sediments all diminish water transparency. Corals derive nutrients from symbiotic dinoflagellate algae (zooxanthellae) that require light. Thus, growth rates of coral and other reef organisms dependent upon photosynthesis decline as light decreases with depth (summarized by Huston 1985a) or reduced water transparency (Tomascik and Sander 1985). Kanwisher and Wainwright (1967) estimated that zooxanthellate corals require a minimum of about 4% of surface radiation for reef development. These corals need at least 0.15% for survival (Reed 1985). Data on water transparency in the Florida Keys area (Hanson and Poindexter 1972, summarized by Jaap 1984) are consistent with the observation that reef growth in the Keys normally occurs to depths of about 35 to 40 m (Jameson 1981).

Literature Review

Ecologic studies of Florida Keys coral reefs began during the late 19th century (Agassiz 1883; Mayer 1914; Vaughan 1915, 1918; Longley and Hildebrand 1941). Since the Carnegie Laboratory (on Loggerhead Key, Dry Tortugas) burned in 1937, laboratory facilities in the Florida Keys have been lacking until quite recently. Thus, our understanding of Florida corals and reefs relies heavily upon studies from other Caribbean and western Atlantic areas.

Tropical coral reefs are characterized by high species diversity (Loya 1972; Connell 1978; Huston 1985b); rapid recycling of nitrogen and phosphorus (Pilson and Betzer 1973; Webb et al. 1975; Muscatine 1980; Johannes et al. 1983); high gross primary productivity and low net primary productivity resulting from high respiration rates (Lewis 1977; Atkinson and Grigg 1984; Gladfelter 1985; Kinsey 1985); highly transparent water (Wells 1957; Yonge 1963; Wethey and Porter 1976); many species with specialized food requirements, narrow niches, and complex life cycles (Ebbs 1966; Colin 1976; Kissling and Taylor 1977); symbiotic relationships (Limbaugh 1961; Goreau and Hartman 1966; Meyer et al. 1983); and primary productivity by microscopic symbiotic algae (zooxanthellae) living within reef-dwelling Cnidaria (Goreau and Goreau 1960; Chalker 1983; Porter et al. 1984).

Because this section can only highlight certain aspects of the Florida Keys coral reefs, the following brief bibliography is provided. Geological background is presented by Hoffmeister (1974) and Shinn (1984, 1988) (the geology of the Florida Keys is discussed in Chapter 2). Synoptic overviews of South Florida coral reefs are found in Multer (1971), Bright et al. (1981), Jaap (1984), Jones et al. (1986), Porter (1987), Voss (1988), and Shinn et al. (1989). General guides to western Atlantic coral reefs include those by Colin (1978) and Kaplan (1982). The four volumes of *Biology and Geology of Coral Reefs* (Jones and Endean 1973-1977) cover a wide spectrum of reef science, as do the Proceedings of the International Coral Reef Symposia (Mukudan and Pillai 1972; Cameron et al. 1974; Taylor 1977; Gomez et al. 1981; Delesalle et al. 1985; Choat et al. 1988). Deep reef surveys off Key Largo are presented by Jameson (1981). The three volume series by Wells (1988) summarizes reef resources and management issues for 109 countries including the U.S. Marine invertebrates inhabiting Florida reefs are identified in Zeiller (1974) and Voss (1976). Field guides to coral reef fish are provided by Chaplin and Scott (1972), Greenberg (1977), and Stokes and Stokes (1980). A diver's guide to the Florida Keys by Halas et al. (1984) contributes practical information on reef diving sites.

Table 8. Species Totals: Ajax Reef

Depth-zone	Shallow			Mid			Deep		
Species	L	N	T	L	N	T	L	N	T
Acropora cervicornis	54	8	3			μ	21	2	1
Agaricia agaricites	34	10	4	3	1	1	54	6	5
Agaricia fragilis							6	1	1
Agaricia lamarcki							51	1	1
Colpophyllia natans				11	1	1			
Dichocoenia stokesii	75	13	5	121	17	8	35	7	4
Diploria clivosa	311	10	4						
Diploria labrynthiformis	19	2	2			μ			
Diploria strigosa				4	2	2	4	1	1
Eusmilia fastigiata				4	3	3	2	1	1
Madracis decactis							58	9	5
Manicina aerolata				7	3	2			
Meandrina meandrites	68	4	3	30	2	2	6	1	1
Montastrea annularis			μ	57	5	3	466	23	5
Montastrea cavernosa	16	4	3	1	1	1	74	8	5
Mycetophyllia ferox							10	2	2
Porites astreoides				16	5	3	21	2	2
Porites furcata	12	4	3						
Porites porites	64	16	7	23	9	3	6	2	1
Siderastrea siderea	32	9	6	63	13	7	315	29	8
Stephanocoenia michelinii				7	3	2	134	14	8
Scolymia lacera				2	1	1			
Zone Total =	685	80		349	66		1263	109	

L = Sum of intercept lengths (cm)
N = Number of colonies intercepted
T = Number of transects on which species occurred
μ Species observed but not intercepted

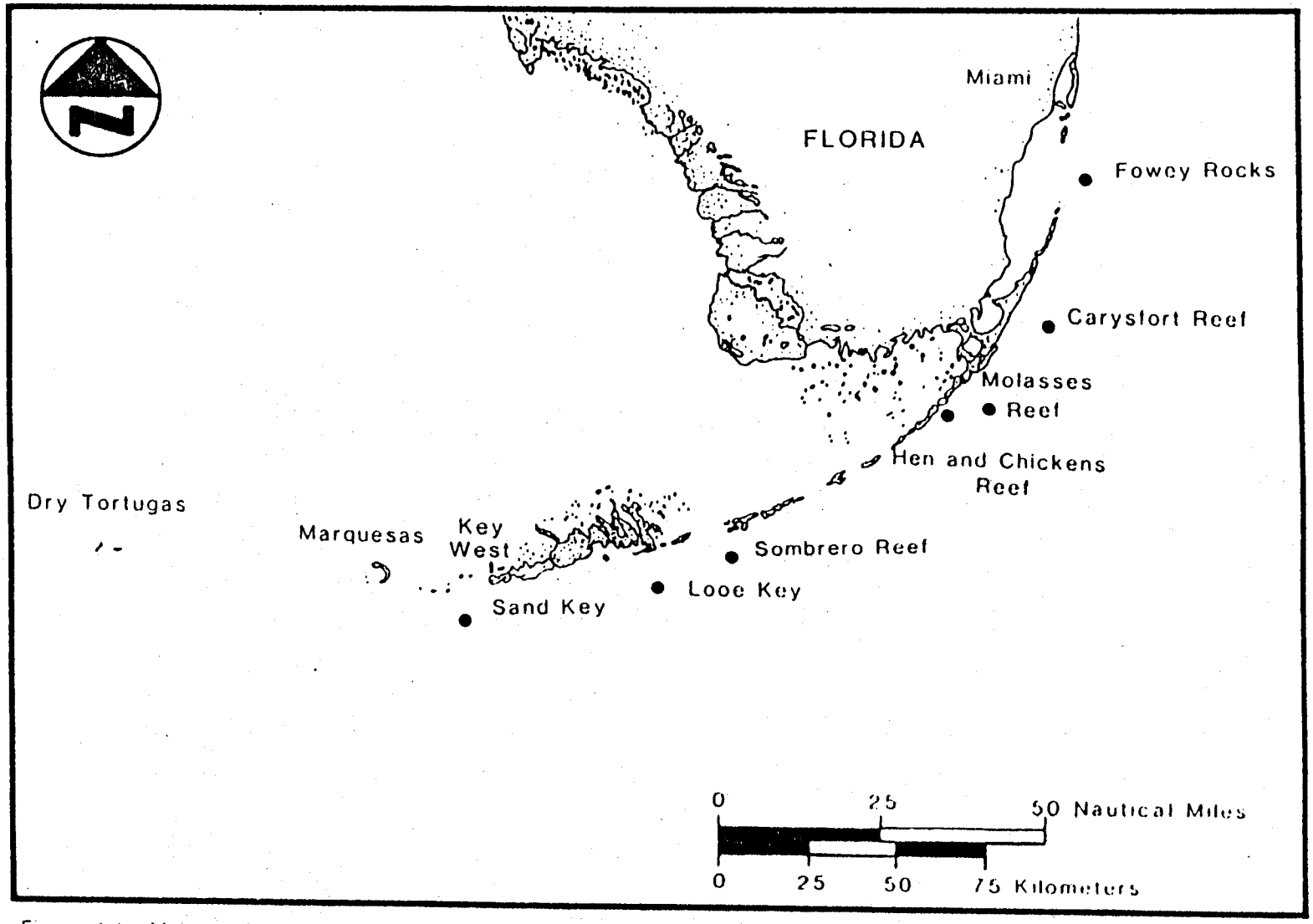


Figure 4.4. Major reefs of the Florida Reef Tract.

B-C index values for this reef are given in Tables 3 and 4. The mid and deep stations are approximately 3 times more similar than the shallow vs. deep or shallow vs. mid pairings. Jaccard values for the zone comparisons are given in Table 5. The mid and deep stations had the most similar species composition.

A comparison of the diversity indices for this reef reveals that the two deeper stations were more diverse (Table 6). The mid-depth station had a higher H'c. This station and the deeper one had equal species diversity, H'n, and a more even distribution of colonies (Dn = .86).

Ajax Reef

Differences were detected among the amounts of coral cover measured in the three depth-zones on Ajax Reef. The deepest station possessed a greater percent cover than the others (7.9), and the mid-depth station had significantly less (2.2) ($P = .004$). Differences were evident in the number of colonies per transect, the density, and the number of species per transect, but they were not significant. Twenty two species of coral were sampled on this reef (Table 8). Eight species showed differences among depth-zones ($P < .05$).

In the shallow station at Ajax Reef, the species with the greatest percent cover and that with the most colonies were the only two to show significant differences between depth-zones. Diploria clivosa was again the species in the shallowest station with the greatest relative cover (45.4%) (Fig. 11), but it was absent from the two deeper zones (Fig. 12). Porites porites possessed the greatest number of colonies in

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Synthesis of Available Biological, Geological, Chemical, Socioeconomic, and Cultural Resource Information for the South Florida Area

May 1990

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U.S. Department of the Interior
Minerals Management Service
Atlantic OCS Region

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predominance of these species in the shallow station is graphically portrayed in Figure 9.

The histogram for the mid fore-reef of Long Reef shows that Dichocoenia stokesii dominated this zone (Fig. 9). It covered 0.8 percent of the sampled substrate (25.9 percent of total coral cover). Nineteen colonies were intercepted. The mid and deep fore-reef stations were significantly greater than the shallow station for all three abundance measures ($P < .01$).

Diploria clivosa and Siderastrea siderea provided the mid-depth station with 12.5 and 13.7 percent of the coral cover. However, these two species were not more abundant in this zone. The former was more abundant in the shallow station, and the latter showed insignificant differences with depth. Colonies of Porites porites were more abundant and more dense ($P < .01$) in this mid fore-reef than in the shallow station (Fig. 10). A total of 10 colonies occurred on 5 of the 8 transects, provided 0.2 percent cover, and a mean density of $2.73/m^2$.

Acropora cervicornis, Dichocoenia stokesii, Montastrea cavernosa, and Siderastrea siderea were relatively abundant species in the deep (12 - 18 m) fore-reef zone (Fig. 9). None of these showed significant differences between this and the mid (6 - 12 m) station. Coral cover on these transects was dominated by the Mountainous Star Coral Montastrea annularis. The amount of cover provided by this massive head-coral (1.5 percent) dwarfed other species in this zone (Fig. 9). This species also showed significant differences between depth-zones in the number of colonies and colony density ($P < .05$). M. annularis was most abundant in the deep fore-reef station and did not occur on the shallow fore-reef station.

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CORAL REEFS

Walter C. Jaap and Pamela Hallock

Introduction

Coral reefs are recognized for their beauty and exceptional variety of life. In reef communities, like forest communities on land, the dominant organisms provide other members of the community with food and shelter. The massive and intricate frameworks constructed by reef-building organisms provide an almost infinite array of habitats for other plants and animals, leading to intense biologic activity and high biotic diversity.

Geographic Relationships

Coral reefs of the Florida Keys are similar to Caribbean-Bahamas tropical reefs in species composition and physiographic characteristics. Bank reefs are the major reefal structures; most occur near the continental margin seaward of large islands. Patch reefs are smaller, roughly circular features that occur in waters inshore of the bank reefs.

The coral reefs of the Florida Keys occur at an environmental threshold (Vaughan 1918): they are restricted to south and west of Cape Florida and do not occur on the West Florida shelf (Jaap 1984). Extensive reefs occur offshore of the Florida Keys archipelago (**Figure 4.4**). This chain of islands, which extends from Soldier Key to the Dry Tortugas, exhibits a diverse array of hardgrounds, patch reefs, and bank reefs from 25 m to 13 km (7 nmi) offshore (Jaap 1984). Coral reefs also extend into the Gulf of Mexico from Key West and Smith Shoal to the Content Keys. West and north of the Keys lie a series of shallow embayments (e.g., Biscayne Bay and Florida Bay), the Everglades, and the continental shelf off Southwest Florida. The Straits of Florida and the Florida Current lie beyond the reefs to the south and east.

Coral reef distribution patterns reflect water exchange between the continental shelf and the Atlantic Ocean. Heavy rainfall, drought, summer doldrums, and winter cold fronts influence temperature, salinity, nutrient supply, and turbidity in the shallow bays and sounds and produce waters unfavorable to reef development. Large islands act as barriers to off-shelf transport from Florida Bay and Biscayne Bay; thus Key Largo and Elliott Key have extensive offshore reefs. The island mass from Big Pine Key to Key West is also a barrier to water transport, fostering extensive reef development off this area (Jaap 1984; Shinn et al. 1989). The Middle Keys, which are smaller and separated by numerous wide channels communicating with Florida Bay, have limited reef development. In the Middle and Lower Keys, isolated large corals can be found inside Florida Bay near major passes (Hudson et al. 1989; Smith et al. 1989)

Environmental Characteristics

Coral reefs thrive in relatively warm (18 to 28° C), clear waters with normal marine salinities (30 to 40 ppt). Environmental conditions, including climate and seawater characteristics in the Florida Keys, are summarized in Schomer and Drew (1982), Jaap (1984), and Jaap and Hallock (in press). Walton et al. (1985) modeled the water column dynamics off Key Largo. Lee (1989) summarized the physical oceanography in the Straits of Florida and eastern Gulf of Mexico.

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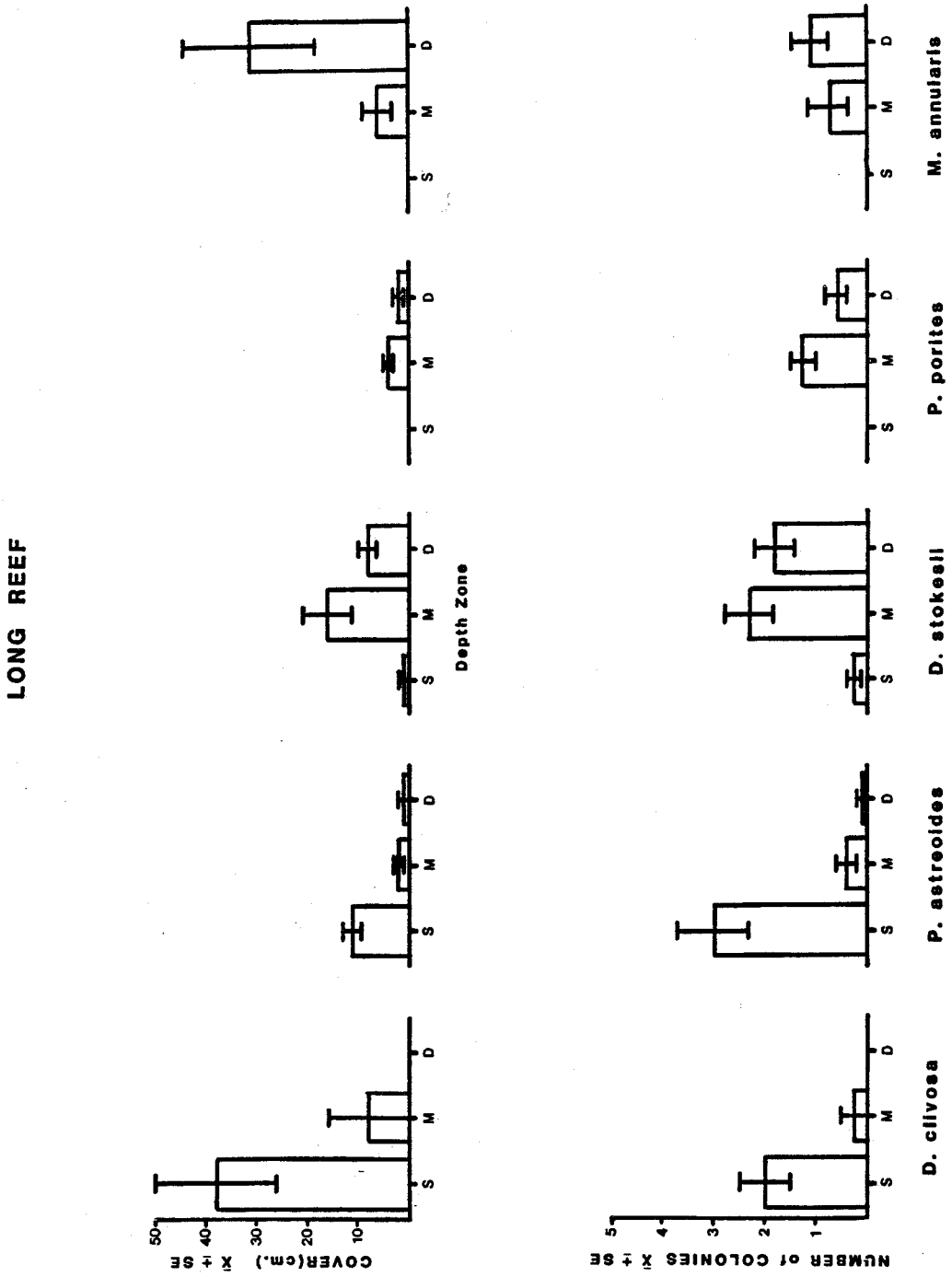

LONG REEF
COVER(cm.) X̄ ± SE
NUMBER of COLONIES X̄ ± SE
Depth Zone
D. clivosa
P. astreoides
D. stokesii
P. porites
M. annularis
S
M
D

Figure 10

Mean coral cover and number of colonies per transect (n = 8) for selected species at Long Reef that showed significant differences among depth-zones by ranks.

Figure 9

Relative abundance of all species for the three depth-zones on Long Reef.

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Table 7. Species Totals: Long Reef

Depth-zone	Shallow			Mid			Deep		
Species	L	N	T	L	N	T	L	N	T
Acropora cervicornis	431	15	4	8	2	2	60	4	1
Acropora palmata	42	1	1						
Agaricia agaricites	4	2	2	32	6	4	6	2	1
Dichocoenia stokesii	8	2	2	128	19	8	64	15	7
Diploria clivosa	301	16	7	62	2	1			
Diploria labrynthiformis						μ	10	1	1
Eusmilia fastigiata							4	3	3
Madracis decactis				2	1	1			
Manicina aerolata				6	2	1			
Meandrina meandrites				32	2	2	16	2	2
Montastrea annularis				49	6	3	246	9	6
Montastrea cavernosa	6	2	2	23	2	2	49	9	4
Porites astreoides	85	24	8	17	3	3	6	1	1
Porites furcata	9	3	2						
Porites porites				31	10	7	17	5	5
Siderastrea siderea	31	5	3	68	10	5	68	14	7
Stephanocoenia michelinii				7	2	2	3	2	2
Solanastrea bournoni				28	1	1	17	1	1
Scolymia lacera				2	1	1	1	1	1
D. stokesii stellaris							10	1	1
Zone Total =	917	70		495	69		577	70	

L = Sum of intercept lengths (cm)
N = Number of colonies intercepted
T = Number of transects on which species occurred
μ Species observed but not intercepted

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(H'c and H'n), although all low, increased with depth and most notably between the shallow and mid zones. Species diversity in the two deeper stations is enhanced by a more even distribution of cover and numbers among the sampled species. This is expressed in the higher values of Simpson's index (Dn).

Long Reef

Long Reef, immediately south of Triumph, had a greater coral cover and was richer in species. Twenty species of hermatypic corals were sampled (Table 7). Nine in the eight shallow transects covered 5.7 percent of the sampled substrate and fifteen in both the mid and deep stations covered 3.1 and 3.6 percent, respectively.

There were no differences among the depth-zones in the total coral cover, colony abundance, and density. Differences in the number of species per transect were minimal.

The importance of the encrusting brain coral Diploria clivosa to the sample-community in the shallow fore-reef is evident from Fig. 9. Colony abundance, cover, and density on these shallow transects were significantly greater than deeper stations ($P < .001$) (Fig. 10). Sixteen large, flattened heads of this coral covered 1.9 percent of the sampled substrate.

Porites astreoides again provided larger values for the three abundance measures in the shallow fore-reef station ($P < .001$) (Fig. 10). Despite the relatively large percent cover of the staghorn coral Acropora cervicornis (2.7), its colonies occurred on too few transects for a significant difference to be detected between this shallow station and deeper areas (Table 7). The overwhelming

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Table 6. Diversity Values for Reef-zones

Reef: zone	S[1]	H'c[2]	H'n[3]	Dn[4]
Triumph: shallow	8	1.40	1.38	0.63
: mid	11	2.00	1.96	0.82
: deep	11	2.17	2.13	0.86
Long: shallow	9	1.32	1.67	0.76
: mid	15	2.29	2.28	0.86
: deep	15	1.92	2.28	0.87
Ajax: shallow	10	1.80	2.16	0.87
: mid	14	1.82	2.22	0.86
: deep	16	1.90	2.19	0.85
Pacific: shallow	13	2.03	1.95	0.81
: mid	11	2.03	1.97	0.83
: deep	18	1.86	2.11	0.78

1. Number of species
2. Shannon-Weaver Index for cover (ln)
3. Shannon-Weaver Index for colony abundace (ln)
4. Simpson's Dominance Index modified (Loya, 1972)

retrofitting of selected stormwater outfalls to contain the heaviest concentrations of pollutants in the stormwater, and removal of inappropriate/unauthorized connections. A "Stormwater Utility" has also been established within D.E.R.M. to monitor the stormwater system and the levels of contamination resulting from the runoff. The County is continuing the monitoring of the landfill leachate and assisting in the development of contamination containment and remediation programs. Other programs within D.E.R.M. that serve to assist the coastal resource include habitat monitoring, enhancement and restoration programs within Biscayne Bay, near-shore reef monitoring, restoration and habitat enhancement, artificial reef placement (both in the Bay and offshore) and utilization of Special Management Zones to assist the beneficial attributes of selected artificial reef areas.

The above mentioned programs do not address all the needs. Programs are added or modified as necessary to address environmental needs or concerns identified by County, State, Federal or private programs. Broward and Palm Beach Counties also have programs to serve a number of concerns addressed above. It will be the concerted efforts of all agencies, user groups and interest groups associated with coastal habitats to affect the protection, conservation and management of the resources.

Acknowledgements

We wish to thank the members of Dade County Department of Environmental Resources Management's Restoration and Enhancement Section and Biological Resources Section for their assistance in the data gathering associated with the North Dade County monitoring programs. Further we wish to thank Mr. Lou Fisher (Broward County Office of Natural Resources Protection), Carmen Vare (Palm Beach County Environmental Resources Management) and Mr. Rick Spaddoni (Coastal Planning and Engineering, Inc.) for information regarding regional habitats.

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Table 1. Reef types and reef areas assessed in the Florida Keys (reefs that were named by the authors and cannot be found on nautical charts are marked with an asterisk). For exact location of the sites studied see the appendix.

Reef type, reef area	distance to shore, km	diameter, m	depth surroun-dings, m	depth top, m	cam-pus	cluster
(1) Marginal reefs						
Alan's Deep*	8	50	7*	6*	-	2
Key Largo D.R.	7.2	200	7*	6*	-	2
White Bank D.R.	8.4	150	7*	2-6*	2	3
(2a) Composite patch reefs						
Bache Shoal	2.8	30-60	4	1-2	4	6
Nirvana North*	5.2	20	3	1	-	2
Buck's Reef*	6.0	30	2	1.5	1	1
Cannon South*	4.4	50	7	1.5	1	-
Triangles	5.6	50	4	2	3	2
Nirvana*	5.2	150	7	1-2	2	6
Alina's Reef*	5.6	150	6	1-2	-	2
Long Reef West*	6.3	150	4	3-4	1	-
Higdon Reef	4.4	300	6	1.5	2	2
Sting Reef*	5.6	250	6	1.5	2	3
Marker 48	3.6	100	8	2	-	2
Ninefoot Shoal	4.5	50	7	5	1	-
West Washerwoman	4.6	150	9	0.5	-	4
(2b) Cluster patch reefs						
Carysfort West*	8	-10	2	<0.5	-	7
The Rocks	1.6	25	3	2	-	4
Cheeca Rocks	1.6	15	4	3-4	-	4
Newfound Harbor*	0.6	50-100	2	<0.5	-	5
Boca Chica*	0.8	20-50	3	1	-	4
Larz Reef*	5.2	30	4	1-2	-	1
Bug Reefs*	4.8	20	5	1	3	3

provide the basis for a multi-million dollar fisheries industry, and a plus-billion dollar tourist industry across the tri-county area.

Unfortunately, the stresses on our systems are also similar. The waste disposal associated with the great density of industry, construction and population in the coastal region, as well as the inland agricultural activities and stormwater runoff, have affected the coastal water quality. These changes are being suggested as causative agents of a number of recent biotic community changes noted on the reef areas (i.e., increased cover by nuisance algae, algal blooms, decreased hard coral cover, decreased light penetration). This includes the blooms of *Lyngba* spp. ("blue-green" algae) and *Codium* sp. (a "green alga") along various portions of the northern and southern Florida Reef Tract. Impacts of these algal blooms have reduced coral cover (both hard and soft corals), decreased benthic community diversity, and reduced the complexity of the habitats in the areas where the algae have become abundant or accumulated.

Shipping and construction activities can have direct mechanical or sediment impacts (Causey 1988; Blair and Flynn 1988; Goldberg 1989; Blair et al. 1990b). Secondary impacts associated with specific construction activities (i.e., beach renourishment) have been postulated, though not well documented. These impacts, although sometimes minor, can involve substantial areas (i.e., 25 acres; Blair et al. 1990b).

Recovery capability of the reef areas discussed in this paper is in question due to the continual and increasing stresses placed on these habitats. The increased stresses associated with both natural processes (i.e., sea level rise, increased natural fluctuations of water temperature and water quality and human activities may result in a limited ability of the affected reef areas to maintain and/or overcome the stress. It is essential that the present resources found along the Florida Reef Tract be managed and protected to conserve the limited hardbottom reef habitats that remain.

The management required to ensure the greatest survivability of these areas must include soundly based resource utilization, protection, restoration and education. Each component has a specific purpose in aiding the protection of the habitats. These needs are neither new or unique. They have been stated for decades. Fortunately, they have brought about programs and actions that are believed to be assisting with the protection of the coastal reef areas. For example, in Dade County, an evaluation, (in conjunction with the South Florida Water Management District), of Biscayne Bay water quality and stormwater runoff, identified numerous unauthorized or inappropriate connections to the storm drains, including industrial and sanitary waste connections, and contamination of bay water by leachate from landfills. Efforts to identify and eliminate the compromises of the stormwater drainage system are continuing. This has involved the

Table 2. Variation of cluster data within two individual clusters at Bache Shoal and three individual clusters at Nirvana North. Percentages are calculated on the basis of numbers given under 'alive' and 'dead'. (For numbers of points counted at each of the 65 clusters see Tab. 5.)

Bache Shoal, cluster 1

line	alive	dead	rubble	substrate	other	total
1	31	41	0	0	2	74
	43%	*57%*				
2	44	21	5	3	0	73
	67%	*33%*				
3	33	33	3	0	0	69
	50%	*50%*				
4	42	24	2	2	1	71
	64%	*36%*				
sum	150	119				287
mean	56%	44%				
std.-dev.		11.4%				

Bache Shoal, cluster 2

line	alive	dead	rubble	substrate	other	total
1	37	26	11	8	2	84
	59%	*41%*				
2	15	32	24	4	8	83
	32%	*68%*				
3	16	19	57	0	1	93
	46%	*54%*				
4	32	17	30	2	10	91
	65%	*35%*				
sum	100	94	122	14	21	351
mean	51%	49%				
std.-dev.		14.7%				

Nirvana North, cluster 1

line	alive	dead	rubble	substrate	other	total
1	56	60	0	2	0	118
	48%	*52%*				
2	46	43	0	4	0	93
	52%	*48%*				
3	42	48	0	6	0	96

Table 2. Jaccard Similarity Index based on hardcoral species composition (PBC = Palm Beach Co., BRW = Broward Co., NDC = North Dade Co.; SDC = South Dade Co., CRY = Carysfort Reef; LOK = Looe Key; DTG = Dry Tortugas).

	PBC	BRW	SDC	CRY	LOK	DTG
NDC	.688	.636	.611	.641	.548	.689
PBC		.586	.516	.447	.486	.489
BRW			.549	.472	.514	.489
SDC				.617	.741	.619
CRY					.579	.721
LOK						.682

Table 3. Hardcoral density and cover by depth range at the selected locations*.

		PBC	BRW	NDC	SDC	CRY	LOK	DTG
Density	5-10m	3.0	1.7	5.2	0.4	0.7	8.4	0.4
	10-20M	3.8	4.0	4.6	0.5	1.9	10.7	2.4
	>20M	-	-	1.7	-	1.1	-	1.7
Cover	5-10m	-	3.3	1.0	2.5	11.3	-	10.6
	10-20m	-	4-12	1.5	4.8	31.8	-	48.3
	>20m	-	-	0.3	-	12.0	-	26.8

REFERENCES: PBC - Coastal Planning & Engineering 1991; BRW - Dodge et al. 1991; NDC - Dade County D.E.R.M.; SDC - Burns 1985; CRY - Dustan and Halas 1987; LOK - Wheaton and Jaap 1988; DTG - Jaap et al. 1989.

* Cover as % cover, density as colonies-m^2, except SDC, CRY and DTG density as colonies-m (from line transect data).

	47%	*53%*				
4	34	56	0	2	3	95
	38%	*62%*				
sum	178	207	0	14	3	402
mean	46%	54%				
std.-dev.		5.9%				

values of the similarity indices. If two locations share 50% of their species (i.e. 25 of 50) and the remaining 50% of the species unique to each site, the JSI for that comparison would be 0.333. If two locations share 75% of their species with 25% being unique to each site, the JSI for the comparison would be 0.600. This relationship, however, gets more complicated when the number of species unique to each location is unequal. Thus, for the comparison of North Dade County with Carysfort, the 80% shared, 20% unique species composition between North Dade and Carysfort equates to a JSI value of 0.641. The North Dade - Dry Tortugas comparison shows 97% of the North Dade County species shared (31 of 32) while only 69% of the Dry Tortugas species are shared (31 of 45). Thus, although they share 25% more species than North Dade County and Carysfort, there is only a modest increase (+0.048) in the respective JSI value, reflecting the magnitude of "non-shared" components of the two locations. With this in mind, a review of Table 2 indicates that a relatively high level of similarity exists between neighboring locations, and a substantial level of similarity exists between all locations evaluated. The consistent level of similarity between North Dade County and all other locations, relative to the lower values of similarity in comparisons with sites north of Dade, reflect the transition-zone character of the North Dade to Palm Beach region.

Differences are more apparent when examining the density and percent cover by hard corals at the various locations (Table 3). As would be expected the high cover by hard corals is found in the more pristine and remote locations (i.e., Dry Tortugas). Note, however, the similar density of hard corals for most locations.

A comparison of the fish populations reported from North Dade County (Dade County D.E.R.M. unpublished), Key Largo's John Pennekamp State Park and the Dry Tortugas (Jones and Thompson 1978) reveal that the similarities are also reflected in these populations. For example, the North Dade County - Key Largo comparison resulted in a JSI of 0.552, with 107 species shared between the two sites. This represented 66% of the North Dade species composition and 73% of the reported Key Largo (Pennekamp) species composition. The North Dade - Dry Tortugas comparison showed a JSI of 0.485 with 98 shared species (representing 60% of North Dade's composition and 73% of the Dry Tortugas composition).

It is not the intent of this paper to state that the reefs of northern Dade, Broward and Palm Beach Counties are the same as those of the southern Florida Reef Tract, but to illustrate the similarities that do exist between them. It is these similarities, which reflect parallels in environmental conditions, that have enabled the reef communities to maintain their high levels of productivity and complexity. The productivity and complexity of the reefs support diverse benthic vertebrate and invertebrate populations and

Table 2. continued.

Nirvana North, cluster 2

line	alive	dead	rubble	substrate	other	total
1	21	50	5	18	0	94
	30%	*70%*				
2	20	45	6	7	4	102
	31%	*69%*				
3	20	43	7	14	1	85
	32%	*68%*				
4	25	55	4	12	0	96
	31%	*69%*				
sum	86	193				377
mean	31%	69%				
std.-dev.		0.82%				

Nirvana North, cluster 3

line	alive	dead	rubble	substrate	other	total
1	23	48	7	11	3	92
	32%	*68%*				
2	29	43	6	8	5	91
	40%	*60%*				
3	45	29	6	11	0	91
	61%	*39%*				
4	38	35	9	7	2	91
	52%	*48%*				
sum	135	155				365
mean	47%	53%				
std.-dev.	12.8%					

Figure 2. NUMBER OF HARD CORAL SPECIES

BOCA RATON TO DRY TORTUGAS

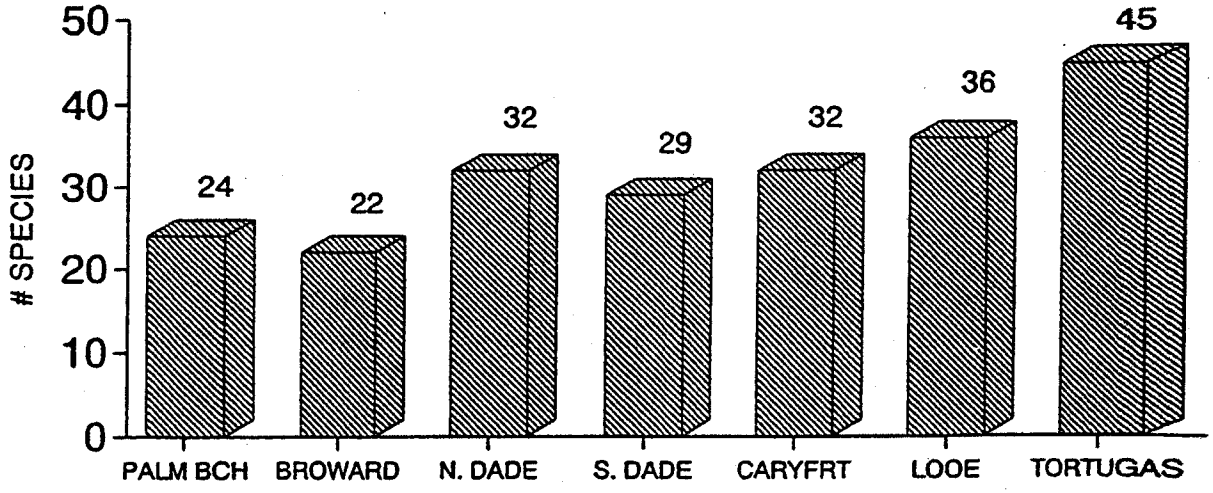


Table 3. Multiple comparison of coral condition at all (22) sites (% < 1/3 dead colony surface). Kruskal-Wallis analysis of variance by ranks (* = significant difference at $p<0.05$).

	1	2	3	4	5	6	7	8	9
M. ann. (1)	1								
M. fav. (2)		1							
M. fra. (3)			1						
M. cav. (4)	*			1					
D. stri. (5)	*	*		*	1				
D. cli. (6)	*	*		*	*	1			
D. lab. (7)	*	*					1		
C. nat. (8)	*					*		1	
S. sid. (9)	*				*	*	*		1

penetration, minimal terrigenous inputs in the Dry Tortugas) to marginally favorable (relatively elevated nutrient levels, decreased water clarity and light penetration, high levels of terrigenous runoffs in Palm Beach County) for the hard coral communities.

Comparison of hard coral components of the reef areas

Three reef areas, or tracts, can be found in the Northern Florida Reef Tract (Blair and Flynn 1989; Goldberg 1973). The reef areas vary somewhat with location, but in general, form three parallel, low relief terraces. The reef terraces lie between 0.25 and 2.5 miles offshore, with the exception of occasional intertidal reefs in Broward and Palm Beach Counties. In Dade County, the depth range of the reefs are: between 15 and 30 feet (first reef, 0.25 - 0.75 miles offshore), 43 and 58 feet (second reef, 1.0 - 1.5 miles offshore) and 55 to +100 feet (third reef, 1.5 - 2.0 miles offshore). These areas show extensive coverage of benthic organisms including relatively high densities of hard corals and high densities of soft corals, algae and sponges. Detailed information regarding the coverage and abundance of various benthic community components is given by Goldberg (1973) and Coastal Planning and Engineering (1991) for Palm Beach County, Fisher and Dodge (1989) and Goldberg (1980) for Broward County, and Blair and Flynn (1989) for the northern Dade County reef areas.

The number of species of hard corals reported from the locations are represented in Figure 2. As would be expected, due to the gradient of environmental conditions, the highest diversity (number of species) is found at the Dry Tortugas. Somewhat surprising, however, are the numbers representing the hard coral diversity of northern Florida Reef Tract locations. The number of species for locations within the northern reef tract is comparable from Looe Key to Northern Dade County, and somewhat less to Palm Beach County. Examination of the number of species shared between the location highlights the differences that are present (Table 1). For example, although North Dade County and Carysfort have the same number of species reported (32), 24 (approximately 80%) are common to both areas, and 8 species (approximately 20%) are unique to each site. Obviously, this alone does not imply high similarity in all the components, but does illustrate the commonness of the regions being compared.

Similarity indices, such as the Jaccard Similarity Index (Krebs 1989), use both the number of common species as well as the number of species unique to each location to derive a number to represent the relative similarity between the two locations. The values can range from 0.00 (no species in common) to 1.00 (all species shared, and no unique species in either location). Table 2 gives the Jacquard Similarity Index (JSI) for hard coral population comparisons between the various locations. A couple of examples will help illustrate the magnitude of the

Table 4. Multiple comparison of *Montastraea* clusters off Elliot Key, Key Largo, and reefs south of Key Largo. Kruskal-Wallis analysis of variance by ranks. *=significant difference at $p < 0.05$.

	Elliot Key vs. Key Largo	Elliot Key vs. Middle Keys	Elliot Key vs. Lower Keys
% dead	0.54	0.11	0.0012*
% rubble	0.007*	0.69	0.075

	Key Largo vs. Middle Keys	Key Largo vs. Lower Keys	Middle Keys vs. Lower Keys
% dead	0.35	0.012*	0.402
% rubble	0.05*	0.468	0.515

6,000 to 8,000 years ago, and extended from the Dry Tortugas to northern Palm Beach County (Lighty et al. 1978; Goldberg 1973). These reef areas are productive regions which add environmental, ecological, economic, aesthetic and biological importance to the southeastern coastal region of Florida. The reef systems are complex and under multiple, often synergistic, stresses (both natural and anthropogenic) that jeopardize the continued health and existence of these habitats. A review of the literature revealed little information has been published on the northern Florida Reef Tract. Substantial data exists, however, in the form of reports to county agencies that were carried out in association with permit conditions for county sponsored projects (i.e., beach restoration, jetty and breakwater construction, artificial reef construction and placement). These reports include preliminary environmental impact assessments, project monitoring reports and assessments of various impacts to hardbottom communities. This paper will compare data available for hard coral communities of the northern reef tract with selected areas of the southern reef tract, to present similarities between the regions with respect to their biological diversity and equivalence of stress (type and magnitude). Although hard corals will be used to characterize the similarities between the areas, equivalent parallels exist between the other components of their benthic communities (i.e., sponges, algae, fish populations, benthic invertebrates).

Literature Sources

The general ecology of the northern Florida Reef Tract has not been extensively documented. Information describing composition and ecology of specific benthic components of the reef areas has been presented by Goldberg (1973, 1981, 1985), Wheaton (1987), Dodge and Fisher (1989), Dodge and Thompson (1974), Dodge and Valsnys (1977) and Dodge et al. (1974). Data from monitoring reports and project environmental impact studies provide the largest source of information regarding the biological components of the hardbottom reefs of this region (e.g. Coastal Planning and Engineering 1991; Fisher et al. 1990; Blair and Flynn 1989; Courtney et al. 1980, 1975, 1972; Continental Shelf Associates 1980, 1984). Additional, though often limited, information is available in reef impact assessment reports (Marszalek 1980, 1981; Britt Associates 1979; Causey 1988; Blair and Flynn 1988; Blair et al. 1990a, 1990b).

The selection of sites for comparison with representative areas of the Florida Reef Tract (Fowey Rocks to the Dry Tortugas) was not meant to be all inclusive, rather, they were selected to provide a gradient from the most protected and pristine habitats (i.e., Dry Tortugas) to those areas under increasing stress by tourism (Key Largo) and/or generalized natural and anthropogenic pressures (Looe Key). The selected areas (Figure 1) also represent a gradient of environmental conditions from most favorable (oligotrophic, high water quality, clarity and light

Appendix

Locations of the reefs studied. For some localities less coordinates than sites are given because the distance between sites is below the resolution of the Magellan GPS-instrument. Localities that were given names by the authors and cannot be found on nautical charts are marked by an asterisk.

Reef	campus sites	cluster sites (points assessed)	Latitude (N)	Longitude (W)
<u>Upper Keys</u>				
Carysfort West*	-	7 (80-181)	25° 13.752	80° 14.050
			25° 13.756	80° 13.823
			25° 13.892	80° 14.041
			25° 11.673	80° 15.967
			25° 11.376	80° 15.522
			25° 11.776	80° 15.850
Bache Shoal	4	6 (100-351)	25° 29.074	80° 08.917
			25° 29.161	80° 08.892
			25° 29.126	80° 08.892
			25° 28.970	80° 08.981
			25° 29.126	80° 08.966
Larz Reef*	-	1 (81)	25° 25.171	80° 09.259
Nirvana North*	-	2 (357, 402)	25° 25.327	80° 08.838
Buck's Reef*	1	1 (101)	25° 25.334	80° 08.843
Bug Reefs*	3	3 (102-204)	25° 21.329	80° 11.402
Cannon South*	1	-	25° 06.150	80° 21.400
Triangles	3	2 (80, 100)	25° 01.121	80° 26.374
			25° 01.182	80° 26.418
Nirvana*	2	6 (78-365)	25° 24.973	80° 09.094
			25° 25.120	80° 09.033
Alina's Reef*	-	2 (180, 204)	25° 23.201	80° 09.768
Long Reef West*	1	-	25° 25.272	80° 08.625
Higdon Reef	2	2 (106, 107)	25° 08.144	80° 18.981
			25° 08.450	80° 18.873
Sting Reef*	2	3 (60-100)	25° 04.170	80° 22.243
			25° 04.165	80° 22.284
Alan's Deep*	-	2 (80, 106)	25° 10.050	80° 15.600
Key Largo D. R.	-	2 (84, 90)	25° 07.357	80° 17.915
White Bank D. R.	2	3 (100-102)	25° 02.430	80° 22.272
			25° 02.605	80° 22.120

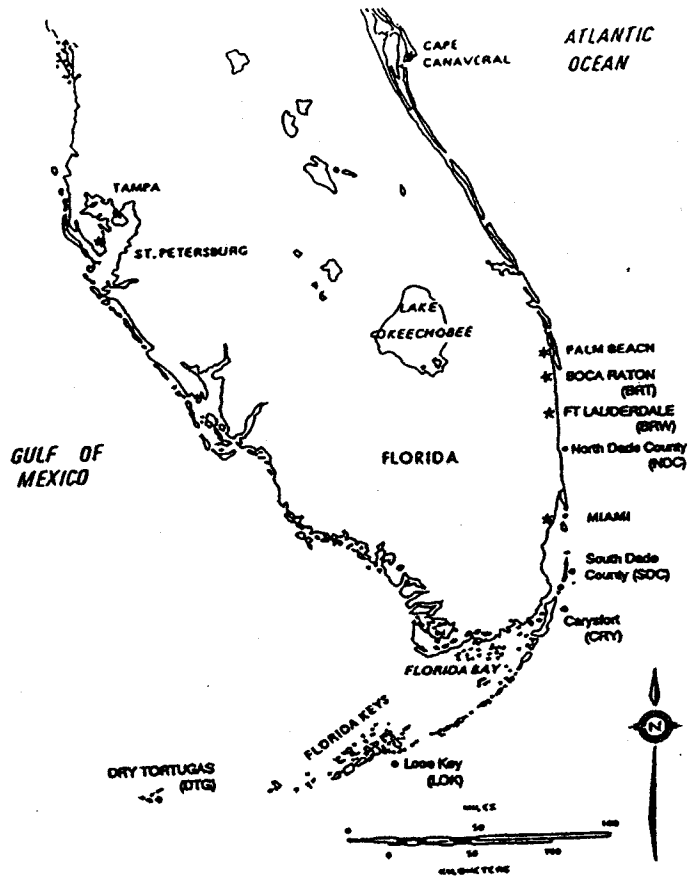


Figure 1. Location of selected comparison sites.

Table 1. Number of species of hardcoral shared between locations (PBC = Palm Beach Co., BRW = Broward Co., NDC = North Dade Co.; SDC = South Dade Co., CRY = Carysfort Reef; LOK = Looe Key; DTG = Dry Tortugas

	PBC	BRW	SDC	CRY	LOK	DTG
NDC	22	21	22	25	23	32
PBC		17	16	17	18	22
BRW			17	17	18	22
SDC				20	19	25
CRY					22	31
LOK						30

Tab. 5: continued.

Middle Keys				
The Rocks	-	4 (79-173)	24° 56.645	80° 33.387
			24° 56.670	80° 33.180
Cheeca Rocks	-	4 (80-142)	24° 54.130	80° 36.920
Marker 48	-	2 (195, 200)	24° 41.330	81° 02.320
Lower Keys				
Newfound Harbor*	-	5 (172-194)	24° 36.987	81° 23.629
			24° 36.946	81° 23.515
West Washerwoman	-	4 (180-201)	24° 37.929	81° 35.396
Boca Chica*	-	4 (96-104)	24° 33.116	81° 42.012
			24° 33.043	81° 42.191
			24° 33.097	81° 42.096
Ninefoot Shoal	1	-	24° 34.177	81° 33.127

Reef areas of southeastern Florida: Hardbottom reef communities of Dade, Broward, and Palm Beach counties.

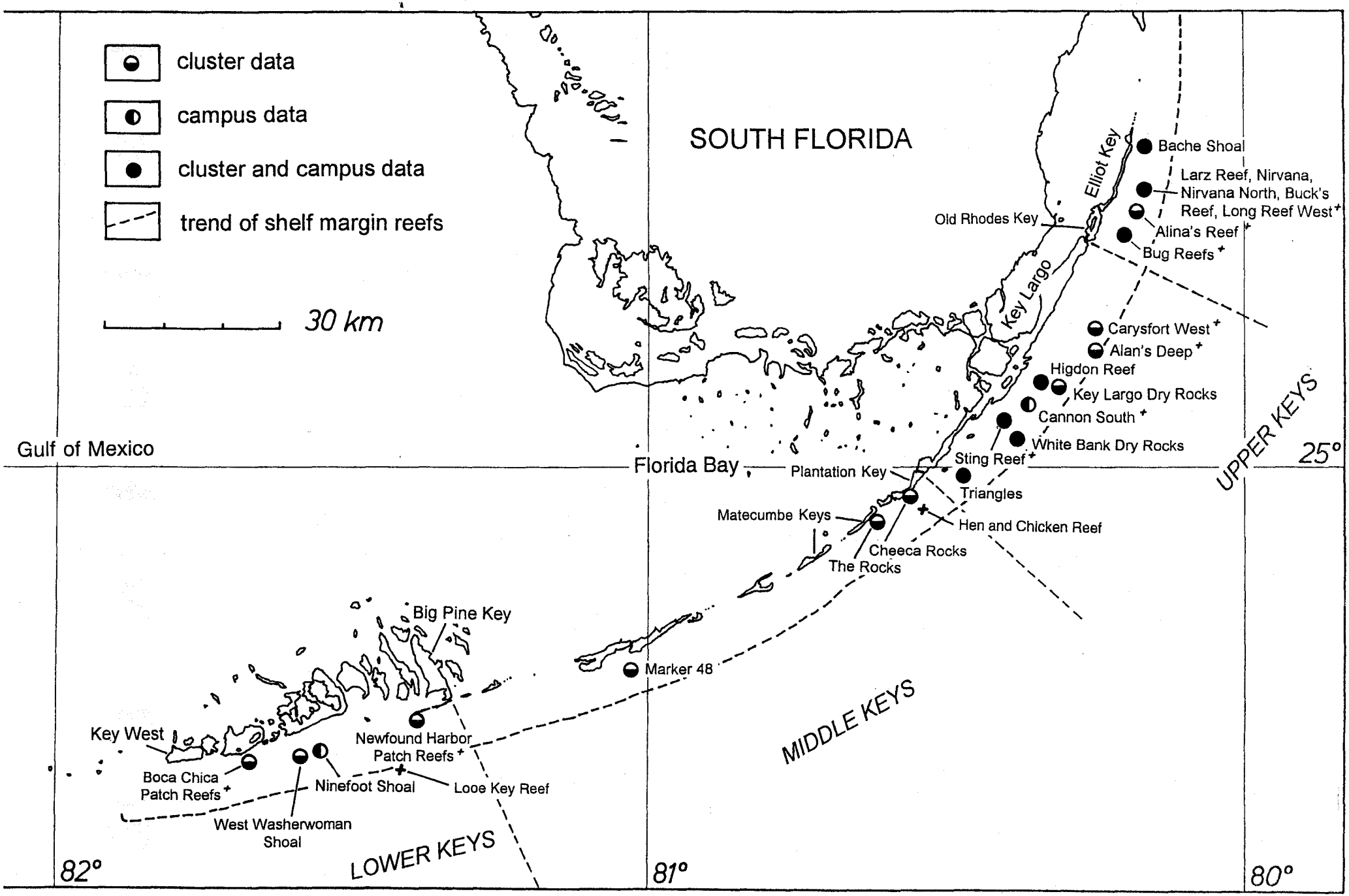
Steven M. Blair
Dade Environmental Resource Management & Biological Resources
111 NW First St., Suite 1310
Miami, FL 33128-1971

Abstract

The benthic reef habitats found offshore of Miami and North to West Palm Beach, lack the coral development commonly associated with the coral reefs to the south (i.e., the Florida Keys). However, the hardbottom reef areas off Dade, Broward, and Palm Beach Counties are thriving habitats which mark the northern extent of numerous hard coral species and serve as a transition zone between tropical, subtropical and warm temperate species. The hardbottom reef areas support numerous species of recreationally and economically important fish which provide a substantial economic resource through tourism (i.e. diving, fishing) and an established commercial fishery. The habitats are characterized by a high density and diversity of soft corals, sponges, and algae. The hardbottom reefs off Dade county are dominated by soft corals, with densities ranging between 2.85 and 26.49 colonies per meter square (m^2). The region (Palm Beach county to Dade County) shows a high diversity of hard corals relative to the total number of species found within Florida (33 of the 45 recorded species). Further, strong similarities in density and diversity of benthic community components (i.e., fish, soft coral, algae, sponges), exist between this region and areas along the Florida Reef Tract. Significant differences exist, however, in hard coral cover (0.28 to 3.78% off Miami to West Palm versus 2.5 to 48.3% on the southern portions of the Florida Reef Tract). Urbanization and tourism have caused broad-based, large-scaled stresses on the resources which are felt both on the northern and southern Florida Reef Tracts. These often synergistic stresses place the health and ecology of these systems in jeopardy. It is essential that the present resources be conserved and action taken to protect the limited hardbottom reefs remaining.

Introduction

The offshore coral reef areas of southeastern Florida make up the Florida REef Tract (Vaughan 1916). The reef tract extends from Fowey Rocks, southern Dade County, to the Dry Tortugas, and supports the only shallow water tropical coral reef system on the continental shelf of North America (Jaap 1984). The Dade, Broward and Palm Beach offshore reefs make up an extension of the reef tract referred to as the "Northern Florida Reef Tract" (Goldberg 1973). This region is a relic of a vastly more extensive system that existed some



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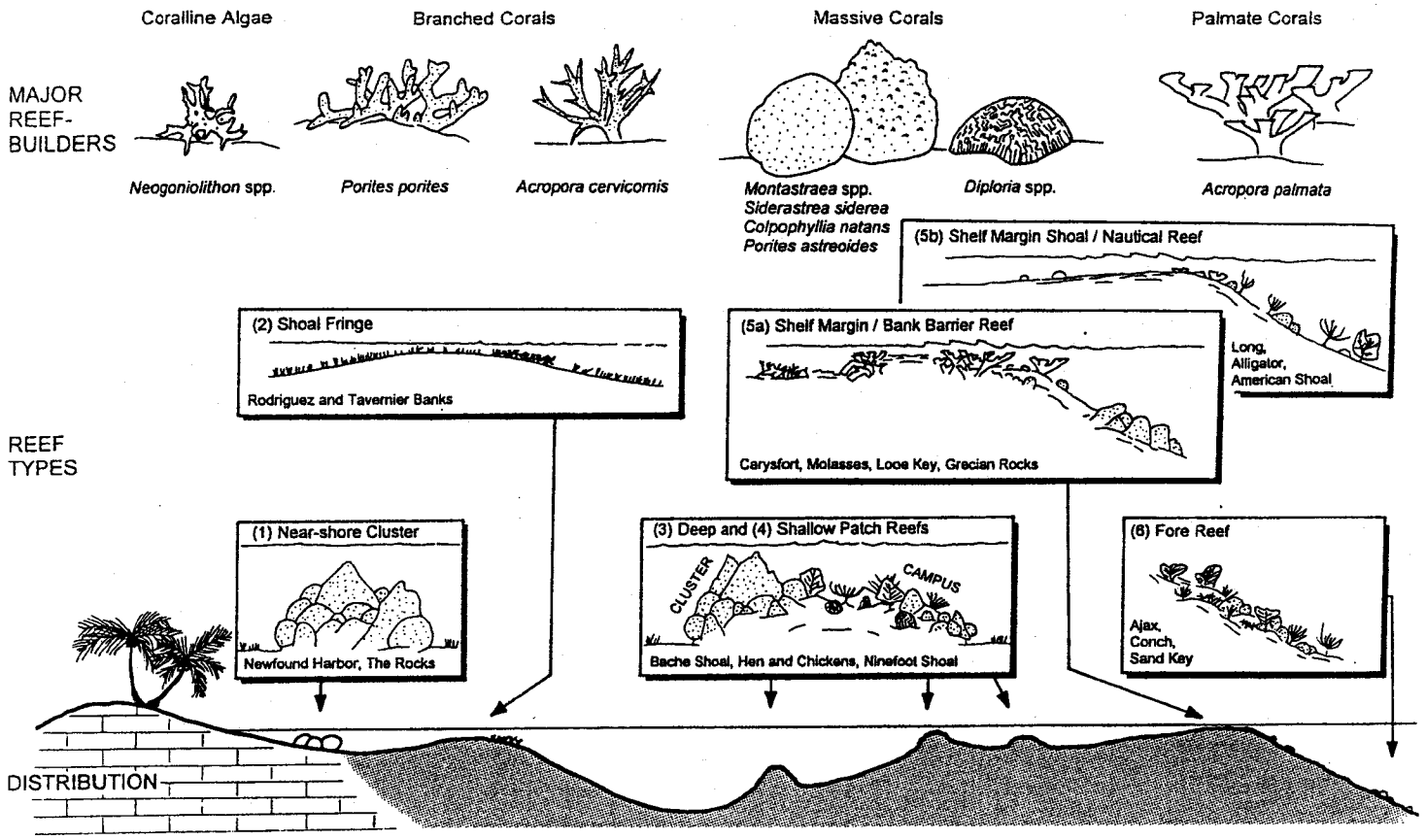
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FLORIDA REEF TYPES: MAJOR COMPONENTS AND DISTRIBUTION

Fig 2

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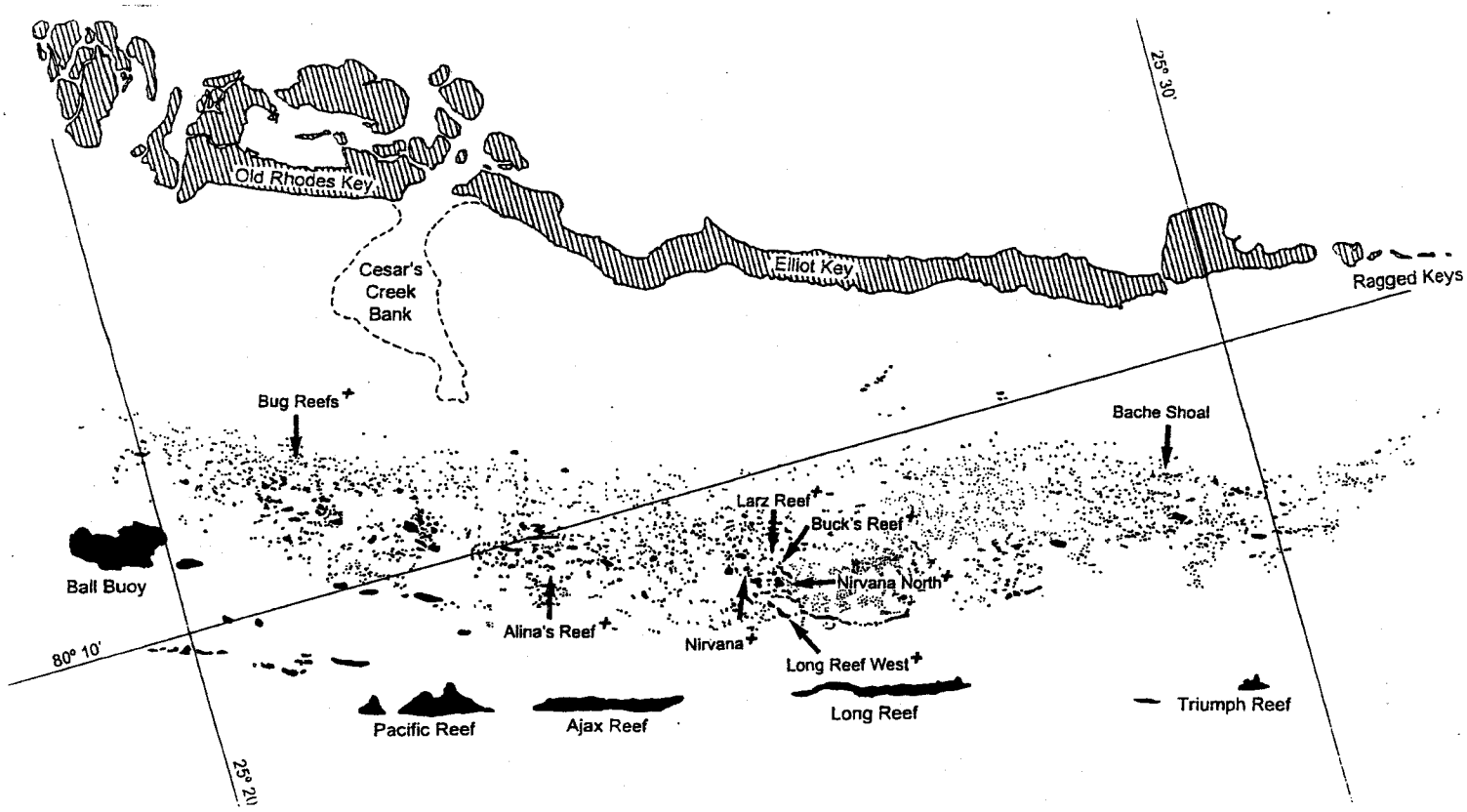

Old Rhodes Key
Cesar's Creek Bank
Elliot Key
Ragged Keys
25° 30'
Bug Reefs
Bache Shoal
Larz Reef
Buck's Reef
Nirvana North
Ball Buoy
Alina's Reef
Nirvana
Long Reef West
80° 10'
Pacific Reef
Ajax Reef
Long Reef
Triumph Reef
25° 21'

Fig 3

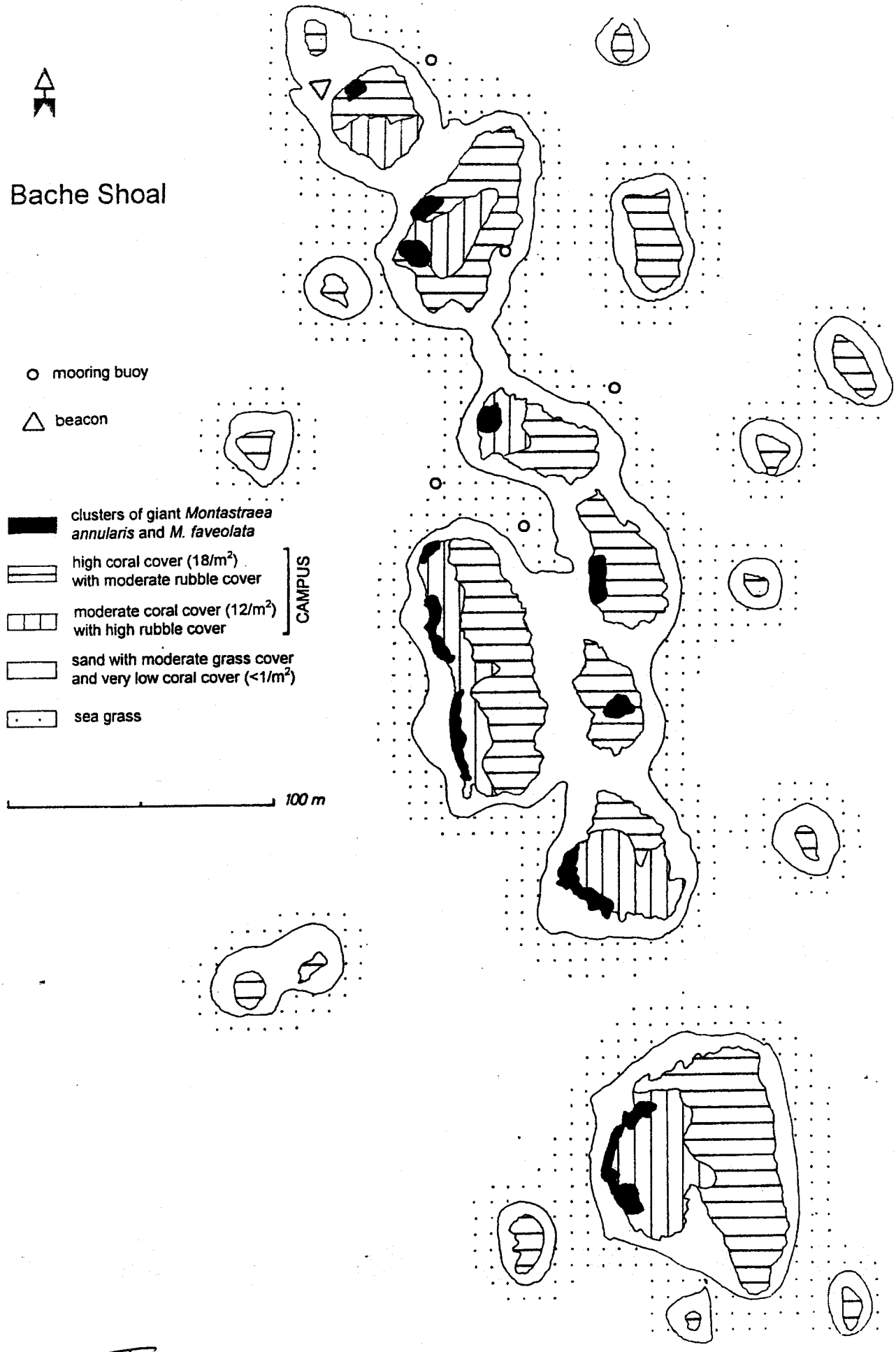

Bache Shoal
mooring buoy
beacon
clusters of giant Montastraea annularis and M. faveolata
high coral cover (18/m²) with moderate rubble cover
moderate coral cover (12/m²) with high rubble cover
CAMPUS
sand with moderate grass cover and very low coral cover (<1/m²)
sea grass
100 m

Fig 44

a

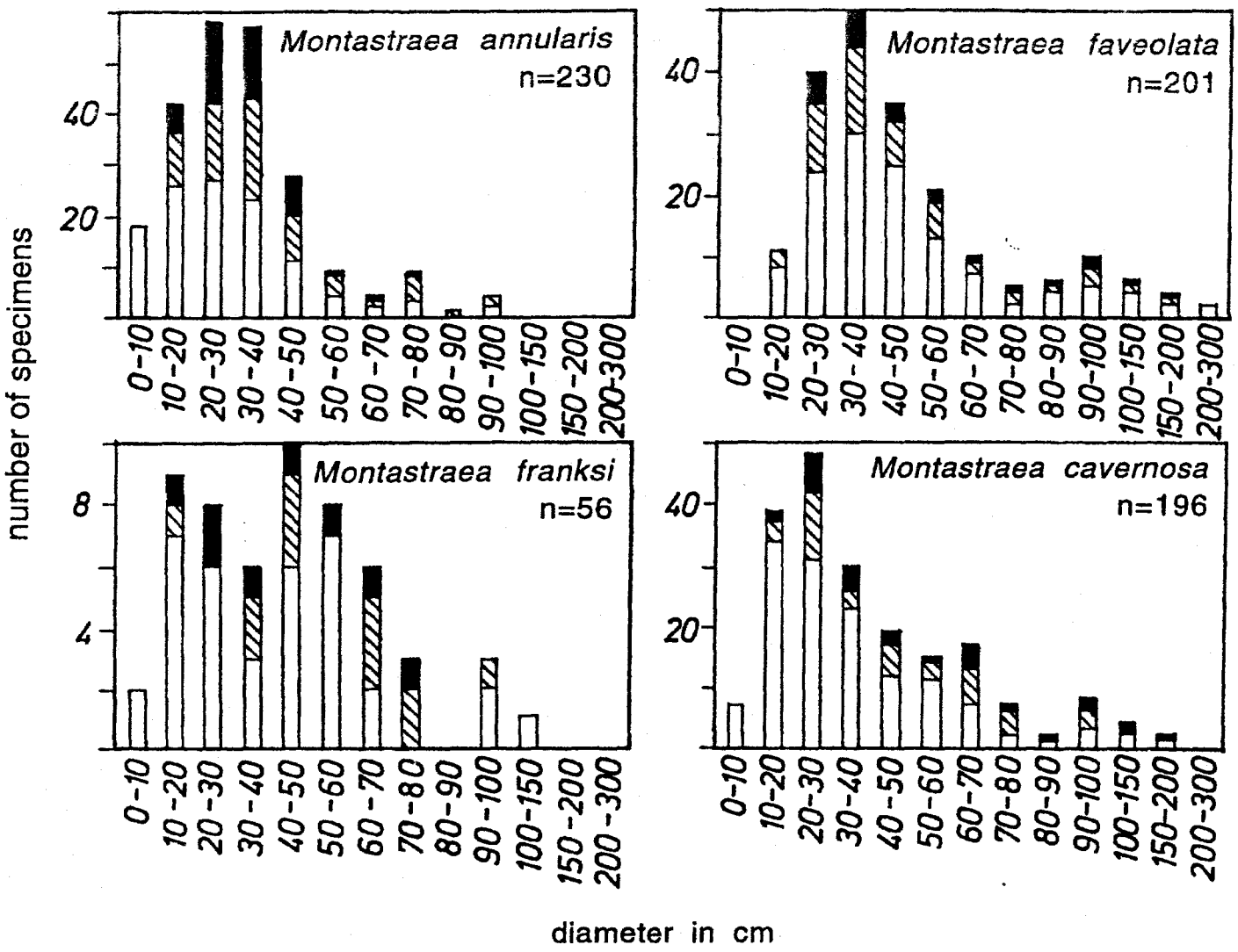

Montastraea annularis
n=230
Montastraea faveolata
n=201
Montastraea franksi
n=56
Montastraea cavernosa
n=196
number of specimens
diameter in cm
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
90-100
100-150
150-200
200-300

Fig 5a

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b

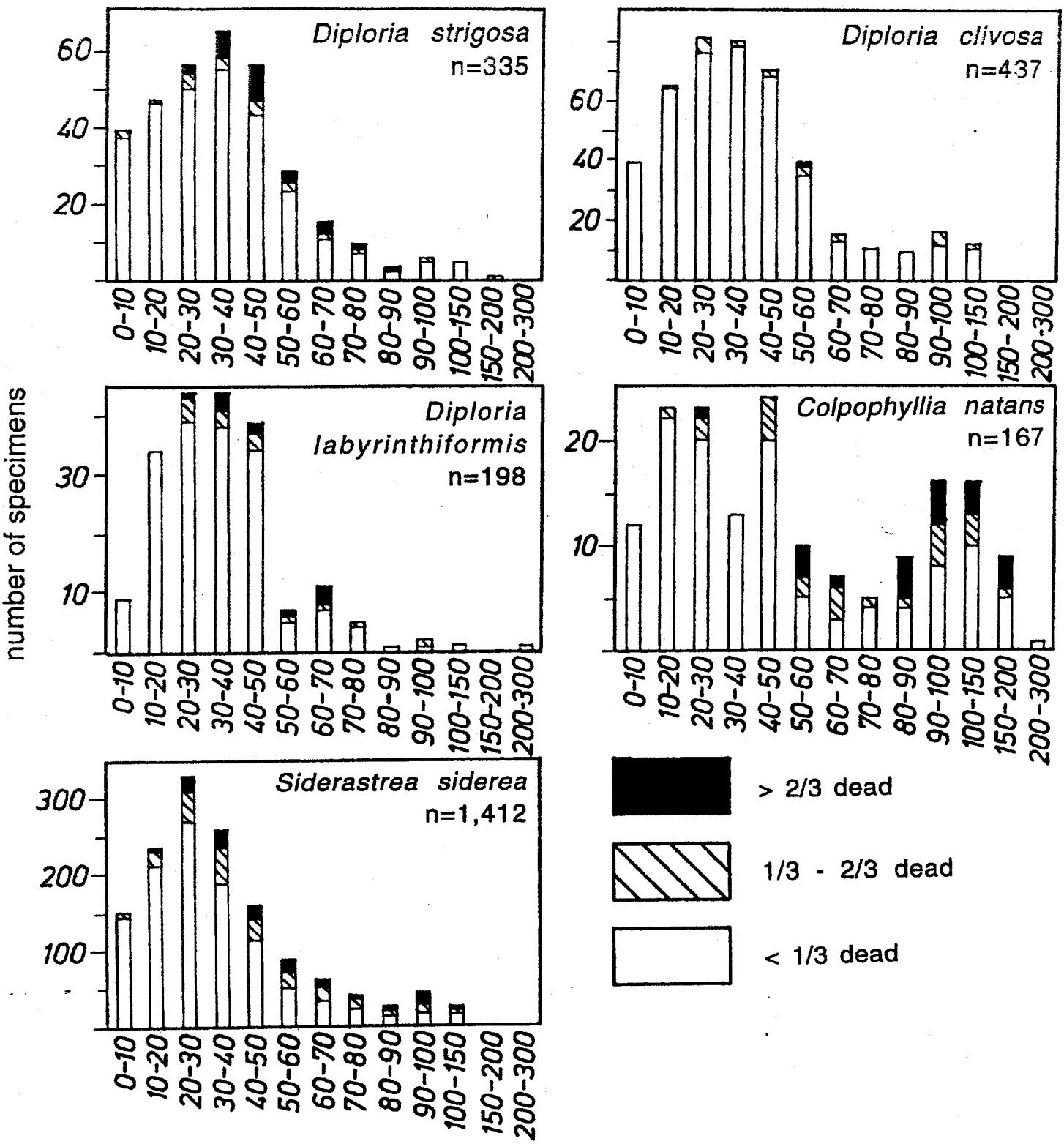

Diploria strigosa
n=335
Diploria clivosa
n=437
Diploria labyrinthiformis
n=198
Colpophyllia natans
n=167
Siderastrea siderea
n=1,412
number of specimens
diameter in cm
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
80-90
90-100
100-150
150-200
200-300
> 2/3 dead
1/3 - 2/3 dead
< 1/3 dead

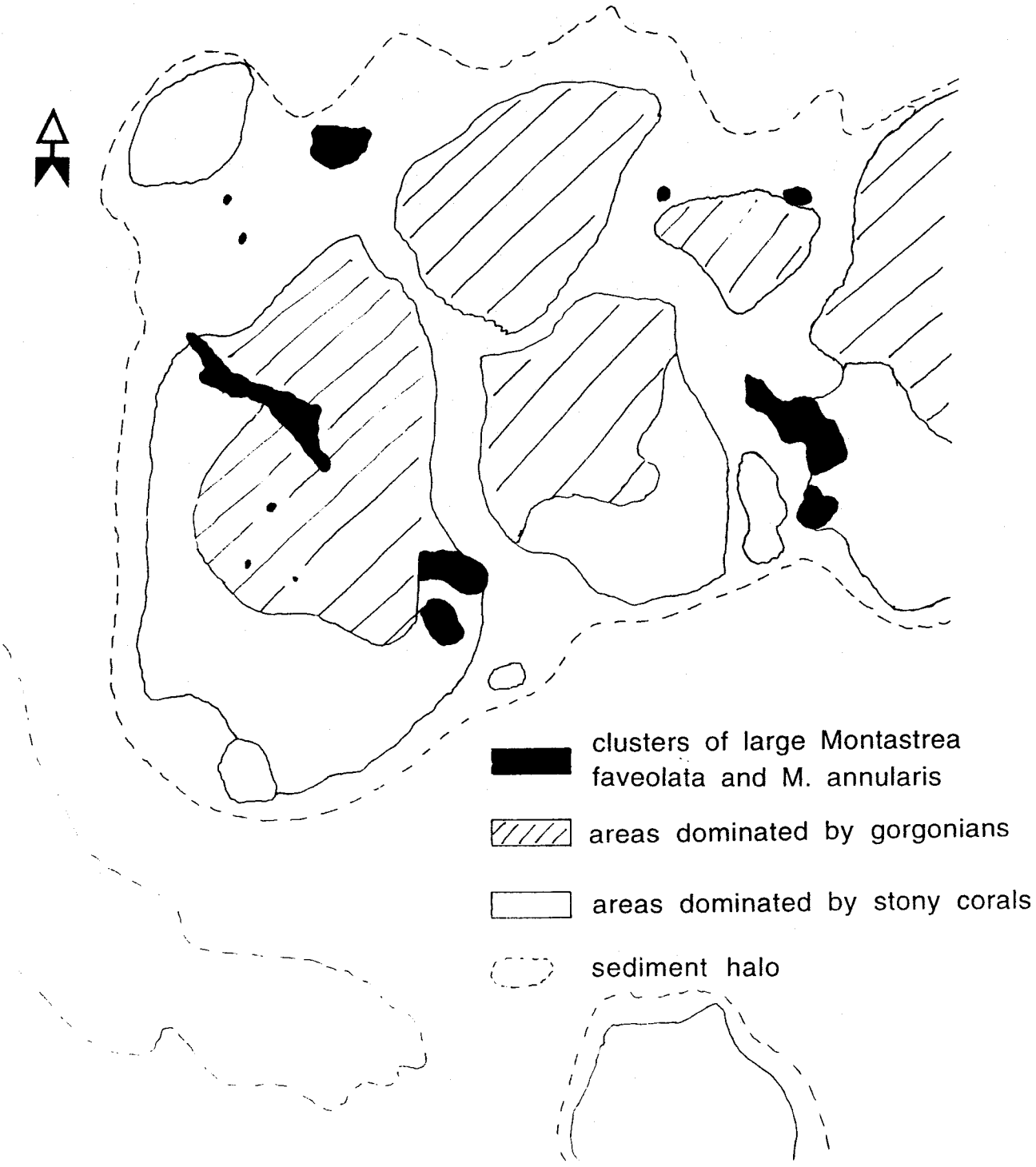
Fig 56

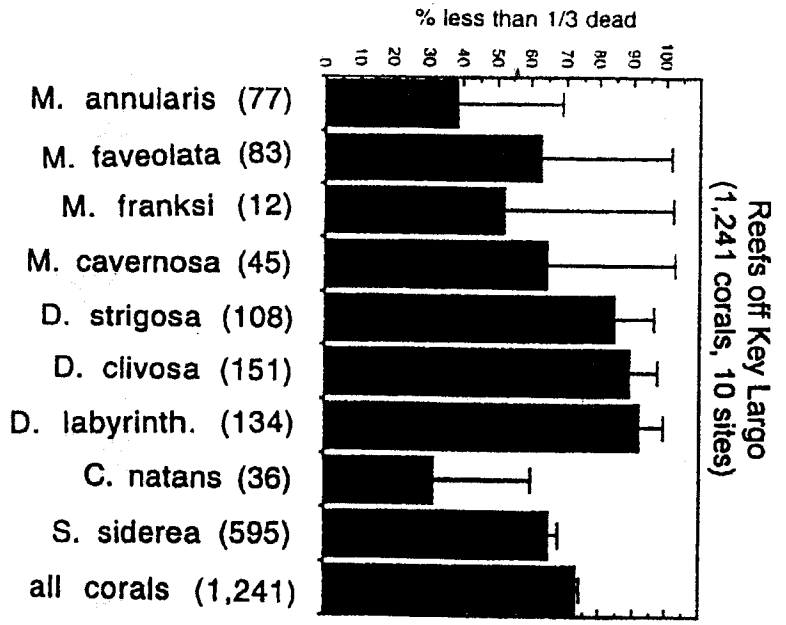
Figure 12

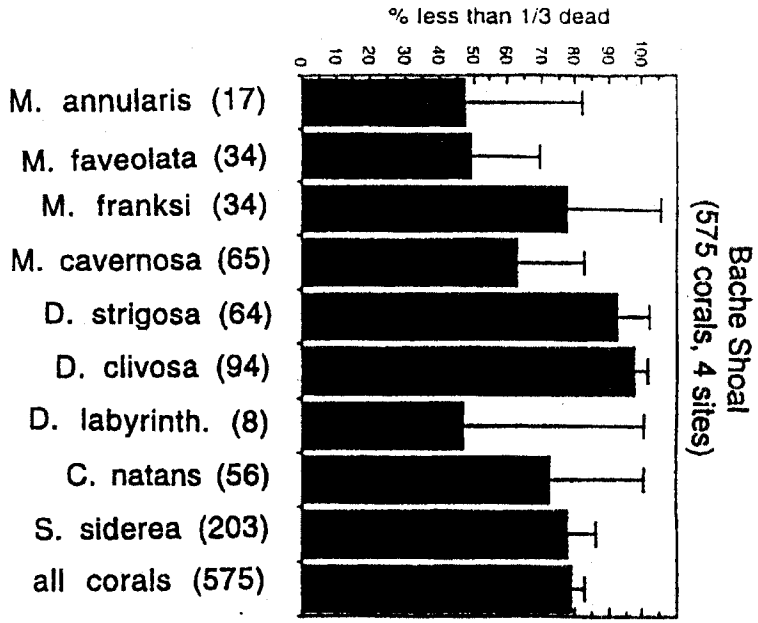
RAPID ASSESSMENT OF REEF CORAL CONDITION
University of Miami, RSMAS-MGG
Robert N. Ginsburg, July 1995

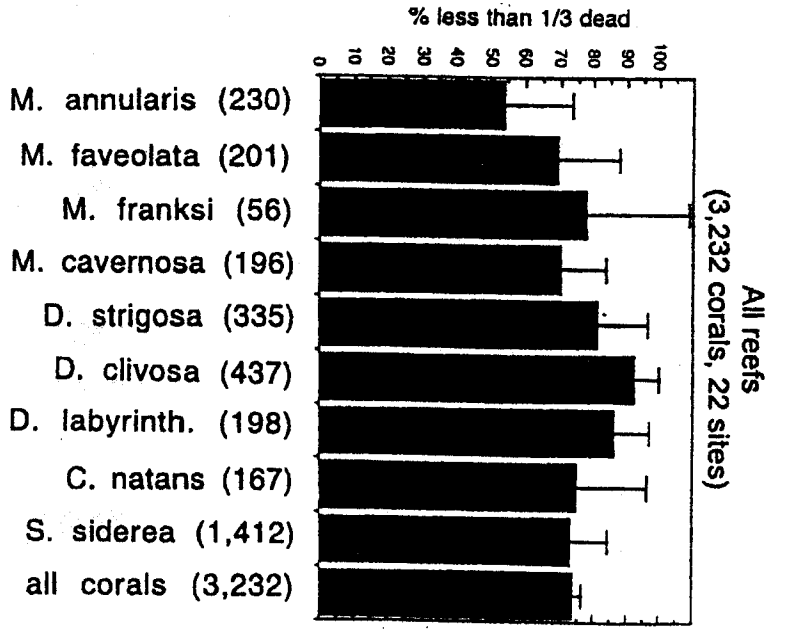
Map of Nirvana
based on aerial photography and field observations

(for location see Figure 1; approximate diameter of the patch reef is 100 meters)




% less than 1/3 dead
0 10 20 30 40 50 60 70 80 90 100
M. annularis (77)
M. faveolata (83)
M. franksi (12)
M. cavernosa (45)
D. strigosa (108)
D. clivosa (151)
D. labyrinth. (134)
C. natans (36)
S. siderea (595)
all corals (1,241)
Reefs off Key Largo
(1,241 corals, 10 sites)


% less than 1/3 dead
0 10 20 30 40 50 60 70 80 90 100
M. annularis (17)
M. faveolata (34)
M. franksi (34)
M. cavernosa (65)
D. strigosa (64)
D. clivosa (94)
D. labyrinth. (8)
C. natans (56)
S. siderea (203)
all corals (575)
Bache Shoal
(575 corals, 4 sites)


% less than 1/3 dead
0 10 20 30 40 50 60 70 80 90 100
M. annularis (230)
M. faveolata (201)
M. franksi (56)
M. cavernosa (196)
D. strigosa (335)
D. clivosa (437)
D. labyrinth. (198)
C. natans (167)
S. siderea (1,412)
all corals (3,232)
All reefs
(3,232 corals, 22 sites)

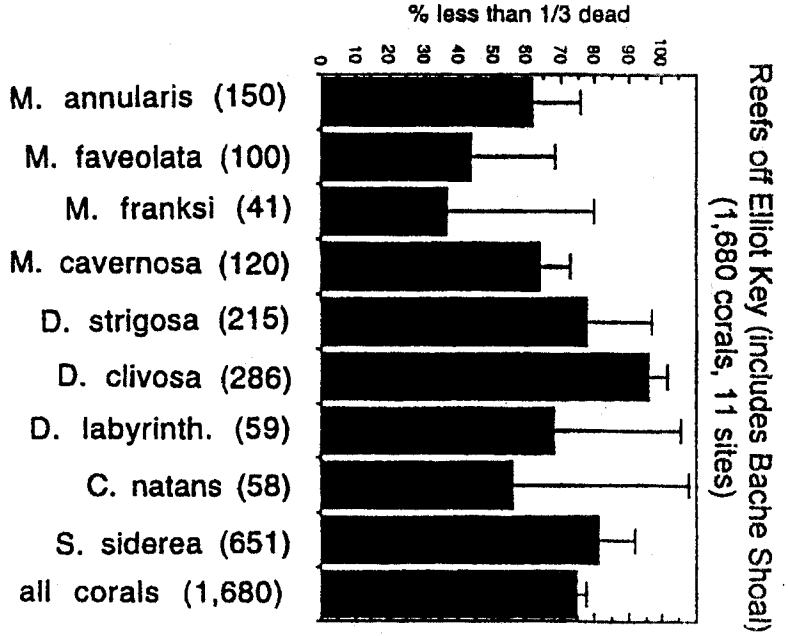
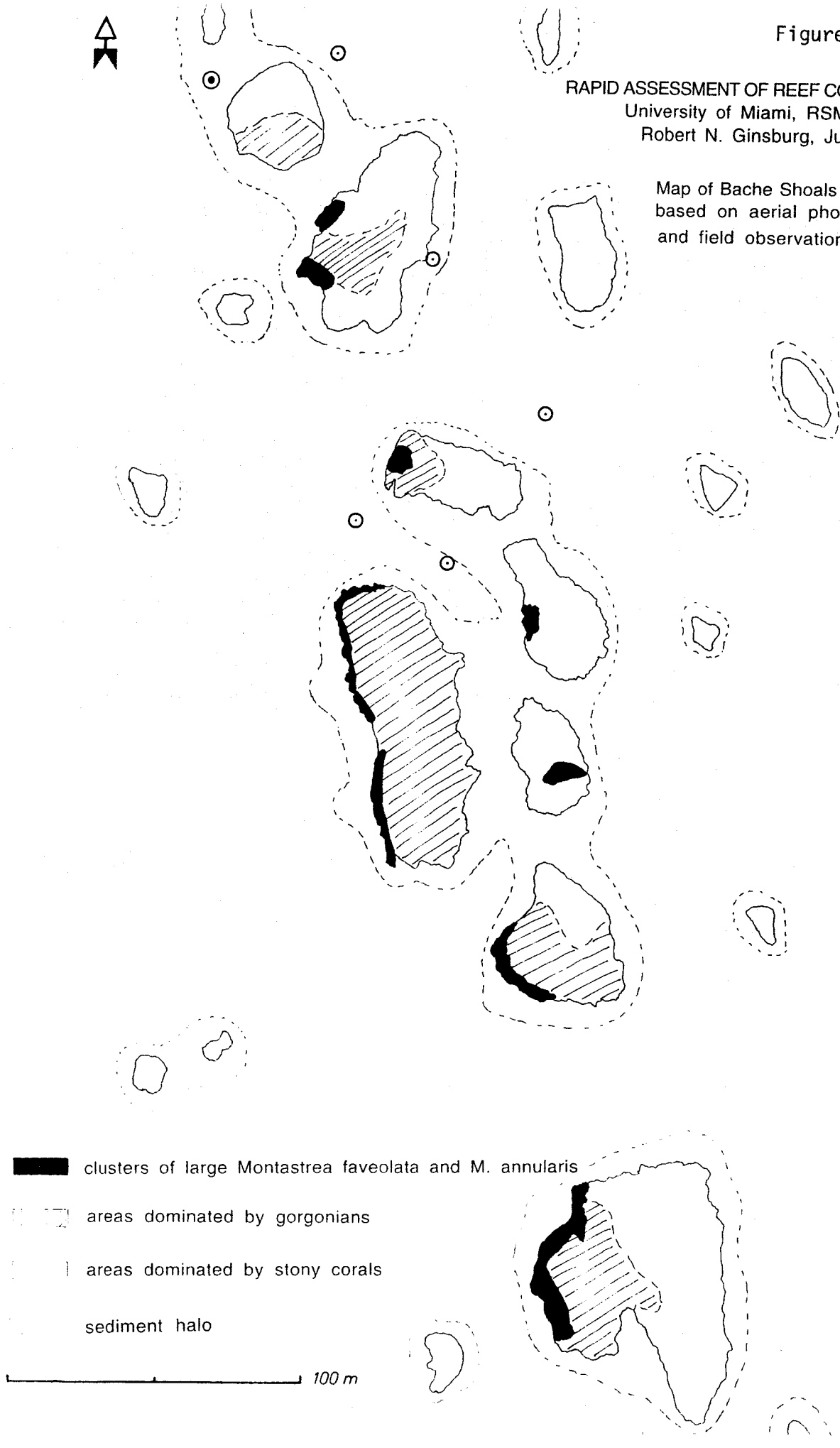

% less than 1/3 dead
0 10 20 30 40 50 60 70 80 90 100
M. annularis (150)
M. faveolata (100)
M. franksi (41)
M. cavernosa (120)
D. strigosa (215)
D. clivosa (286)
D. labyrinth. (59)
C. natans (58)
S. siderea (651)
all corals (1,680)
Reefs off Elliot Key (includes Bache Shoal)
(1,680 corals, 11 sites)

Fig 6

Figure 11

RAPID ASSESSMENT OF REEF CORAL CONDITION
University of Miami, RSMAS-MGG
Robert N. Ginsburg, July 1995

Map of Bache Shoals
based on aerial photography
and field observations



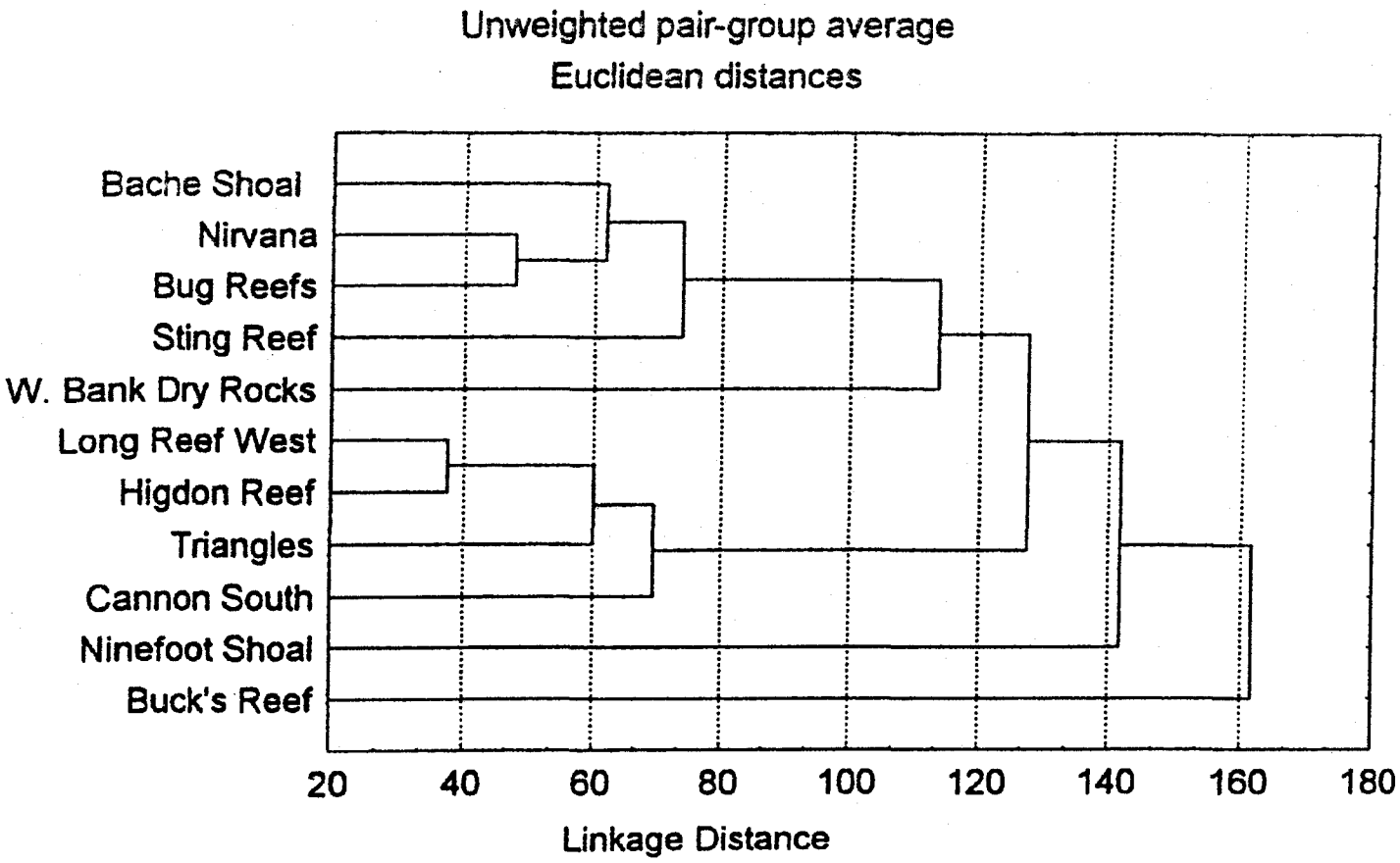

Unweighted pair-group average
Euclidean distances
Bache Shoal
Nirvana
Bug Reefs
Sting Reef
W. Bank Dry Rocks
Long Reef West
Higdon Reef
Triangles
Cannon South
Ninefoot Shoal
Buck's Reef
20
40
60
80
100
120
140
160
180
Linkage Distance

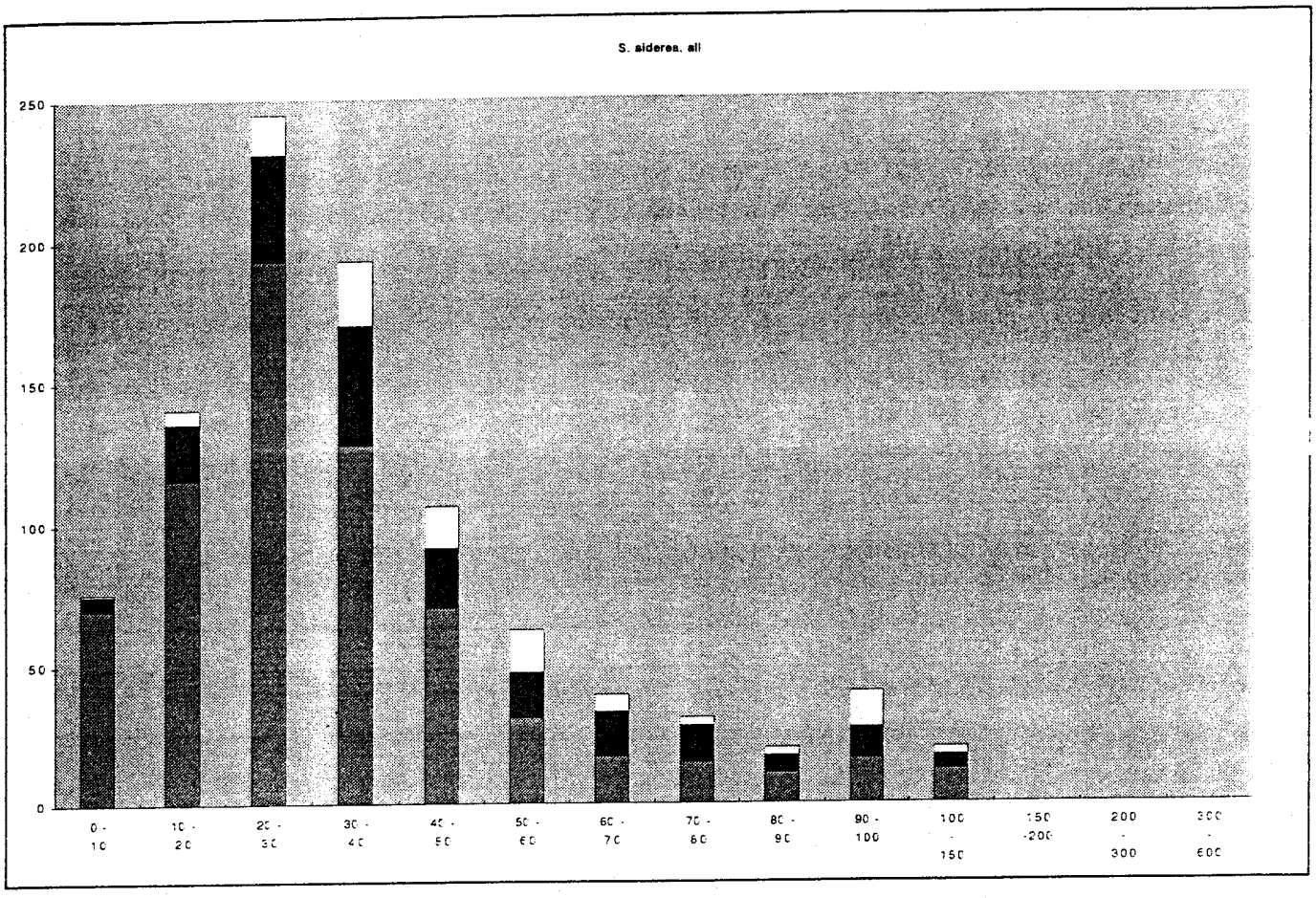
Fig 7

Figure 10

RAPID ASSESSMENT OF REEF CORAL CONDITIO

University of Miami, RSMAS-MGG

Robert N. Ginsburg, July 1995



SIZE DISTRIBUTION OF CORALS

grey = less than 1/3 dead
black = 1/3 - 2/3 dead
white = more than 2/3 dead

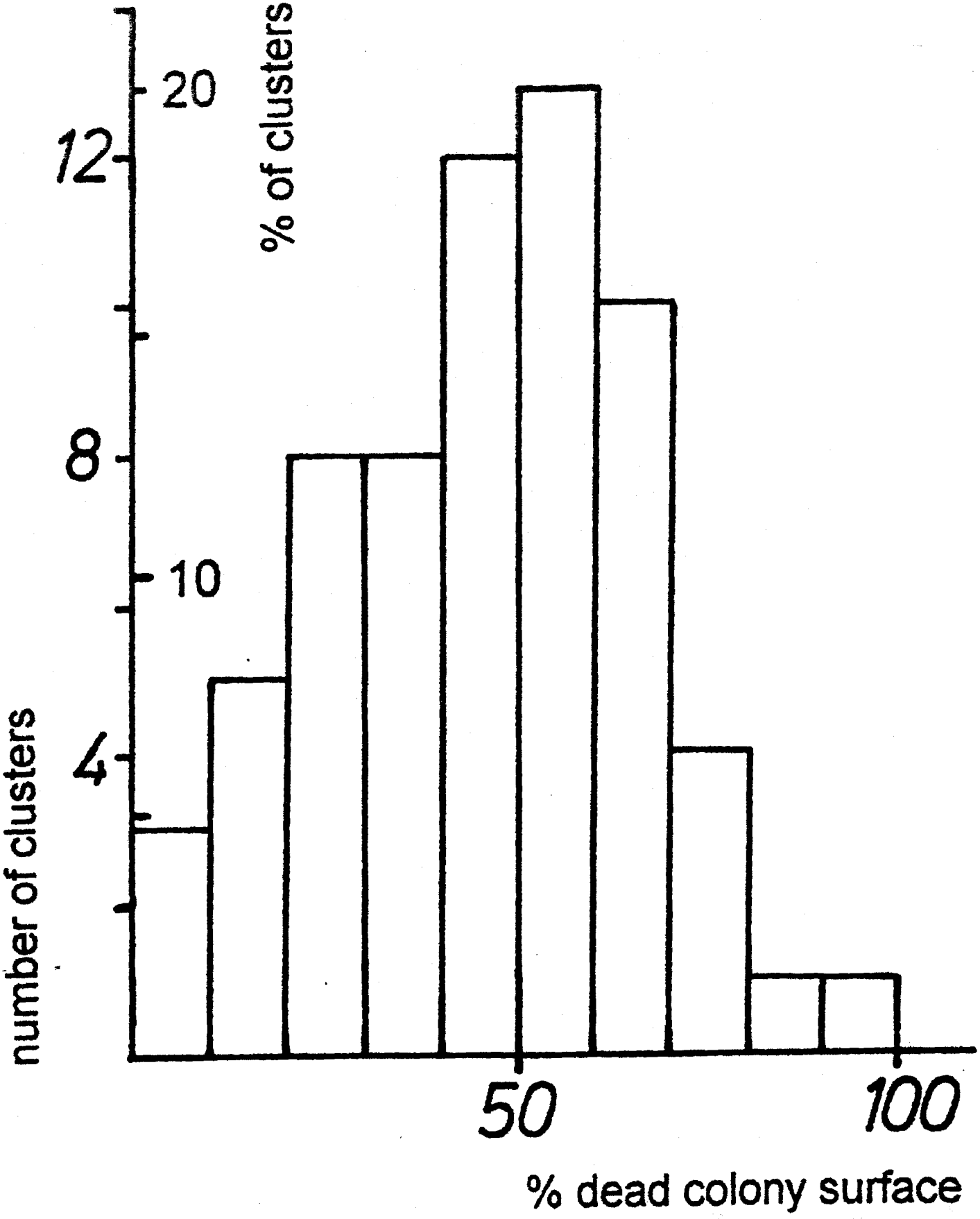
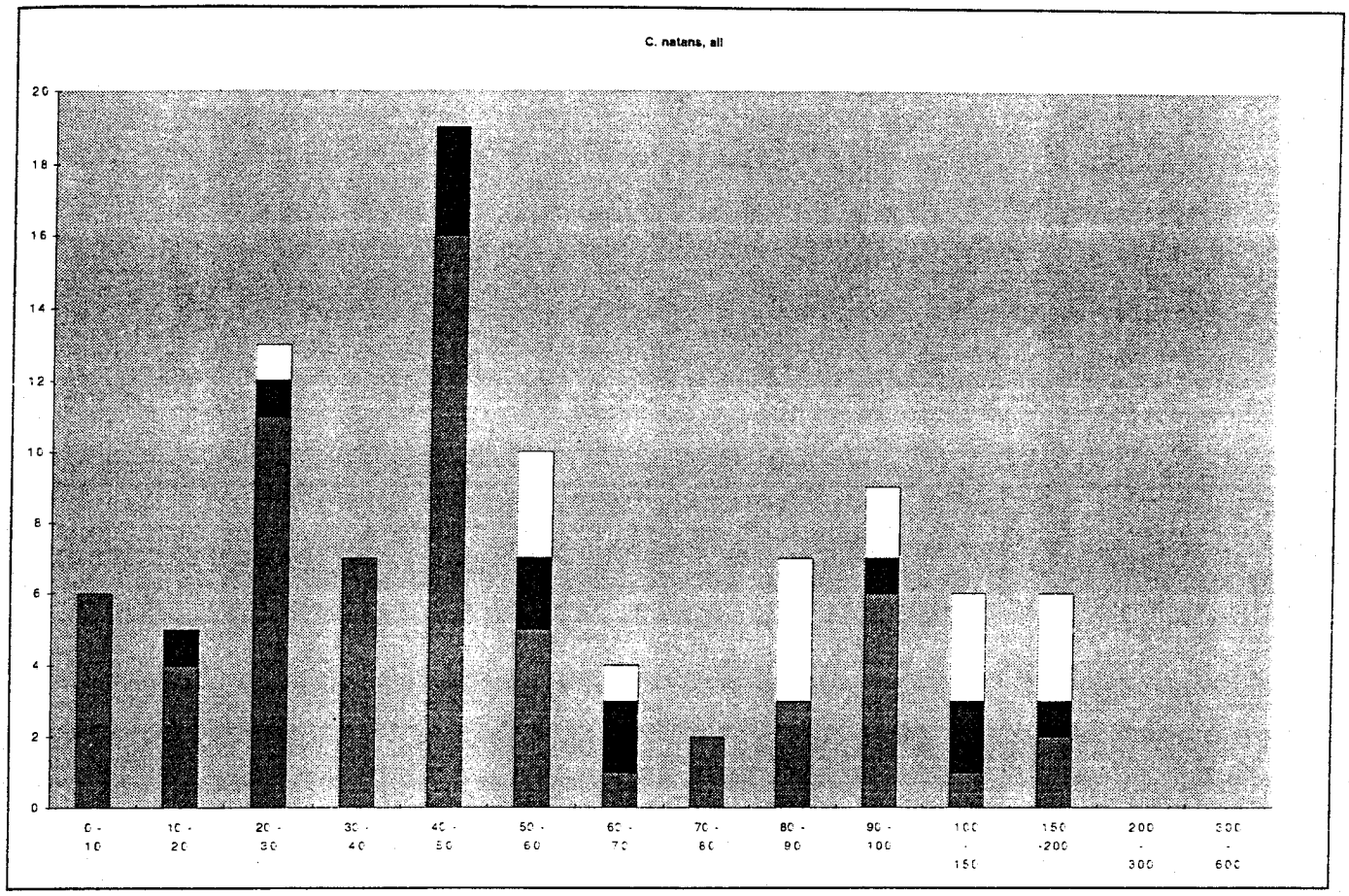

20
12
8
10
4
% of clusters
number of clusters
50
100
% dead colony surface

Fig 8

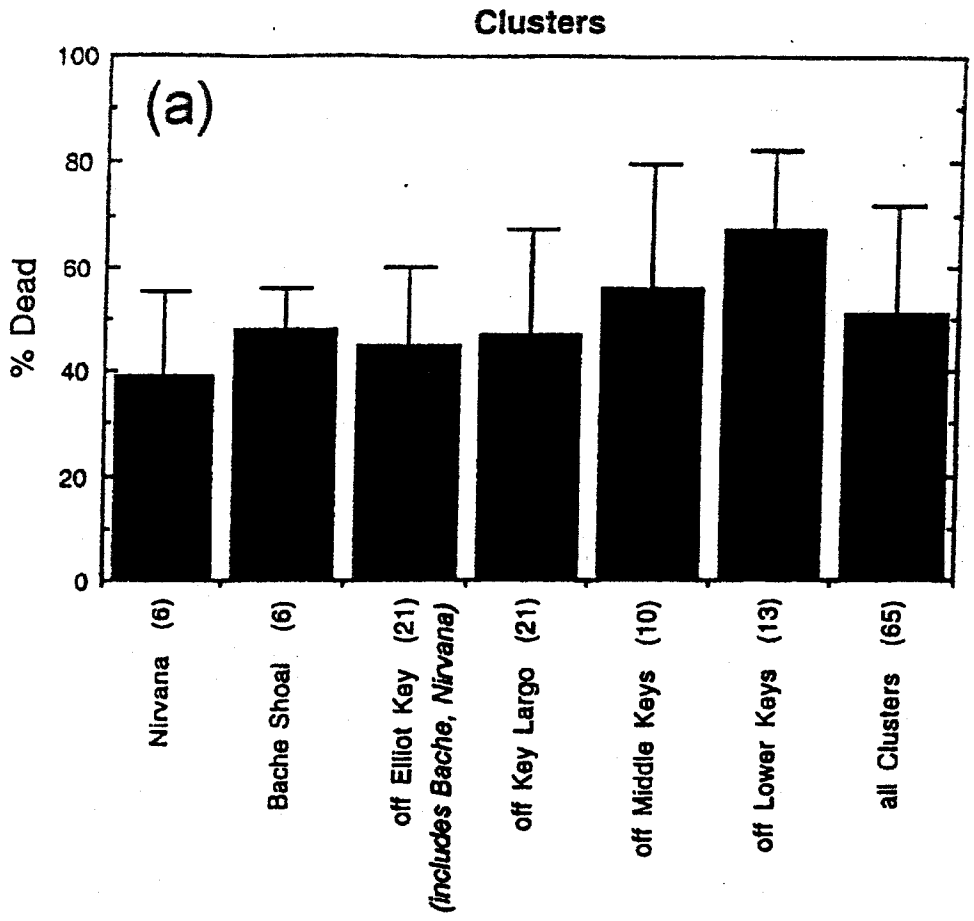
Figure 9

RAPID ASSESSMENT OF REEF CORAL CONDITIOI
University of Miami, RSMAS-MGG
Robert N. Ginsburg, July 1995



SIZE DISTRIBUTION OF CORALS

grey = less than 1/3 dead
black = 1/3 - 2/3 dead
white = more than 2/3 dead


Clusters
(a)
% Dead
100
80
60
40
20
0
Nirvana (6)
Bache Shoal (6)
off Elliot Key (21)
(includes Bache, Nirvana)
off Key Largo (21)
off Middle Keys (10)
off Lower Keys (13)
all Clusters (65)

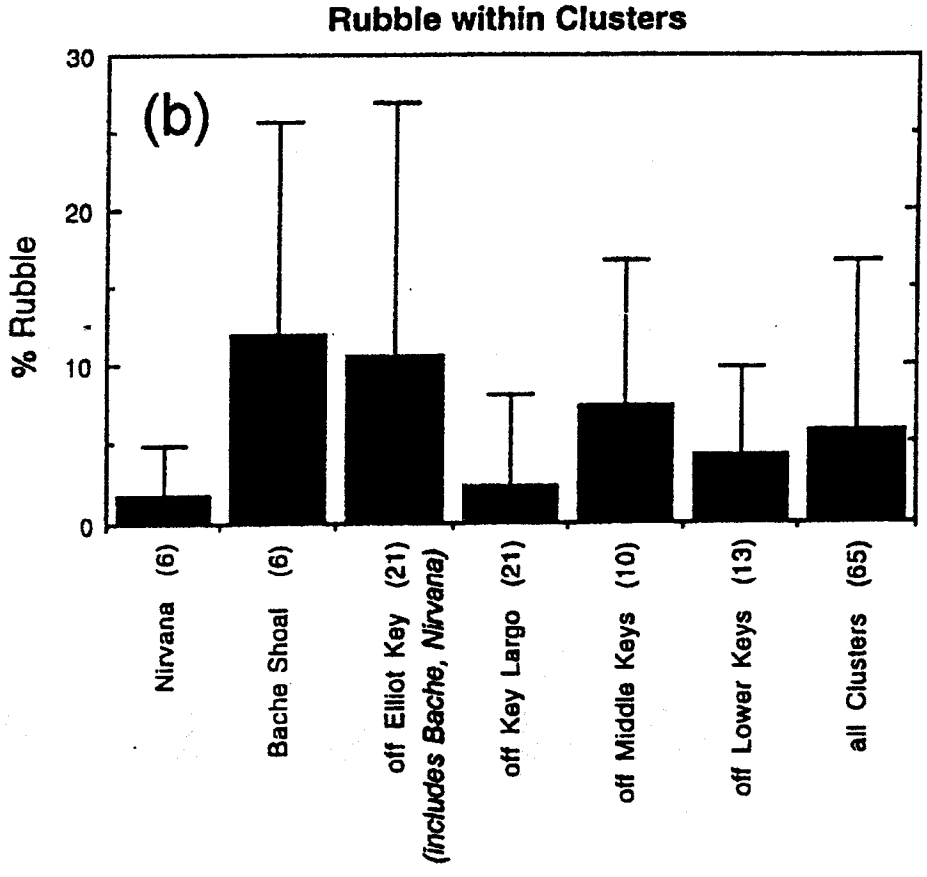

Rubble within Clusters
(b)
% Rubble
30
20
10
0
Nirvana (6)
Bache Shoal (6)
off Elliot Key (21)
(includes Bache, Nirvana)
off Key Largo (21)
off Middle Keys (10)
off Lower Keys (13)
all Clusters (65)

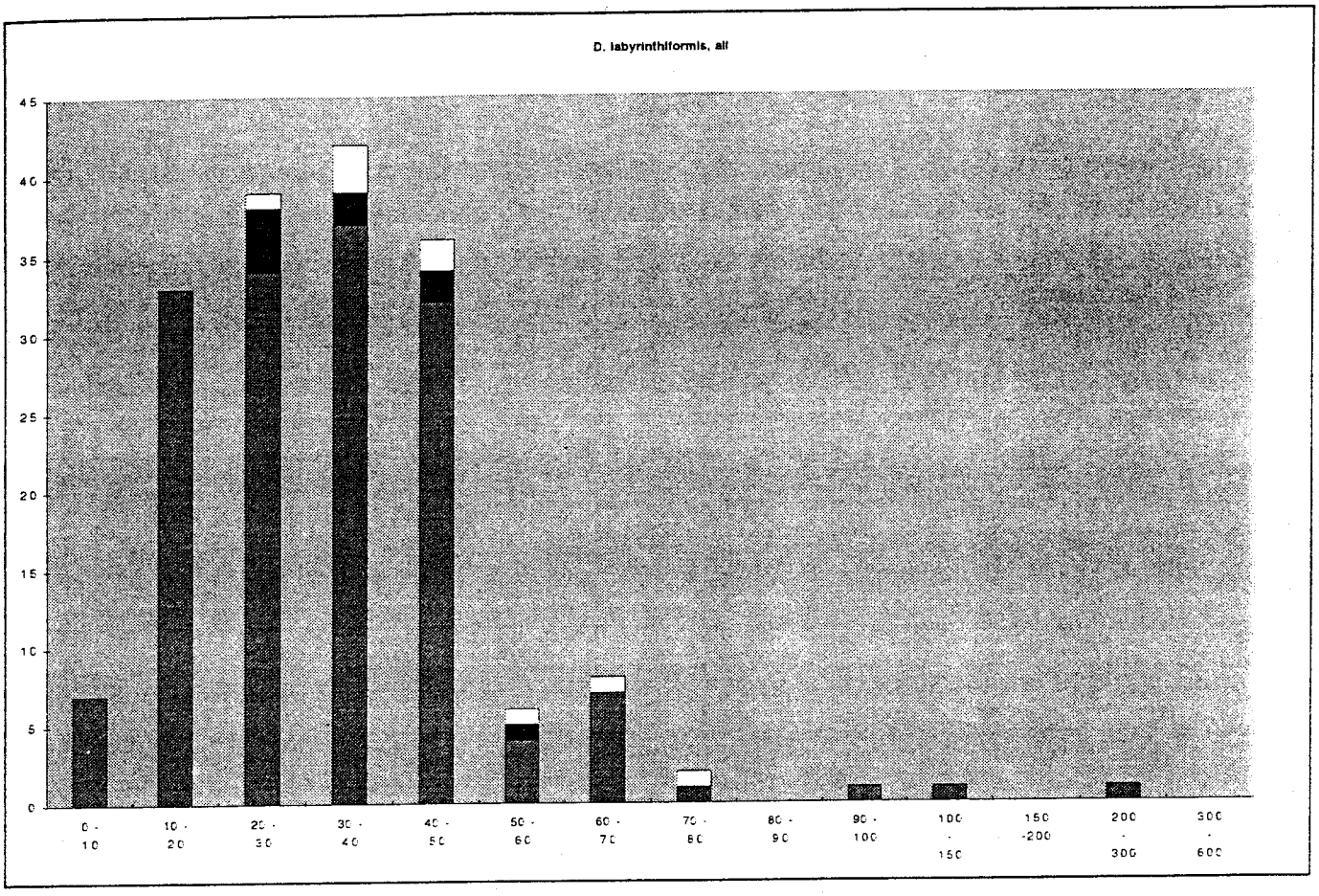
Fig 9

Figure 8

RAPID ASSESSMENT OF REEF CORAL CONDITIO

University of Miami, RSMAS-MGG

Robert N. Ginsburg, July 1995



SIZE DISTRIBUTION OF CORALS

grey = less than 1/3 dead
black = 1/3 - 2/3 dead
white = more than 2/3 dead

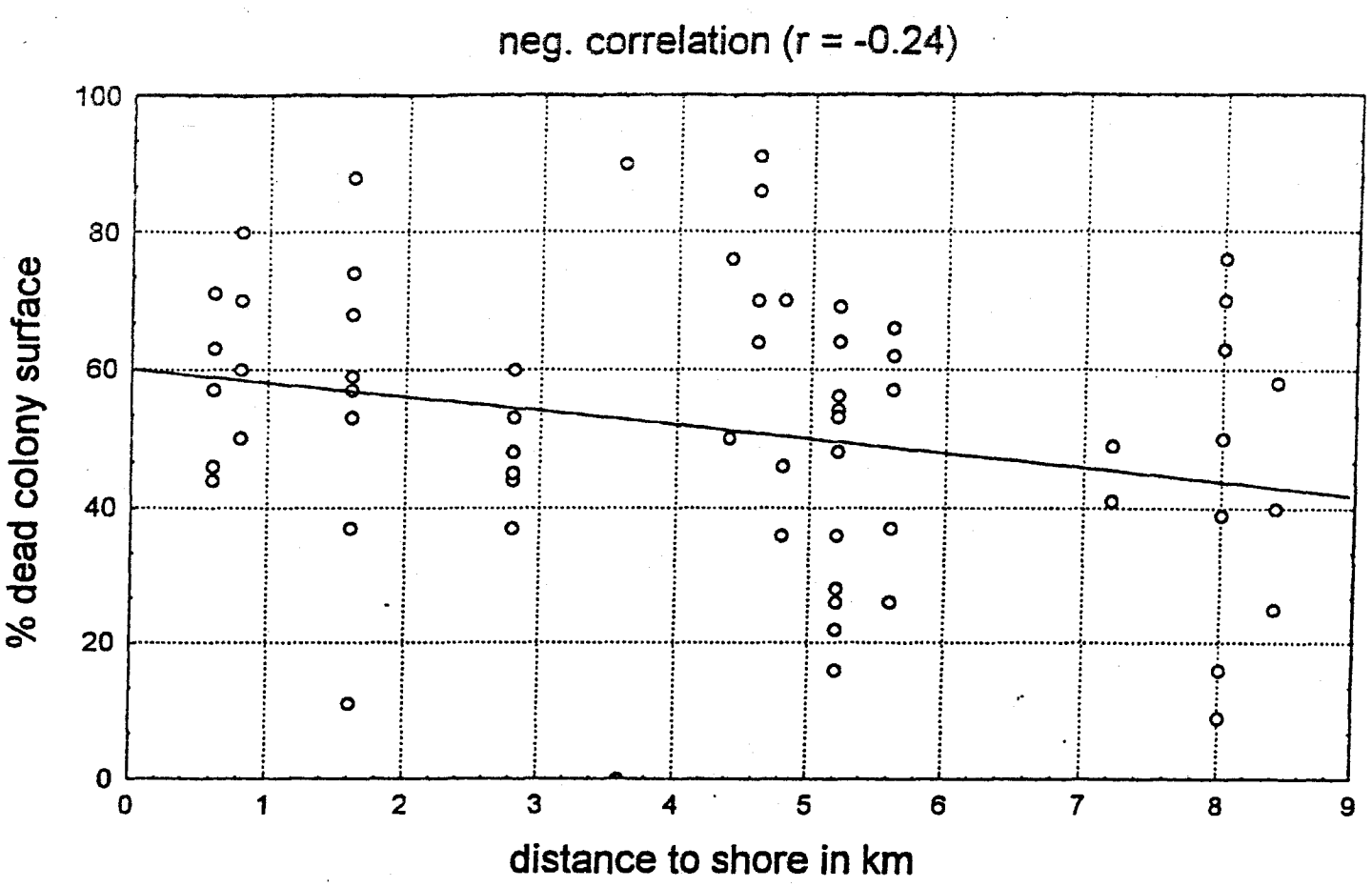
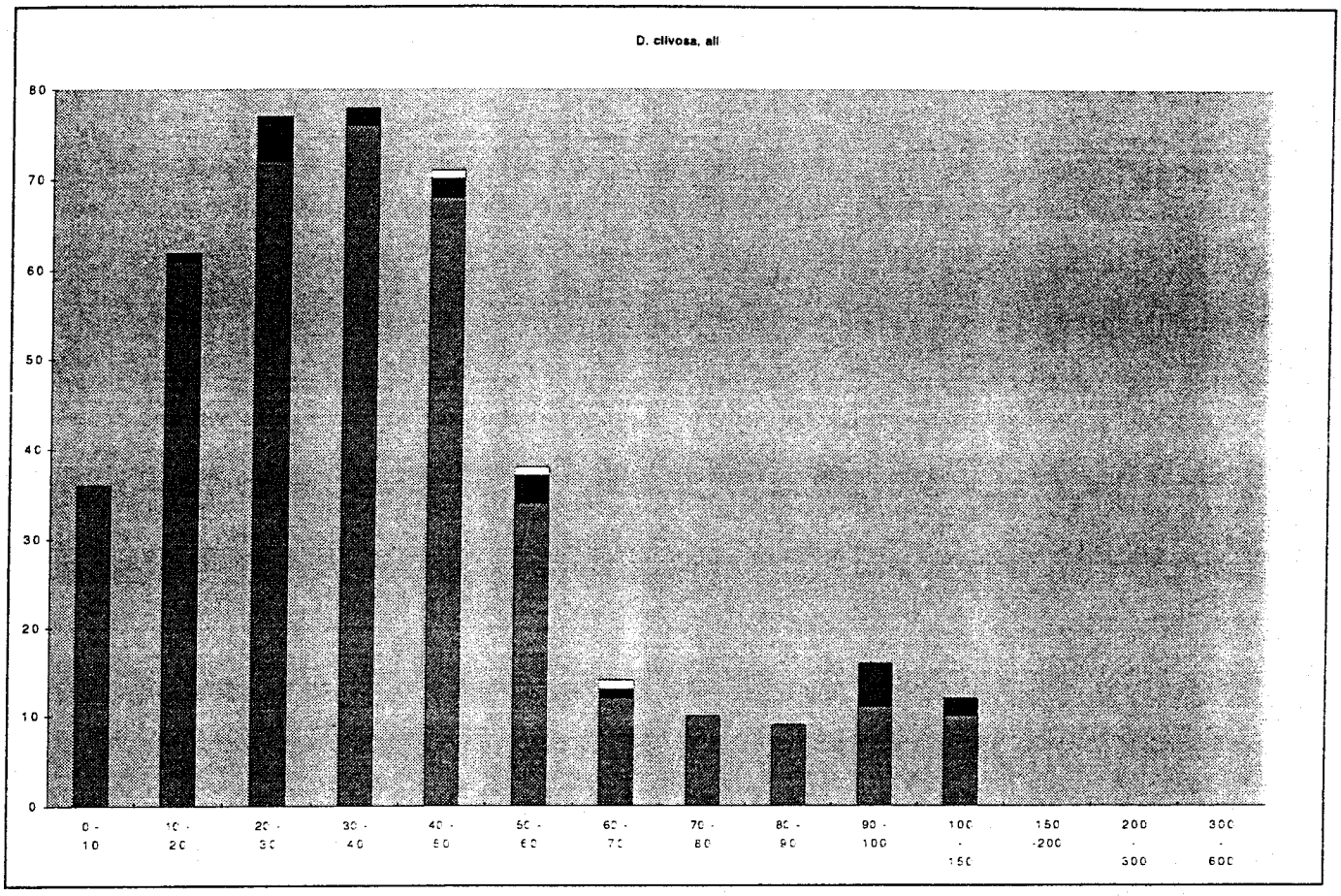

neg. correlation (r = -0.24)
% dead colony surface
distance to shore in km
0
20
40
60
80
100
0
1
2
3
4
5
6
7
8
9

Fig 10

Figure 7

RAPID ASSESSMENT OF REEF CORAL CONDITIOI
University of Miami, RSMAS-MGG
Robert N. Ginsburg, July 1995



SIZE DISTRIBUTION OF CORALS

grey = less than 1/3 dead
black = 1/3 - 2/3 dead
white = more than 2/3 dead

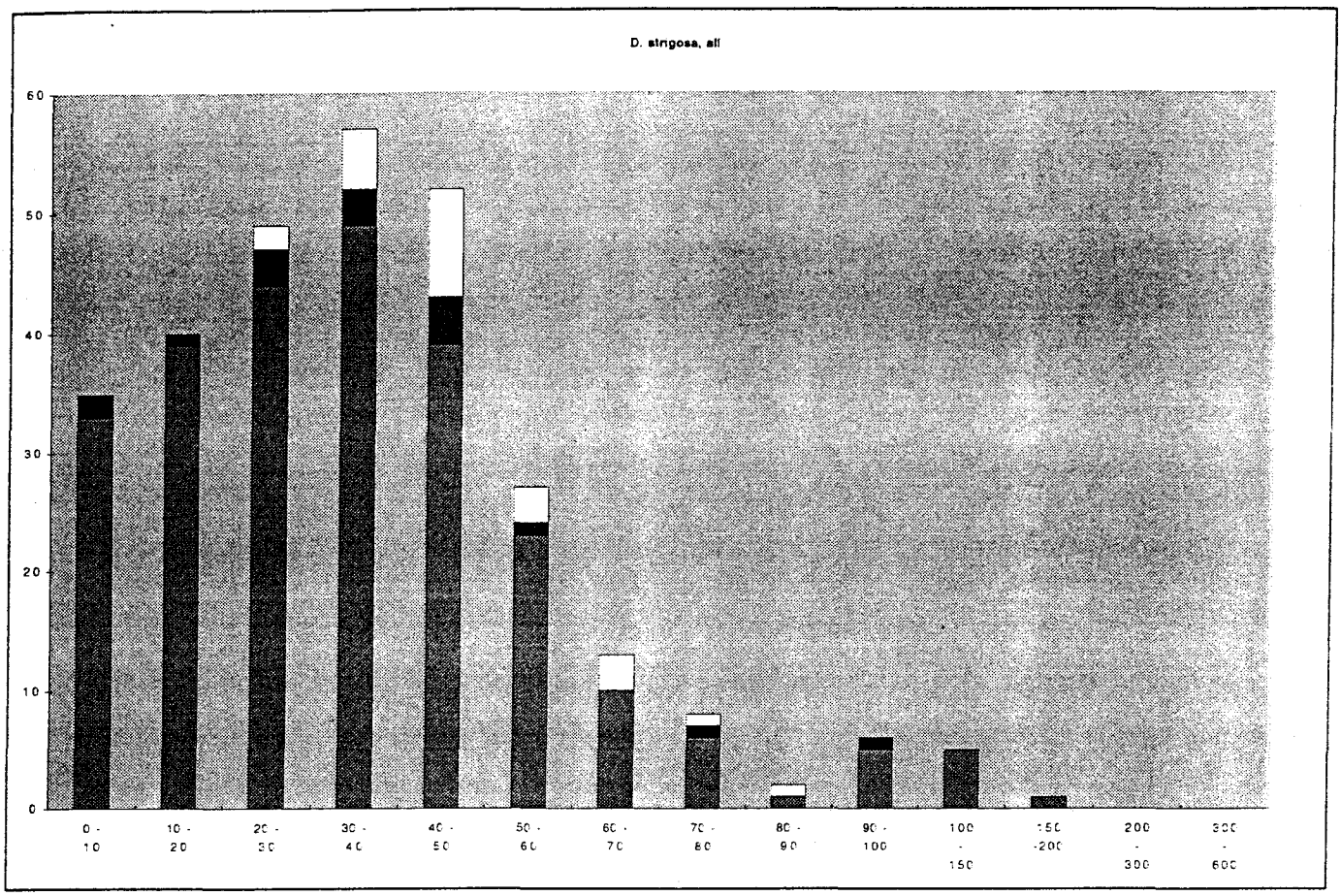
DUPLICATE:
Original in
Museum Archives

Figure 6

RAPID ASSESSMENT OF REEF CORAL CONDITION

University of Miami, RSMAS-MGG

Robert N. Ginsburg, July 1995



SIZE DISTRIBUTION OF CORALS

grey = less than 1/3 dead
black = 1/3 - 2/3 dead
white = more than 2/3 dead

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UNIVERSITY OF
Miami

Mr. Richard Curry,
Science Coordinator
Biscayne National Park
P.O.Box 1369
Homestead, FL. 33030

August 14, 1995

Dear Richard,

We had a most successful cruise last month and I thought you would be interested to know what we have been doing on patch reefs, especially on those within Biscayne National Park. Attached is a Progress Report that will I think bring you up to date on the questions being addressed, our methods and our results.

I am also including the results of a census of patch reefs in Biscayne National Park that should be of interest.

As indicated at the end of the Progress Report, I want to continue this kind of assessment and also see how we can use aerial photographs for detailed mapping of reef-building communities. In that regard, we need some help in getting out in the reef areas. Is it possible for the park to provide a boat for several days during August and the first part of September? Our schedule is reasonably flexible such that we can adapt to availability.

I will be away until August 16 and hope that you can give me an answer to this request.

Sincerely,

Robert N. Ginsburg

Rosenstiel School of Marine & Atmospheric Science
T. Wayland Vaughan Laboratory for Comparative Sedimentology
Mailing Address: University of Miami, RSMAS / MGG
4600 Rickenbacker Causeway
Miami, Florida 33149-1098
(305) 361-4684 or 361-4875

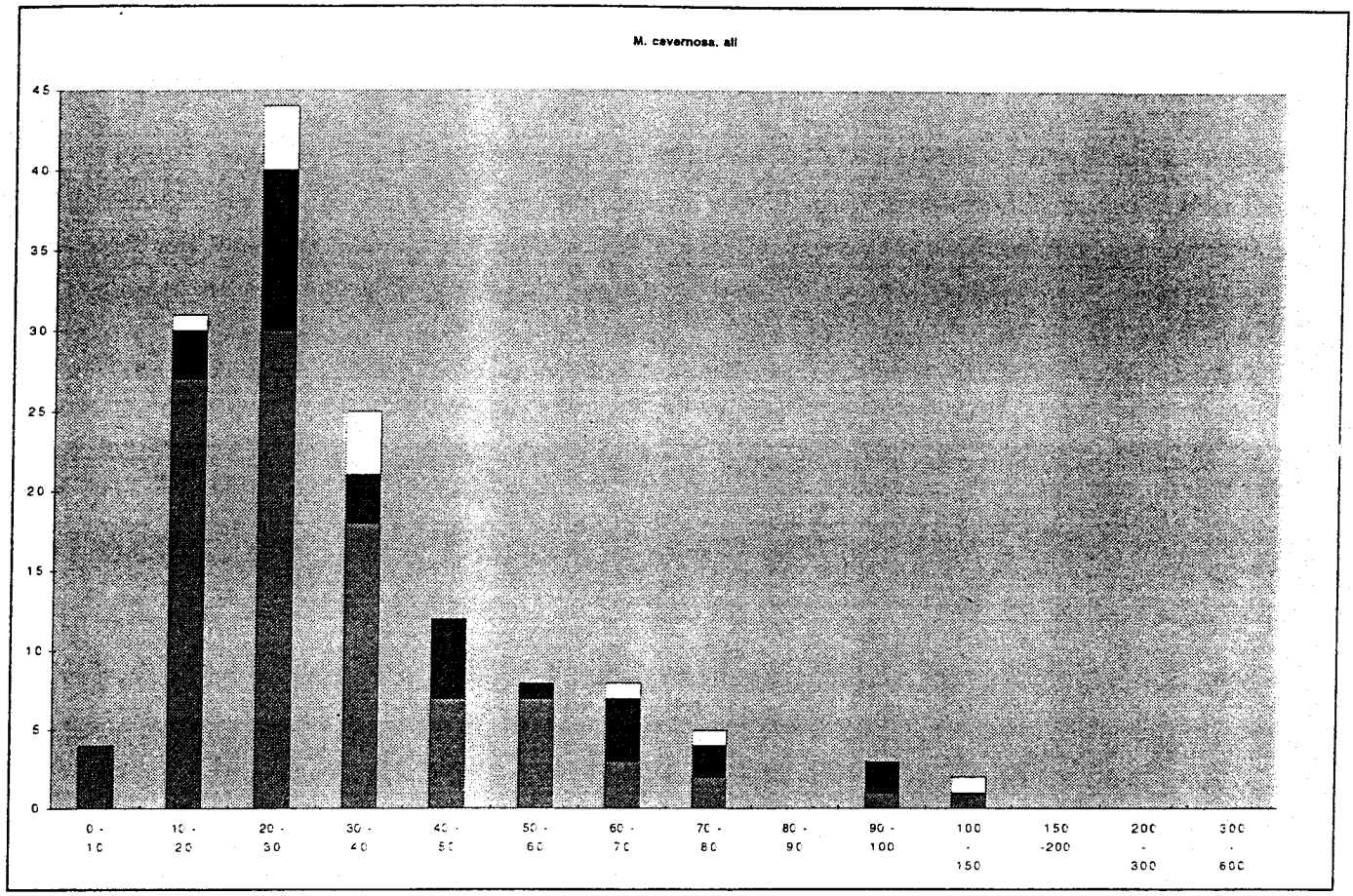
ax (305) 361-4632

Telex 7401484

Figure 5

RAPID ASSESSMENT OF REEF CORAL CONDITION

University of Miami, RSMAS-MGG
Robert N. Ginsburg, July 1995



SIZE DISTRIBUTION OF CORALS

grey = less than 1/3 dead
black = 1/3 - 2/3 dead
white = more than 2/3 dead

Progress report on
RAPID ASSESSMENT OF REEF CORAL CONDITION
Upper and Middle Florida Keys

Prepared by
Robert Ginsburg, Eberhard Gischler, William Kiene[1]
Rosenstiel School of Marine and Atmospheric Science
University of Miami

Purpose of the assessment

Concern about the condition of Florida's coral reefs is widespread given their extensive use by divers, tourists, and fisher persons. Local declines in coral cover are well-documented, but the areal extent of these declines is not known. To fill this gap, a study of the current condition of the major massive, reef-building corals on patch reefs has been initiated at the Rosenstiel School of Marine and Atmospheric Science with support from a private foundation. Patch reefs are by far the most abundant reef type off the Florida Keys. In Biscayne National Park alone, there are some 2500 patch reefs as explained in the attached census.

This progress report was prepared by Robert Ginsburg, Eberhard Gischler, and William Kiene on the basis of data collected during a field trip to the Upper Keys from 18-28 July, 1995. They were assisted by Alan Buck, David Lehman, and Steven Lutz.

Census of abundant massive, reef-building corals

The current condition of nine abundant massive reef corals (*Montastrea annularis, M. faveolata, M. franksi, M. cavernosa, Diploria strigosa, D. clivosa, D. labyrinthiformis, Colpophyllia natans, Siderastrea siderea*) was assessed by divers at nine localities in the Upper Keys from Bache Shoals to Cheeca Rocks (Fig. 1). 2450 corals were assigned to three "health-classes", namely 'less than 1/3 dead', '1/3 - 2/3 dead', '> 2/3 dead'. Assuming a general correlation between colony size and age, the diameter of each coral was measured to assess the age distribution of coral species, to decipher possible patterns of recent recruitment. and to see whether or not there is a correlation between age and general condition.

The preliminary results show that the corals assessed are in good condition. More than 75 % fall into the class '< 1/3 dead' (Tab. 1). *In Montastrea, Colpophyllia, and Siderastrea* 50 - 70 % fall in this class. The species of the brain coral *Diploria* are in even better condition with around 90 % of the colonies in the '<1/3 dead'-class (Tab. 1). The condition of the corals at the individual localities is more or less similar to the overall percentages (Tab. 2-10). There seems to be no geographical gradient in the health of the corals assessed in the Upper Keys.

The size distributions of the corals is similar among the nine species assessed (Fig. 2-10). Most of the corals are 20 - 50 cm in diameter. It appears that there is recent

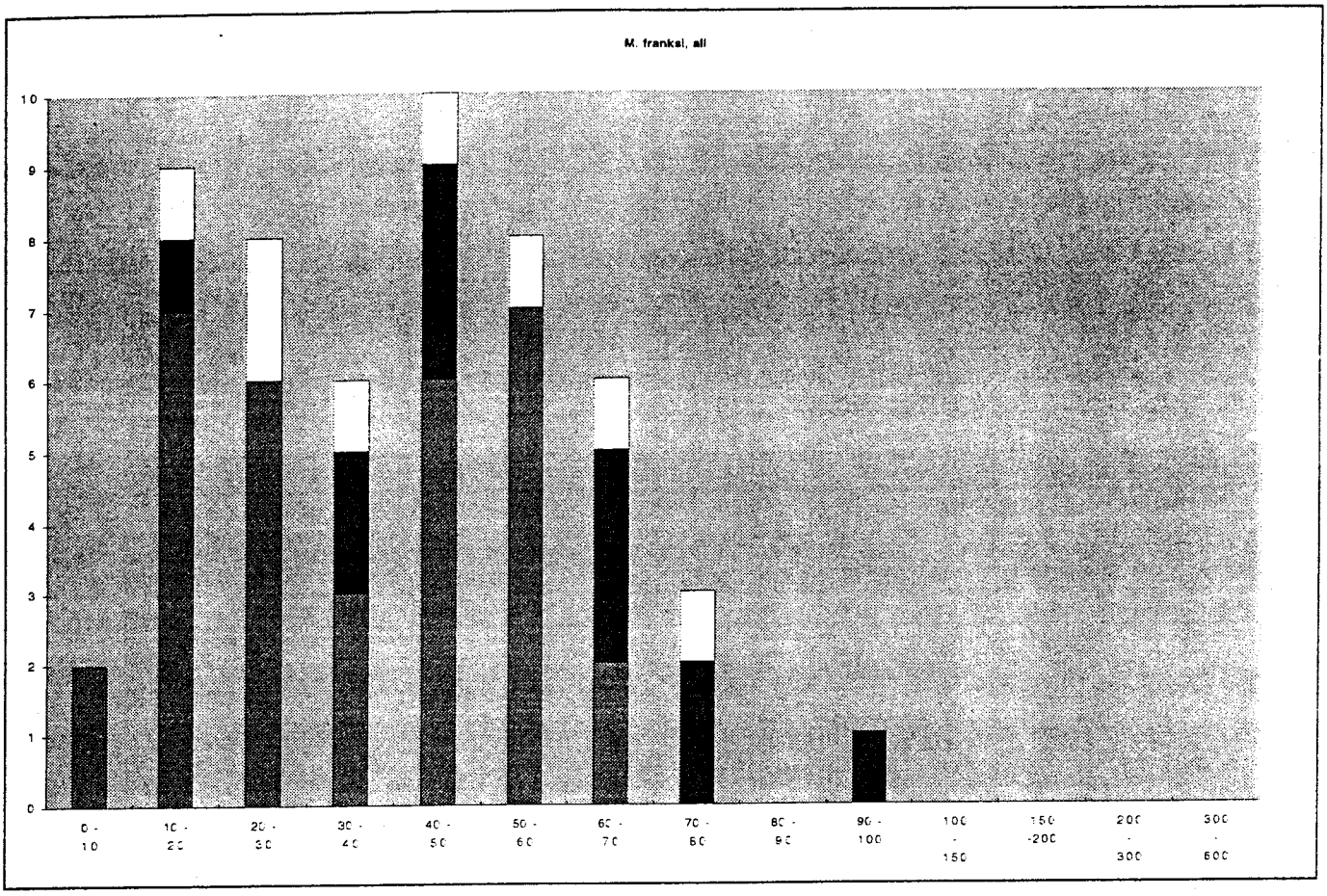
[1] University of Frankfurt, Germany

Figure 4

RAPID ASSESSMENT OF REEF CORAL CONDITION

University of Miami, RSMAS-MGG

Robert N. Ginsburg, July 1995



SIZE DISTRIBUTION OF CORALS

grey = less than 1/3 dead
black = 1/3 - 2/3 dead
white = more than 2/3 dead

recruitment as there are considerable numbers of corals in the smallest size class of all corals assessed. It is noreworthy that the numbers of colonies decrease in the larger size classes. The reason for that is not understood. In colonial organisms such as corals that are not senescent an increase towards the larger size classes should be expected.

There exists no correlation between colony size and general condition (Tab. 1).

Condition of clusters of large colonies of *Montastrea*

In the Floridian patch reefs, species of the massive coral *Montastrea* occur as isolated colonies up to a few meters in diameter and in clusters of huge colonies of 1 - 4 meters in diameter. These clusters that cover as much as 100 m^2 have up to 5 m of relief over the surrounding sea floor. Such large clusters are a major element of reef architecture as they produce the highest relief and provide varied habitats for other invertebrates and fish. For these reasons *Montastrea* may be described as a "keystone species" in the patch reefs. Two examples of the distribution of *Montastrea* clusters in patch reefs are shown on the maps of Figure 11 and Figure 12. The *Montastrea* clusters in the study area were assessed separately by point-counting dead versus alive tissue (Fig. 1).

As in the coral census there was no general geographical gradient in the general condition of the *Montastrea* clusters detected. Some of the clusters that are located closer to the shelf margin (Alan's Deep, Key Largo Dry Rocks, White Bank Dry Rocks) are in better condition than those closer to the shores of the keys. Clusters in the southernmost part of the study area (The Rocks, Cheeca Rocks) appear to be in worse condition than the other clusters. The condition seen there might still reflect the influence of the 1969 and 1977 cold winters that killed high numbers of corals in the Middle Keys.

Future plans

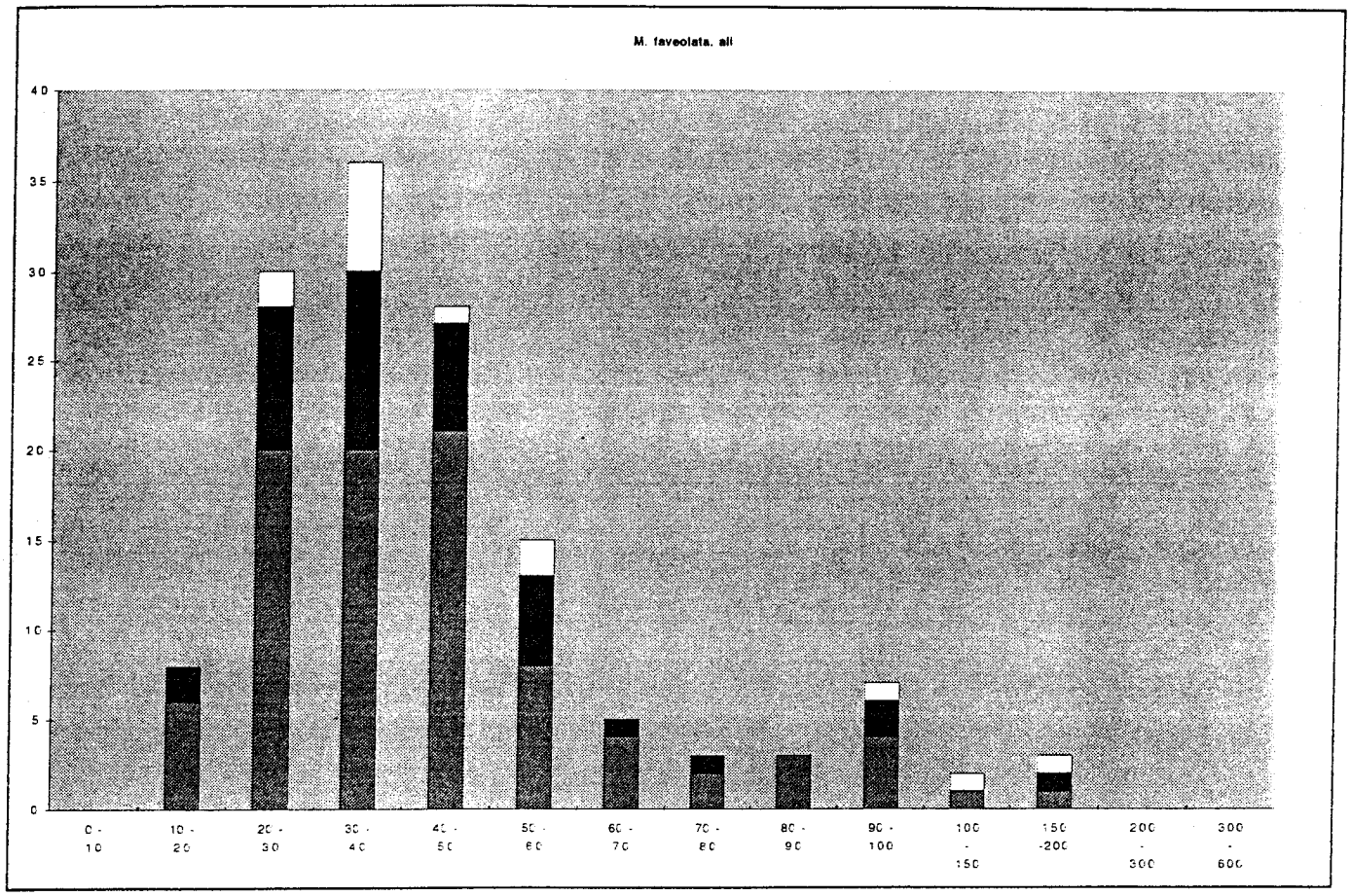
As can be seen on the map (Fig. 1) there is a larger gap in coverage within Biscayne National Park off Broad Key and the northernmost part of Key Largo. It is planned to assess coral condition in that area both by a census and by point-counting clusters of *Montastrea*. Furthermore, the patch reef 'Nirvana' west of Long Reef will be mapped in detail to evaluate the use of aerial photography in mapping of coral reefs.

Figure 3

RAPID ASSESSMENT OF REEF CORAL CONDITION

University of Miami, RSMAS-MGG

Robert N. Ginsburg, July 1995



SIZE DISTRIBUTION OF CORALS

grey = less than 1/3 dead
black = 1/3 - 2/3 dead
white = more than 2/3 dead

Biscayne National Park Patch Reef Census

Robert N. Ginsburg, David A. Lehman
University of Miami - Rosenstiel School of Marine and Atmospheric Science
4600 Rickenbacker Causeway Miami, Fl 33149

Biscayne National Park has the densest concentration of patch reefs in the Florida Reef Tract, estimated at over 3000 (Shinn et al., 1989). However, no accurate census of these reefs is known. To address this lack of data and fill the gap, we counted and classified almost all of the patch reefs of BNP according to size and shape. Transparencies of aerial photographs at a scale of 1 : 48,000 (National Geodetic Survey, NOAA, 1/92; # 2918, 2867, 2865, 2862) were overlain by a grid composed of 4 cm^2 cells. Patch reefs whose borders were readily definable (clearly separated form other patches) were then counted within these cells, measured (approx. 1 mm = 50 m) and classified according to shape. Areas of small, dense coral heads were not included, as distinct patch reefs were to variable and difficult to define (i.e., patch reef area directly West of Long Reef).

Total # patch reefs counted: 2411
Four areas counted in 2 cm x 2 cm cells:
1) N. end of Ragged Keys to Triumph Reef (app. 25° 33.7' N to 25°30.5' N)
2)Triumph Reef to N. end of Long Reef (to app. 25°26.0' N)
3)N. end of Long Reef to N. end of Pacific Reef (to app. 25°22.7' N)
4)Pacific Reef to Ball Buoy (to app. 25° 19.9' N)

Size Distribution

	0 - 25 m	25 - 50 m	50 - 100 m	100 - 150 m	Total
1)	84 (49%)	67 (39%)	16 (9%)	5 (3%)	172
2)	462 (59%)	236 (30%)	62 (8%)	27 (3%)	787
3)	596 (65%)	242 (26%)	61 (7%)	18 (2%)	917
4)	265 (50%)	198 (37%)	50 (9%)	22 (4%)	535
Tot:	1407 (58%)	743 (31%)	89 (8%)	72 (3%)	2411

Shape Classification

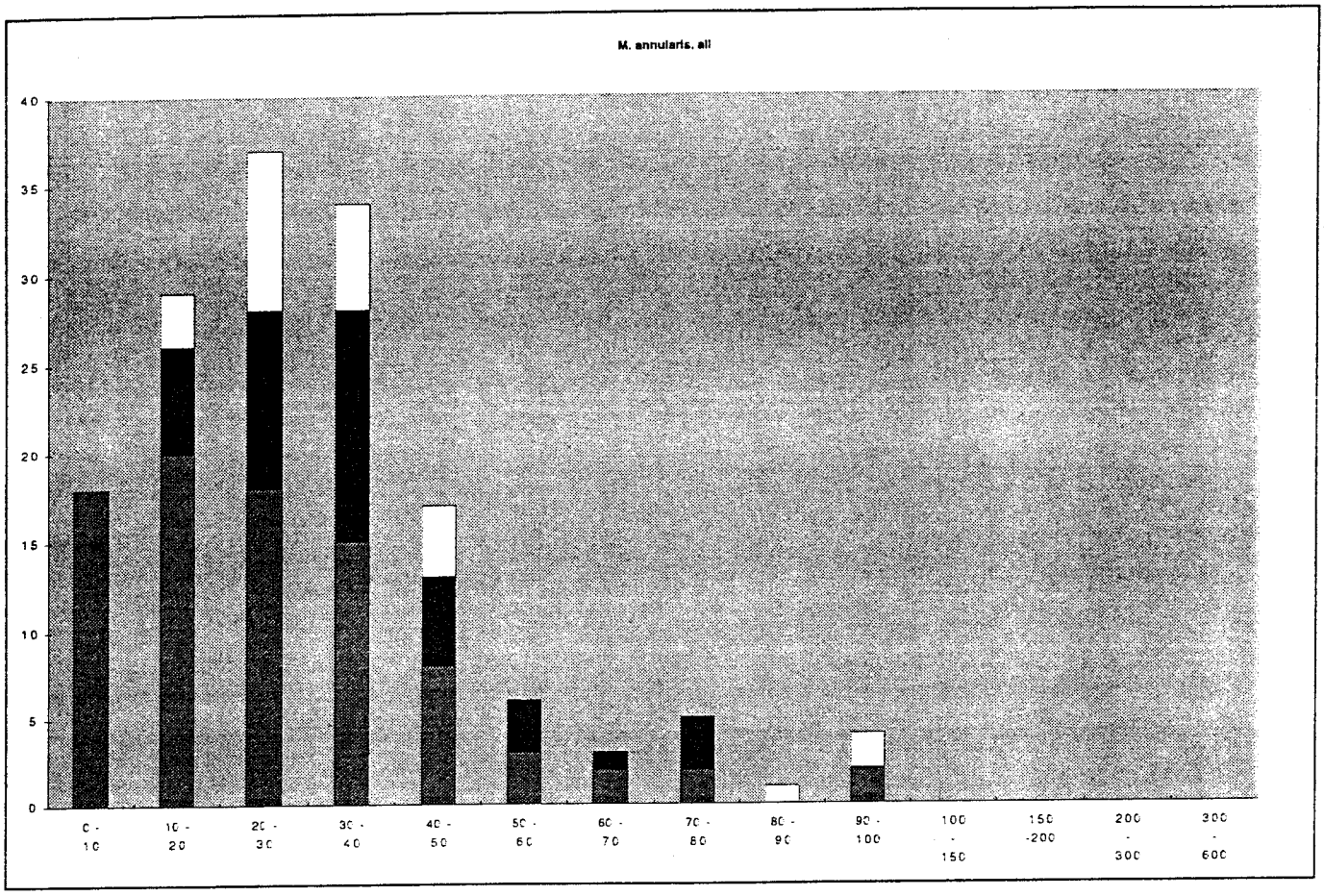
	circular	well-rounded non-circular	elongate	irregular	Total
1)	51 (30%)	70 (41%)	0 (0%)	51 (30%)	172
2)	173 (22%)	473 (60%)	9 (1%)	132 (17%)	787
3)	244 (27%)	476 (52%)	14 (2%)	183 (20%)	917
4)	128 (24%)	289 (54%)	8 (1%)	110 (21%)	535
Tot:	596 (25%)	1308 (54%)	31 (1%)	476 (20%)	2411

Figure 2

RAPID ASSESSMENT OF REEF CORAL CONDITION

University of Miami, RSMAS-MGG

Robert N. Ginsburg, July 1995



SIZE DISTRIBUTION OF CORALS

grey = less than 1/3 dead
black = 1/3 - 2/3 dead
white = more than 2/3 dead

Table 1: Census data of all corals assessed between Bache Shoals and Triangles. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, Univ. of Miami, Robert N. Ginsburg, July 1995.

Montastrea annularis		
< 1/3 dead	88	57 %
1/3 - 2/3 dead	41	27 %
>2/3 dead	25	16 %
total	154	
Montastrea faveolata		
< 1/3 dead	90	64 %
1/3 - 2/3 dead	36	26 %
> 2/3 dead	14	10 %
total	140	
Montastrea franksi		
< 1/3 dead	33	62 %
1/3 - 2/3 dead	12	23 %
> 2/3 dead	8	15 %
total	53	
Montastrea cavernosa		
< 1/3 dead	100	70 %
1/3 - 2/3 dead	30	21 %
> 2/3 dead	12	8 %
total	142	
Diploria strigosa		
< 1/3 dead	255	86 %
1/3 - 2/3 dead	16	5 %
> 2/3 dead	24	8 %
total	295	
Diploria clivosa		
< 1/3 dead	399	94 %
1/3 - 2/3 dead	21	5 %
> 2/3 dead	3	1 %
total	423	
Diploria labyrinthiformis		
< 1/3 dead	158	90 %
1/3 - 2/3 dead	9	5 %
> 2/3 dead	9	5 %
total	176	
Colpophyllia natans		
< 1/3 dead	64	68 %
1/3 - 2/3 dead	13	14 %
> 2/3 dead	17	18 %
total	94	
Siderastrea siderea		
< 1/3 dead	679	70 %
1/3 - 2/3 dead	193	20 %
> 2/3 dead	101	10 %
total	973	
all corals		
< 1/3 dead	**1866**	**76 %**
1/3 - 2/3 dead	**371**	**15 %**
> 2/3 dead	**213**	**9 %**
total	**2450**	

Figure 1

RAPID ASSESSMENT OF REEF CORAL CONDITION
University of Miami, RSMAS-MGG
Robert N. Ginsburg, July 1995

LOCALITIES OF THE STUDY

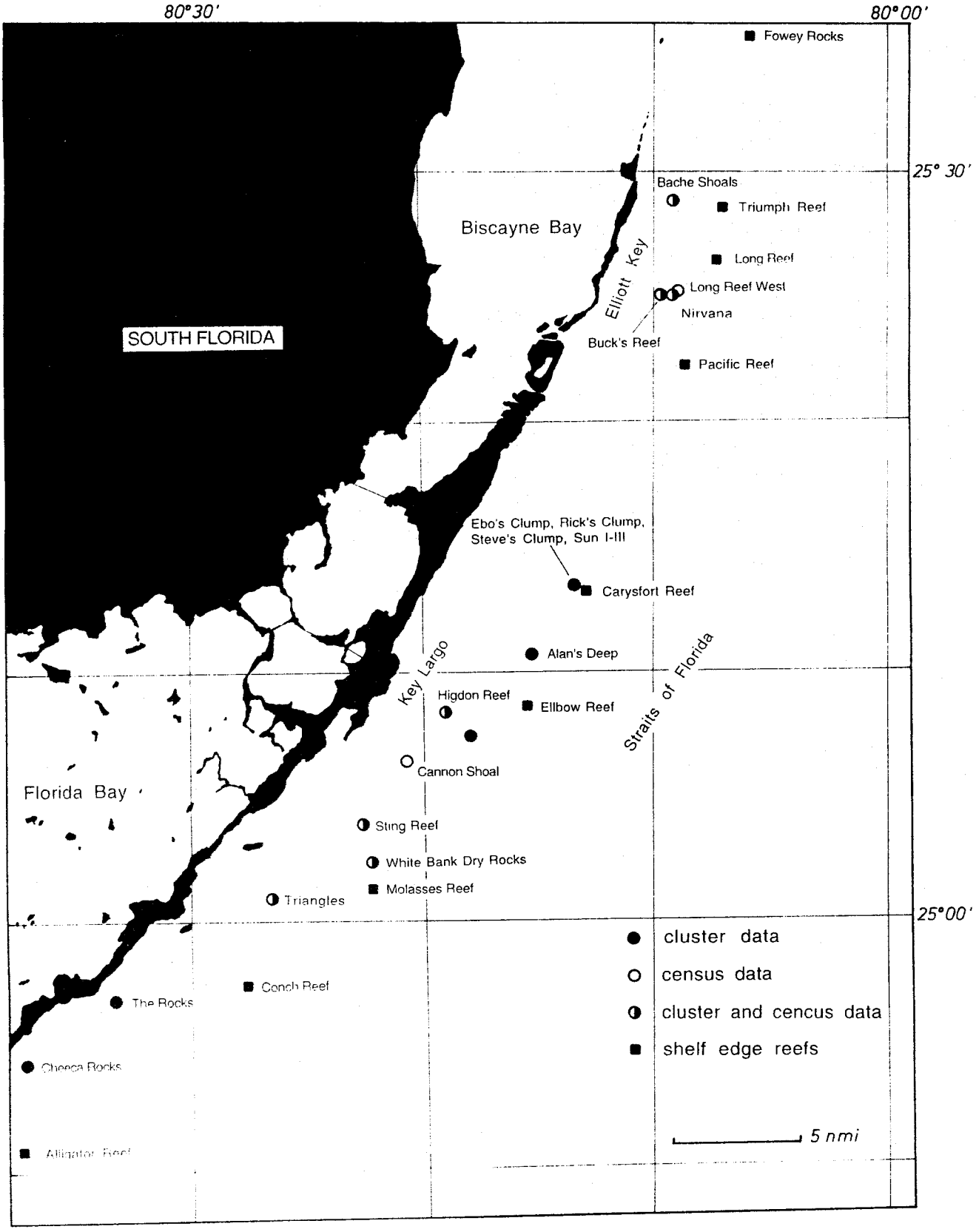


Table 2: Census at Bache Shoals. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, Univ. of Miami, Robert N. Ginsburg, July 1995.

Montastrea annularis		
< 1/3 dead	11	65 %
1/3 - 2/3 dead	3	18 %
>2/3 dead	3	18 %
total	17	
Montastrea faveolata		
< 1/3 dead	17	50 %
1/3 - 2/3 dead	11	32 %
> 2/3 dead	6	18 %
total	34	
Montastrea franksi		
< 1/3 dead	21	62 %
1/3 - 2/3 dead	10	29 %
> 2/3 dead	3	9 %
total	34	
Montastrea cavernosa		
< 1/3 dead	43	66 %
1/3 - 2/3 dead	18	28 %
> 2/3 dead	4	6 %
total	65	
Diploria strigosa		
< 1/3 dead	57	89 %
1/3 - 2/3 dead	3	5 %
> 2/3 dead	4	6 %
total	64	
Diploria clivosa		
< 1/3 dead	90	96 %
1/3 - 2/3 dead	4	4 %
> 2/3 dead	0	0 %
total	94	
Diploria labyrinthiformis		
< 1/3 dead	7	88 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	1	12 %
total	8	
Colpophyllia natans		
< 1/3 dead	44	79 %
1/3 - 2/3 dead	5	9 %
> 2/3 dead	7	13 %
total	56	
Siderastrea siderea		
< 1/3 dead	162	80 %
1/3 - 2/3 dead	23	11 %
> 2/3 dead	18	9 %
total	203	
all corals		
< 1/3 dead	**452**	**79 %**
1/3 - 2/3 dead	**77**	**13 %**
> 2/3 dead	**46**	**8 %**
total	**575**	

Table 11: Montastrea-cluster data. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, University of Miami, Robert N. Ginsburg, July 1995. Numbers are in %.

	alive	dead
Bache Shoals A	63	37
Bache Shoals B	40	60
Bache Shoals C	47	53
Bache Shoals D	50	50
Bache Shoals E	55	45
Bache Shoals F	52	48
Buck's Reef	44	56
Nirvana 1	36	64
Nirvana 2.1	72	28
Nirvana 2.2	67	33
Ebo's Clump 1	37	63
Ebo's Clump 2	30	70
Rick's Clump	61	39
Steve's Clump	24	76
Sun 1	50	50
Sun 2	84	16
Alan's Deep 1	91	9
Alan's Deep 2	85	15
Higdon Reef 1	50	50
Higdon Reef 2	24	76
Key Largo Dry Rocks 1	59	41
Key Largo Dry Rocks 2	51	49
Sting Reef 1	34	66
Sting Reef 2.1	43	57
Sting Reef 2.2	74	26
White Bank Dry Rocks 1.1	75	25
White Bank Dry Rocks 1.2	42	58
White Bank Dry Rocks 2	60	40
The Rocks 1	12	88
The Rocks 2	43	57
The Rocks 3	89	11
The Rocks 4	32	68
Cheeca Rocks 1	47	53
Cheeca Rocks 2	41	59
Cheeca Rocks 3	26	74
Cheeca Rocks 4	50	50
Triangles 1	38	62
Triangles 2	63	37

Table 3: Census at Long Reef West. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, Univ. of Miami, Robert N. Ginsburg, July 1995.

Montastrea annularis		
< 1/3 dead	2	67 %
1/3 - 2/3 dead	0	0 %
>2/3 dead	1	3 %
total	3	
Montastrea faveolata		
< 1/3 dead	2	67 %
1/3 - 2/3 dead	1	33 %
> 2/3 dead	0	0 %
total	3	
Montastrea franksi		
< 1/3 dead	2	100 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	2	
Montastrea cavernosa		
< 1/3 dead	8	73 %
1/3 - 2/3 dead	1	9 %
> 2/3 dead	2	18 %
total	11	
Diploria strigosa		
< 1/3 dead	56	88 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	8	12 %
total	64	
Diploria clivosa		
< 1/3 dead	113	99 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	1	1 %
total	114	
Diploria labyrinthiformis		
< 1/3 dead	6	86 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	1	14 %
total	7	
Colpophyllia natans		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	0	
Siderastrea siderea		
< 1/3 dead	48	80 %
1/3 - 2/3 dead	3	5 %
> 2/3 dead	9	15 %
total	60	
all corals		
< 1/3 dead	**237**	**71 %**
1/3 - 2/3 dead	**5**	**1 %**
> 2/3 dead	**94**	**28 %**
total	**336**	

Table 10: Census at Triangles. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, Univ. of Miami, Robert N. Ginsburg, July 1995.

Montastrea annularis		
< 1/3 dead	18	44 %
1/3 - 2/3 dead	14	34 %
>2/3 dead	9	22 %
total	41	
Montastrea faveolata		
< 1/3 dead	28	72 %
1/3 - 2/3 dead	8	21 %
> 2/3 dead	3	8 %
total	39	
Montastrea franksi		
< 1/3 dead	2	100 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	2	
Montastrea cavernosa		
< 1/3 dead	11	79 %
1/3 - 2/3 dead	3	21 %
> 2/3 dead	0	0 %
total	14	
Diploria strigosa		
< 1/3 dead	40	98 %
1/3 - 2/3 dead	1	2 %
> 2/3 dead	0	0 %
total	41	
Diploria clivosa		
< 1/3 dead	40	98 %
1/3 - 2/3 dead	1	2 %
> 2/3 dead	0	0 %
total	41	
Diploria labyrinthiformis		
< 1/3 dead	35	94 %
1/3 - 2/3 dead	1	3 %
> 2/3 dead	1	3 %
total	37	
Colpophyllia natans		
< 1/3 dead	3	50 %
1/3 - 2/3 dead	2	33 %
> 2/3 dead	1	17 %
total	6	
Siderastrea siderea		
< 1/3 dead	127	68 %
1/3 - 2/3 dead	50	27 %
> 2/3 dead	11	6 %
total	188	
all corals		
< 1/3 dead	**304**	**74 %**
1/3 - 2/3 dead	**80**	**20 %**
> 2/3 dead	**25**	**6 %**
total	**409**	

Table 4: Census at Buck's Reef. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, Univ. of Miami, Robert N. Ginsburg, July 1995.

Montastrea annularis		
< 1/3 dead	15	71 %
1/3 - 2/3 dead	6	29 %
>2/3 dead	0	0 %
total	21	
Montastrea faveolata		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	0	
Montastrea franksi		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	0	
Montastrea cavernosa		
< 1/3 dead	2	50 %
1/3 - 2/3 dead	1	25 %
> 2/3 dead	1	25 %
total	4	
Diploria strigosa		
< 1/3 dead	3	43 %
1/3 - 2/3 dead	1	14 %
> 2/3 dead	3	43 %
total	7	
Diploria clivosa		
< 1/3 dead	2	100 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	2	
Diploria labyrinthiformis		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	1	100 %
total	1	
Colpophyllia natans		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	0	
Siderastrea siderea		
< 1/3 dead	16	94 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	1	6 %
total	17	
all corals		
< 1/3 dead	**38**	**73 %**
1/3 - 2/3 dead	**8**	**15 %**
> 2/3 dead	**6**	**12 %**
total	**52**	

Table 9: Census at White Bank Dry Rocks. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, Univ. of Miami, Robert N. Ginsburg, July 1995.

Montastrea annularis		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
>2/3 dead	0	0 %
total	0	
Montastrea faveolata		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	0	
Montastrea franksi		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	0	
Montastrea cavernosa		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	0	
Diploria strigosa		
< 1/3 dead	14	93 %
1/3 - 2/3 dead	1	7 %
> 2/3 dead	0	0 %
total	15	
Diploria clivosa		
< 1/3 dead	37	82 %
1/3 - 2/3 dead	8	18 %
> 2/3 dead	0	0 %
total	45	
Diploria labyrinthiformis		
< 1/3 dead	15	100 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	15	
Colpophyllia natans		
< 1/3 dead	9	53 %
1/3 - 2/3 dead	2	12 %
> 2/3 dead	6	35 %
total	17	
Siderastrea siderea		
< 1/3 dead	22	65 %
1/3 - 2/3 dead	8	24 %
> 2/3 dead	4	12 %
total	34	
all corals		
< 1/3 dead	**97**	**77 %**
1/3 - 2/3 dead	**19**	**15 %**
> 2/3 dead	**10**	**8 %**
total	**126**	

Table 5: Census at Nirvana. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, Univ. of Miami, Robert N. Ginsburg, July 1995.

Montastrea annularis		
< 1/3 dead	25	69 %
1/3 - 2/3 dead	9	25 %
>2/3 dead	2	6 %
total	36	
Montastrea faveolata		
< 1/3 dead	10	50 %
1/3 - 2/3 dead	8	40 %
> 2/3 dead	2	10 %
total	20	
Montastrea franksi		
< 1/3 dead	1	20 %
1/3 - 2/3 dead	1	20 %
> 2/3 dead	3	60 %
total	5	
Montastrea cavernosa		
< 1/3 dead	11	61 %
1/3 - 2/3 dead	2	11 %
> 2/3 dead	5	28 %
total	18	
Diploria strigosa		
< 1/3 dead	44	85 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	8	15 %
total	52	
Diploria clivosa		
< 1/3 dead	61	98 %
1/3 - 2/3 dead	1	2 %
> 2/3 dead	0	0 %
total	62	
Diploria labyrinthiformis		
< 1/3 dead	23	88 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	3	12 %
total	26	
Colpophyllia natans		
< 1/3 dead	1	100 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	1	
Siderastrea siderea		
< 1/3 dead	64	65 %
1/3 - 2/3 dead	16	16 %
> 2/3 dead	18	18 %
total	98	
all corals		
< 1/3 dead	**240**	**75 %**
1/3 - 2/3 dead	**37**	**12 %**
> 2/3 dead	**41**	**13 %**
total	**318**	

Table 8: Census at Sting Reef. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, Univ. of Miami, Robert N. Ginsburg, July 1995.

Montastrea annularis		
< 1/3 dead	2	16 %
1/3 - 2/3 dead	5	42 %
>2/3 dead	5	42 %
total	12	
Montastrea faveolata		
< 1/3 dead	10	56 %
1/3 - 2/3 dead	6	33 %
> 2/3 dead	2	11 %
total	18	
Montastrea franksi		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	1	100 %
> 2/3 dead	0	0 %
total	1	
Montastrea cavernosa		
< 1/3 dead	14	78 %
1/3 - 2/3 dead	4	22 %
> 2/3 dead	0	0 %
total	18	
Diploria strigosa		
< 1/3 dead	24	86 %
1/3 - 2/3 dead	3	11 %
> 2/3 dead	1	4 %
total	28	
Diploria clivosa		
< 1/3 dead	26	79 %
1/3 - 2/3 dead	5	15 %
> 2/3 dead	2	6 %
total	33	
Diploria labyrinthiformis		
< 1/3 dead	38	83 %
1/3 - 2/3 dead	6	13 %
> 2/3 dead	2	4 %
total	46	
Colpophyllia natans		
< 1/3 dead	7	54 %
1/3 - 2/3 dead	4	31 %
> 2/3 dead	2	15 %
total	13	
Siderastrea siderea		
< 1/3 dead	75	66 %
1/3 - 2/3 dead	28	25 %
> 2/3 dead	10	9 %
total	113	
all corals		
< 1/3 dead	**196**	**70 %**
1/3 - 2/3 dead	**62**	**22 %**
> 2/3 dead	**24**	**8 %**
total	**282**	

Table 6: Census at Cannon South. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, Univ. of Miami, Robert N. Ginsburg, July 1995.

Montastrea annularis		
< 1/3 dead	7	78 %
1/3 - 2/3 dead	1	11 %
>2/3 dead	1	11 %
total	9	
Montastrea faveolata		
< 1/3 dead	6	100 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	6	
Montastrea franksi		
< 1/3 dead	3	60 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	2	40 %
total	5	
Montastrea cavernosa		
< 1/3 dead	7	100 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	7	
Diploria strigosa		
< 1/3 dead	6	75 %
1/3 - 2/3 dead	2	25 %
> 2/3 dead	0	0 %
total	8	
Diploria clivosa		
< 1/3 dead	10	91 %
1/3 - 2/3 dead	1	9 %
> 2/3 dead	0	0 %
total	11	
Diploria labyrinthiformis		
< 1/3 dead	7	7 %
1/3 - 2/3 dead	1	1 %
> 2/3 dead	0	0 %
total	8	
Colpophyllia natans		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	0	
Siderastrea siderea		
< 1/3 dead	67	66 %
1/3 - 2/3 dead	21	21 %
> 2/3 dead	13	13 %
total	101	
all corals		
< 1/3 dead	**113**	**73 %**
1/3 - 2/3 dead	**26**	**17 %**
> 2/3 dead	**16**	**10 %**
total	**155**	

Table 7: Census at Higdon Reef. Data from RAPID ASSESSMENT OF REEF CORAL CONDITION, Univ. of Miami, Robert N. Ginsburg, July 1995.

Montastrea annularis		
< 1/3 dead	8	53 %
1/3 - 2/3 dead	3	20 %
>2/3 dead	4	27 %
total	15	
Montastrea faveolata		
< 1/3 dead	17	85 %
1/3 - 2/3 dead	2	10 %
> 2/3 dead	1	5 %
total	20	
Montastrea franksi		
< 1/3 dead	4	100 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	4	
Montastrea cavernosa		
< 1/3 dead	4	66 %
1/3 - 2/3 dead	1	17 %
> 2/3 dead	1	17 %
total	6	
Diploria strigosa		
< 1/3 dead	11	69 %
1/3 - 2/3 dead	5	31 %
> 2/3 dead	0	0 %
total	16	
Diploria clivosa		
< 1/3 dead	20	95 %
1/3 - 2/3 dead	0	5 %
> 2/3 dead	1	0 %
total	21	
Diploria labyrinthiformis		
< 1/3 dead	27	96 %
1/3 - 2/3 dead	1	4 %
> 2/3 dead	0	0 %
total	28	
Colpophyllia natans		
< 1/3 dead	0	0 %
1/3 - 2/3 dead	0	0 %
> 2/3 dead	0	0 %
total	0	
Siderastrea siderea		
< 1/3 dead	98	61 %
1/3 - 2/3 dead	44	28 %
> 2/3 dead	18	11 %
total	160	
all corals		
< 1/3 dead	**189**	**70 %**
1/3 - 2/3 dead	**57**	**21 %**
> 2/3 dead	**24**	**9 %**
total	**270**	

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Effects of fish predation and seaweed competition on the survival and growth of corals

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Abstract On Caribbean coral reefs, high rates of grazing by herbivorous fishes are thought to benefit corals because fishes consume competing seaweeds. We conducted field experiments in the Florida Keys, USA, to examine the effects of grazing fishes on coral/seaweed competition. Initially, fragments of *Porites divaracata* from an inshore habitat were transplanted into full-cage, half-cage, and no-cage treatments on a fore-reef. Within 48 h, 56% of the unprotected corals in half-cage and no-cage treatments (62 of 111) were completely consumed. Stoplight parrotfish (*Sparisoma viride*) were the major coral predators, with redband parrotfish (*S. aurofrenatum*) also commonly attacking this coral. Next, we transplanted fragments of *P. porites* collected from the fore-reef habitat where our caging experiments were being conducted into the three cage treatments, half in the presence of transplanted seaweeds, and half onto initially clean substrates. The corals were allowed to grow in these conditions, with concurrent development of competing seaweeds, for 14 weeks. Although seaweed cover and biomass were both significantly greater in the full-cage treatment, coral growth did not differ significantly between cage treatments even though corals placed with pre-planted seaweeds grew significantly less than corals placed on initially clean substrate. This surprising result occurred because parrotfishes not only grazed algae from accessible treatments, but also fed directly on our coral transplants. Parrotfish feeding scars were significantly more abundant on *P. porites* from the half and no-cage treatments than on corals in the full cages. On this Florida reef, direct fish predation on some coral species (*P. divaracata*) can exclude them from fore-reef areas, as has previously been shown for certain seaweeds and sponges. For other corals that live on the fore-reef (*P. porites*), the benefits of fishes removing seaweeds can be counterbalanced by the detrimental effects of fishes directly consuming corals.

Key words Coral · Corallivory · Florida · Predation · Seaweed competition

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Introduction

Invertebrate corallivores are widely recognized as having important effects on reef development and reef coral populations in both the Caribbean (e.g., the gastropod *Coralliophila*: Ott and Lewis 1972; Brawley and Adey 1982; Knowlton et al. 1990) and Pacific (e.g., *Acanthaster* and other echinoderms: Endean 1973; Glynn et al. 1979; Glynn and Krupp 1986). In contrast, much of the literature on corallivory by reef fishes refers to specialized Pacific butterflyfishes (Reese 1977; Neudecker 1979; Cox 1986). Most research in the Caribbean and temperate Atlantic has focused on how grazing fishes indirectly benefit corals by consuming seaweeds and thus reducing competitive pressure (Birkeland 1977; Lewis 1986; Steneck 1988; Hughes 1994; Miller and Hay 1996). These studies suggest that a significant reduction of fish grazing can result in the overgrowth of juvenile and adult corals by other benthic life forms, especially fleshy macroalgae. Observations by Birkeland (1977) in the tropical eastern Pacific indicate that herbivorous fishes actively avoid consuming juvenile corals greater than a few millimeters in size. A similar result was reported by Brock (1979) for Hawaiian parrotfish. In his laboratory study, field densities of parrotfish were determined to be "optimal" in promoting coral recruitment and benthic community development.

DUPLICATE:
Original in
Museum Archives

The exceptions to this rule are an anecdotal account from Barbados of substantial direct predation on corals by parrotfishes (Frydl 1979) and a careful experimental study by Littler et al. (1989) showing that direct predation by parrotfishes on *Porites porites*, but not *P. astreoides*, is a primary factor controlling the distinct zonation of these two coral species on the protected side of a Belizean reef flat.

Long-term overfishing of grazers as well as piscivores in many areas of the Caribbean (Hay 1984a; Hughes 1994), in combination with the loss of the echinoderm grazer *Diadema antillarum* in a pandemic die-off in 1982–1983 (Lessios 1988), is implicated in the proliferation of macroalgae and the loss of live coral from many Caribbean reefs (Liddell and Ohlhorst 1986; de Ruyter van Steveninck and Bak 1986; Hughes et al. 1987; Carpenter 1990a; Hughes 1994). Though many reef fisheries in the Florida Keys are also classified as overfished (J. Ault and J. Bohnsack, personal communication), these fisheries are primarily of a recreational rather than a subsistence nature, and the overfished stocks are primarily carnivores, such as grouper and snapper, rather than grazing scarids and acanthurids.

Our study was designed to test the direct effect of large grazing fishes on the accumulation of seaweed standing stock, as well as the indirect effect of fish grazing on coral growth and survivorship on a fore-reef in the Florida Keys. Our a priori hypothesis, based on our own and others' previous results (Lewis 1986; Morrison 1988; Hughes 1994; Miller and Hay 1996), was that the exclusion of large grazing fishes would result in a proliferation of seaweeds and a decrease in coral growth and/or survivorship due to competition from these seaweeds. This is not what we found.

Materials and methods

Field experiments were conducted in the relict spur and groove zone at Pickles Reef, Key Largo, Fl, USA (24°59.200′ N, 80°25.133′ W). We used flat cinder blocks (20 × 41 × 5 cm) as our experimental units. A 2-cm hole was drilled in the center of each cinder block and a large galvanized steel stake was hammered through the hole and driven into the reef substrate to secure the blocks in place. Forty-five blocks were arranged in 15 groups of three (n = 15, each with three treatments) in an approximately linear arrangement running northeast to southwest at a depth of 6–8 m. Each group of three blocks was separated from adjacent groups by at least 2–3 m. One of each group of three blocks was left bare (no cage), one was completely enclosed in plastic mesh (full-cage treatment), and one was partially enclosed (two walls and a top, half-cage control; see Fig. 1). A large mesh size (2-cm openings) was used to exclude large grazing fishes while allowing access to smaller predatory fishes such as wrasses and blennies. Access by these smaller fishes should minimize potential artifacts resulting from cages providing predation refuges for mesograzers (Lewis 1986).

A second factor was also used in the experiments. Because we were starting with clean substrates, we chose to preplant seaweeds into one end of every cinder block. Clumps of *Dictyota* spp. and of *Halimeda opuntia* were attached with cable ties to a 5-cm wide strip of mesh cut from a seine. This mesh was cable-tied around one end of each cinder block so that it held the algae firmly against the block and allowed them to attach to the block and grow up

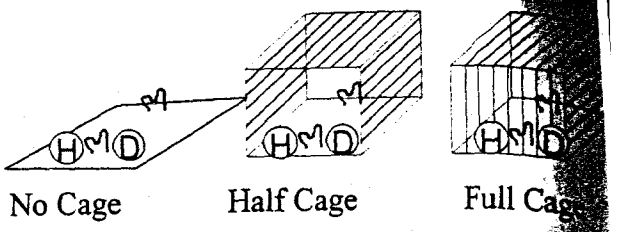


Fig. 1 Schematic design of one replicate of the field experime... *D* represent preplanted clumps of the seaweeds *Halimeda op...* *Dictyota* spp., respectively. In the experiment with *Porites d...* two coral transplants were placed on each end of each cinde...

through the mesh. A bare strip of mesh was cable-tied aro... other end of the block as a control. One or two corals (de... on the experiment, see below) were then attached through... the mesh onto each end of each block (i.e., attached betw... clumps of preplanted algae on one end and through the me... the bare block on the other end; see Fig. 1). Because each... mental unit (cinder block) received both levels of the prep... factor but only one level of the caging factor, we had a two... split-plot experiment for which we used an ANOVA desig... gested by Milliken and Johnson (1984) with the error mean... term associated with the cinder block used to test significance... cage treatment. Over the course of the experiment, a few... cages were lost due to rough weather, yielding a sample s... analysis of 12 or 13. Due to this imbalance, we report sta... results of type III sum-of-squares calculated by PROC GL... SAS (Shaw and Mitchell-Olds 1993).

Experiment with *P. divaracata*

On 28 July 1996, we collected fragments of the slender bran... coral *P. divaracata* from the grass flats around Rodriguez ... approximately 3 km inshore from the fore-reef site at Pickles ... The fragments were returned to the National Undersea Rese... Center in Key Largo and kept in flowing seawater until ... buoyant weight of each fragment was determined (Davies 1... On 29 July, each fragment was placed in an individually numbe... plastic bag, transported back to Pickles Reef, and attached to ... numbered cinder block using Petit Polypoxy Underwater Patchi... Compound. In this experiment, two small fragments were glued to ... each end of each cinder block (i.e., four coral pieces/cinder block).

Two days later (31 July), we found that many of the corals ... the no-cage and half-cage treatments were missing, apparently ... bitten off at the base which remained embedded in the epoxy. ... At this time, each of the four corals in each cage was scored as ... undamaged, one-quarter, one-half, three-quarters, or completely ... eaten. These scores were averaged to obtain the percentage of ... corals remaining for each cage. We had 12 excess corals that had ... not been used in the initial experiment, so these were affixed to the ... blocks at 1100 hours. We observed several of these corals for the ... next hour (to see if they were attacked by fishes) and then revisited ... them 4 h later. At this time, the experiment was ended because all ... of the corals had been completely consumed.

Because of the short duration of this experiment, the preplanted ... seaweed factor was ignored and a Kruskal-Wallis nonparametric ... one-way ANOVA followed by Dunn's pairwise comparisons was ... used to detect significant differences in coral survival between the ... cage treatments.

Video assay

To determine which fishes were consuming corals, four underwate... video cameras were set up at haphazard positions in the vicinity of ... the experimental cages on 31 July 1996. Fist-sized aggregations of ... four species of corals collected from grassbeds near Rodriguez Key

ASTRÆANS: tentacles not definitely limited in number, though usually not exceeding one hundred, and generally much below this number; transverse floors. Mæandrinas, generally referred to Astræans, are higher than the true Astræans, on account of their compound Polyps.
FUNGIDÆ: indefinite multiplication of tentacles; imperfect transverse beams.
ACTINIÆ: indefinite multiplication of tentacles; soft bodies and no transverse beams.

If now we compare this structural gradation among Polyps with their geological succession, we shall find that they correspond exactly. The following table gives the geological order in which they have been introduced upon the surface of the earth:—

GEOLOGICAL SUCCESSION.

Present,	Halcyonoids.
Pliocene, Miocene, Eocene,	Madrepores.
Cretaceous, Jurassic, Triassic, Permian,	Porites and Astræans.
Carboniferous, Devonian, Silurian,	Fungidæ.

With regard to the geological position of the Actiniæ we can say nothing, because, if their soft, gelatinous bodies have left any impressions in the rocks, none such have ever been found; but their absence is no proof that they did not exist, since it is exceedingly improbable that animals destitute of any hard parts could be preserved. . . . .

P. divaricata, *Cladocora arbuscula*, *Siderastrea radians*, and *Madracis* sp.) were placed at the corners of a 50-cm square in view of each camera and filmed for 2 h. The number of bites of each coral species taken and the identity of fishes attacking the corals were quantified.

Experiment with *P. porites*

We repeated the above experiment using *P. porites* collected from the fore-reef near our cages. On 1 August 1996, these corals were weighed and one piece of coral was transplanted onto each end of each cinder block as described above. This experiment ran for 14 weeks at which time (20 November 1996), the corals were harvested and seaweed cover was estimated on each half of each cinder block using a 50-point grid to determine the number of points intersecting macroalgae. Corals were returned to the laboratory at the Rosenstiel School of Marine and Atmospheric Science at the University of Miami where they were buoyant-weighed and examined carefully to quantify the number of bite scars. Number of bite scars, seaweed cover, and coral growth were analyzed by the ANOVA design described above.

Results

Experiment with *P. divaricata*

When we first monitored the *P. divaricata* transplants, 48 h after placing them in the field, we found that 56% of the corals (62 of the 111) in no-cage and half-cage treatments were missing. In most cases, it appeared that they had been bitten off at the base, leaving what looked like parrotfish feeding scars in the bit of skeleton remaining embedded in the epoxy. All corals in full cages remained intact. New corals transplanted onto the cinder blocks at 1100 hours were immediately attacked and completely consumed by stoplight parrotfish (*Sparisoma viride*). All of these transplants were consumed within 4 h. Stoplight parrotfish were also observed nosing against the full cages, apparently trying to access the corals they protected.

Kruskal-Wallis one-way ANOVA followed by Dunn's test showed that survivorship in closed cages was significantly greater than in either half-cage or no-cage treatments; these last two treatments did not differ from each other (Fig. 2). One striking aspect of these results was that the corals consumed were not evenly distributed among replicates (Fig. 3). Replicates were arranged approximately linearly from southwest to northeast; all of the corals consumed were from the southwest end. None of the corals that were in replicates on the extreme northeast end were consumed (Fig. 3).

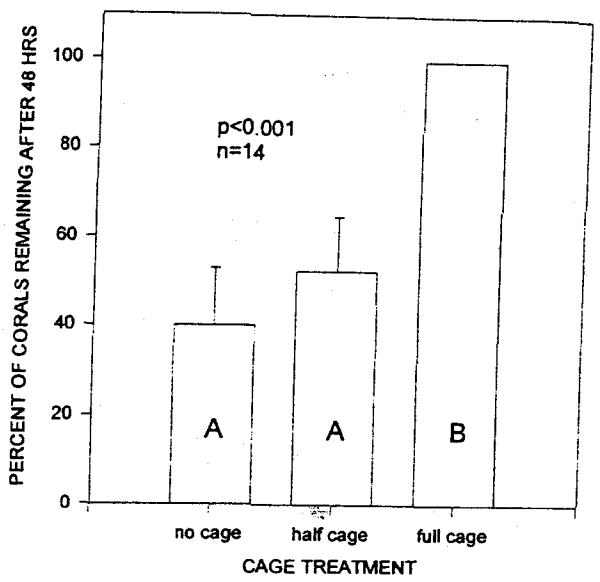


Fig. 2 Results of the experiment with *P. divaracata*. *Bars* represent means + 1 SE. *P*-value from Kruskal-Wallis one-way ANOVA. Treatments with the *same letter* are not significantly different ($P > 0.05$) by Dunn's post hoc pairwise comparisons

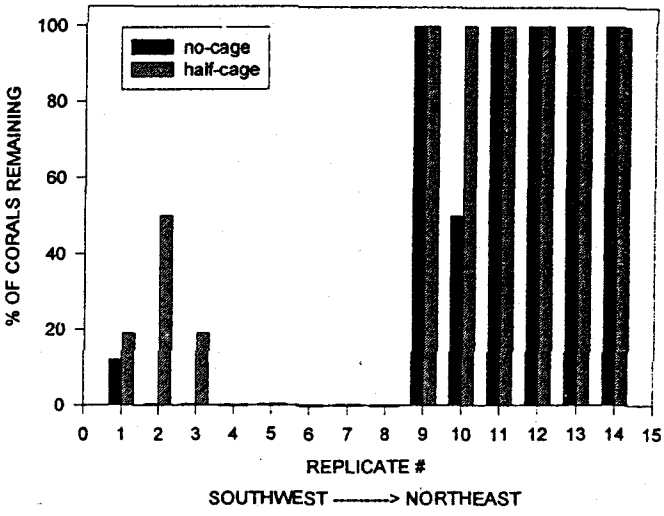


Fig. 3 Forty-eight-hour *P. divaracata* survival in individual replicates of the no-cage and half-cage treatments. Virtually all the corals consumed were at the southwest end of the experimental array

Video assays

The video-taped assays documented rapid consumption of *P. divaracata* by stoplight parrotfish (*S. viride*) and redband parrotfish (*Sparisoma aurofrenatum*). Our field observations and these videos both suggested that large parrotfish were responsible for the majority of damage to these corals. They bit off large portions of whole branches, while redband parrotfish appeared to scrape only the surface of the corals. *P. divaracata* was much more attractive to both species of parrotfish than were any of the other three species of corals tested. This experiment also suggested considerable small-scale spatial variation in the intensity of coral predation. Corals at two of our four video stations received a large number of bites from the beginning of our filming, while two other stations showed very low activity until just before filming ended (Fig. 4).

single, and, though they are stony corals, they have no share in the formation of reefs. In these, also, the tentacles multiply throughout life, though they are usually not so numerous as in the Actiniæ. But a new feature is added to the complication of their structure, as compared with Actiniæ, in the transverse beams which connect their vertical partitions, though they do not stretch across the chambers so as to form perfect floors, as in some of the higher Polyps.

In the Astræans, the multiplication of tentacles is more definite and limited, rising sometimes to ninety and more, though often limited to forty-eight in number, and the transverse floors between the vertical partitions are more complete than in the Fungidæ. The Porites have twelve tentacles only (Pl. XVI., Figs. 15 and 16), never more and never less, and in them the whole solid frame presents a complicated system of connected beams. The Madrepores have also twelve tentacles, but they have a more definite character than those of the Porites, on account of their regular alternation in six smaller and six larger ones (Pl. XVIII., Figs. 5, 6, and 7); in these also the transverse floors are perfect, but exceedingly delicate. Another remarkable feature among the Madrepores consists in the prominence of one of the Polyps on the summit of the branches (Pl. XIX., Fig. 7), showing a kind of subordination of the whole community to these larger individuals, and thus sustaining the view expressed above, that the combination of many individuals into a connected community is among the Polyps a character of superiority when contrasted with the isolation of the Actiniæ. In the Sea-Fans, the Halcyonoids, as they are called in our classification, the number of tentacles is always eight, four of which are already present at the time of their birth, arranged in pairs, while the other four are added later. Their tentacles are lobed all around the margin, and are much more complicated in structure than those of the preceding Polyps.

According to the relative complication of their structure, these animals are classified in the following order: —

STRUCTURAL SERIES.

HALCYONOIDS: eight tentacles in pairs, lobed around the margin, always combined in large communities, some of which are free and movable like single animals.

MADREPORES: twelve tentacles, alternating in six larger and six smaller ones; frequently a larger top animal standing prominent in the whole community, or on the summit of its branches.

PORITES: twelve tentacles, not alternating in size; system of connected beams.

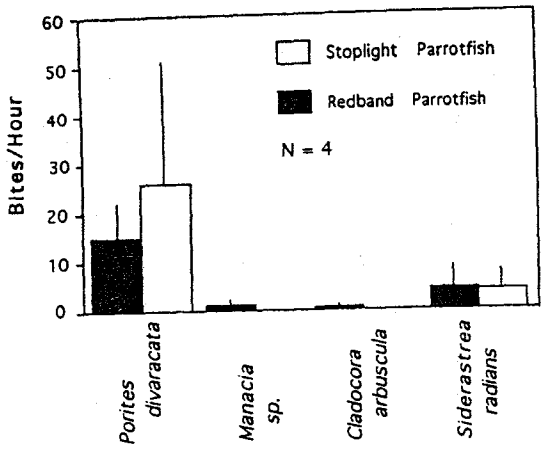


Fig. 4 Number of bites/h (mean + 1 SE) on approximately equal sized clumps of four species of corals transplanted from a seagrass bed to a fore-reef habitat. All bites were by the two species of parrotfishes indicated. The large SE is due to two sites being rapidly found and attacked by fishes while two other sites were found only near the end of the 2-h filming period

Experiment with *P. porites*

At the end of the 14-week experiment, seaweed percent cover was significantly higher (approximately double, Fig. 5A) in full-cage treatments than in the half-cage and no-cage treatments ($P = 0.002$). In addition, seaweed cover on the preplanted side of each block remained significantly greater (by 5–10%) than on the initially bare side ($P = 0.002$). There was also a significant spatial effect of cinder block ($P < 0.002$). *Dictyota* spp. that had been preplanted were the most abundant seaweed present in all replicates of all cage treatments. *H. opuntia* was also present in all types of cage treatments, but at lower abundance that *Dictyota*. Colonizing species of seaweed (mostly reds) were largely restricted to full-cage treatments (Fig. 6).

Contrary to our a priori hypothesis, there was no significant cage effect on coral growth (Fig. 5B, $P = 0.886$) even though there was a significant effect of the initial planting of seaweeds on coral growth ($P = 0.007$). Thus, seaweed competition clearly has an important detrimental effect on coral growth based on the significant effect of preplanting of seaweeds. However, the significant difference in seaweed cover between cage treatments was not reflected in a significant effect on coral growth associated with treatments that had low algal cover due to their open access to grazers. This may be because the reduction in seaweed cover that occurred in the presence of grazers (Fig. 5A) was offset by significantly higher rates of direct predation (as measured by bite scars) on corals (Fig. 5C, $P < 0.001$). The two treatments that had the highest coral growth rates were ones that had both few grazing scars on the corals (Fig. 5C) and relatively less algal competition (Fig. 5A). The full-cage treatment without preplanted seaweeds had relatively high coral growth despite having the second highest incidence of seaweed cover, seemingly because of protection from predation (zero bite scars in all replicates). Thus, protection of *P. porites* from direct predation in our full cages appears to counterbalance the detrimental effects of increases in competing seaweeds when fishes are excluded.

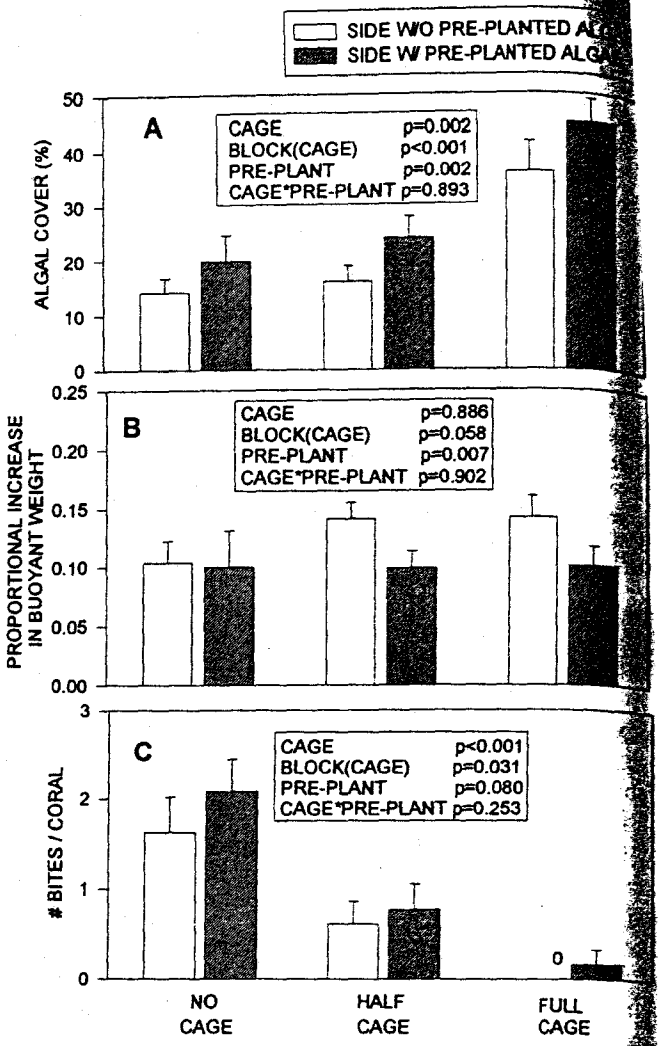


Fig. 5A–C Results of the experiment with *P. porites*. Bars represent means + 1 SE. *P*-values from two-factor split-plot ANOVA ($n = 12$–13). A Macroalgal percent cover in the six treatment groups after 14 weeks. B Coral growth as relative change in buoyant weight over the course of the experiment. C Grazing scars on corals in the six treatment groups

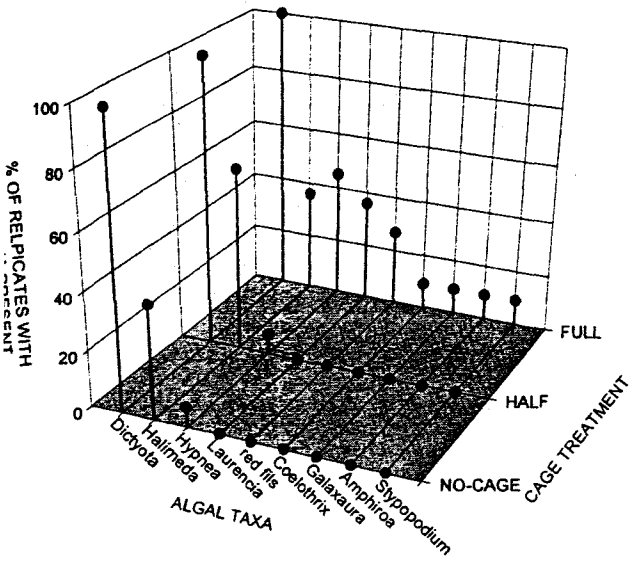
We used the half-cage treatment to control for artifacts associated with caging (e.g., water movement and shading). In the case of algal proliferation, the half-cage treatments behaved similarly to the no-cage controls, suggesting that these effects were due to grazers rather than cage artifacts. In contrast, the number of bite scars on corals in half cages was intermediate between those in the open and in the full cages. It appears that coral-eating fishes were somewhat deterred by half cages, probably because larger individuals were responsible for most of the coral predation (video observations) while all sizes of fish eat seaweeds. Thus, the half-cage treatment may more accurately be considered an intermedi-

which time we have no evidence of any change in species, but, on the contrary, the strongest proof of the absolute permanence of those species whose past history we have been able to trace.

Before leaving the subject of the coral reefs, I would add a few words on the succession of the different kinds of Polyp corals on a reef as compared with their structural rank and also with their succession in time, because we have here another of these correspondences of thought, those intellectual links in creation, which give such coherence and consistency to the whole and make it intelligible to man.

The lowest in structure among the Polyps are not corals, but the single, soft-bodied Actiniæ. They have no solid parts, and are independent in their mode of existence, never forming communities, like the higher members of the class. It might at first seem strange that independence, considered a sign of superiority in the higher animals, should here be looked upon as a mark of inferiority. But independence may mean either simple isolation, or independence of action; and the life of a single Polyp is no more independent in the sense of action than that of a community of Polyps. It is simply not connected with or related to the life of any others. The mode of development of these animals tells us something of the relative inferiority and superiority of the single ones and of those that grow in communities. When the little Polyp coral — the Astræan or Madrepore, for instance — is born from the egg, it is as free as the Actinia, which remains free all its life. It is only at a later period, as its development goes on, that it becomes solidly attached to the ground, and begins its compound life by putting forth new beings like itself as buds from its side. Since we cannot suppose that the normal development of any being can have a retrograde action, we are justified in believing that the loss of freedom is in fact a stage of progress in these lower animals, and their more intimate dependence on each other a sign of maturity.

There are, however, structural features by which the relative superiority of these animals may be determined. In proportion as the number of their parts is limited and permanent, their structure is more complicated; and the indefinite multiplication of identical parts is connected with inferiority of structure. Now in these lowest Polyps, the Actiniæ, the tentacles increase with age indefinitely, never ceasing to grow while life lasts, new chambers being constantly added to correspond with them, till it becomes impossible to count their numbers. Next to these come the true Fungidæ. They are also



. 6 Seaweed composition of each cage treatment indicated by the cent of replicates with each taxa present (n = 11 for full cages, = 14 for half cages, and n = 15 for no cages) (*red fils* multiple dentified red filamentous species)

treatment with regard to coral predation while it ıctioned more as the described control with regard to ızing on seaweeds.

cussion

rotfish grazing on corals in the Caribbean is thought be low and relatively inconsequential for both the ıes and the corals (Randall 1974; Bruggemann et al.)6). Grazing fishes are, however, thought to be es- tial components of healthy reefs because they remove weeds, avoid eating corals, and thus prevent seaweeds m excluding corals via competition (Birkeland 1977;)ck 1979; Lewis 1986; McClanahan and Muthiga :8; Hughes 1994). Our data suggest that the beneficial :cts of fish grazing are not generalizable to all loca- ıs or all corals, but vary greatly depending on the al species and parrotfish species involved. Stoplight l redband parrotfishes rapidly consumed most of our *divaracata* transplants. They completely consumed r 50% of our transplants in 48 h (Fig. 2) and sys- ıatically removed all transplants from some areas of reef (Fig. 3). When four coral species typical of ssbed habitats were moved to the fore-reef, parrot- es rapidly consumed *P. divaracata*, commonly bit *adians*, but paid minimal attention to *Manicina* sp. or *arbuscula* (Fig. 4). Additionally, placing *P. porites* on same cinder blocks used in the *P. divaracata* exper- nt showed that, even though it was grazed, *P. porites* ld persist and grow (Fig. 5) in areas where grazing es excluded *P. divaracata*. Thus, even within the us *Porites*, there is considerable variation in suscep- lity to parrotfish grazing, as shown previously by ler et al. (1989). Similarly, Neudecker (1979) showed strong intragenus variation in susceptibility of *Pocillopora* species to fish predation in Guam, even between species whose taxonomic distinctness was debated by taxonomists.

Parrotfish corallivory: do they or don't they?

Our data contribute to an ongoing debate regarding the importance of direct fish grazing on corals. A recent field study in Bonaire (Bruggemann et al. 1996) concluded, "Living coral is rarely eaten by scarids, and largely escapes erosion by grazing." A recent review by Hixon (1997) states that "outside of damselfish territories, the reported direct effects of herbivorous fishes on corals are contradictory (and) ... appear to depend on the particular system." Frydl (1979) shows photographs of extreme parrotfish grazing of coral colonies, including *Montastraea annularis* and *P. porites*, but notes that this intensity of damage is unusual. Randall (1974) and Bak and Engle (1979) reported that grazing fishes damage juvenile corals, while Birkeland (1977) reported that grazing fishes avoided damaging even very small juveniles. Other recent observations suggest that the reproductive status of the corals may also be important. Developing gonads held in coral tissue might provide a particularly rich nutritional source, and *M. annularis* in the Florida Keys appears to suffer increased predation in the weeks before the annual mass spawn (A.M. Szmant, personal communication).

In developing countries, intense overfishing often results in direct depletion of herbivore fish guilds (Hay 1984a; McClanahan and Muthiga 1988; Hughes 1994). However, in the Florida Keys, the fisheries are recreational and commercial in nature, and reef piscivores such as grouper and snapper are targeted while grazing fishes are not considered desirable. It is plausible that overfishing in the Florida Keys has reduced predation on grazers. Combined with the virtual absence of *Diadema*, which competes with grazing fishes (Hay and Taylor 1985; Carpenter 1990b; Robertson 1991), these decreases in predators and competitors could result in abnormally high intensities of parrotfish grazing on reefs in the Florida Keys. Other caging experiments in Biscayne National Park, just north of our study site, have shown that grazing fishes consume transplanted juvenile corals of many species (including *P. astreoides*, *S. radians*, and *Favia fragum*, as well as *P. divaracata*) to extinction if they are not protected in full cages (Miller et al., in preparation). At Conch Reef (adjacent to our study site in the Key Largo area), video assays have also shown that *Sparisoma* parrotfishes consume substantial amounts of sponges (Dunlap and Pawlik 1996). Dunlap and Pawlik (1996) note that numerous previous studies of parrotfish foraging have not reported parrotfishes as sponge feeders (Hanley 1984; Bellwood and Choat 1990; Bruggemann et al. 1994). It may be that Florida Keys reefs are overpopulated with *Sparisoma* parrotfishes and that their foraging has

began. Leaving aside, however, all that part of its history which is not susceptible of positive demonstration in the present state of our knowledge, I will limit my results to the evidence of facts already within our possession; and these give us as the lowest possible estimate a period of seventy thousand years for the formation of that part of the peninsula which extends south of Lake Okee-cho-bee to the present outer reef.

So much for the duration of the reefs themselves. What, now, do they tell us of the permanence of the species by which they were formed? In these seventy thousand years has there been any change in the corals living in the Gulf of Mexico? I answer most emphatically, *No.* Astræans, Porites, Mæandrinas, and Madrepores were represented by exactly the same species seventy thousand years ago as they are now. Were we to classify the Florida corals from the reefs of the interior, the result would correspond exactly to a classification founded upon the living corals of the outer reef to-day. There would be among the Astræans the different species of Astræa (Pl. IV.) proper, forming the close, round heads, — the Mussa, growing in smaller stocks, where the mouths coalesce and run into each other as in the Brain-Corals, but in which the depressions formed by the mouths are deeper, — and the Caryophyllians (Cladocora Pl. III., Figs. 1–7), in which the single individuals stand out more distinctly from the stock; among Porites, the P. Astræoides (Pl. XVI., Figs. 1–12), with pits resembling those of the Astræans in form, though smaller in size, and growing also in solid heads, though these masses are covered with club-shaped protrusions, instead of presenting a smooth, even surface like the Astræans, — and the P. Clavaria (Pl. XII., Figs. 4, 5, and 6), in which the stocks are divided in short, stumpy branches, with club-shaped ends, instead of growing in close, compact heads; among the Mæandrinas we should have the round heads we know as Brain-Corals (Pl. IX.), with their wavy lines over the surface, and the Manicina (Pls. V., VI.), differing again from the preceding by certain details of structure; among the Madrepores we should have the Madrepora prolifera (Pl. XIX.), with its small, short branches, broken up by very frequent ramifications, the M. cervicornis (Pl. XVIII.), with longer and stouter branches and less frequent ramifications, and the cup-like M. palmata (Pl. XVII.), resembling an open sponge in form. Every species, in short, that lives upon the present reef is found in the more ancient ones. They all belong to our own geological period, and we cannot, upon the evidence before us, estimate its duration at less than seventy thousand years, during

expanded from herbivory (Bruggemann et al. 1994) to include novel foods such as sponges and corals. This hypothesis is not consistent, however, with the conventional view that reefs in the Florida Keys are overgrown with macroalgae and thus rich in algal foods relative to other reefs (Ward 1990; Torrence 1991; Hallock et al. 1993).

Does it matter?

The studies of Bruggemann et al. (1994) from Bonaire demonstrated that up to 9% of bites by the parrotfish *S. viride* were on live coral, primarily *M. annularis*. In many cases, however, bites of coral were dropped and not consumed. They speculated that coral bites may serve more of a social than a nutritional function, creating territory markers by leaving a conspicuous white spot on the live coral colony. Although they concluded that corallivory was of negligible nutritional importance for parrotfish, this would not prevent parrotfish corallivory from having a significant impact on populations of some coral species. In our study, parrotfishes were not observed dropping the corals they had bitten, and the fact that they rapidly consumed our transplants suggests that they were not biting these merely to mark territory boundaries but that some species were being targeted as desirable foods.

In agreement with our findings, Littler et al. (1989) documented that grazing fishes had a large impact on some corals in Belize. The distribution of *P. porites* and *P. astreoides* as a function of distance from the reef flat was controlled by differential palatability to grazing fish. In areas with sufficient structure to harbor larger fishes, *P. porites* was rapidly eaten while *P. astreoides* was largely ignored.

Our a priori hypothesis was that reduced grazing in full cages would allow macroalgae to proliferate and overgrow corals, substantially reducing their growth. While filamentous algae have been shown to compromise and/or kill corals in damselfish territories (Potts 1977) and under natural nutrient enrichment (Genin et al. 1995), Lewis (1986) found that filamentous algae decreased significantly in caged experimental treatments and noted that macroalgae, rather than filamentous algae, overgrew and killed corals. We observed no differences in filamentous algal abundance between treatments, but did observe a significant proliferation of macroalgae in the full cages (Fig. 5A). Contrary to expectation, this increased macroalgal cover in full cages had no significant cage effect on *P. porites* growth (Fig. 5B). However, our study does confirm previous results regarding the clear importance of seaweed competition to corals (when they are not eaten directly by fishes) in that the preplanted seaweeds significantly inhibited coral growth (Fig. 5B). The intensity of direct predation on corals in our manipulations, as estimated by the number of bite scars, was inverse to the proliferation of seaweeds. Thus, it appears that parrotfish predation had a negative impact on *P. porites* growt that matched and offset the positive effects of herbivore removing competing seaweeds (Fig. 5A).

Even more dramatically, on some portions of th reef, all *P. divaracata* transplants were eaten completel in only a few hours (Fig. 3). High susceptibility to par rotfish predation may explain the restriction of thi species from reef slopes to inshore habitats with lesse grazing intensity. Similar distributional restrictions du to grazing have been shown for numerous seaweed (Hay 1981, 1985) and, more recently, for sponge (Dunlap and Pawlik 1996). Greater chemical defense against predation have been shown in relatively unpal atable reef species versus palatable nonreef species fo both seaweeds (Hay 1984b; Paul and Hay 1986) anc sponges (Pawlik et al. 1995). Chemical defenses in harc corals remain largely unexplored, but given the large variance in susceptibility to fish grazing that occurs be tween coral species (Fig. 4) and even among specie within a genus (Neudecker 1979; Littler et al. 1989; thi paper), investigations of hard coral defenses seem warranted.

Another unexpected aspect of our results is the considerable small-scale (a few meters) spatial variation in corallivory (Fig. 3). In both the cage experiments anc the video assays, corals transplanted to some areas were consumed rapidly while those transplanted a few meters away appear to have been found and consumed much more slowly, or not at all. Spatial variation in predation intensity, both herbivory and corallivory, is well documented between sites, habitats, and depth zones (Neudecker 1979; Hay 1981, 1985; Steneck 1988; Littler et al. 1989; reviewed in Glynn 1990). Work with seaweeds and reef herbivores has demonstrated that grazing pressure can vary dramatically over spatial scales of only centimeters to meters due to effects of territorial damselfishes or of noxious seaweeds creating microsites of associational escapes for more palatable seaweeds (Hay 1985, 1986, 1996). However, to our knowledge, there are no previously published reports of such significant variation in predation of corals on such a small scale (2–3 m) within a single habitat/depth zone (7–8 m, fore-reef relict spur and groove). The spatial pattern of coral consumption we document (Fig. 3) could have resulted from territorial behavior of parrotfishes. *S. viride* are known to be territorial (Bruggemann et al. 1994) and the video assays showed this species to be the primary feeder on *P. divaracata* with all *S. viride* that we saw feeding being large individuals that could bite off entire coral branches.

In conclusion, direct feeding by parrotfishes in the Florida Keys can substantially reduce the abundance and distribution of some coral species (*P. divaracata*) while other corals (*P. porites*) can be negatively affected by both direct fish predation and, in the absence of grazing fishes, by seaweed competition. The effects of parrotfish feeding on coral populations are not generalizable to all corals and will depend on species-specific traits of the corals and parrotfishes involved.

united to the main-land by the complete filling up and consolidation of the channel which once divided it from the extremity of the peninsula, as a channel now separates the keys from the shore-bluffs, and the outer reef, again, from the keys. These three concentric reefs, then, — the outer reef, the keys, and the shore-bluffs, — if we measure the growth of the two latter on the same low estimate by which I have calculated the rate of progress of the former, cannot have reached their present condition in less than twenty thousand years. Their growth must have been successive, since, as we have seen, all corals need the fresh action of the open sea upon them, and if either of the outer reefs had begun to grow before the completion of the inner one, it would have effectually checked the growth of the latter. The absence of an incipient reef outside of the outer reef shows these conclusions to be well founded. The islands capping these three reefs do not exceed in height the level to which the fragments accumulated upon their summits may have been thrown by the heaviest storms. The highest hills of this part of Florida are not over ten or twelve feet above the level of the sea, and yet the luxuriant vegetation with which they are covered gives them an imposing appearance, recalling the islands of the Pacific.

But this is not the end of the story. Travelling inland from the shore-bluffs, we cross a low, flat expanse of land, the Indian hunting-ground, which brings us to a row of elevations called the Hummocks. This hunting-ground, or Everglade as it is also called, is an old channel, changed first to mud-flats and then to dry land by the same kind of accumulation that is filling up the present channels, and the row of hummocks is but an old coral reef with the keys or islands of past days upon its summit. Seven such reefs and channels of former times have already been traced between the shore-bluffs and Lake Okee-cho-bee, adding some fifty thousand years to our previous estimate. Indeed, upon the lowest calculation, based upon the facts thus far ascertained as to their growth, we cannot suppose that less than seventy thousand years have elapsed since the coral reefs already known to exist in Florida began to grow.

When we remember that this is but a small portion of the peninsula, and that, though we have no very accurate information as to the nature of its interior, yet the facts already ascertained in the northern part of the State formed, like its southern extremity, of coral growth, justify the inference that the whole peninsula is formed of successive concentric reefs, we must believe that hundreds of thousands of years have elapsed since its formation

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by Captain Woodbury of Tortugas, with the view of determining the rate of growth of corals, when taken up in 1858 had a crust of Mæandrina upon it a little more than half an inch in thickness. Mr. Allen also sent me from Key West a number of fragments of Mæandrina from the breakwater at Fort Taylor; they had been growing from twelve to fifteen years, and have an average thickness of about an inch. The specimens vary in this respect, — some of them being a little more than an inch in thickness, others not more than half an inch. Fragments of Oculina gathered at the same place and of the same age are from one to three inches in height and width; but these belong to the lighter, more branching kinds of corals, which, as we have seen, cannot, from their brittle character, be supposed to add their whole height to the solid mass of the coral wall. Millepora gives a similar result.

Estimating the growth of the coral reef according to these and other data of the same character, it should be about half a foot in a century; and a careful comparison which I have made of the condition of the reef as recorded in an English survey made about a century ago with its present state would justify this conclusion. But, allowing a wide margin for inaccuracy of observation or for any circumstances that might accelerate the growth, and leaving out of consideration the decay of the soft parts and the comminution of the brittle ones, which would subtract so largely from the actual rate of growth, let us double this estimate and call the average increase a foot for every century. In so doing, we are no doubt greatly overrating the rapidity of the progress, and our calculation of the period that must have elapsed in the formation of the reef will be far within the truth.

The outer reef, still incomplete, as I have stated, and therefore of course somewhat lower than the inner one, measures about seventy feet in height. Allowing a foot of growth for every century, not less than seven thousand years must have elapsed since this reef began to grow. Some miles nearer the main-land are the keys, or the inner reef; and though this must have been longer in the process of formation than the outer one, since its growth is completed, and nearly the whole extent of its surface is transformed into islands, with here and there a narrow break separating them, yet, in order to keep fully within the evidence of the facts, I will allow only seven thousand years for the formation of this reef also, making fourteen thousand for the two.

This brings us to the shore-bluffs, consisting simply of another reef exactly like those already described, except that in course of time it has been

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there an island. This is accounted for by the sensitiveness of the corals to any unfavorable circumstances impeding their growth, as well as by the different rates of increase of their different kinds. Wherever any current from the shore flows over the reef, bringing with it impurities from the land, there the growth of the corals will be less rapid, and consequently that portion of the reef will not reach the surface so soon as other parts, where no such unfavorable influences have interrupted the growth. But in the course of time the outer reef will reach the surface for its whole length, and become united to the inner one by the filling up of the channel between them, while the inner one will long before that time become solidly united to the present shore-bluffs of Florida by the consolidation of the mud-flats, which will one day transform the inner channel into dry land.

What is now the rate of growth of these coral reefs? We cannot, perhaps, estimate it with absolute accuracy, since they are now so nearly completed; but coral growth is constantly springing up wherever it can find a foothold, and it is not difficult to ascertain approximately the rate of growth of the different kinds. Even this, however, would give us far too high a standard; for the rise of the coral reef is not in proportion to the height of the living corals, but to their solid parts which never decompose. Add to this that there are many brittle, delicate kinds that have a considerable height when alive, but contribute to the increase of the reef only so much additional thickness as their branches would have if broken and crushed down upon its surface. A forest in its decay does not add to the soil of the earth a thickness corresponding to the height of its trees, but only such a thin layer as would be left by the decomposition of its whole vegetation. In the coral reef, also, we must allow not only for the deduction of the soft parts, but also for the comminution of all these little branches, which would be broken and crushed by the action of the storms and tides, and add, therefore, but little to the reef in proportion to their size when alive.

The foundations of Fort Jefferson, which is built entirely of coral rock, were laid on the Tortugas Islands in the year 1846. A very intelligent head-workman watched the growth of certain corals that established themselves on these foundations, and recorded their rate of increase. He has shown me the rocks on which corals had been growing for some dozen years, during which they had increased at the rate of about half an inch in ten years. I have collected facts from a variety of sources and localities that confirm this testimony. A brick placed under water, in the year 1850,

owe their knowledge of the coast to their former occupation. It is a singular fact, that at this very time, when the whole country feels its obligation to the men who have devoted so many years of their lives to these investigations, a proposition should have been brought forward in Congress for the suspension of the Coast Survey on economical grounds. Happily, the almost unanimous rejection of this proposition has shown the appreciation in which the work is held by our national legislature. Even without reference to their practical usefulness, it is a sad sign, when, in the hour of her distress, a nation sacrifices first her intellectual institutions. Then, more than ever, when she needs all the culture, all the wisdom, all the comprehensiveness of her best intellects, should she foster the institutions that have fostered them, and in which they have been trained to do good service to their country in her time of need.

Several of the Florida keys, such as Key West and Indian Key, are already large, inhabited islands, several miles in extent. The interval between them and the main-land is gradually filling up, by a process similar to that by which the islands themselves were formed. The gentle landward slope of the reef, and the channel between it and the shore, are covered with a growth of the more branching lighter corals, such as Sea-Fans, Coral-lines, &c., answering the same purpose as the intricate roots of the mangrove-tree. All the débris of the reef, as well as the sand and mud washed from the shore, collect in this net-work of coral growth within the channel, and soon transform it into a continuous mass, with a certain degree of consistence and solidity. This forms the foundation of the mud-flats which are now rapidly filling the channel, and must eventually connect the keys of Florida with the present shore of the peninsula.

Outside the keys, but not separated from them by so great a distance as that which intervenes between them and the main-land, there stretches beneath the water another reef, abrupt, like the first, on its seaward side, but sloping gently toward the inner reef, and divided from it by a channel. This outer reef and channel are, however, in a much less advanced state than the preceding ones. Only here and there a sand-flat large enough to afford a foundation for a beacon, or a lighthouse, shows that this reef also is gradually coming to the surface, and that a series of islands corresponding to the keys must eventually be formed upon its summit.

Some of my readers may ask why the reef does not rise evenly to the level of the sea, and form a continuous line of land, instead of here and

After a time, an immense quantity of such materials is formed about a coral reef. Tides and storms constantly throw them up on its surface, and at last a soil collects on the top of the reef, wherever it has reached the surface of the water, formed chiefly of its own débris, of coral sand, coral fragments, even large masses of coral rock, mingled with the remains of the animals that have had their home about the reef, with sea-weeds, with mud from the neighboring land, and with the thousand loose substances always floating about in the vicinity of a coast, and thrown upon the rocks or shore with every wave that breaks against them. Add to this the presence of a lime-cement in the water, resulting from the decomposition of some of these materials, and we have all that is needed to make a very compact deposit and fertile soil, on which a vegetation may spring up, whenever seeds floating from the shore, or dropped by birds in their flight, take root on the newly-formed island. . . . .

Such caps of soil on the summit of a coral reef are of course very insecure, till they are consolidated by a long period of accumulation, and they may even be swept completely away by a violent storm. It is not many years since the lighthouse, built on Sand Key for the greater security of navigation along the reef, was swept away, with the whole island on which it stood. Thanks to the admirably conducted investigations of the Coast Survey, this part of our seaboard, formerly so dangerous on account of the coral reefs, is now better understood, and every precaution has been taken to insure the safety of vessels sailing along the coast of Florida.

I cannot deny myself the pleasure of paying a tribute here to the high scientific character of the distinguished superintendent of this survey, who has known so well how to combine the most important scientific aims with the most valuable practical results in his direction of it. If some have hitherto doubted the practical value of such researches, — and unhappily there are always those who estimate intellectual efforts only by their material results, — one would think that these doubts must be satisfied, now that the Coast Survey is seen to be the right arm of our navy. Most of the leaders in our late naval expeditions have been men trained in its service, and familiar with all the harbors, with every bay and inlet of our southern coasts, from having been engaged in the extensive researches undertaken by Dr. Bache, and carried out under his guidance. Many even of the pilots of our southern fleets are men who have been employed upon this work, and

Jim Tilmant, Gary Davis
1976

A SKIN DIVER'S GUIDE

TO THE MARKED PATCH REEFS

IN BISCAYNE NATIONAL MONUMENT, FLORIDA

Coral reefs are some of the most beautiful and interesting of all living communities. We hope this guide will help you find and safely enjoy a few typical coral reefs in Biscayne National Monument.

The only living coral reefs in the continental United States are found along the scimitar-shaped arc of the Florida Keys. The Upper Keys themselves were once coral reefs, over 100,000 years ago when sea level was much higher than it is today. Now shallower portions of that ancient reef form the limestone foundations of the Keys, while deeper parts of the old reef provide the hard bottom needed as a foothold by today's living coral reef. With a sunny place to stand, and the warm clear waters of the northward flowing Florida current bringing them food and oxygen, colonies of tiny coral animals, called polyps, create massive, intricate, limestone condominiums that are used by thousands of plants and animals as shelter.

The ancient reef forms a shallow curved shelf. On the eastern edge of the shelf, the outer reef drops off to depths greater than 100 feet (30 m). Behind the outer reef, in sheltered lagoon-like waters, small reef patches rise to the surface in a complex irregular pattern. It is on these shallow patch reefs where novice and intermediate skin divers can easily get acquainted with Florida's coral reefs.

The patch reefs described in this guide are marked by small blue and white mooring buoys and are typical of nearly a hundred such reefs in the monument. They are located two to three miles (3-5 km) east of Old Rhodes and Elliott Keys, as shown on the chart. They can be easily reached by boat from Caesar's Creek. Bearings from the marker buoys to prominent landmarks and navigational aids are indicated on the individual reef maps. These maps show the outlines of the reefs and the general locations of different types of corals. One patch reef includes an adjacent schooner wreck. Water depths are also indicated for your convenience. A careful lookout must be kept for shallow coral heads that seem to pop up everywhere when operating boats in this area. Remember that the reefs are here because they need sunlight and flowing water, so don't get sunburned and always swim with a buddy up current from your boat. Tie to the buoy to prevent damaging the reef with your anchor, and have fun.

increase. Here, as elsewhere, destruction and construction go hand in hand, and the materials broken or worn away from one part of the reef help to build it up elsewhere. The corals forming the reef are not the only beings that find their home there: many other animals, — shells, worms, crabs, star-fishes, sea-urchins, — establish themselves upon it, work their way into its interstices, and seek a shelter in every little hole and cranny made by the irregularities of its surface. In the Zoölogical Museum at Cambridge there are some large fragments of coral reef which give one a good idea of the populous aspect that such a reef would present, could we see it as it actually exists beneath the water. Some of these fragments consist of a succession of terraces, as it were, in which are many little miniature caves, where may still be seen the shells or sea-urchins which made their snug and sheltered homes in these recesses of the reef.

We must not consider the reef as a solid, massive structure throughout. The compact kinds of corals, giving strength and solidity to the wall, may be compared to the larger trees in a forest, giving it shade and density; but beneath these larger trees grow all kinds of trailing vines, ferns, and mosses, wild-flowers, and low shrubs, filling the spaces between them with a thick underbrush. The coral reef also has its underbrush of the lighter, branching, more brittle kinds, filling its interstices, and fringing the summit and the sides with their delicate, graceful forms. Such an intricate underbrush of coral growth affords an excellent retreat for many animals that like its protection better than exposure to the open sea, just as many land-animals prefer the close and shaded woods to the open plain. A forest is not more thickly peopled with birds, squirrels, martens, and the like, than is the coral reef with a variety of animals which do not contribute in any way to its growth, but find shelter in its crevices, or in its near neighborhood.

But these larger animals are not the only ones that haunt the forest. There is a host of parasites besides, principally insects and their larvæ, which bore their way into the very heart of the tree, making their home in the bark and pith, and not the less numerous because hidden from sight. These also have their counterparts in the reef, where numbers of boring shells and marine worms work their way into the solid substance of the wall, piercing it with holes in every direction, till large portions become insecure, and the next storm suffices to break off the fragments so loosened. Once detached, they are tossed about in the water, crumbled into coral sand, crushed, often ground to powder by the friction of the rocks and the constant action of the sea.

SAFETY TIPS TO REMEMBER

1. Always swim in pairs; use the buddy system.
2. Be aware of tidal currents; stay upstream of the boat.
3. Coral is sharp and will cause painful, easily infected cuts.
4. Beware of sunburn, even when you are in the water.
5. Sea urchins have sharp spines.
6. Most animals bite; leave them alone.
7. Display a dive flag.

This booklet was prepared for your enjoyment by the staff of Biscayne National Monument, National Park Service., U. S. Department of the Interior. The Superintendent of Biscayne National Monument, whose address is P.O. Box 1369, Homestead, Fl., 33030, is in immediate charge.

As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's Department of Natural Resources. The Department works to assure the wisest choice in managing all our resources so each will make its full contribution to a better United States--now and in the future.

National Park Service
U.S. Department of the Interior

of these little germs are poured into the water surrounding a reef. There they swim about till they find a genial spot on which to establish themselves, when they become attached to the ground by one end, while a depression takes place at the opposite end, which gradually deepens to form the mouth and inner cavity, while the edges expand to form the tentacles, and the productive life of the little coral begins: it buds from every side, and becomes the foundation of a new community.

I should add, that, beside the Polyps and the Acalephs, Mollusks also have their representatives among the corals. There is a group of small Mollusks called Bryozoa, allied to the Clams by their structure, but excessively minute when compared to the other members of their class, which, like the other corals, harden in consequence of an absorption of solid materials, and contribute to the formation of the reef. Beside these, there are certain plants, limestone Algæ, — Corallines (Plate XXII.), as they are called, — which have their share also in the work. . . . .

A few miles from the southern extremity of Florida, separated from it by a channel, narrow at the eastern end, but widening gradually toward the west, and rendered every year more and more shallow by the accumulation of materials constantly collecting within it, there lies a line of islands called the Florida Keys. * They are at different distances from the shore, stretching gradually seaward in the form of an open crescent, from Virginia Key and Key Biscayne, almost adjoining the main-land, to Key West, at a distance of twelve miles from the coast, which does not, however, close the series, for sixty miles farther west stands the group of the Tortugas, isolated in the Gulf of Mexico. Though they seem disconnected, these islands are parts of a submerged coral reef, parallel with the shore of the peninsula and continuous underneath the water, but visible above the surface at such points of the summit as have fully completed their growth.

This demands some explanation, since I have already said that no coral growth can continue after it has reached the line of high water. But we have not finished the history of a coral wall, when we have followed it to the surface of the ocean. It is true that its normal growth ceases there, but already a process of partial decay has begun that insures its further

* See Map of Florida Keys, by Pourtalès, Memoirs, M. C. Z., Vol. II., Ill. Cat., No. IV. Also Pl. XXIII. of this Memoir, Sketch Map of the Straits of Florida.

ELKHORN REEF (Buoy No. 1)*

Named for the large branching colonies of elk, or moose, horn coral that dominate its northern and eastern flanks, Elkhorn Reef is a shallow, small scale piece of the deeper offshore reef. It is approximately 1600 feet (500 m) long, from north to south, and 640 feet (200 m) wide, from east to west. Even though the deepest water near the reef is less than 25 feet (7.5m), much of the biological zonation typical of deeper, offshore reefs is present.

From a seagrass and sand bottom to the east, the reef rises abruptly as small finger-like ridges alternate with sand bottomed ravines. The tops of the ridges are covered with elkhorn coral, which absorbs the energy of the gentle summer waves from the southeast, and filters the plankton from the open sea. Behind these front line defenders, is a shallow fire coral and rubble zone where the turbulence and sand from spent waves prevents all but the most hardy reef dwellers from living. As the water deepens slightly to the west, sea fans and sea whips wave and bend before the currents, and low profile brain and starlet corals hug the bottom. In the quieter waters of the back reef, small thickets of delicate finger coral and patches of lettuce coral are common. At the northwest corner of the reef, which receives the brunt of the winter storms, several large heads of common star coral and brain corals provide shelter for reef fishes.

Just as the corals on the reef are found in zones or patterns, the fishes that seemingly flit all over the reef can also be found in specific places. A few minutes of careful observation will reveal that some of the fishes, particularly the damsels, seldom leave the small areas of the reef they call home. The sponge eating queen angelfish, and their photogenic cousins, the French and gray angelfish, are typically found swimming amongst the elkhorn coral and crevasses on the eastern front of the reef. Others, like the grunts and black margates, select favorite resting places where they spend the daylight hours waiting to feed in the surrounding area at night. Groupers and barracudas also patrol certain portions of the reef, and can be predictably found, once you get to know the reef community and its various neighborhoods. On the other hand, some fish, like the blue tangs, ocean surgeons, wrasses, and parrotfish, are citizens-at-large and wander about the reef all day. Wander with them and enjoy the beauty and grace of the reef.

*25°21.7'N, 80°10'W

such an animal fully expanded, and found it to be a true Acaleph. It is exceedingly difficult to obtain a view of them in this state, for, at any approach, they draw themselves in, and remain closed to all investigation.*

With these branching corals the reef reaches the level of high water, beyond which, as I have said, there can be no further growth, for want of the action of the fresh sea-water. This dependence upon the vivifying influence of the sea accounts for one unfailing feature in the coral walls. They are always abrupt and steep on the seaward side, but have a gentle slope towards the land. This is accounted for by the circumstance that the corals on the outer side or the reef are in immediate contact with the pure ocean-water, while by their growth they partially exclude the inner ones from the same influence, — the rapid growth of the latter being also impeded by any impurity of foreign material washed away from the neighboring shore and mingling with the water that fills the channel between the main-land and the reef. Thus the coral reefs, whether built around an island, or along a straight line of coast, or concentric to a rounding shore, are always shelving toward the land, while they are comparatively abrupt and steep toward the sea. This should be remembered, for, as we shall see hereafter, it has an important bearing on the question of time as illustrated by coral reefs.

I have spoken of the budding of corals, by which each one becomes the centre of a cluster; but this is not the only way in which they multiply their kind. They give birth to eggs also, which are carried on the inner edge of their partition-walls, till they drop into the sea, where they float about, little, soft, transparent, pear-shaped bodies (Plate XVI. Figs. 7, 10, and 11), as unlike as possible to the rigid stony structure they are to assume hereafter. In this condition they are covered with vibratile cilia or fringes, that are always in rapid, uninterrupted motion, and by means of which they swim about in the water. These little germs of the corals, swimming freely about during their earliest phases of life, continue the growth of the reef, those that prosper at shallower depths coming in at the various heights where their predecessors die out; otherwise it would be impossible to understand how this variety of building material, as it were, is introduced wherever it is needed. This point, formerly a puzzle to naturalists, has become quite clear since it has been found that myriads

* See also Agassiz, L., Cont. Nat. Hist. U. S., Vol. III. Pl. XV. and H. N. Moseley, Phil. Trans. R. S., Vol. CLXVII. Part 1.

INTERPRETIVE
REEF

home nearer the surface; such a home being made ready for them by their predecessors, they now establish themselves on the top of the coral wall and continue its growth for a certain time. These are the Mæandrinas (Plate IX.), or the so-called Brain-Corals, and the Porites (Plates XII. and XVI.). The Mæandrinas differ from the Astræans by their less compact and definite pits. In the Astræans the place occupied by the animal in the community is marked by a little star-shaped spot, in the centre of which all the partition-walls meet. But in the Mæandrinas, although all the partitions converge toward the central opening, as in the Astræans, these central openings elongate, run into each other, and form waving furrows all over the surface, instead of the small round pits so characteristic of the Astræans. The Porites resemble the Astræans, but the pits are smaller, with fewer partitions and fewer tentacles, and their whole substance is more porous.

But these also have their bounds within the sea: they in their turn reach the limit beyond which they are forbidden by the laws of their nature to pass, and there they also pause. But the coral wall continues its steady progress; for here the lighter kinds set in, — the Madrepores (Plates XVII., XVIII., and XIX.), the Millepores (Plate XX.), and a great variety of Sea-Fans (Plate XXI.), and Corallines (Plate XXII.), and the reef is crowned at last with a many-colored shrubbery of low feathery growth. These are all branching in form, and many of them are simple calciferous plants, though most of them are true animals, resembling, however, delicate Algæ more than any marine animals; but, on examination of the latter, one finds them to be covered with myriads of minute dots, each representing one of the little beings out of which the whole is built, while nothing of the kind is seen in Algæ.

I would add here one word on the true nature of the Millepores, long misunderstood by naturalists. While pursuing my investigations on the coral reefs of Florida, one of these Millepores revealed itself to me in its true character of Acaleph. It must be remembered that they belong to the hydroid group of Acalephs, of which our common jelly-fishes do not give a correct idea. It is by their soft parts alone, — those parts which are seen only when these animals are alive and fully open, — that their Acalephian character can be perceived, and this accounts for their being so long accepted as Polyps, when studied in the dry coral stock. Nothing could exceed my astonishment when for the first time I saw

Schooner Wreck (Buoy No. 2)*

For centuries the Gulf Stream along Florida's east coast has formed an important shipping lane for vessels of both the new and old worlds. In the early 1700's, Spanish galleons laden with silver, gol and riches were sailing from the harbor of San Cristobal de la Habana (Havana) northward along the curving arc of the Florida Keys enroute to Spain's ports. In later years, sleek fast schooners engaged in inter-island and coastal trade, transited these waters.

The journey through the straits of Florida held many unpleasant possibilities. To the west, the great line of Florida reefs fringed the Keys and eastward were the shoals of the Bahama banks. Both coasts converge to a passage only fifty miles wide. With scarcely twenty five miles of water off either bow, early sailing ships blown only a little off course by storm winds or caught in a hurricane stood a high chance of running aground. In addition, strong currents of the Gulf Stream and prevailing southeasterly winds reduced the accuracy of navigation.

In 1733, a Spanish Armada of over twenty ships, each laden with riches, was caught in a hurricane in the straits. Nineteen of the galleons were washed onto the reefs and sunk during the storm. For centuries the lower coast of Florida became the graveyard of storm wrecked galleons and schooners. During the 1800's, coastal schooners carrying commercial trade goods frequently ran aground and salvaging wrecks became a profitable business for many residents along the Keys. With the development of steam engines, the construction of lighthouses to warn ships of danger, and weather services to forecast storms, passage through the straits of Florida became safer and the profits of salvaging died.

The name and fate of the ship sunk at this site is unknown, but it is believed to be a late 18th century schooner. A short swim over the remains of this schooner is a direct link to the great sailing days of the past. Typical of most wrecks, all that remains today are the piles of ballast rock which served to weight the hull of the ship, and a few scraps of coral encrusted iron. The wooden hull has long ago rotted away. Careful observation will reveal the original position of the keel left lying between the two piles of ballast rock. On the north side of the largest ballast pile, a large iron gear box (encrusted with fire coral) remains. White sand outlines the original extent of the wreckage.

Numerous species of tropical reef fish can be seen darting in and out of the mounds of ballast. A survey to the north will reveal three large beautiful star coral heads with several grouper and large snapper lying in holes underneath. To the south a short distance is a patch reef rising to within a few feet of the surface. Perhaps it was this reef that dealt the final blow to the ill-fated schooner. This small reef has an interesting variety of corals, sea fans, whips and plumes.

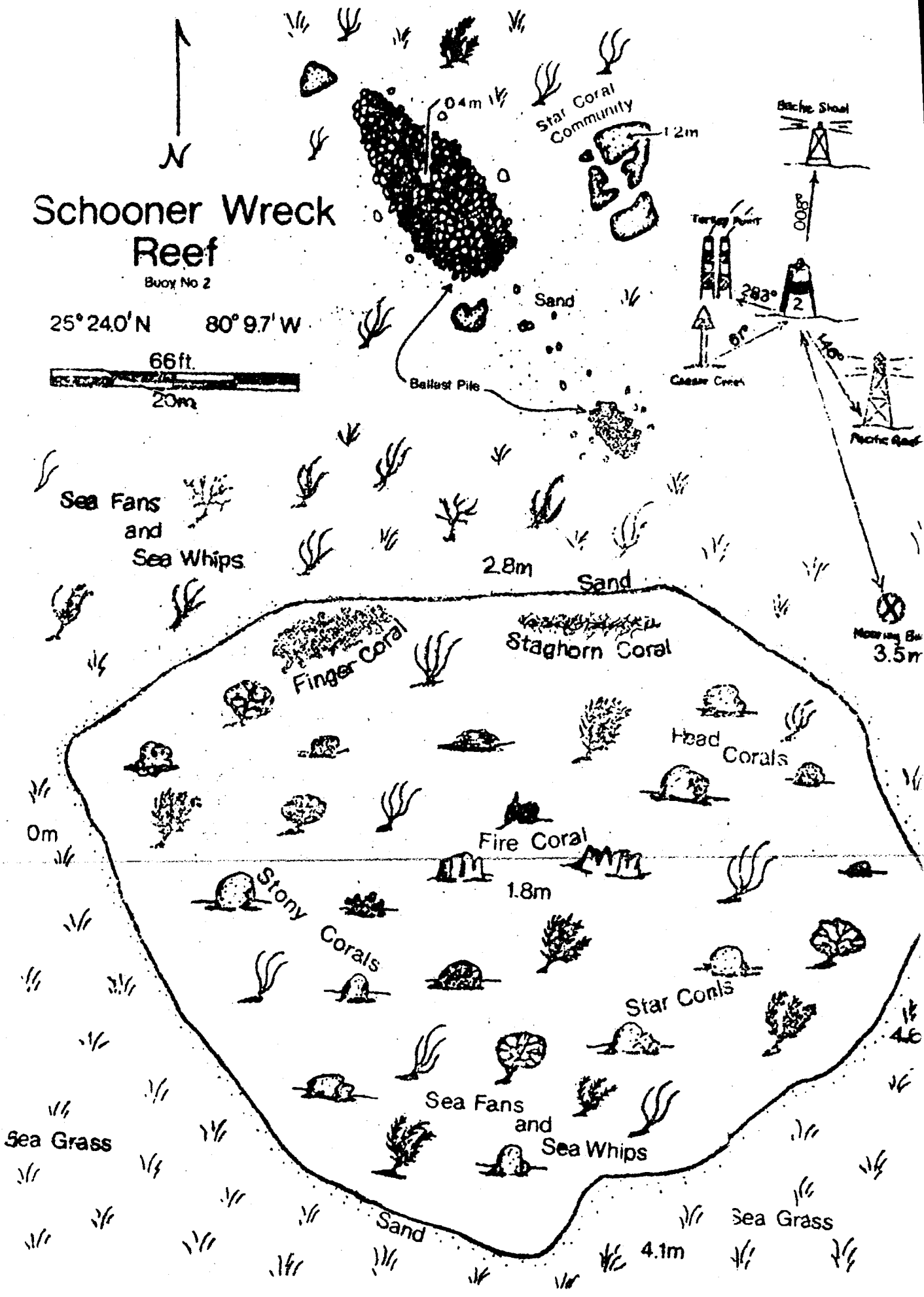
*25°24.0'N, 80°9.7'W

igneous mass of materials which formed its earliest condition, their investigation mingles with that of the astronomer, and we cannot trace the limestone in a little coral without going back to the creation of our solar system, when the worlds that compose it were thrown off from a central mass in a gaseous condition.

When the coral has become in this way permeated with lime, all parts of the body are rigid, with the exception of the upper margin, the stomach, and the tentacles. The tentacles are soft and waving, projected or drawn in at will; they retain their flexible character through life, and decompose when the animal dies. For this reason the dried specimens of corals preserved in museums do not give us the least idea of the living corals, in which every one of the millions of beings composing such a community is crowned by a waving wreath of white or green or rose-colored tentacles.

As soon as the little coral is fairly established and solidly attached to the ground, it begins to bud. This may take place in a variety of ways, dividing at the top or budding from the base or from the sides, till the primitive animal is surrounded by a number of individuals like itself, of which it forms the nucleus, and which now begin to bud in their turn, each one surrounding itself with a numerous progeny, all remaining, however, attached to the parent. Such a community increases till its individuals are numbered by millions; and I have myself counted no less than fourteen millions of individuals in a coral mass of Porites (Plate XVI.) measuring not more than twelve feet in diameter. The so-called coral heads, which make the foundation of a coral wall, and seem by their massive character and regular form especially adapted to give a strong, solid base to the whole structure, are known in our classifications as the Astræans, so named on account of the star-shaped form of the little pits crowded upon their surface, each one of which marks the place of a single more or less isolated individual in such a community.

Thus firmly and strongly is the foundation of the reef laid by the Astræans (Plate IV.); but we have seen that for their prosperous growth they require a certain depth and pressure of water, and, when they have brought the wall so high that they have not more than six fathoms of water above them, this kind of coral ceases to grow. They have, however, prepared a fitting surface for different kinds of corals that could not live in the depths from which the Astræans have come, but find their genial


Schooner Wreck Reef
Buoy No 2
25° 24.0' N
80° 9.7' W
66ft.
20m
N
0.4m
Star Coral Community
1.2m
Sand
Ballast Pile
Sea Fans and Sea Whips
2.8m
Sand
Finger Coral
Staghorn Coral
Head Corals
0m
Fire Coral
1.8m
Stony Corals
Star Corals
Sea Fans and Sea Whips
Sea Grass
Sand
4.1m
Sea Grass
Beacon Shoal
Turkey Point
283°
2
Cheese Creek
3.5m

with all these chambers. At the top is an aperture serving as a mouth, surrounded by a wreath of hollow tentacles, each one of which connects at its base with one of the chambers, so that all parts of the animal communicate freely with each other. But though the structure of the coral is identical in all its parts with that of the sea-anemone, it nevertheless presents one important difference. The body of the sea-anemone is soft, while that of the coral is hard.

It is well known that all animals and plants have the power of appropriating to themselves and assimilating the materials they need, each selecting from the surrounding elements whatever contributes to its well-being. Now corals possess, in an extraordinary degree, the power of assimilating to themselves the lime contained in the salt water around them; and as soon as our little coral is established on a firm foundation, a lime deposit begins to form in all the walls of its body, so that its base, its partitions, and its outer wall, which in the sea-anemone remain always soft, become perfectly solid in the polyp coral, and form a frame as hard as bone.

It may naturally be asked where the lime comes from in the sea which the corals absorb in such quantities. As far as the living corals are concerned, the answer is easy, for an immense deal of lime is brought down to the ocean by rivers that wear away the lime deposits through which they pass. The Mississippi, whose course lies through extensive lime regions, brings down yearly lime enough to supply all the animals living in the Gulf of Mexico. But behind this lies a question not so easily settled, as to the origin of the extensive deposits of limestone found at the very beginning of life upon earth. This problem brings us to the threshold of astronomy, for the base of limestone is metallic in character, susceptible, therefore, of fusion, and may have formed a part of the materials of our earth, even in an incandescent state, when the worlds were forming. But though this investigation as to the origin of lime does not belong either to the naturalist or the geologist, its suggestion reminds us that the time has come when all the sciences and their results are so intimately connected that no one can be carried on independently of the others. Since the study of the rocks has revealed a crowded life whose records are hoarded within them, the work of the geologist and the naturalist has become one and the same, and, at that border-land where the first crust of the earth was condensed out of the

STAR CORAL REEF (Buoy No. 3)*

This small patch reef is very similar to the reefs that built the Florida Keys 100,000 years ago. The bulk of the reef is made up of limestone skeletons from corals cemented together with a mortar of algae, broken shells and sea water. The huge, golden brown, living coral colonies along the western edge of the reef are common star coral, Montastrea annularis. This coral is the chief architect of most patch reefs in the monument.

The shallow center of the reef, only 8 feet (2.5 m) from the surface, is cluttered with purple sea fans and other soft corals. A quick swim around the reef reveals nearly half of the 50 kinds of stony corals found in Florida. Large spherical starlet and brain corals are readily apparent. The small and delicate cactus, flower, and leaf corals can be found by the careful observer on the edge of the reef where they are not exposed to storm waves that pound the flexible sea ships and sea feathers that occupy the top. Small clumps of staghorn coral are found on the southeastern, windward, edge, where they can take advantage of the turbulent water that the other stony corals dislike.

Over 50 kinds of tropical fish call this reef home, and many more can be seen just paying an occasional visit. A large school of hatchet-shaped glassy sweepers usually seeks shelter under the massive star coral heads on the northwest corner of the reef. Coppery reef crokers, with a black spot at base of each pectoral fin, are also commonly seen hiding behind the larger corals. The bolder damsel fishes like the sergeant major and dusky damsel hover over the corals, rise slightly to greet swimmers, and then dart back to their homes. Generally indifferent to human intruders, the colorful parrot fishes chew away at the stony corals with their bird-like beaks. If you listen carefully, you can hear each bite as they make sand out of the coral. The sand fills the crevasses in the reef, is cemented into rock, and more reef is built

Spiny lobsters hide in holes in the reef during the day, and range out onto the surrounding sea grass flats at night in search of sea biskets, young conchs, and other favorite foods. Heavy fishing pressure has severely reduced the number of lobsters found on this reef in recent years, so you will have to look hard to find the waving antennae that give them away as they sit far back in their lairs.

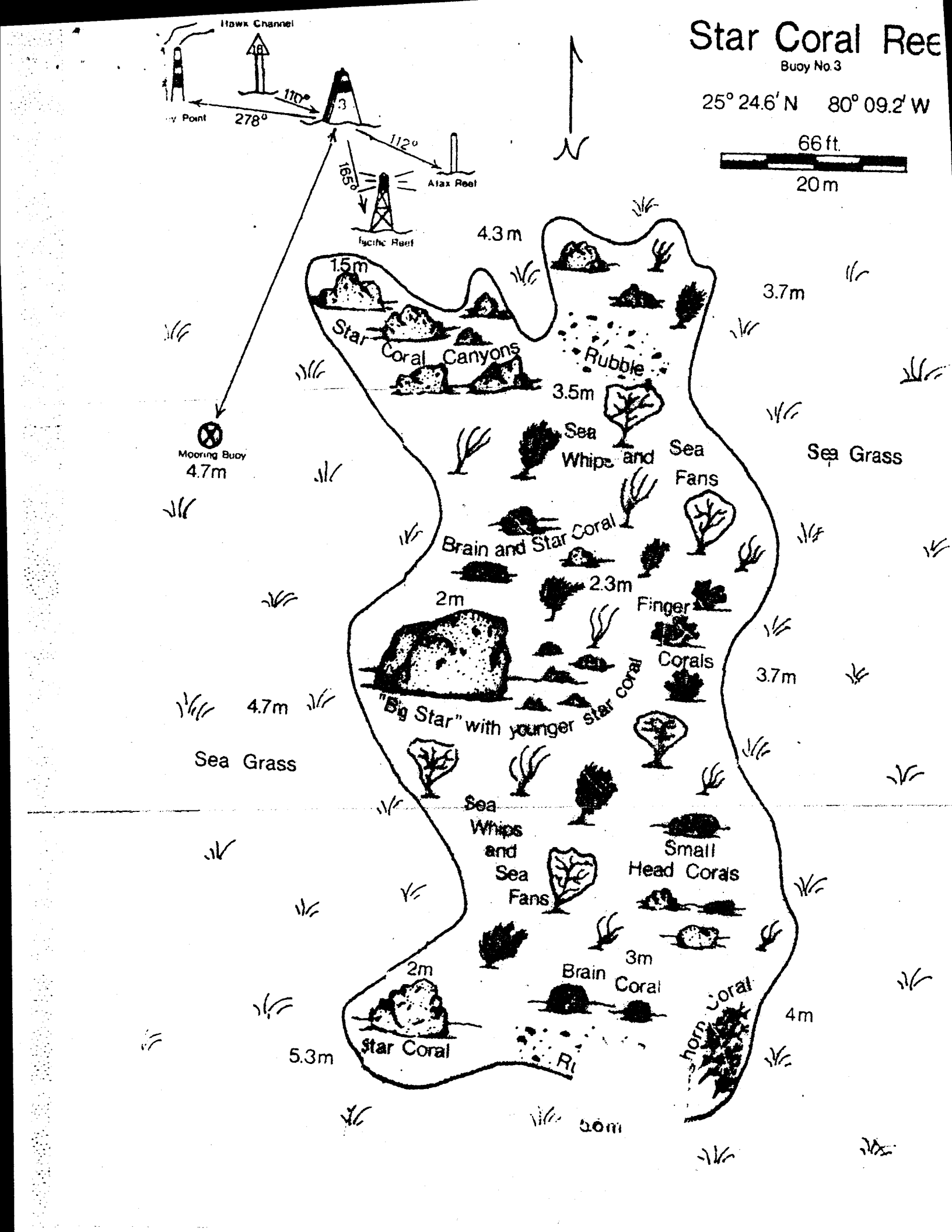
*25°24.6'N, 80°09.2'W

weight equal to that of three such atmospheres, which is reduced to one when it reaches the sea-level. The change is proportionally greater for those fishes that come from a depth of several hundred feet. These laws of limitation in space explain many facts in the growth of coral reefs that would be otherwise inexplicable, and which I now will endeavor to make clear to my readers.

For a long time it was supposed that the reef-builders inhabited very deep waters, for they were sometimes brought up on sounding-lines from a depth of many hundreds, or even thousands, of feet, and it was taken for granted that they must have had their home where they were found; but the facts recently ascertained respecting the subsidence of ocean-bottoms have shown that the foundation of a coral wall may have sunk far below the place where it was laid. And it is now proved, beyond a doubt, that no reef-building coral can thrive at a depth of more than fifteen fathoms, though corals of other kinds occur far lower, and that the dead reef-corals, sometimes brought to the surface from much greater depths, are only broken fragments of some reef that has subsided with the bottom on which it was growing. But though fifteen fathoms is the maximum depth at which any reef-builder can prosper, there are many which will not sustain even that degree of pressure; and this fact has, as we shall see, an important influence on the structure of the reef.

Imagine now a sloping shore on some tropical coast descending gradually below the surface of the sea. Upon that slope, at a depth of from ten to twelve or fifteen fathoms, and two or three or more miles from the main land, according to the shelving of the shore, we will suppose that one of those little coral animals, to whom a home in such deep waters is genial, has established itself. How it happens that such a being, which we know is immovably attached to the ground, and forms the foundation of a solid wall, was ever able to swim freely about in the water till it found a suitable resting-place, I shall explain hereafter, when I say something of the mode of reproduction of these animals. Accept, for the moment, my unsustained assertion, and plant our little coral on this sloping shore, some twelve or fifteen fathoms below the surface of the sea.

The internal structure of such a coral corresponds to that of the sea-anemone. The body is divided by vertical partitions from top to bottom (Plate I. Figs. 2, 3, and 4), leaving open chambers between; while in the centre hangs the digestive cavity, connected by an opening in the bottom


Star Coral Ree
Buoy No.3
25° 24.6' N 80° 09.2' W
66 ft.
20 m
Hawk Channel
110°
278°
112°
165°
Alax Reef
Pacific Reef
4.3 m
1.5m
3.7m
Star Coral Canyons
Rubble
3.5m
Mooring Buoy
4.7m
Sea Whips and Sea Fans
Sea Grass
Brain and Star Coral
2.3m
2m
Finger Corals
3.7m
"Big Star" with younger star coral
4.7m
Sea Grass
Sea Whips and Sea Fans
Small Head Corals
3m
Brain Coral
2m
Star Coral
5.3m
Elkhorn Coral
4m

We all live under the pressure of the atmosphere. Now, thirty-two feet under the sea doubles that pressure. At the depth of thirty-two feet, then, any marine animal is under the pressure of two atmospheres, — that of the air, which surrounds our globe, and of a weight of water equal to it; at sixty-four feet he is under the pressure of three atmospheres, and so on. There is a great difference in the sensitiveness of animals to this pressure. Some fishes live at a great depth, and find the weight of water genial to them; while others would be killed at once by the same pressure; and the latter naturally seek the shallow waters. Every fisherman knows that he must throw a long line for a halibut, while with a common fishing-rod he will catch plenty of perch from the rocks near the shore; and the differently colored bands of sea-weed revealed by low tides, from the green line of the ulvas through the brown zone of the common fucus, to the rosy and purple-hued sea-weeds of the deeper water, show that the floræ as well as the faunæ of the ocean have their precise boundaries.

This wider or narrower range of marine animals is in direct relation to their structure, which enables them to bear a greater or less pressure of water. All fishes, and, indeed, all animals having a wide range of distribution in ocean-depths, have a special apparatus of water-pores, so that the surrounding element penetrates their structure, thus equalizing the pressure of the weight, which is diminished from without in proportion to the quantity of water they can admit into their bodies. Marine animals differ in their ability to sustain this pressure, just as land animals differ in their power of enduring great variations of climate and of atmospheric pressure.

Of all air-breathing animals, none exhibits a more surprising power of adapting itself to great and rapid changes of external influences than the condor. It may be seen feeding on the sea-shore under a burning tropical sun, and then, rising from its repast, it floats up among the highest summits of the Andes, and is lost to sight beyond them, miles above the line of perpetual snow, where the temperature must be lower than that of the Arctics. But even the condor, sweeping at one flight from tropic heat to arctic cold, although it passes through greater changes of temperature, does not undergo such changes of pressure as a fish that rises from a depth of sixty-four feet to the surface of the sea; for the former remains within the air that surrounds our globe, and therefore the increase or diminution of pressure to which it is subjected must be confined within the limits of one atmosphere; while the latter, at a depth of sixty-four feet, is under a

DOME REEF (BUOY No. 4)*

Just east of turbid Hawk Channel, northeast of Margot Fish Shoal, this small patch of large coral heads demonstrates some corals' ability to withstand the cloudy water spilling out of the channel displacing the clearer reef tract waters. Although not as conspicuous as coral on this reef, algae are very important to reef growth and development. The decomposed skeletons of calcareous algae, like the bright green fingernail-sized plates of Halimeda growing amongst the corals, make up a significant portion of the sand that helps cement the reef structures together.

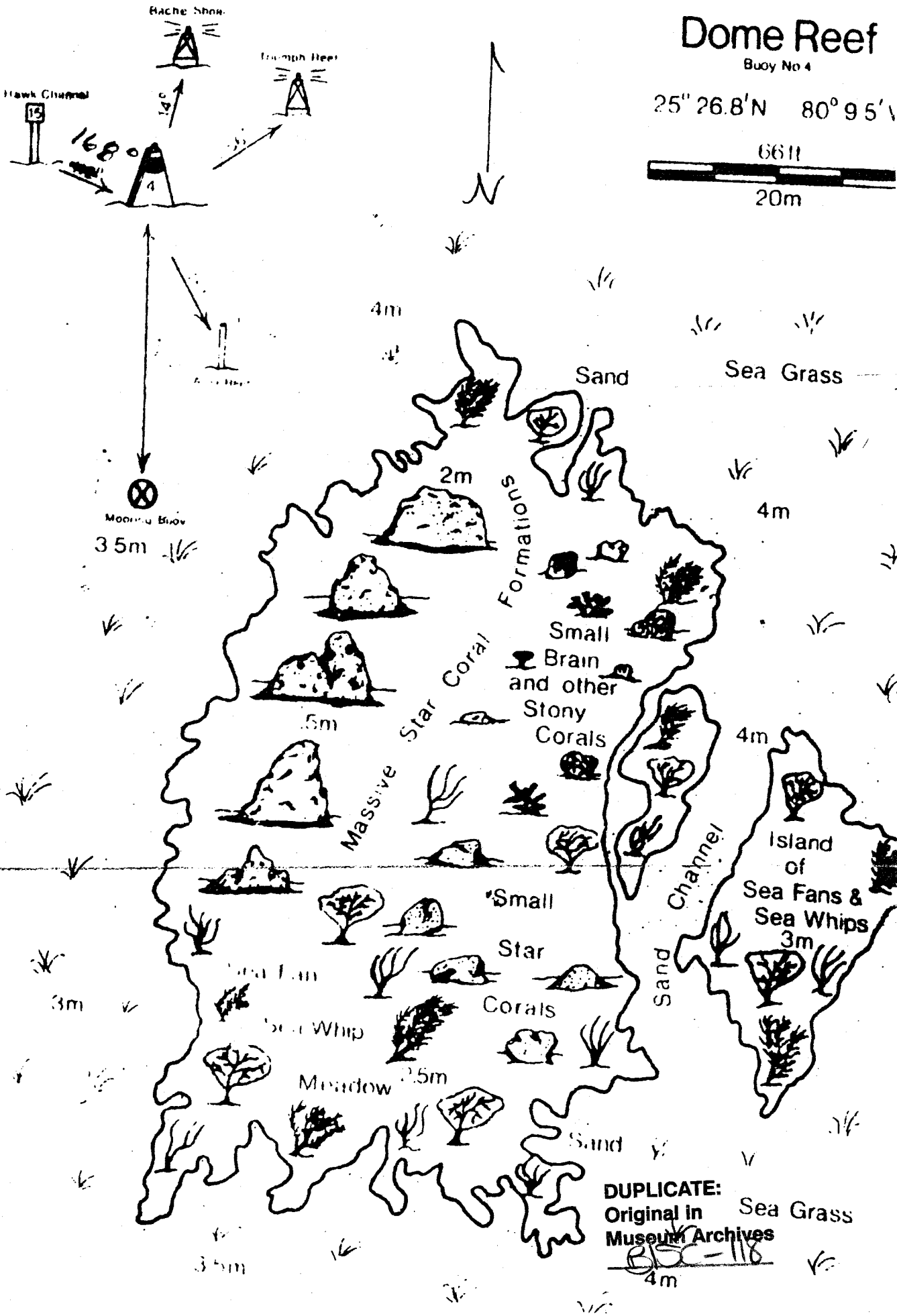
Another important non-coral reef builder is also common on this reef. More closely related to the dangerous stinging Portuguese Man-of-War than to the reef corals, the mustard colored Fire Coral encrusts the upper surfaces of many of the large coral heads along the western edge of the reef. All corals are sharp and can cause painful easily infected, cuts if touched. Fire Coral adds the sting of its microscopic harpoons to the problem. "Look; don't touch" is the slogan for the safe reef browser.

Other members of the reef community to watch from afar are the walking pincushions, or sea urchin s. Scientists call the large black spiny urchin Diadema for the jewel like spots nestled amongst its spines like a crown, or diadem. These urchins seek the shelter of the reef during the day, and graze on the sea grasses nearby at night, maintaining the sandy halo common around most patch reefs.

Brilliant colors and bizarre shapes identify yet another unsung group of reef builders, the sponges. They filter hundreds of gallons of sea water a day for food and oxygen, taking the water in through tiny holes all over their bodies, and pumping it out with their wastes through a few large holes on their upper sides. Their semi-rigid bodies contain thousands of intricate brittle spicules, shaped like children's jacks, dumb-bells, and other geometric designs. Released by the death of sponge, these spicules also add to the mortar of the reef.

The fish of Dome reef are typical of many patch reefs in this part of the Monument. Juvenile and adult parrotfish are especially common. The striped Tom Tate grunts school, while school master snappers hide between the corals, and daring seargeant major damsels challenge the swimmers to their piece ofthe rock.Many juvenile reef fishes use the patch reefs as nursery areas, or way stations on their journey to the outer reefs. It is a good place to look for the brilliantly colored juvenile angelfishes, porkfish, and several damsel fish that will display completely different color patterns as adults.

*25°26.8'N, 80°9.5'W



DUPLICATE:
Original in
Museum Archives
BSC-118

the slope of a high mountain in the Tropics, from base to summit, presents in a condensed form, an epitome, as it were, of the same kind of gradation in vegetable growth that may be observed from the Tropics to the Arctics. At the base of such a mountain we have all the luxuriance of growth characteristic of the tropical forest, — the palms, the bananas, the bread-trees, the mimosas; higher up, these give way to a different kind of growth, corresponding to our oaks, chestnuts, maples, &c.; as these wane, on the loftier slopes comes in the pine forest, fading gradually, as it ascends, into a dwarfish growth of the same kind; and this at last gives way to the low creeping mosses and lichens of the greater heights, till even these find a foothold no longer, and the summit of the mountain is clothed in perpetual snow and ice. What have we here but the same series of changes through which we pass, if, travelling northward from the Tropics, we leave palms and pomegranates and bananas behind, where the live-oaks and cypresses, the orange-trees and myrtles of the warmer temperate zone come in, and these die out as we reach the oaks, chestnuts, maples, elms, nut-trees, beeches, and birches of the colder temperate zone, these again waning as we enter the pine forests of the Arctic borders, till, passing out of these, nothing but a dwarf vegetation, a carpet of moss and lichen, fit food for the reindeer and the Esquimaux, greets us, and beyond that lies the region of the snow and ice fields, impenetrable to all but the daring arctic voyager?

I have thus far spoken of the changes in the vegetable growth alone as influenced by altitude and latitude, but the same is equally true of animals. Every zone of the earth's surface has its own animals, suited to the conditions under which they are meant to live; and, with the exception of those that accompany man in all his pilgrimages, and are subject to the same modifying influences by which he adapts his home and himself to all climates, animals are absolutely bound by the laws of their nature within the range assigned to them. Nor is this the case only on land, where river-banks, lake-shores, and mountain-ranges might be supposed to form the impassable boundaries that keep animals within certain limits; but the ocean, as well as the land, has its faunæ and floræ bound within their respective zoölogical and botanical provinces; and a wall of granite is not more impassable to a marine animal than that ocean-line, fluid, and flowing, and ever-changing though it be, on which is written for him, "Hitherto shalt thou come, but no farther." One word as to the effect of pressure on animals will explain this.

the rate of increase in the wall is greater than that of subsidence in the island, while the latter gradually sinks below the surface, the former rises in proportion, and by the time it has completed its growth the central island has vanished, and there remains only a ring of coral reef, with here and there a break, perhaps, at some spot where the more prosperous growth of the corals has been checked. If, however, as sometimes happens, there is no such break, and the wall is perfectly uninterrupted, the sheet of sea-water so enclosed may be changed to fresh water by the rains that are poured into it. Such a water-basin will remain salt, it is true, in its lower part, and the fact that it is affected by the rise and fall of the tides shows that it is not entirely secluded from communication with the ocean outside; but the salt water, being heavier, sinks, while the lighter rain-water remains above, and it is to all appearance actually changed into a fresh-water lake.

I need not dwell here on the further history of such a coral island, or follow it through the changes by which the summit of its circular wall becomes covered with a fertile soil, a tropical vegetation springs up upon it, and it is at last, perhaps, inhabited by man. There is something very attractive in the idea of these green rings enclosing sheltered harbors and quiet lakes in mid-ocean, and the subject has lost none of its fascination since the mystery of their existence has been solved by the investigations of several contemporary naturalists, who have enabled us to trace the whole story of their structure. I would refer all who wish for a more detailed account of them to Charles Darwin's charming little volume on "Coral Reefs," where their mode of formation is fully described, and also to James D. Dana's "Geological Report of the United States Exploring Expedition."

Coral reefs are found only in tropical regions: although Polyps, animals of the same class as those chiefly instrumental in their formation, are found in all parts of the globe, yet the reef-building Polyps are limited to the Tropics. We are too apt to forget that the homes of animals are as definitely limited in the water as on the land. Indeed, the subject of the geographical distribution of animals according to laws regulated by altitude, by latitude and longitude, by pressure of atmosphere or pressure of water, by temperature, light, &c., is exceedingly interesting, and presents a most important field of investigation.

The climatic effect of different levels of altitude upon the growth of animals and plants is the same as that of different degrees of latitude; and

early days. The stony face of the Sphinx is not more true to its past, nor the massive architecture of the Pyramids more unchanged, than they are. But the advocates of the mutability of species say truly enough that the most ancient traditions are but as yesterday in the world's history, and that what six thousand years could not do sixty thousand years might effect. Leaving aside, then, all historical chronology, how far back can we trace our own geological period, and the species belonging to it? By what means can we determine its duration? Within what limits, by what standard, may it be measured? Shall hundreds, or thousands, or hundreds of thousands, or millions of years be the unit from which we start?

I will begin this inquiry with a series of facts which I myself have had an opportunity of investigating with especial care, respecting the formation and growth of the coral reefs of Florida. But first a few words on coral reefs in general. They are living limestone walls, built up from certain depths in the ocean by the natural growth of a variety of animals, but limited by the level of high water, beyond which they cannot rise, since the little beings that compose them die as soon as they are removed from the vitalizing influence of the pure sea-water. These walls have a variety of outlines: they may be straight, circular, semicircular, or oblong, according to the form of the coast along which the little reef-builders establish themselves; and their height is, of course, determined by the depth of the bottom on which they rest. If they settle about an island on all sides of which the conditions for their growth are equally favorable, they will raise a wall all round it, thus encircling it with a ring of coral growth. The atolls in the Pacific Ocean, those circular islands enclosing sometimes a fresh-water lake in mid-ocean, are coral walls of this kind, that have formed a ring around a central island.

This is easily understood, if we remember that the bottom of the Pacific Ocean is by no means a stable foundation for such a structure. On the contrary, over a certain area, already surveyed with some accuracy by Professor Dana, during the United States Exploring Expedition, it is subsiding; and if an island upon which the reef-builders have established themselves be situated in that area of subsidence, it will, of course, sink with the floor on which it rests, carrying down also the coral wall to a greater depth in the sea. In such instances, if the rate of subsidence be more rapid than the rate of growth in the corals, the island and the wall itself will disappear beneath the ocean. But whenever, on the contrary,

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REEF DISTRIBUTION IN SOUTH FLORIDA

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ABSTRACT

The Florida Reef Tract contains approximately 96 km (kilometers) of outer bank reefs along the shallow shelf edge and more than 6000 patch reefs in the inner lagoon. Most reefs are located in the upper Keys seaward of Elliot Key and Key Largo Key. Patch reefs are extremely rare in the middle Keys although outer bank reefs are occasionally developed along the platform edge. Outer bank reef and patch reef development increases in the lower Keys between Big Pine Key and Dry Tortugas.

Reef distribution is controlled mainly by factors affecting exchange between the Reef Tract and coastal lagoons and Florida Bay. Of primary importance are: relative development of land barriers and tidal passes; orientation of the Reef Tract in relation to wind-driven winter currents; and exposure to Loop Current water and the effects of the Loop Current on local circulation.

KEY WORDS: Coral Reefs, Florida Reef Tract, Distribution (Reef), Circulation

SKETCH OF

THE FLORIDA REEFS AND KEYS.

REPRINTED FROM THE "METHODS OF STUDY."

THE physical as well as the human history of the world has its mythical age, lying dim and vague in the morning mists of creation, like that of the heroes and demigods in the early traditions of man, defying all our ordinary dates and measures. But if the succession of periods that prepared the earth for the coming of man, and the animals and plants that accompany him on earth, baffles our finite attempts to estimate its duration, have we any means of determining even approximately the length of the period to which we ourselves belong? If so, it may furnish us with some data for the further solution of these wonderful mysteries of time, and it is besides of especial importance with reference to the question of permanence of species.

Those who maintain the mutability of species, and account for all the variety of life on earth by the gradual changes wrought by time and circumstances, do not accept historical evidence as affecting the question at all. The relics of those oldest nations, all whose history is preserved in monumental records, do not indicate the slightest variation of organic types from the earliest epoch to this day. The animals preserved within their tombs or carved upon the walls of their monuments by the ancient Egyptians were the same as those that have their home in the valley of the Nile to-day; the negro, whose peculiar features are unmistakable even in their rude artistic attempts to represent them, was the same woolly-haired, thick-lipped, flat-nosed, dark-skinned being in the days of the Rameses that he is now. The apis, the ibis, the crocodiles, the sacred beetles, have brought down to us unchanged all the characters that superstition hallowed in those

REEF DISTRIBUTION IN SOUTH FLORIDA

D.S. Marszalek, G. Babashoff, Jr., M.R. Noel, and D.R. Worley

Introduction

The Florida Reef Tract extends from Miami southward along the Keys to Dry Tortugas. The reefs are within easy access of the densely populated Miami-Homestead area, and are important to the tourist based economy of the State as well as to the seafood and baitfish industries. The Keys have recently undergone large-scale development usually accompanied by removal of natural vegetation and shoreline modification. Increasing evidence of reef deterioration prompted the State Bureau of Coastal Zone Planning (Department of Natural Resources) to initiate a research and marine resource management program, the initial phase of which is an inventory of marine benthic communities and substrate-types, and the compilation of distribution maps. Aerial photography of the Reef Tract from Miami to the Marquesas Keys was completed last year using water-penetration aerial color film. Aerial photography coupled with ground-truthing reveals the accurate spatial distribution of benthic communities. Aerial photomosaics and color-coded maps at a scale of 1:24000 will be published upon completion of the project. Preliminary data focusing on coral reef distribution are presented in this report.

Distribution

Outer bank reefs

Approximately 96 km of outer bank reefs occur along the shallow platform edge between Fowey Rocks Lighthouse near Miami and the Marquesas Keys west of Key West, a distance of about 270 km measured at the 20 meter depth contour. The distribution of outer bank reefs is shown on Figs. 1-4. Table 1 indicates the extent of outer bank reef development at various locations in the Florida Reef Tract.

TABLE 1

Outer bank reef distribution in the Florida Reef Tract

Area	Outer Bank Reef (in kilometers)
Fowey Rocks to Broad Creek	22.2
Broad Creek to Tavernier Creek	34.3
Tavernier Creek to Big Pine Key	16.6
Big Pine Key to Marquesas Keys	22.6
TOTAL	95.8 km

The outer bank reefs are typically elongate features of variable vertical relief which occur at the shallow shelf edge between the 5 m (meters) and 10 m depth contours. Their long axes form a discontinuous line of reefs oriented parallel to the shelf edge. The northernmost reefs trend N-S and the reefs near Key West E-W reflecting the change in orientation of the arcuate shelf edge. Approximately 56 km of linear bank reefs are located north of Tavernier Creek (at the south end of Key Largo Key), 17 km of reefs in the middle Keys and 23 km in the lower Keys (west of Bi Pine Key). A spur and groove system is developed o the seaward face of most of the bank reefs, with th spurs and grooves oriented generally perpendicular t the shelf edge and to the incoming waves of the Florid Current. Spurs and grooves are best developed on oute bank reefs of the upper Keys (Figs. 1 and 2) and lowe Keys (Fig. 4); the spur and groove pattern on reefs ir the middle Keys (Fig. 3) is generally less developed an exhibits a more random orientation.

In an ecological sense Florida outer bank reefs are roughly comparable to the barrier reefs of the Caribbean and the Pacific but are biologically less diverse, relatively small in aerial extent, and lack the vertical reflief characteristic of true barrier reefs. Typically less than 10 m of vertical relief is formed by living corals in the Florida Reef Tract.

Florida outer bank reefs are highly variable in their degree of development. Our calculations of shelf-edge reef development are based on aerial photography and ground-truthing and include both well developed and poorly developed reefs.

Well developed outer bank reefs are characterized by a reef-flat formed of *in situ* dead encrusted *Acropora palmata* skeletons and rubble. Dominant reef-flat benthic macrobiota includes small heads of *Acropora*, *Porites*, and *Siderastrea*, encrusting *Millepora*, the echinoid *Diadema antillarum*, sponges, and the codiacean calcareous alga *Halimeda opuntia*. A fringe of massive oriented colonies of *Acropora palmata* forms the seaward face of the reef to a depth of about 4 m. *Millepora complanata* and the colonial zooanthid *Palythoa* also occur in the turbulent shallow zone. Deeper portions of the reef exhibit a diverse coral assemblage dominated by large heads of *Montastrea annularis*. Carysfort Reef and Key Largo Dry Rocks are representative of well-developed outer bank reefs.

At the other end of the spectrum of outer bank reefs included in our calculations are those reefs of sparse coral growth which lack the *A. palmata* zone. Although these reefs may have been *Acropora palmata* reefs in the past, they are now limestone ridges capped by a veneer of living coral and other reef organisms; most of the vertical relief including spurs and grooves is relict structure. Long Reef and French Reef in the upper Keys are representative of poorly developed outer bank reefs. Thus although approximately 34% of the platform edge between Miami and the Marquesas Keys is occupied by outer bank reefs, only a fraction of that percentage represents prolific *Acropora palmata* reefs.

Patch reefs

More than 6,000 patch reefs are found in the Florida Reef Tract between Miami and the Marquesas Keys. Most patch reefs occur 3 to 7 km from land between Hawk Channel and the outer bank reefs. A few isolated patch reefs, however, are found seaward of the

the keys and the main-land. In still more remote ages the present mud flats may become swamps, elevated above the reach of the tide-waters, like the Everglades; and this process may perhaps be extended to the present ship-channel. But unless some great revolution in nature modifies the present relative level between land and sea, it may safely be maintained that the present outer reef is the final southern boundary of the North American continent, and that the sooner a system of lighthouses and signals is established along the whole reef, the better; for this is, after all, the shore which is to be lighted, and not the range of keys which is within the reef. In relation to the western range of keys, and the western extremity of the reef, we may expect, in course of time, to see the depression between the Marquesas and Tortugas gradually lessened by the increase of the reef, so that the westernmost group of islands may finally stand in as close connection with the keys more to the west as they now bear to each other, the passage between them being reduced to as narrow a channel as Boca Grande, between the Marquesas and the Mangroves.

The shoals west of Cape Sable may, undoubtedly, also increase in extent westward; but how far the currents from the northwest may limit this accumulation, in connection with the changes which the currents themselves may undergo by the increase of the keys to the west, it is beyond the power of human foresight to determine.

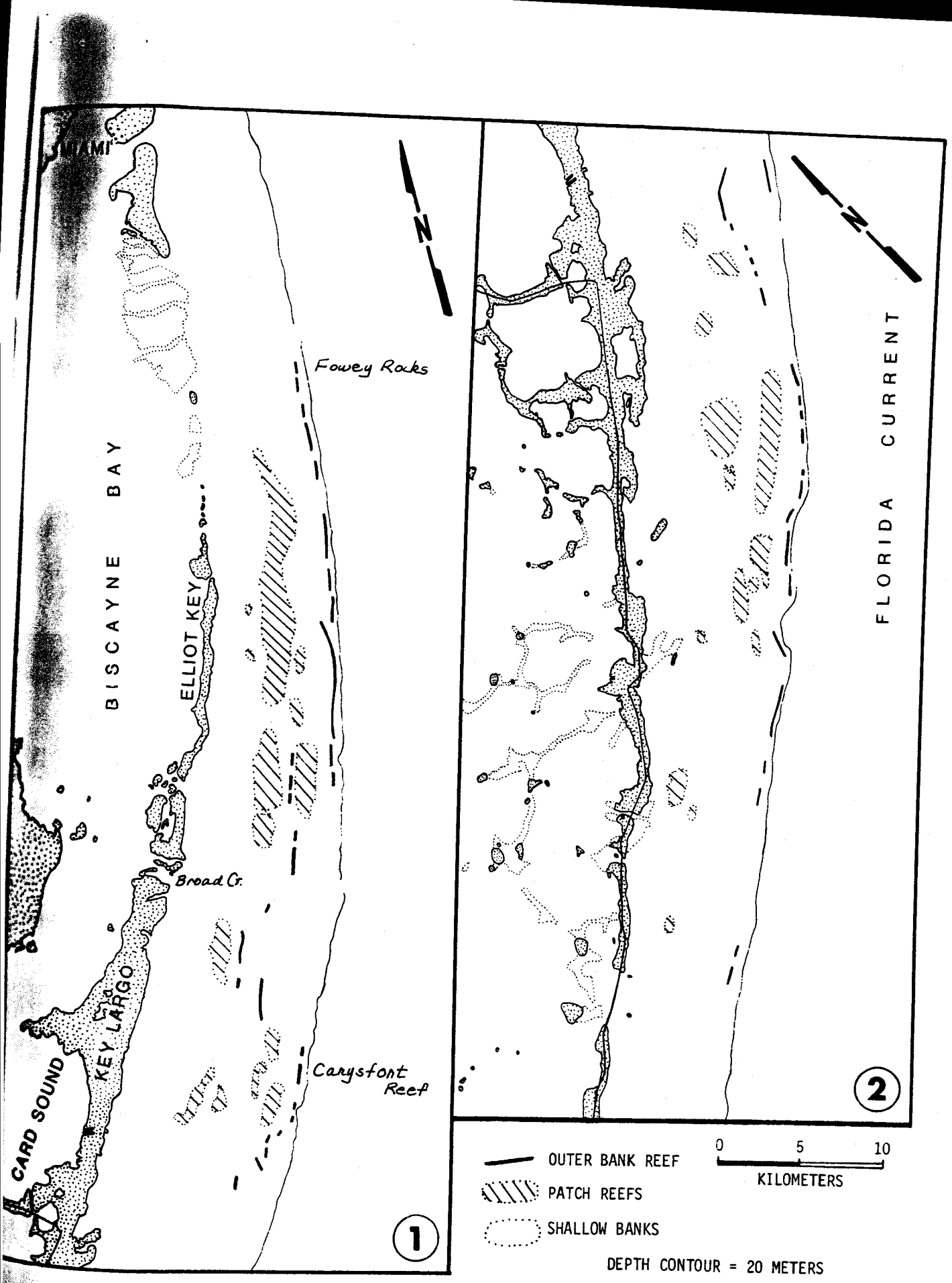
These practical results, — for so we venture to call the general conclusions last presented, — although they are purely scientific deductions from general principles, may satisfy the most obstinate supporters of the matter-of-fact side of all questions, of the advantages of scientific illustrations in the daily walks of life, and also justify the course which has been followed with so much success by the Coast Survey, in combining the strictest scientific methods with its practical operation.

Respectfully submitted,

L. AGASSIZ.

Professor A. D. BACHE,

Superintendent of the Coast Survey.


MIAMI
BISCAYNE BAY
ELLIOT KEY
Fowey Rocks
Broad Cr.
KEY LARGO
CARD SOUND
Carysfort Reef
FLORIDA CURRENT
N
N
1
2
OUTER BANK REEF
PATCH REEFS
SHALLOW BANKS
0 5 10
KILOMETERS
DEPTH CONTOUR = 20 METERS

Changes in Ages to come.

Among the questions contained in your instructions, you ask whether the growth of coral reefs can be prevented, or the results remedied, which are so unfavorable to the safety of navigation. I may say that here, as in most cases where the operations of nature interfere with the designs of man, it is not by a direct intervention on our part that we may remedy the difficulties, but rather by a precise knowledge of their causes, which may enable us, if not to check, at least to avoid the evil consequences. I do not see the possibility of limiting in any way the extraordinary increase of corals, beyond the bounds which nature itself has assigned to their growth. We have seen how successfully several reefs have been formed, more or less parallel, within the limits of the peninsula of Florida, as well as beyond the main-land. We have seen, also, how these parallel or concentric reefs have been gradually transformed into main-land by the accumulation of coral sand and mud with other loose materials, and also that the keys are now slowly annexed to the main-land, by the same process. We may, therefore, safely infer that, as far as the conditions exist for the formation of similar accumulations of loose materials, they will continue to occur, but they will never extend beyond the natural foundation from which a coral reef may rise; and as we now have sufficient evidence that this foundation is a sea-bottom, under from twelve to twenty fathoms, we may be satisfied that outside of the present outer reef, where the slope is steep, sinking rapidly to unfathomable depths, there is no opportunity for the growth of a new reef.

Here and there the reef may widen somewhat, towards the Gulf Stream, within those limits at which the depth does not exceed twenty fathoms; and from the knowledge we already possess of the soundings outside the reef we know positively that this is nowhere a broad stream. We may therefore rest assured that the changes which are going on will chiefly consist in bringing up the reef, for its whole extent, to the surface of the water, with occasional intervening channels kept open by the currents, such as exist now between the keys; that this reef once matured, will be covered by coral débris, becoming transformed into a range of keys, similar to that which exists now inside of it; that the depth of the ship-channel between the reef and the main range of keys will gradually lessen, and the channel itself be changed into mud flats, similar to those stretching now between


FLORIDA BAY
BIG PINE KEY
3
KEY WEST
MARQUESAS KEYS 5 KM
4

formed, and that then the channel between Cuba and Florida was wider still, washing freely over the grounds now known as the mud flats, between the keys and the main-land, and that there was then nothing to impede a free communication between the Gulf of Mexico and the Atlantic Ocean. The channel of the Gulf Stream was not only wider, — it was also less shallow along its northern borders; for the whole extent of soundings south of the main-land of Florida was an uncovered coral ground, upon which the deep-water species were just beginning to spread. But we may trace the change farther. There was a time when neither the southern bluffs of the continent, nor Long Key within the Everglades, nor even the Everglades themselves, existed; when, therefore, the Gulf Stream had a broad communication with the Atlantic, and the southern shores of the United States extended in almost unbroken contiguity from west to east, from the shores of Texas and Louisiana to St. Augustine. At that time the gulf-channel was, in reality, a broad bay, as broad as the gulf itself, destitute of all those obstructions which now cause the tropical current to follow such a circuitous course between the West India Islands, through the Caribbean Seas, and around the peninsula of Florida. The influence which the Gulf Stream has upon the climate of the Atlantic is so well known that its connection with the changes which the current itself has undergone within a comparatively recent period cannot be overlooked. If it is true, as we have every reason to believe, that the temperature of the Gulf Stream, in connection with the temperature of the southwesterly winds blowing obliquely across the Atlantic, modifies that of the western coast of Europe; if it is true that the Gulf Stream and the southwest winds have an influence in determining the course of the isothermal lines upon the two sides of the Atlantic, and of raising beyond their normal altitude the mean annual temperatures of northwest Europe, — then we may look to the physical changes which have occurred on the southeastern extremity of the North American continent for the cause — or at least a partial cause — of those changes of temperature which have taken place, in the beginning of the present period, in those very northwestern portions of Europe which are now so much warmer than the corresponding latitudes on the American continent, and which, soon after the accumulation of the glacial drift, had as low mean annual temperatures as the coasts of Labrador, Nova Scotia, and New England in our day.

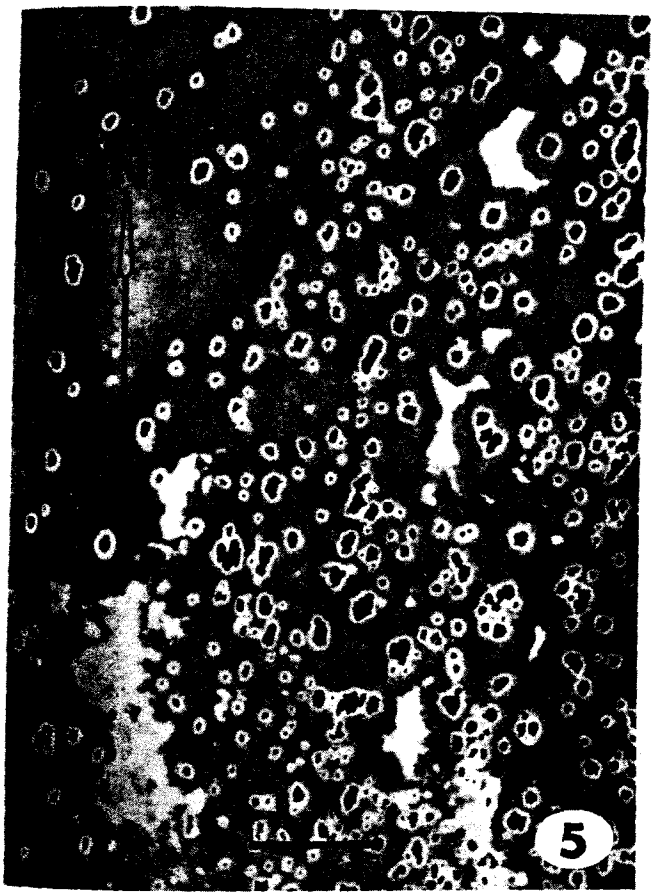


Figure 5. Patch reef density near Elliot Key, upper Keys. Note sand halos and topographic control on distribution. Dark areas are sea grasses, mainly Thalassia testudinum. Lighter areas indicate sparse sea grass cover or barren sand areas. Water depth approximately 7 m.

shallow shelf edge; others are found within 1.5 km of the Keys. Two basic types of patch reefs are recognizable: a) dome-type patch reefs, and b) linear-type patch reefs.

Dome-type patch reef are roughly circular or elliptical in plan view, show well developed sand halos, and usually occur in clusters. They range in size from a few meters to several hundred meters in diameter. Although generally less than 5 m in height, some exhibit as much as 9 m vertical relief. The patch reefs typically support a varied assemblage of scleractinian and octacorals, sponges, other invertebrates and algae. Except for the lack of A. palmata, the biota of dome-type patch reefs is similar to that found on the outer bank reefs but lacks the coral zonation characteristic of most shelf-edge reefs. Some dome-type patch reefs are formed of single enormous colonies of Montastrea annularis, usually with hollow cavernous interiors. M. annularis typically forms the highest relief on patch reefs more than 5 m in height.

Linear-type patch reefs are generally found seaward of the dome-type reefs, are arcuate or linear in plan view, tend to occur end to end in single or multiple rows, and exhibit the same orientation as nearby outer bank reefs. Unlike the dome-type patch reefs, these reefs are frequently colonized by Acropora palmata. When found on patch reefs, A. palmata colonies are smaller, more widely spaced, and lack the orientation characteristic of this species on the outer bank reefs. Linear patch reefs are clearly transitional between the bank reefs and the more numerous dome-type patch reefs.

The distribution of patch reefs in the Florida Reef Tract is highly irregular with most of the reefs clustered in relatively few areas. As seen in Table 2 and Figs. 1-4, most of the patch reefs are found in the upper Keys, very few in the middle Keys and the remainder in the lower Keys.

TABLE 2

Patch reef distribution in the Florida Reef Tract

Area	Approx. no. patch reefs
Fowey Rocks to Broad Creek	3,975
Broad Creek to Tavernier Creek	1,590
Tavernier Creek to Big Pine Key	50
Big Pine Keys to Marquesas Keys	420
TOTAL	6,035

Discussion

The preceeding data shows that south Florida reefs are not uniformly distributed along the coast but rather occur primarily in the upper Keys and secondarily in the lower Keys. Outer bank reefs are more evenly distributed than are patch reefs, which show their maximum development in the upper Keys. Field observations indicate that the most luxurient coral reefs are concentrated in the Key Largo Key area, especially within and seaward of John Pennekamp Coral Reef State Park. The observed distribution pattern is unusual in that the most prolific reef growth occurs near the northern limit for reef development in the Caribbean region. The lower Keys, although more "tropical", support fewer reefs. The remainder of this report will attempt to identify factors responsible for the observed distribution.

Factors controlling reef distribution

The Florida Reef Tract is bounded on the seaward side by the Florida Current (Gulf Stream) and on the landward side by the Keys. Exchange between the Reef Tract and coastal lagoons and Florida Bay is through a series of passes between the Keys. Tides at Miami are semidiurnal with a mean range of about 0.7 m which decreases gradually to the south. At Key West mean tidal range is about 0.4 m and tides are somewhat mixed reflecting the diurnal tides of the northern Gulf of Mexico.

Prevailing winds are from the southeast during

All the keys, all the islands along the whole extent of the reef, and all that part of the peninsula which consists of coral formations, have been formed by subaerial deposits accumulated under tidal agencies. The contrast between these subaerial deposits and the rock of submarine origin is striking. Near the shore the torrential character of the stratification is still evident; but at some distance from the islands and the main-land the strata are more regular, and contain, also, more and better-preserved fossil remains. The depth at which coral reefs start from some given foundation is stated by different authors to be from twelve to twenty fathoms. It would seem that the Florida reef has sprung up in somewhat shallower waters, for below ten or twelve fathoms there are no indications of living coral growth. The outer reef ends off the Marquesas in a depth of about ten fathoms. The ship-channel itself is only some ten fathoms in depth there, and very few coral heads are found in it. Add to this, that the depression between the Marquesas and Tortugas, though for the greater part not exceeding twelve or thirteen fathoms, is entirely unobstructed by coral heads, and that in the ship-channel there are very few coral heads noticed below a depth of six or seven fathoms. We are therefore inclined to believe that, in latitudes bordering on the Tropics, the normal depth for the foundation of a coral reef is from ten to twelve fathoms, and that, if they spring up from greater depths, it must be in the Tropics proper.

Physical Changes in the Gulf Stream.

There are several questions of the deepest scientific interest, which may be advanced by a due consideration of the facts observed upon the reefs of Florida. There we have a peninsula — a narrow, flat strip of land, projecting for about five degrees from the main-land — between the Atlantic Ocean and the Gulf of Mexico, and forming an effective barrier between the waters of the two seas, which otherwise, even by the change of a few feet in the relative level of the intervening peninsula, would communicate freely with one another; and this peninsula we now know to have been added to the continent, step by step, in a southerly direction.

We know that the time cannot be far behind us when the present reef, with its few keys, did not exist, and when the channel, therefore, was broader, and the Gulf Stream flowed directly along the main range of keys. We know, further, that at some earlier period the keys themselves were not yet

most of the year. Cold fronts are common during the winter and are accompanied by northerly winds, an increase in wind velocity, and a sharp drop in temperature. Circulation on the Reef Tract is affected by tides and wind-driven currents.

The northern portion of the Reef Tract exhibits the most extensive reef development. The area of luxurient reef growth is flushed by oceanic waters of the Florida Current which consistently flows near and occasionally over the platform edge in the upper Keys; the position of the Florida Current is more variable off the lower Keys, as explained later. Key Largo Key and Elliot Key effectively prevent exchange of shelf water with Barnes Sound, Card Sound, and Biscayne Bay. Outer bank reefs deteriorate from luxurient at Carysfort Reef to semi-barren rubble at Fowey Rocks over a distance of 48 km. Measurements of minimum water temperatures over various outer reefs made by Vaughn (1) during a 20 year period were 17.9°C off Key West, 18.2°C at Carysfort Reef, and 15.6°C at Fowey Rocks. The absence of coral reefs along the coast north of Biscayne Bay where tidal passes are not found indicates that waters north of Miami are generally too cold for coral reef development.

The northern extent for patch reef development, however, appears to be limited locally by tidal and wind-driven exchange between Biscayne Bay and the inner shelf, through the open area (known locally as the "Safety Valve") between Key Biscayne and the Ragged Keys. Patch reefs are extremely abundant off Elliot Key and disappear abruptly opposite the tidal passes north of the Ragged Keys. The northernmost patch reefs are mostly encrusted rubble and may have developed when sea level was lower and tidal exchange with Biscayne Bay reduced or non-existant.

Caesar's Creek and Broad Creek are tidal passes located between Elliot Key and Key Largo Key and connect the Reef Tract with south Biscayne Bay and Card Sound respectively (see Fig. 1). Patch reefs are present directly seaward of these tidal passes but are more numerous off Elliot Key (Fig. 5) to the north and Key Largo Key to the south. The presence of patch reefs near Ceasar's Creek and Broad Creek and their absence north of the Ragged Keys indicates that tidal exchange through the creeks is minimal compared to the Safety Valve. The mean tidal range which is 0.6 m in Biscayne Bay near the Safety Valve decreases to 0.22 m in Card Sound and 0.12 m in Barnes Sound (2). In a study of Biscayne Bay circulation Lee and Rooth (2) concluded that tides are not the primary flushing mechanism of the Bay, their effect being confined to the vicinity of the tidal passes. Flushing of Biscayne Bay occurs primarily through the Safety Valve (and artificial inlets to the north) during the winter months when south winds preceeding cold fronts push Card Sound water into Biscayne Bay, and Bay water out through the Safety Valve. They also observed that south winds may cause shelf water to flow into Card Sound, and Florida Bay water to flow into Barnes Sound through Jewfish Creek (2). The observed circulation in Biscayne Bay explains why patch reefs are abundant north of Ceasar's Creek and Broad Creek, and absent seaward of the Safety Valve.

Coral reefs are least developed in the middle Keys where passes between the Keys are most developed. Ginsburg and Shinn (3) noted that reefs occur mainly opposite land, where they are less exposed to Florida Bay water. The location of outer bank reefs relative to the tidal passes and the absence of patch reefs (Figs. 2 and 3) attest to the open circulation between the Reef Tract and adjacent Florida Bay. Although normal tidal exchange through the broad passes would be expected to affect reef development, the effect is intensified by the E NE - W SW orientation of the middle Keys. Northerly winds associated with cold fronts cool the shallow (2-4 m deep) Bay water and in effect push the turbid cool Bay water over the Reef Tract. During severe cold fronts and high wind velocities, Florida Bay water is likely to reach temperatures of 15°C or less. Wind-driven currents from the north coupled with the orientation of the middle Keys significantly increases the normal tide-induced encroachment of Florida Bay water over the Reef Tract. Abnormally cold water and the relative narrowness of the Reef Tract in this area prevent the development of patch reefs.

The increased land area of the lower Keys which reduces exchange of the Reef Tract with Florida Bay accounts for the observed increase in reef development west of Big Pine Key. The vast shallow shelf to the north and the E-W trend of the Reef Tract in this area, however, makes the reefs vulnerable to cold wind-driven currents during the winter months. Also detrimental to reef development are the effects of the Loop Current on circulation in the lower Keys. The Loop Current connects the Yucatan and Florida Curents in the eastern Gulf of Mexico. When least developed it occurs only in the southern Gulf; during times of maximum development the Loop Current may extend as far north as the Mississippi delta and may reach the west Florida shelf. Its exact location is highly variable throughout the year (4). Before flowing southward and eventually reaching the Keys, the Loop Current may interact with coastal water masses. Maul (4) reports the tracking of a low salinity water mass within the Loop Current which was 24 °/oo near the edge of the west Florida shelf, less than 30 °/oo along the cyclonic boundary in the Straits of Florida, and still showing low salinity values of 34.5 °/oo off the Georgia Coast. The westernmost Keys are most exposed to the Loop Current which may account for the absence of outer bank reefs along the shallow shelf edge near Dry Tortugas.

During a one year study of variation in Loop Current migration, Maul (4) observed that when found at its southernmost extent (off the coast of Cuba), the Loop Current affected circulation in the Keys causing Florida Bay water to flow south through the Keys. The Bay water moving over the shelf edge was visible in LANDSAT images and in ship track data. The combined effect of these factors is to make the lower Keys less hospitable than the upper Keys to the development of coral reefs.

least deranging the level of the latter. We must suppose this to be true for the main bluffs also, and for all the concentric ranges of hummocks and swamps lying within them. To suppose that in each instance these upheavals were strictly limited to one such narrow belt would be contrary to all our knowledge of such agencies. To suppose all the upheavals to have been simultaneous would be equally opposed to what we know of the mode of growth of coral reefs. Their formation must be successive, since the outer one cannot start till the completion of the previous one furnishes the necessary conditions for its foundation.

There is in reality but one way of accounting for this equality of level in the successive reefs; which is, to suppose that their loftiest ridges are the maximum height at which materials can be accumulated by the natural agency of gales, and we have sufficient evidence to justify the adoption of this view.

The fact that, at present, the highest tides, during the most severe gales, do not reach the level of the bluff summits along the shores of the main-land, or even that of the maximum height of Key Largo or Key West, does not invalidate this supposition, for when the shore bluffs of the main-land were formed, the ocean had full sweep over the ground now occupied by the reef and mud flats, which did not then exist; and when Key Largo and Key West attained their maximum height, the outer reef did not yet form a barrier, checking the violence of the Gulf Stream in that direction. But, even with the present obstruction, we have evidence of the occasional rise of the water to heights which fully justify our assumption that even the highest ridges on the shores of the main-land and on the reef have been formed by the action of severe gales. For, in the year 1846, the water rose eight and a half feet above high-water mark at Key Vacas. Key West was entirely inundated during the same gale; and though that island is somewhat protected by the reef, even at present, the rushes, driven upon it by the flood, may be seen among the trees and bushes, at a height almost equal to its loftiest summit. In 1841 the water rose ten feet above high-water mark at Cape Romaine, on the western shore of the peninsula.

These facts suffice to show that the explanation we have given of the formation of the reef is in accordance with the powers of the agencies to which it is ascribed, and, when taken in connection with the peculiar arrangement of the materials of which they consist, seems to us to prove the justness of this view.

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of paramount importance, were it only with reference to the position of lighthouses. But there is another subject connected with this investigation which is not less momentous. It is well known that, in the Pacific, coral reefs have been raised above the levels at which they were formed, by the agency of the living animals, and also that in other localities, sometimes in close connection with those just mentioned, the ground is subsiding. These changes have been so often observed, whenever coral reefs occur, that the idea of subsidence and upheaval is naturally connected with the features of coral reefs, and the question at once arises, whether the reefs on our shores are thus undergoing variations of level, independently of their natural growth. We have seen how extensive are the changes produced merely by the normal growth of the corals, and the facts accompanying their increase. It now remains for us to ascertain whether this growth has taken place, or does at present take place, upon ground which has changed or is now changing its relative level in reference to the sea.

The facts already described afford a sufficient answer to the question. We are satisfied that as far as coral formations have been observed upon the main-land of Florida, and within the present extent of the coral reefs, no change of the relative level has taken place either by subsidence or upheaval of the coral ground, and that all the modifications which the reef has presented at successive periods have been the natural consequence of the growth of reef-building corals, with the subsequent accumulation of their products in the manner described above.

I am sorry to differ from my friend, Mr. Tuomy, who, in an interesting account of an excursion to Florida, considers the upright coral heads standing above the water level as evidence of the upheaval of the reef. I have already shown that, although at the first glance the position of these heads suggests that they have grown where they are found, they are, in fact, detached boulders, accumulated where they now lie. Setting this aside, the whole coral field of Florida furnishes connected evidence that neither upheaval nor subsidence of the ground on which the coral formations rest has taken place. The maximum height of all these formations including the bluffs on the main-land, is the same, — between twelve and thirteen feet above high-water mark. If we ascribe their present level to a series of upheavals rather than to the natural accumulation on the spot, we must suppose each successive disturbance to have raised the more recent reef and range of keys to exactly the same height as the earlier ones, without in the

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Key, then a growing reef. Here we will stop, since our knowledge of the interior is not sufficiently exact to justify us in pushing our retrograde history farther. Let us reverse the process now, and, starting from Long Key as the then southernmost point of Florida, build seaward. Twelve or twenty miles from the shore the sea has a depth of some twelve to twenty fathoms, and there a reef begins to grow. Gradually it rises, till here and there it reaches the sea level in patches. On such patches broken fragments of coral, sand, and mud accumulate, and they are gradually fashioned into keys. Between this growing reef and Long Key there flows at first a channel; but by the accumulation of coral sand, mud, and débris of all sorts, from the reef or from the main-land, this channel is gradually transformed into a tract of mud flats. These flats are gradually raised to the surface of the water, and they, as well as the shore bluffs, become dry land. Perhaps before this process comes to an end another reef begins to rise, the conditions for its formation being pushed a little farther south by the shore bluffs themselves, since the corals prosper only on a certain slope and at a certain distance from the land. The foundation for the main range of keys is now laid; but the tract now occupied by the mud flats is still open sea, the powerful action of which we may trace to this day in the excavations and erosions of the shore bluffs. At last this new reef reaches the surface, here and there gradually forming the present main range of keys, while the open channel is transformed, by accumulation, into the present mud flats. The main range of keys, like the shore bluffs, determines the position for the next coral wall, and the present outer reef begins to rise, though nearer to the main range of keys then they had been to the shore bluff, because the sea bottom is steeper. As this last reef rises, it modifies, in its turn, the course of the surrounding waters, the channel between it and the keys begins to fill, the shoals encircling the islands increase, and we arrive at last at the present condition of things. We have thus followed the extension of the peninsula of Florida, through the successive annexation of a series of coral reefs, the most recent of which is still in the stage of active and rapid growth.

But it may be asked, What is the practical use of such detailed descriptions of the coral reefs for the coast survey? We need only allude to the universal impression of the dangers arising to navigation from the growth of such reefs to satisfy the most sceptical that a minute knowledge of the extent and mode of formation of those belonging to our own shores must be

almost entirely of fragments of shells, but the fact that the same shell-conglomerate occurs at Cape Sable, in the immediate prolongation of the southernmost shore bluff, convinces me that one and the same geological formation, identical in lithological character with the reef of Florida, and presenting only slight local modifications, extends all over the peninsula of Florida, at least as far north as St. Augustine. Leaving this point, for the settlement of which we have not yet sufficient data, let us limit our comparison to the southernmost extremity of the peninsula and the keys. Here, at least, there can be no doubt that the southernmost shore bluff represents another range of keys similar to the main keys lying north of the mud flats, and that the Everglades within those bluffs are in reality another more extensive mud flat, agreeing in every respect with those lying between the main range of keys and the main-land. The only difference is that the Everglades have risen, with time, above the level of the sea. Were the present mud flats partially drained, or were a few additional feet of soil accumulated and consolidated upon them, their depressions would then correspond to the swampy ground, and their raised portions to the dry patches on the Everglades, while the Mangrove Islands would represent the hummocks. Nor does the agreement end here. About twenty miles from the southernmost shore, within the first prairies, another line of hummocks runs parallel with the first, and with the shore. This ridge, with an instinctive appreciation of its true character, has been called the Long Key. In short, these hummocks and Everglades represent as many ranges of keys divided by mud flats, showing that the present keys and reefs of Florida are the last of a series of reefs advancing gradually from north to south, in a more or less concentric succession. Endeavoring to reconstruct this process, we should suppose that a long time ago, before the outer reef had grown up from its foundation, the present range of main keys was itself a growing reef, not yet reaching the surface. In the place of the mud flats now filling the space between the keys and the main-land was a channel as deep and unobstructed as that now lying between the main range of keys and the reef. Carrying the scene still farther back to an age for the duration of which we have no measure, the present shore bluffs are then the growing reef, rising to the surface here and there so as to form keys, while the southernmost part of the Everglades is changed to an open channel between the Long Key and the shore bluffs. Another backward step, and no reef rises between Cape Sable and Cape Florida, but the ocean beats against the Long

to the Post-pliocene, and does not seem to have noticed that it is of coral origin. The connection of these deposits with the Post-pliocene formations of South Carolina, although it seems very probable, needs further proof; but a fact of greater importance, and one about which there can be no doubt, is, that the shore bluffs of the main-land are identical in structure and mode of formation with the subaerial deposits of the main keys. The lithology of the main-land is identical with the rocks of the keys as well as its mode of formation. Along the whole course of the main-land to the edge of the Everglades the appearance is the same. Indeed, a belt of coral rock, several miles in width, encircles the southern coast of the peninsula of Florida. This belt seems like a range of elongated hillocks, because it is broken here and there by cuts and depressions similar to those which separate the successive islands in the main range of keys. Within this belt, on the landward side, begin those inundated prairies known as Everglades. The bottom of these fresh-water swamps consists of the same muddy, semi-oolitic and concretionary limestone so characteristic of the northern shore of Key West, especially about the barracks. The bottom is very uneven, so that the sheet of water covering it varies in depth from a few inches to four or five feet, and in more extensive depressions forms shallow lakes. Where the ground is completely inundated, silicious sand covers it; but wherever the solid foundation rises to the surface, a soft soil is formed by the accumulation of decomposing vegetable matter. Such patches are here and there quite extensive, rising sometimes like islands one or two or even three feet above the shallow waters, and sustaining large trees and a rich vegetation. Such overgrown islands are called *hummocks*, and they make picturesque breaks in the otherwise monotonous flats of the Everglades. I have not yet ascertained by direct observation the extent of this formation in a northerly direction; but Lieutenant Rodgers, who has crossed the Everglades in all directions, informs me that as far north as Lake Okeechobee, near the 27th degree of northern latitude, the character of the peninsula is the same as in those more southern portions which we visited together. Specimens from the shores of Lake Munroe, which I owe to the kindness of Count Pourtalès, satisfy me that these formations extend beyond the 29th degree of northern latitude. Even the Coralline in the neighborhood of St. Augustine, specimens of which have been furnished me by Lieutenant Rodgers, and by Captain Curtis, of Key West, must be, as I believe, the northern prolongation of the same deposits. It is true that the rock there consists

Dauphin Island Sea Lab

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CORAL FAUNAS OF THE FLORIDA KEYS: A REPORT ON THE KEYSWIDE CORAL REEF EXPEDITION

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higher and higher points on the stem, all of which throw out again fresh shoots. As these mangrove seeds are stranded in great numbers and often close together, such a plantation soon becomes the nucleus around which sand and mud accumulate. The most extensive and shoalest mud flats occur, therefore, wherever the mangrove islands rise. Here the Holothuria are most abundant, while the Gorgonia thrive better on a harder bottom, where the flats are covered with four or five feet of water. The flats and mangrove islands to the north of the Pine Islands and Boca Chica are less muddy, consisting rather of a coral sand resembling very minute oolites. The bottom becomes rather softer, however, to the seaward and north of Key West and Boca Chica. Sea-fans (Gorgonias) frequently occur in this region upon the harder bottom, especially where the flats slope northward into two or three fathoms of water. The sponges are generally found upon hard, smooth sand, or upon coral rock in five or six feet of water. They occur, however, even at a depth of three to five fathoms. We cannot explain the greater prevalence of the oolitic sand in the Pine Islands and Boca Chica group of keys. It may be owing to the greater width of this range of islands, or to the greater width of the reef which gave rise to their formation. Nowhere else do the keys cover so wide an area.

The Main-land.

A careful survey of all the varieties of rock occurring at Key West, as well as their peculiar superposition, had prepared us for a minute comparison between the keys and the main-land; but, nevertheless, we were no less surprised than delighted to find that the solid foundation of the main-land consisted of the same identical modifications of coral rocks which form the keys. Along all that part of the shore which was examined, as well as upon the shores of the Miami, we found everywhere the same coarse, oolitic rock, with cross-stratification, consisting of thin beds, dipping at various angles in different directions, precisely as we find it at the western extremity of Key West, excepting, perhaps, that the cross-stratification is here more prominent, the strata dipping more frequently in several directions within the same extent.

Attention has been called to the resemblance of the main-land to the keys, by Buckingham Smith, Esq., in his Report to the House of Representatives respecting the drainage of the Everglades. He refers the formation, however,

Ragged Keys and Soldier Key, the shoals are more distinct from one another, divided by broader and deeper channels than occur in any other part of the tract lying between the main keys and the main-land. This is explained by the freer influence of the Atlantic tides on this part of the reef, as compared with its more western range. West of a line extending from Black Point to Elliott's Key, the whole space between the main-land and the main keys is occupied by an almost uninterrupted mud flat, covered by a shallow sheet of water varying from four to five feet in depth, though in some occasional depressions it may measure seven feet or thereabouts. The monotony of this great stretch of mud flat is broken by the innumerable mangrove islands already mentioned, as well as by the shoaler flats left dry at very low water. What has been said of the shoals off Cape Florida applies equally to those here mentioned, and needs no repetition. The mode of formation of the Mangrove Islands, however, is both peculiar and interesting, and demands a few words of explanation. The mangroves are among the most important geological agents in this region; but for them the loose sand and mud would remain an ever-shifting ground of movable particles. To understand this we must know something of the mode of growth of the mangrove seed. Like that of all viviparous plants it germinates upon the parent stock, the new plant attaining a length of some six inches before it drops from the old tree. As these trees grow down to the water's edge, and as at high tide the interior of the Mangrove Islands is submerged, the new plants are of course dropped into the water, and are swept about and scattered by its movements. Like brownish-green sticks, fusiform in shape, they float about in great numbers, with the heavier end, where the root is to be, slightly sunk below the surface. Floating thus, they suggest the idea that a ship-load of cigars has been wrecked upon the reef, and swept inland by the tides. Presently these fusiform bodies are stranded along the edge of some mud flat, touching ground at last with their heavier loaded end. Their hold is at first very loose, but made to turn, by the rising and falling tides, like a rod upon a pivot, they soon work their way into the soft mud and plant themselves firmly. Immediately the long, rapidly-growing roots begin to shoot out and soon form a close screen, giving stability to all the loose materials about them and holding the mud and sand in place. So spreading is the root that a young mangrove, not more than two feet in height, will send its roots out in all directions over an area of some six feet. As it rises it constantly sends down new roots to reach the ground from

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CORAL FAUNAS OF THE FLORIDA KEYS: A REPORT ON THE KEYSWIDE CORAL REEF EXPEDITION

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tains which Gressly has called "Terrains de charriage." They show signs of attrition, but at the same time are so incrusted as to be protected from farther disintegration, during the transportation of the mud in which they are embedded. The general aspect of the reef indicates that all this mud is slowly moving from east to west, and encroaching upon the free growth of the corals; while it furnishes at the same time the minute materials, which in connection with coral sand fill the intervals between the coral heads and coral boulders. Where it is accumulated by eddies so as to approach the surface, it forms mud flats or may have given rise to the layers of muddy limestone described above.

Several of the keys adjoining the main range, and standing out somewhat into the channel, differ in structure greatly from the main keys. They are not formed by the accumulation of coral boulders and coral fragments upon the edge of the reef, but by the accumulation of coral sand and mud in eddies or shoals. They are, in fact, the highest mud flats, to the consolidation of which the mangrove growth upon them has contributed. Such are Rodriguez Key, Tavernier Key, Sister Key, Loggerhead Key. The formation of similar keys in the course of time may be foretold, off Old Rhodes, upon the Washerwoman's Shoal, and upon the middle ground off Sand Key. Let us suppose the accumulation of coral sand and mud between the main range of keys and the outer reef to have increased so as almost to fill the ship-channel, reducing its deepest part to some eight or nine feet of water, and a number of mangrove keys like Rodriguez and Tavernier to have been formed where we now have only sand shoals or banks and coral heads, as between Carysfort and Key Largo, for instance; we should then have precisely the same conditions as are now presented by the extensive mud flats lying between the main-land and the keys from Cape Sable to Cape Florida. Although we infer by analogy that, when the main keys were only a reef, their inner side supported live coral heads and was bordered by larger or smaller shoals of coral, and inhabited by a fauna similar to that now found in the ship-channel, nothing of all this is now to be seen in that locality. The coral heads and sand ridges have given place to extensive mud flats, intersected by shallow channels and shallow depressions, interspread with innumerable low mangrove islands arranged in little groups, or forming more continuous chains such as the Walker Keys, which stretch almost uninterruptedly, in a southerly direction, from the main-land to Key Largo. In the northernmost part of the reef west of the

the turning-point of the direction of the reef. Such heads occur again about a mile and a half off Vermont Key, half way between Key Tavernier and Indian Key, outside of which Gorgonia and sponges are very abundant, upon a hard, white sand bottom. Similar heads are seen between Long Key and Tennessee Reef, and nearer the reef there are shoals of white coral sand, covered with Gorgonia; but farther west, off Duck Key, the bottom becomes softer. Off Bahia Honda, again, it is rocky, — that is, studded with large heads, surmounted with soft, muddy sand. This change in the character of the bottom is more obvious westward, where the heads are fewer and the bottom more generally muddy, or covered with finer-grained sand. For instance, hard sand is observed between Loggerhead Key and Saddle bluff; but nearer the reef, as far as the American Shoals, we have soft mud, with shoals and coral heads. Off Boca Chica, the channel way has also a bottom of soft coral mud, while shoals, with coral heads, may be traced for three fourths of a mile along the shores, as, again, towards the Sambos, in a depth of from three to two fathoms. The softness of the bottom in the vicinity of Key West, considered in connection with the scarcity of coral heads in that region, shows that a soft mud formation is unfavorable for the growth of corals; and, indeed, this holds also good for the flats north of tke keys.

Between the main-land and the main range of keys, and north of Pine and Mangrove Islands where the mud flats are most extensive, no coral heads are seen. Some of the Gorgonias grow upon hard sand, others chiefly upon coral heads, others in the more muddy places. Gorgonia flabellum, for instance, is most abundant upon hard sand, while Gorgonia anceps is found on the mud flats, and Gorgonia dicotoma, again, upon coral heads. If the mud flats, especially when the mud is very soft and deep, are poor in animal life, they are favorable to the growth of the sea weeds known as limestone algæ, the tissues of which are filled with lime. The Nullipores, also of this family, grow either upon the dying corals near the level of low water or upon mud flats that are almost dry. We have been surprised at the general lack of animal remains in this mud, as well as at the singular appearance of such as were found in it. Shells otherwise well preserved were incrusted with Bryozoa or with patches of hardened mud. Neither did the corals show a clean surface; indeed, all the solid parts of animal remains brought up with this mud reminded us, in their state of preservation, of the fossils found in those beds of the Jura Moun-

INTRODUCTION

The scientific and popular literature agree that coral reefs of the western Atlantic have degraded over the past several decades (e.g., Shinn 1989; Aronson et al. 1994; Ginsburg 1994). In general, the cover of reef-building corals has decreased and the cover of fleshy, non-coralline macroalgae (henceforth "macroalgae") has increased. In the Florida Keys, the severity of this degradation and its causes remain controversial (Porter et al. 1982; Jaap 1984; Dustan and Halas 1987; Porter and Meier 1992; Jaap et al. 1994; Lapointe et al. 1994; Szmant and Forrester 1996). Little is known about the usual condition of western Atlantic coral reefs, because rigorous ecological studies began only a few decades ago. The first monitoring effort at the scale of the Florida reef tract began in 1995 (Wheaton et al. 1996). Debate currently centers on whether the decline in coral cover and the increase in macroalgal cover in the western Atlantic are novel occurrences, or whether such changes occurred in the past (Jackson 1991, 1992; Woodley 1992; Aronson and Precht in press).

Reef ecologists have recognized the need for large-scale surveys and long-term monitoring studies of coral reefs, especially where declines appear to be associated with coastal development and expanding human populations (Buddemeier and Smith 1988; Rogers 1988; Ray and Grassle 1991; Ginsburg and Glynn 1994; Ogden et al. 1994; Chiappone et al. 1996). Unfortunately, surveys and monitoring programs are not popular in the scientific community at large, because most such programs lack guiding hypotheses that are of general interest (Hughes 1992; Aronson et al. 1994). Furthermore, research grants tend to be limited in size and of short duration. The Keyswide Coral Reef Expedition was conceived as a multidisciplinary effort to conduct a hypothesis-driven, synoptic survey of the biota of the entire Florida reef tract. The Expedition emphasized deeper reef habitats, which are not normally studied in the Florida Keys and which are not part of other monitoring efforts.

Twenty named and unnamed reefs were surveyed at 13-19 m depth from Biscayne Bay to the Dry Tortugas during the summer and fall of 1995. On most of the reefs, this depth range is characterized by spur-and-groove habitat. The primary goal of the project was to identify the spatial scales at which significant variation occurs in the structure of floral and faunal assemblages. The portion of the project reported here involved videographic sampling of sessile faunas at each reef to measure variation at the following spatial scales (Fig. 1):

(1) among 25-m long transects on adjacent spurs, which are separated by several meters,
(2) among subsections of reefs ("subreefs") within reefs, where subreefs are defined as portions of a reef approximately 1250 m^2 in area and separated by a linear distances of 0.5-1 km,
(3) among adjacent reefs, separated by several kilometers, within each of the five regions of the Florida Reef Tract (the Upper, Middle and Lower Keys, the Marquesas, and the Dry Tortugas), and
(4) among adjacent regions, each up to 50 km long, within the 250-km long reef tract.

Scales 3 and 4 were of primary interest for testing hydrographic and biogeographic hypotheses. For example, if the ecology of reefs is strongly influenced by the flow of inimical waters from Florida Bay through passes between the Keys (e.g., Ginsburg and Shinn 1964, 1994), there should

width throughout, with the exception of those few places where the reef widens, or the mud flats from the keys encroach upon it. Its narrowest passages are between Looe Key and the Pine Islands, between Pickle's and French Reefs, and between Key Rodriguez and Tavernier. Is is also somewhat narrowed between Alligator Reef and Indian Key, and is widest off Key West. Its depth varies also slightly, being shoaler in its eastern range than to the west. The shallowest part is between Pickle's Reef and Key Rodriguez, and between Looe Key and Pine Islands.

But if we do not take into account those spots where the depth is reduced from local circumstances, we may say that, as a whole, the ship-channel begins to the east, with a depth of about two fathoms between Fowey Rocks and Soldier Key, increasing gradually thence until it reaches three fathoms between Pacific Reef and Old Rhodes, then becomes again slightly reduced between Carysfort Reef and Key Largo; after which, with the exception of the shoals between Pickle's Reef and Key Rodriguez, it deepens again to three, four, five, or even six fathoms, until, between Looe Key and Pine Islands, it shoals once more to fourteen feet. Farther on, it increases again to five, six, and seven fathoms, the average depth between Key West and the Reef being five or six fathoms; and still beyond, more towards the west, sinks to eight, nine, and ten fathoms between the western extremity of the Marquesas and the western end of the reef, where it spreads into the great depression separating the Tortugas from the Marquesas. The character of the bottom varies in different parts, as do also the living beings which it supports. Where it is the most shoal, as between Fowey Rocks, Triumph Reef, and Long Reef, on one side, and Soldier Key and the Ragged Keys on the other, the bottom consists of coral sand, overgrown with what is called the country *grass;* that is to say, a variety of the limestone algæ mingled with Gorgonia, among which rise a number of coral heads.

These heads are hemispheres of Porites or Astræa. In the shoaler parts Mæandrinas and Millepora alcicornis also occur; they are more numerous near the reef than near the keys, and are, indeed, the inner expansion of the reef itself where the corals are less continuous, forming isolated patches rising out of coral sands.

To the west of Long Reef, especially between Carysfort and Key Largo, the coral sand rises here and there in the form of shoal sand-banks, intermixed with coral heads, — an arrangement which is probably owing to the more rapid currents flowing in that part of the channel, which is precisely

SUMMARY

Coral reef communities have declined along the Florida reef tract, but the magnitude and causes of that degradation remain controversial. Part of the problem stems from the inappropriate extrapolation of small-scale patterns observed on individual reefs to much larger scales. The Keyswide Coral Reef Expedition was conceived as a multidisciplinary effort to conduct a hypothesis-driven, synoptic survey of the biota of the entire Florida reef tract.

To achieve a better understanding of patterns of variation among regions of the reef tract, variation among reefs within regions, and variation within reefs, we videographically sampled replicate transects on 20 reefs at 13-19 m depth from Biscayne Bay to the Dry Tortugas. Of the 20 reefs sampled, 16 were characterized by spur-and-groove habitat in this depth range. Three of the 16 spur-and-groove sites--Carysfort, Tennessee and Western Sambo Reefs--were each sampled in three areas ("subreefs"); these subreefs, or reef subsections, were separated by <1 km.

Coral cover (from point counts), species diversity (*H'*; also from point counts), and the number of coral colonies were estimated for each video transect. A nested Analysis of Variance (ANOVA) design was used to compare the variation among Carysfort, Tennessee and Western Sambo Reefs to the variation among subreefs within those reefs. For both coral cover and *H'*, this analysis revealed low variation among subreefs within reefs but significant variation among reefs. A nested ANOVA on the coral colony count data revealed significant variation at both the among-subreef and among-reef levels. Cluster analysis of multivariate coral cover data (point counts partitioned by species) showed that subreefs within reefs were more similar to each other than they were to subreefs from different reefs. Cluster analysis of multivariate coral colony count data yielded similar results.

A second series of nested ANOVAs compared variation among reefs (10-km scale) to variation among regions of the reef tract (50-km scale), again based on coral cover, *H'* and coral colony counts. Variation in these univariate measures was again significant at the among-reef scale. Significant inter-regional variation was also detected. That variation became non-significant for coral cover and *H'*, but not for coral colony counts, when the isolated reefs of the Dry Tortugas region were removed from the analysis. Thus, variation among subreefs adequately predicted variation within the reef as a whole, but variation among reefs within regions outweighed variation among regions. Cluster analyses of multivariate coral cover, coral colony count and species presence/absence data supported these conclusions. When the four hardground sites were included in these cluster analyses, they generally clustered together, indicating that substratum type influences the composition of the coral assemblage living in this depth range.

The results suggest that there are no geographic gradients in coral cover or the composition of coral assemblages in the habitat and depth range studied. Coral cover and assemblage composition may be related to the distances reefs from passes between the Keys; community structure in this depth range may be affected by inimical waters from Florida Bay. Thus, reef community composition is probably determined by the interaction of multiple factors that act at the scale of the individual reef and at larger scales.

water mark, but lies several feet below that. The able engineer now building a lighthouse on that very spot has provided against a similar misfortune by uncovering the reef as the first step in his work. Mr. Dana has already pointed out another fact of the utmost importance, with reference to the construction of lighthouses. Even the lower and more solid mass of the reef is not continuous throughout, but has cavities filled with sand, débris, loose material of all kinds. Any point selected for the erection of a lighthouse should, therefore, be carefully surveyed, and the solidity of the reef should be tested by boring small holes throughout its thickness. If not weakened by such cavities, it will afford a safe foundation for beacons, signals, or lighthouses. The reef-building corals are, indeed, not only the largest, but also the most compact and hardest, and their order of succession in their growth, with the closer, heavier kinds below and the lighter ones above, give durability and strength to their masonry. The foundation of the reef is built by the massive heads of Astræa and Porites, in the middle range Mæandrinas and Milleporas come in, and only above these do we find the Madreporas, the stoutest and strongest of which form the uppermost growth upon the reef of Florida. As if to give additional firmness to the structure, the dying corals, as they reach the surface, become incrusted with Nullipores of different kinds. One species forms a close coating of the hardest limestone, not less than half an inch thick, over the dead corals. In the empty spaces grow other more branching kinds, which gradually fill the small cavities and act as a natural mortar cementing the whole. Upon this basis the broken, floating materials are thrown up, forming that loose cap of sand and débris which rests on the top of the reef and is liable to be carried away by storms.

The reef in its easternmost part north of Fowey Rocks, and in the direction of Bearcut and Virginia Bay, converges toward Cape Florida. Here it is covered by silicious drift sand, as are also the keys north of Cape Florida. The character of these formations, evidently the work of corals like other parts of the reef, favors the supposition that the longitudinal narrow islands stretching in almost unbroken continuity along the eastern coast of the peninsula are, like the Everglades upon the main-land, a prolongation of the reef now covered by drift sand.

Ship-Channel.

The broad channel extending the whole range of the reef, between the main keys and the outer reef, is rather uniform, having the same

be significant variation in community composition among reefs within regions. However, understanding variation at scales 1 through 3 was an important prerequisite to testing those hypotheses; the search for pattern and process on a large scale is meaningless unless it can be asserted with confidence that the sampling protocol selected provides a representative sample of each reef.

This report first examines variation in coral assemblages at the smaller scales. We compare the variation among subreefs within reefs to (1) the variation among reefs, and (2) the variation within subreefs, in order to answer the question: does a sample of transects from a subreef adequately represent the community composition of the reef as a whole? We then ask a question about variation at the two larger scales: does greater variability in community composition occur at the scale of the individual reef or at the scale of the region within the Florida reef tract? After answering these questions, we test explanations for the observed patterns of large-scale variability.

STUDY AREAS

The locations of the 20 sampled reefs are shown in Fig. 2. Study sites were selected based on the following criteria:

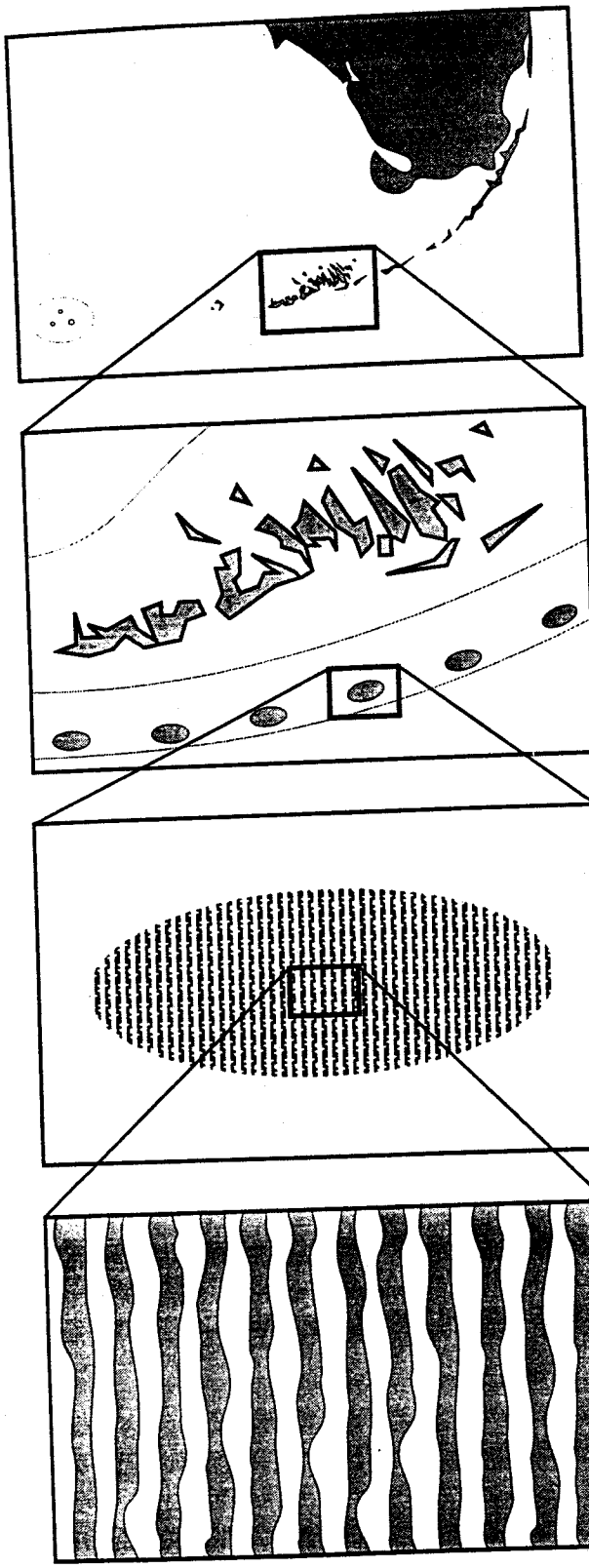
(1) evidence of a deep spur-and-groove zone in aerial photographs (when available), or
(2) the occurrence of hard substratum in the 13-19 m depth range.

Sites were selected so as not to be directly opposite emergent areas of reefs; where portions of a reef were emergent, the area sampled was located away from that section (i.e., up or down the reef tract from the emergent area). In order to select the precise spot at which sampling commenced, a buoy on a weighted line was dropped from the surface at a haphazard position in the area of interest. Each site was then assessed visually to determine the type of habitat that occurred at 13-19 m depth. Although most of the areas sampled were in fact spur-and-groove habitats, four of the reefs were characterized by limestone pavement (hardground) habitats (Table 1). This report is primarily concerned with data from the 16 spur-and-groove sites, which comprise a large sample size of the same habitat type on different reefs. The four hardground sites are then considered in relation to the spur-and-groove sites.

The reefs were numbered for reference during the survey work. At the analysis stage, they were re-designated with letters, beginning with Tortugas Bank, the westernmost site in the Dry Tortugas, and proceeding in order along the Reef Tract to the northernmost site, Fowey Rocks. Reefs were partitioned into regions following two schemes: (1) the hydrographically-based classification of Klein and Orlando (1994), and (2) the more traditional classification used, for example, by Shinn et al. (1989).

Three spur-and-groove reefs were sampled repeatedly in different locations for the reef-subreef comparison: Western Sambo Reef (reef G), Tennessee Reef (reef M), and Carysfort Reef (reef Q). These reefs are situated in the Southern, Middle, and Northern Keys, respectively. The Carysfort site was the outer of two fore reef terraces (Dustan 1985). Apart from their location in different regions of the Keys, the three reefs were chosen arbitrarily and for logistical

island formed chiefly of broken shells and coral fragments thrown up on the edge of the reef, a new feature begins. The higher ledges approach each other again, and the depressions between them are shallower than those to the east. We have here in close succession from east to west the American Shoal under six feet of water, the Pelican Reef with about four feet of water, and East, Middle and West Sambos, three little keys of a few acres in extent, consisting chiefly, like Looe Key, of broken shells and coral fragments, forming so light a crust upon the edge of the reef that storms occasionally wash away the whole accumulation. Between West Sambo and Sand Key, another depression on the reef, with a depth of water varying from four to five fathoms, forms the main channel leading into Key West. Toward Sand Key the reef widens considerably, but the corals are less crowded upon it. Large accumulations of coral sand intervene between the living heads, and detached masses and fragments of corals are thrown up in quantities upon the ridge, forming extensive shoals. To the east of Sand Key these shoals are known as the Eastern Dry Rocks and Rock Key; to the west, as the Western Dry Rocks. Sand Key itself is a small island also consisting chiefly of coral fragments and coral sand heaped above the field of large coral boulders stretching almost uninterruptedly from Eastern Dry Rocks to Western Dry Rocks. This part of the reef contrasts remarkably with the Sambos, and, taken together, they explain the process by which a living reef is transformed into a dry key. At the Sambos as at Carysfort we have a field of Madrepora palmata mixed with a few stocks of Millepora alcicornis and bunches of Gorgonia rising as a level ledge to the surface of the water at low tide. Upon the most prominent points of this ledge, coral boulders and sand are accumulated, every such accumulation forming the nucleus for a key. Comparing such incipient keys with Sand Key, we there find that the collection of coral boulders and sand has increased so much as to cover entirely the summit of the once living reef, spreading also far down upon its slopes. Before the storm of 1846, vegetation was spreading over Sand Key, and a lighthouse was built upon it. In the hurricane of the 11th of October, the lighthouse was washed away with the mass of coral boulders on which it stood. This mass of loose materials had in fact been mistaken for continuous coral rock sufficiently solid to support the structure based upon it. This unfortunate event has shown that the loose cap resting upon the more solid reef should always be removed before laying the foundation of a lighthouse. The solid rock is not to be reached at the level of low-



100-km scale: Regions within the Keys province.

10-km scale: Reefs within regions.

1-km scale: Subreefs within reefs.

0.1-km scale: Transects along spurs within subreefs.

Fig. 1. Hierarchy of scales of analysis of the Keyswide Coral Reef Expedition.

Madrepora palmata) as with a close shrubbery. One is reminded of the bank or beds of Kalmia or rhododendron spreading so uniformly over certain favorable spots. These beds of Madrepora palmata are yellowish in color, and broken here and there by a few heads of Millepora alcicornis or Mæandrina labyrinthica. The growth is so close that there are hardly any intervals to be filled by dead corals. Only on the borders of the ledge, and especially to the leaward where it slopes to the ship-channel, do we find accumulations of coral sand and coral débris between the heads of the Mæandrinas and Porites. These become more numerous as the depth increases, and are accompanied by a great variety of Gorgonia. Within the ship-channel the accumulation of coral sand increases, and several sand ridges may be traced parallel to Carysfort Reef along its inner slope, rising to some eight or nine feet below the surface of the water. Upon these sand ridges may be seen occasional heads of Mæandrina, patches of Millepora and Madrepora, and also a variety of Gorgonia, especially the beautiful purple Gorgonia flabellum, known as the sea-fan. On the steep seaward slope, and below the range of the Madrepora palmata, the heads of Mæandrina and Porites are very numerous. To the west of Carysfort, the edge of the reef sinks to a depth of some nine or ten feet, the greatest depression on the reef west of Cape Florida. Between the reefs above mentioned, for instance, there is hardly anywhere more than six or seven feet of water, so that from Fowey Rocks to Carysfort Reef we have an unbroken range of living corals. French Reef, again, is separated from Pickle's Reef by a depression of about ten feet, as is also Conch Reef from Crocker's Reef. Between this and Alligator Reef the depression is still greater; about twelve feet. The outer reef itself rises for a longer stretch near the surface at Alligator Reef than anywhere else west of Carysfort or east of Sombrero. Between Alligator and Tennessee Reefs, and between these and Coffins Patches, there is upon the edge of the reef not less than fifteen to seventeen feet of water, and about twenty between Coffins Patches and Sombrero. Sombrero is a small island of a few acres, formed of large coral fragments heaped up on the edge of the reef. Between Sombrero and Looe Key another large depression occurs on the reef some twenty feet deep throughout.

Thus not only are the higher ledges upon the reef gradually separated by wider intervals, but the reef itself, as a whole, is deepening westward, as is shown by the increasing depth and extent of the depressions. In fact the reef, as well as the mud flats, dips from east to west. At Looe Key, a small

Table 1. List of reefs surveyed during the Keyswide Coral Reef Expedition. Letter designations correspond to geographic position; the original numbering scheme is also presented for reference. Regional classifications: Klein and Orlando (1994); Shinn et al. (1989). Shading indicates hardground habitats.

Regional Classification					
Klein	**Shinn**	**Reef**	**Habitat Type**	**Letter**	**Number**
Dry Tortugas	Dry Tortugas	Tortugas Bank	Hardground	A	28
		Bird Key Reef	Spur & Groove	B	27
		Pulaski Shoal	Spur & Groove	C	30
Marquesas Key	Lower Keys	28-ft Shoal	Hardground	D	31
		Cosgrove Shoal	Spur & Groove	E	24
		Sand Key Reef	Spur & Groove	F	21
Lower Keys		W. Sambo Reef	Spur & Groove	G	20
		American Reef	Spur & Groove	H	18
		Looe Key Reef	Spur & Groove	I	17
Middle Keys	Middle Keys	No Name Reef	Spur & Groove	J	15
		Sombrero Reef	Spur & Groove	K	14
		Love Reef	Spur & Groove	L	32
		Tennessee Reef	Spur & Groove	M	11
		Alligator Reef	Spur & Groove	N	10
Upper Keys	Upper Keys	Pickles Reef	Spur & Groove	O	8
		The Elbow	Spur & Groove	P	6
		Carysfort Reef	Spur & Groove	Q	5
		Ajax Reef	Spur & Groove	R	3
		Triumph Reef	Hardground	S	2
		Fowey Rocks	Hardground	T	1

selves. Living in communities, death begins first at the base or centre of the group, while the surface or tips still continue to grow, so that it resembles a dying centennial tree, rotten at the heart, but still apparently green and flourishing without, till the first heavy gale of wind snaps the hollow trunk and betrays its decay. Again, innumerable boring animals establish themselves in the lifeless stem, piercing holes in all directions into its interior, like so many augers, dissolving its solid connection with the ground, and even penetrating far into the living portion of these compact communities. The number of these boring animals is quite incredible, and they belong to different families of the animal kingdom: among the most active and powerful we would mention the date-fish, Lithodomus, several Saxicava, Petricola, Arca, and many worms, of which the Serpula is the largest and most destructive, inasmuch as it extends constantly through the living part of the coral stems, especially in Mæandrina.

On the loose basis of a Mæandrina, measuring less than two feet in diameter, we have counted not less than fifty holes of the date-fish, — some large enough to admit a finger, — besides hundreds of small holes made by worms.

But however efficient these boring animals may be in preparing the coral stems for decay, there is yet another agent, perhaps still more destructive. We allude to the minute boring-sponges, which penetrate them in all directions, until they appear at last completely rotten throughout.

The outer reef, or, as it is generally called on the spot, *The Reef*, is the main seat of the present activity and growth of the reef-building corals in Florida. This reef consists of a narrow wall, rising nearly to the surface of the water, with a steep seaward slope, and a gentler one on the inner side toward the ship-channel. Its greatest width varies from one to two miles, though it is frequently not more than half a mile wide. This is true, for instance, of all those narrow ledges which have risen to within a few feet of the surface, such as Fowey Rocks off Soldier Key, Triumph Reef off Ragged Key, Long Reef off Elliott's Key, Ajax Reef off Cæsar's Creek, Pacific Reef off Old Rhodes, Turtle Reef off the eastern extremity of Key Largo, and the extensive reef of Carysfort facing for several miles Key Largo. This spot is one of the most instructive on the reef. Here the reef, for a stretch of several miles, nearly reaches the surface and forms a long level ledge entirely covered with living corals (chiefly the large spreading

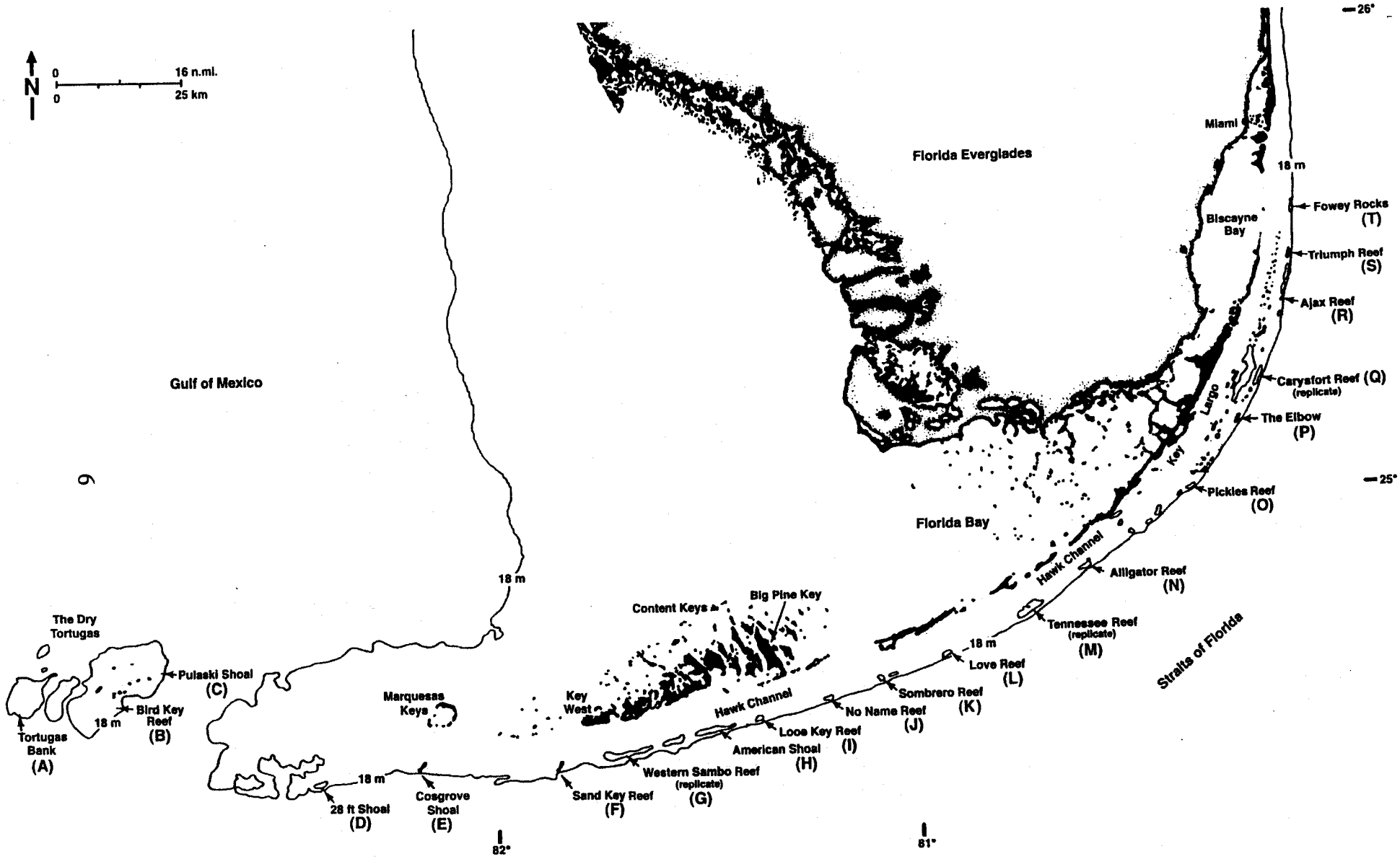


Fig. 2. Study sites of the Keyswide Coral Reef Expedition. Modified from Shinn et al. (1989).

around a submarine hill. The group consists of a circle of flat, low islands, not far apart from one another, divided by deep channels and enclosing a sheet of water, — a circular harbor as it were. Instead of steep walls like the Pacific lagoons, these islands have extensive shoals; but the channels and the harbor are deep, safe, and accessible, so that the fort now rising upon Garden Key will have especial advantages as a maritime station. These islands are not built of the débris of coral animals. The rock consists chiefly of the remains of corallines. This confirms my belief that they have grown up around a submarine rising ground; for the coralline or limestone Algæ, especially that kind of coralline of which the Tortugas rock is chiefly composed, do not prosper in deep water, but thrive on shoal flats. The reef-building corals have combined with this extensive coral vegetation to bring the Tortugas to their present condition. It seems, at first, astonishing that a sea-plant should build these extensive rocky islands. But we must remember that the corallines absorb lime and form limestone secretions no less than the stony corals themselves. Indeed, the coralline rocks of the Tortugas are no more an anomaly than the coal beds: in the former, the rock is built of the limestone secretions of the plants; in the latter, of their woody or cellulose tissue.

Coral Reefs.

After examining a growing coral reef, so full of life, so fresh in appearance, so free from heterogeneous materials, in which the corals adhere so firmly to the ground, or, if they rise near the surface, seem to defy the violence of the ocean, standing uninjured amid the heaviest breakers, an observer cannot but wonder why, in the next reef, the summit of which begins to rise above the level of the water, the scene is so completely changed. Huge fragments of corals, large stems, broken at their base, gigantic boulders, like hemispheres of Porites and Mæandrina, lie scattered about in the greatest confusion, — flung pell-mell among the fragments of more delicate forms, and heaped upon those vigorous madrepores which reach the surface of the sea.

The question at once arises, how is it that even the stoutest corals, resting with broad base upon the ground, and doubly secure from their spreading proportions, become so easily a prey to the action of the same sea which they met shortly before with such effectual resistance? The solution of this enigma is to be found in the mode of growth of the corals them-

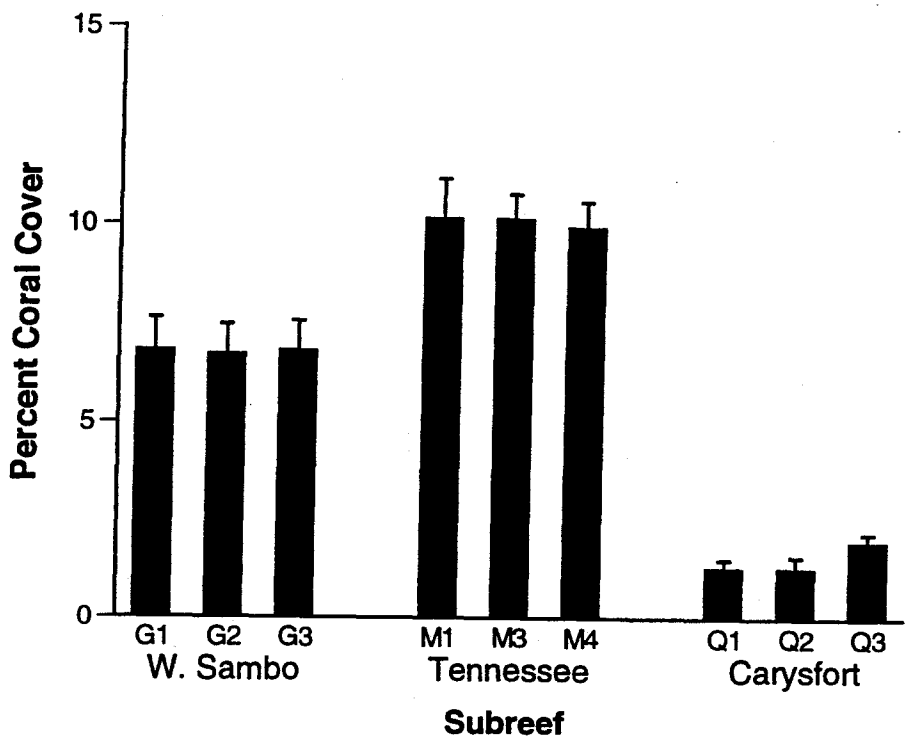


Fig. 3. Mean percent coral cover at the 9 subsites. Error bars represent standard errors.

Table 2. Results of one-way nested ANOVA on arcsine-transformed coral cover.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Reef	0.651	2	0.323	323.000	< 0.0005
Subreef{Reef}	0.006	6	0.001	0.561	0.760
Error	0.141	81	0.002		

promontory of Key West. Upon this island, also, the intervening seams of compact limestone between layers of oolite are especially numerous; and here the superficial crust is more continuous than elsewhere, frequently consisting, beside the compact limestone, of small fragments of oolite rock, with patches here and there of oolitic sand. Occasionally such a mixture entirely fills large excavations, — excavations worn by the tides in former ages, and filled again by later deposits. Along the northern shores, where flat beds, similar to those of the Pine Islands, extend under the mud flats, their dip is but from two to three or four degrees. Near the fort, where the oolitic beds have been quarried for building purposes, they have a dip of seven or eight degrees, the stratification being clearly indicated by successive seams of compact limestone, and also by the projecting edges of the seams of coarser oolite rising from the vertical walls of the artificial excavations. The so-called Mangrove Islands, west of Key West, constitute a group of low keys connected by mud flats, similar to all the other mangrove islands north of the Pine Islands and of Key West. They may be considered a prolongation of the extensive flats encircling the whole group of keys from the upper Bahia Hondas to Boca Grande. They are separated from Key West by a navigable ship-channel, running north-northwest like those intersecting the Pine Islands, showing that, notwithstanding the more westerly course of Key West and the whole Boca Chica group, all this part of the reef has a common character. The westernmost groups, the Marquesas and Tortugas, although they lie in the direction of the main range of keys, have again another character.

The islands forming this group are among the most interesting of the whole reef, because, without the phenomena of subsidence to which the Atoll or Lagoon Islands of the Pacific are due, they nevertheless closely resemble them in character. The Atolls in the Pacific are formed by the sinking of some island around which corals have established themselves. By the growth of the corals the reef rises as the foundation subsides, and finally reaches the surface as a ring often broken by channels and enclosing a harbor. In such cases the wall of the reef is precipitous and often sinks to a depth at which the reef-building corals cannot live. But, as the process is very gradual, the dead base of the reef affords a foundation for the living portion until the latter finally reaches the water level.

It is my belief that the Tortugas (though no change has taken place in the sea-bottom on which they rest) were built up by the coral growth

convenience, with no *a priori* regard to their community composition. The subreef areas were designated by numbers (e.g., M1, C3), which did not correspond to their locations on the reef. The subreefs were separated by distances of approximately 0.8 km.

METHODS

Ten transects, each 25 m long by 0.4 m wide, were videotaped on adjacent, parallel spurs within each reef or subreef. Each 10-transect sample covered an area of approximately 1250 m^2. The sampling protocol required less than one day at each reef or subreef, an important logistical consideration in a large-scale study. The hardground sites were sampled by placing the transects on the substratum in the same parallel pattern as for the spur-and-groove sites.

The videotapes were analyzed in the laboratory, according to the methods described in Aronson et al. (1994). Estimates of the cover of hard corals (Scleractinia plus Milleporina) by species were obtained by point counts (500 random points per transect), and the abundance of hard coral colonies by species was assessed by viewing the entirety of the videotape for each transect. These methods and sample sizes allow statistically powerful, univariate among-site comparisons of coral cover, Shannon-Wiener diversity (*H'*; calculated from the point counts), and colony abundance (Aronson et al. 1994). The sampling protocol also allows powerful multivariate comparisons of coral cover and colony abundance data (Aronson and Swanson in press).

Data on the presence/absence of coral species were also collected for each reef sampled (though not for each subreef). The identities of the coral species present at each reef were determined from the 10 video transects plus 10 additional transects of the same dimensions. The 10 additional transects were assessed visually for species presence/absence in the field. Previous work has shown that a sample size of 20 transects is adequate for assessing species richness (Aronson et al. 1994).

RESULTS AND DISCUSSION

Comparison of Subreefs to Reefs

To compare the variability among subreefs within reefs to the variability among reefs, 90 video transects from 9 subreefs on 3 reefs were analyzed. Thirty-five species of hard corals were recorded on the 9 subreefs. Total coral cover, estimated from a data set of 45,000 point counts, varied dramatically among the three reefs (Fig. 3). However, coral cover appeared to be relatively homogeneous among transects within subreefs, judging from the small variances. There also appeared to be little variation among subreefs within reefs.

These qualitative impressions were tested statistically by Analysis of Variance (ANOVA). The 9 subreef samples of 10 transects each did not conform to the homoscedasticity assumption of parametric statistics (F_{max} test), and so the data were arcsine-transformed. F_{max} and Lilliefors tests confirmed that the transformed data met the assumptions of homoscedasticity and normality,

rated from the layers below. There could hardly be a more conclusive evidence that the keys have been formed above high-water mark. These islands take their name from the pine woods with which they are partially covered. A beautiful palmetto flourishes there also, considerably smaller than the cabbage-palmetto of the Southern States, and, as far as I can ascertain, an undescribed species. It is remarkable for its smooth stem, and for the silvery lustre of the lower surface of its leaves. The great width of the mud flats surrounding the Pine Islands, and the peculiar direction of that group of keys, suggest the idea that they were formed when the Gulf discharged its waters more freely from the north into the Gulf Stream, and when the range of keys extended only abreast of Cape Sable. This supposition is sustained by the fact that the whole reef dips to the west. The outer reef rises to the same level as the Marquesas; but west of Key West, as far as the Tortugas, the main range of keys has not yet reached the same height above the sea level as the eastern parts of the reef. We may therefore suppose, that the group of Key West, which is again as high as Key Largo, stood to the Key Vaccas in the same relation as the Tortugas now stand to the Marquesas, leaving a broad, deep depression between them. This has gradually been filled by drifting sand, just as the Marquesas, by like accumulations, are spreading toward the Tortugas. The groups of Boca Chica, of which Key West and Saddle Bunch Key are the largest, have again a more westerly direction, corresponding with the general curve of the reef. These islands share the character of the eastern reef, but have also some features of the Pine Islands. Their lower strata consist of coral boulders and coral breccia, as was ascertained during the excavation preparatory to the foundation of the fort of Key West. Their upper layers, however, namely, all that portion which rises above low-water mark, rest upon a coarse oolite, above which follow layers of finer grain, overlaid by very thin layers of muddy limestone. These surface layers resemble those of the Pine Keys, especially on their northern and northeastern shores, which are very level, spreading out into submarine mud flats, while the southern shore is more abrupt, and worn by the action of the tides. The stratification of Key West is not, however, so regular as that of the Pine Islands, nor do the strata dip so uniformly to the north as in the latter. They incline, indeed, in all directions on the western shore, showing that the trend of the tidal deposits has been constantly shifting. The cross-stratification is nowhere better seen, in the main range of keys, than on the westernmost

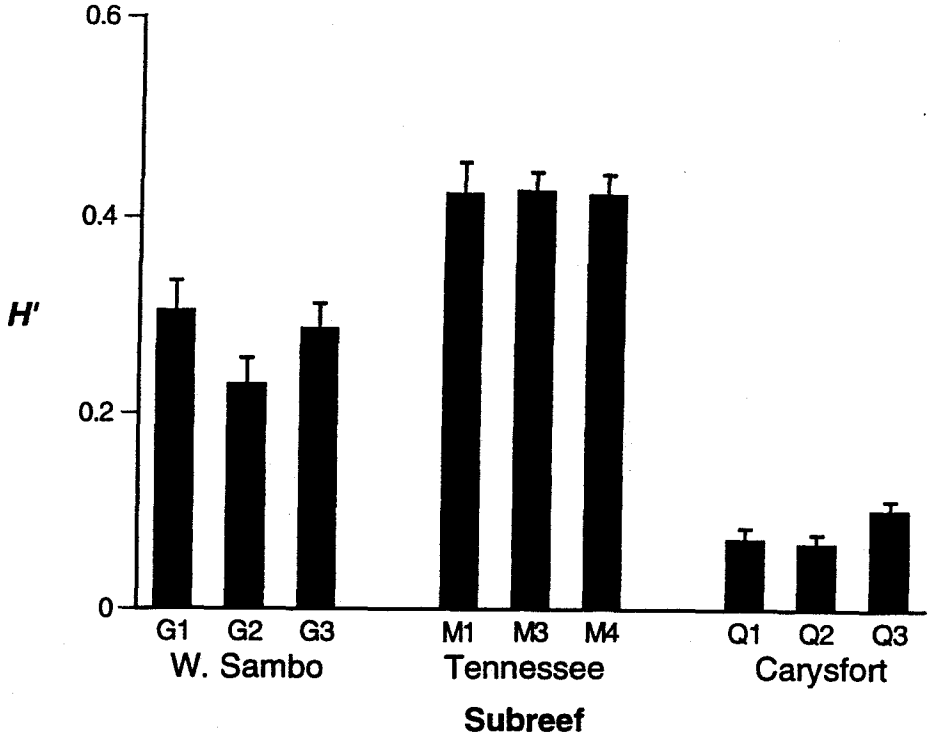


Fig. 4. Mean Shannon-Weiner diversity, H', of hard corals at the 9 subsites. Error bars represent standard errors.

Table 3. Results of a one-way nested ANOVA on coral diversity H'.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Reef	1.84	2	0.920	920.000	< 0.0005
Subreef{Reef}	0.009	6	0.001	0.974	0.94
Error	0.407	81	0.005		

respectively. A one-way, nested ANOVA, with subreefs nested within reefs, revealed a highly significant among-reef effect but no significant within-reef (i.e., among subreef) effect (Table 2). Tukey *a posteriori* pairwise comparisons revealed that each of the 3 reefs was significantly different from both other reefs in coral cover.

The point count data were also used to calculate Shannon-Wiener diversity indices, *H'*, for each transect based on coral cover (Aronson et al. 1994; Fig. 4). Heteroscedasticity was eliminated by logarithmic transformation (F_{max} test), which also ensured normality (Lilliefors tests). A one-way, nested ANOVA showed a highly significant among-reef effect and no significant within-reef effect (Table 3). Tukey pairwise comparisons again showed the 3 reefs to be significantly different from each other.

Cluster analysis was used to determine if subreefs within a reef were more similar to each other than they were to subreefs from other reefs in multivariate space. The point count data were pooled by coral species across transects within subreefs. Species that accounted for <0.5% cover in all subreefs were eliminated. A Euclidean distance matrix was calculated for the 9 subreefs, and the subreefs were clustered by the average linkage method. Euclidean distance is calculated based on species abundance, and it is weighted toward the dominant species. All subreefs clustered by reef, as expected, with the exception of Tennessee subreef M4 (Fig. 5). Tennessee Reef and Western Sambo Reef clustered together, and they were distinct from Carysfort Reef. The 3 most abundant species, in descending order of overall cover, were *Montastraea franksi, Siderastrea siderea*, and *M. faveolata*. Removal of all but these species from the cluster analysis did not alter the clustering pattern.

The same statistics were applied to the data on coral colony counts (Fig. 6). Total colony counts were again heteroscedastic; after logarithmic transformation they met the homoscedasticity and normality assumptions of parametric statistics. A nested ANOVA revealed significant effects both among reefs and within reefs (among subreefs) (Table 4). Tukey comparisons showed all 3 reefs to be significantly different from each other. Tukey comparisons of the subreefs revealed that Carysfort subreef Q1 was significantly different from the other Carysfort subreefs, but all other subreefs were homogeneous within reefs. Yet cluster analysis showed that subreefs within reefs, including Carysfort Q1, were more similar to each other than they were to subreefs from other reefs (Fig. 7; species with ≤4 colonies in all transects were eliminated). As with the point counts, Tennessee and Western Sambo were more similar to each other than they were to Carysfort. The dominant species in the colony count analysis were, in descending order, *Millepora alcicornis, Siderastrea siderea, Montastraea franksi, M. cavernosa, Porites astreoides, Agaricia agaricites,* and *M. faveolata*. Cluster analysis with only these species produced the same results as clustering with all species.

Comparison of Reefs to Regions

Comparison of the variation among reefs within regions to the variation among regions involved the analysis of 160 video transects from the 16 reefs with a deep spur-and-groove habitat. Thirty-eight species of hard corals were recorded at the 16 reefs. Total coral cover, estimated from a data set of 80,000 point counts, showed substantial among-reef variation (Fig. 8). As with the

have been formed in the same manner as the other keys, is found in the fact that a brig was drifted in a heavy gale half way across the Island off French Reef. Plantation Island, Windly's Island, the upper and lower Matecumbe which follow Key Largo, are not so high, and are more like Elliott's Key. Plantation Island is encircled to the seaward by a spreading mud flat, from which, upon an extensive spur, Key Tavernier rises to the east. The others, Upper and Lower Matecumbe, as well as Long Key, Tea-table Key, and Lignum Vitæ Key are connected with Mangrove Keys. To the seaward of the two Matecumbes, however, there are sand beaches, while Indian Key, which stands out into the ship-channel, is entirely rocky, resembling, as already stated, the eastern shore of Key Largo. A mud flat runs along the inside of all these keys, from Lower Matecumbe to the northernmost extremity of Key Largo. It extends for several miles to the north of the keys, and is separated from the mud flats which reach the main-land only by a narrow channel varying from three to four or five feet in depth. This channel is marked by dots upon the map. Another mud flat projects like a spur from Lignum Vitæ Key between Upper and Lower Matecumbe. Yewfish Key, Duck Key, and the Grassy Keys, as well as Key Vaccas, Boot Key, and The Sisters, constitute a series of small low keys, mostly covered by mangroves, with here and there a sand beach on the seaward side, while spurs of mud flats jut out from the leaward side. The Bahia Hondas have a similar appearance, but here the reef begins to change its character. Indeed, the change is already marked farther east, west of Key Vaccas and the Boot Keys. Instead of longitudinal islands bearing east, northeast and west-northwest, we now have an archipelago of low islands rising above extensive mud flats which are also interspersed with innumerable mangrove islands crowded together in small groups, the main islands bearing north-northwest. The principal of these islands are known as Little Pine Island and Pine Island. The main channels intersecting this archipelago run also north-northwest, between Little Pine Islands and the Bahia Hondas, and between the western and eastern Pine Islands. The main islands of this group are very flat, and consist of thin layers of a regularly stratified and somewhat oolitical limestone, evidently formed by deposits of limestone mud. The uppermost layers have evidently been solidified above the level of the sea, for they present numerous cracks of shrinkage such as are everywhere observed upon dry mud flats; the edges of these fissures being here and there slightly raised, and even upturned, so as to be sepa-

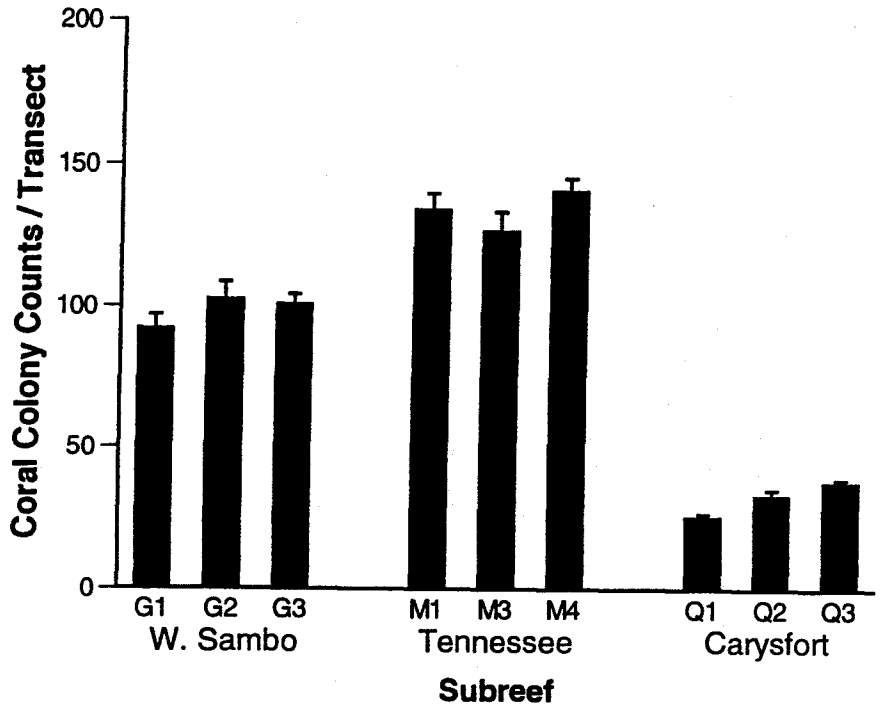


Fig. 6. Mean number of coral colonies at the 9 subreefs. Error bars represent standard errors.

Table 4. Results of a one-way nested ANOVA on log transformed coral colony counts.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Reef	34.816	2	17.408	104.87	< 0.0005
Subreef{Reef}	0.998	6	0.166	6.126	< 0.0005
Error	2.200	81	0.027		

in width. Nowhere does it rise more than thirteen feet above the level of the sea. The hill ninety feet high, said to exist on its eastern extremity, resolves itself into a tuft of very high mangroves.

The vegetation of the whole key is very rich, the trees more diversified and larger than on any other island in the range. The rock formations are also very diversified. The seaward shore is rather abrupt, the ocean having worn away the sloping edges. The foundation of the key consists chiefly of large coral boulders, the flat Mæandrina heads being most numerous, though Porites and Astræans are also abundant. They are so distributed upon the lower level of the island that one would think they had grown where they are found. On closer examination they are seen to be detached coral heads heaped together, and, owing to their peculiar form, stranded in an upright position. Whoever has seen Mæandrina heads broken off by boring shells will not wonder to see these flat hemispheres resting on their broad, flat bases rather than on their rounded side. But though they are thus found in their natural position, suggesting the idea that they have grown where they now lie, the fact that among them are some which are overturned, and others broken in halves, contradicts this conclusion, and show that, notwithstanding the regularity of the foundation, this key, like the others, rests on an accumulation of detached coral boulders. Indian Key has a similar foundation; the evenness of the accumulation and the natural position of the heads misled me at first into the belief that I had found a proof of the upheaval of the keys. But a closer survey satisfied me that their upper formations consist here, as elsewhere, of coarse and fine oolites, with intervening seams, as at Key West, of compact limestone, and an overlying crust whereon the sea does not encroach upon the older formations.

As has already been remarked, the shore is rocky, and, except in small patches, no sand beach is seen along this extensive island. There are, however, large mud flats along its southeastern extremity, among which rise Key Rodriguez, Dove Island, two Mangrove Keys, and another off Plantation Island, known as Tavernier Key. These mud flats abound in animals of all kinds. Nowhere are Holothuria more numerous; cartloads might easily be gathered. The Eunices are also more numerous than elsewhere, and nothing can exceed the beauty of the Actinias, Gorgonias, and Chitons to be found on every rock upon the shore. The best evidence that Key Largo, notwithstanding the fictitious height assigned to some parts of it, may

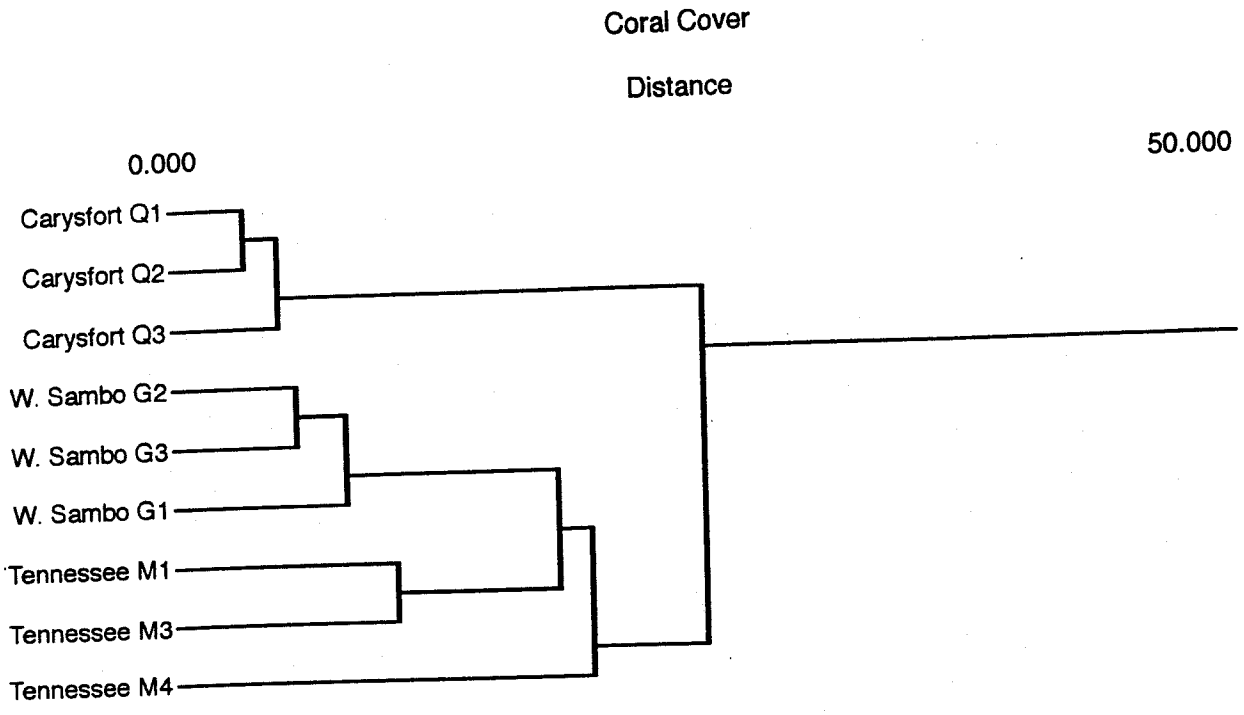


Fig. 5. Dendrogram showing relationships among the 9 subreefs, based on multivariate coral cover. Euclidean distances were calculated from the point count data, and sites were clustered using the average linkage method.

and one sinks ankle-deep in the dense coral growth. A most astonishing variety of sea-worms is found between the branches of the Porites and Oculina. This is also the play-ground of many Ophiurans and Asterians. Cidaris metularia are found here also, and other species of Echini. Such mud-shoals, composed of the most minute sand and mud, frequently encircle the keys, often extending for miles beyond their shores. Wherever they are laid bare at low water they are overgrown by Milleporas; but where they are always covered, even at the lowest tides, with a few inches of water, the Porites take the ascendency. The latter are chiefly of two species, the Porites furcata and Porites clavaria. A black Ascidian is often attached to their branches in great numbers. Great numbers of Holothurians make their home upon these mud flats. Large holes, sometimes close together, sometimes at small distances from each other, are frequently to be met with. These holes, widening at the surface in the shape of a funnel, having a depth of several feet and a diameter of several inches, are occupied by a gigantic worm of the genus Eunicea. Large Actiniæ of various colors are also numerous, and a deep orange colored Starfish and Manicinas show themselves also, though not in great numbers, and an endless variety of Gorgonias. Such shoals are the best field for the collector. Similar mud flats are found everywhere around the Mangrove Islands. But of these, more presently.

Soldier Key rises about five miles to the south of Cape Florida. It is connected with an extensive mud flat, which stretches nearly to the lighthouse, being separated from it only by a narrow channel from nine to ten feet deep. The Ragged Keys come next, — a series of some half-dozen small islands formed by coral boulders rising but little above the surface of the water, and surrounded on both sides, and especially on their western shores, by wide mud flats. These keys, as well as Soldier Key, are covered by mangroves. It is noticeable that some of the Mangrove Islands have beaches, — a fact explained by their mode of formation. To the westward follows Elliott's Key, the first whose surface does not consist solely of coral boulders, coral sand having formed a succession of layers of oolitic rock upon it. Here also we first find white sand beaches dipping to seaward, and see a variety of trees mingling with the mangroves. On the southernmost extremity there is a spur formed by a mud flat, while another more extensive one juts to the eastward, and is connected with Old Rhodes, the next key. Key Largo, which follows, is the largest of all the islands in the main range of keys. It is not less than twenty-five miles long and from one to three miles

subreef-reef comparison, the coral cover data did not conform to the assumptions of parametric statistics. This problem was again corrected with the arcsine transformation.

A one-way nested ANOVA on the coral cover data revealed significant among-reef variation ($P<0.05$), as well as significant variation from region to region, regardless of which regional classification scheme was used (Table 5A, C). When the Dry Tortugas reefs were removed from the analysis, variation among reefs remained significant, but variation among regions was no longer significant (Table 5B, D). Similar results were obtained for the Shannon-Wiener diversity index, *H'*, although in this case the regional effect was marginally non-significant even with the Dry Tortugas included (Fig. 9, Table 6). The *H'* data had to be square-root transformed in this case.

The 16 reefs were clustered based on multivariate coral cover using the Euclidean distance metric. Cluster analysis confirmed that the main source of variation occurred at the reef level; reefs did not cluster by region (Fig. 10). The dominant species were *Montastraea franksi, M. faveolata,* and *M. cavernosa*; removing all but these 3 species did not affect the outcome of the cluster analysis.

Square root-transformed data on coral colony counts yielded ANOVA results somewhat different from those obtained for coral cover and *H'*. High variability from reef to reef was again reflected in significant reef effects (Fig. 11, Table 7). However, the regional effect became more significant once the Dry Tortugas were removed, using either regional classification scheme. Cluster analysis again showed no pattern of similarity among sites within regions (Fig. 12). The dominant species based on colony counts were *Millepora alcicornis, Montastraea franksi, Siderastrea siderea, Porites astreoides, M. cavernosa, M. faveolata, Agaricia agaricites, Stephanocoenia michelinii, Siderastrea radians,* and *Madracis decactis*; cluster analysis with only these species produced the same results.

The reefs were also clustered based on the species presence/absence data, using Jaccard dissimilarities. This presence/absence analysis differed from the analyses using Euclidean distance in that all species were weighted equally. As with the coral cover and colony count data, the species presence/absence data showed no geographic pattern of site clustering; the analysis once again did not cluster sites by region (Fig. 13).

Hardground Sites

Four sites were were characterized by hardground habitat at the depth range studied: Tortugas Bank (site A), 28 ft Shoal (D), Triumph Reef (S), and Fowey Rocks (T). These sites are distributed throughout the reef tract, with Tortugas Bank in the Dry Tortugas, 28 ft Shoal in the Lower Keys, and Triumph Reef and Fowey Rocks in the Upper Keys. Despite their geographic distance, the hardground communities clustered relatively close together based on coral cover (Fig. 14) and coral colony counts (Fig. 15). The pattern was more ambiguous when species presence/absence data were clustered, although Triumph Reef and Fowey Rocks clustered together (Fig. 16).

upon all keys, whatever be their height; and, lastly, that the level of the highest keys, such as Key Largo and Key West, marks the height above the sea-level to which the severest hurricanes, like that of 1846, have been known to drive the loose materials.

These facts in their connection are especially important, as giving us the means of settling the question about the upheaval, depression, or permanence of level of the coral fields of Florida. It should be mentioned here that the fossil remains of animals and plants are rare in coral rock. It will be seen hereafter that the mode of formation and accumulation to which the reefs and keys owe their origin would be unfavorable to the preservation of such remains. When they are found in the coral rock, it is chiefly in the brecciform limestone, where they have been sheltered in some excavation, and thus protected from complete attrition. Here and there small species of thick-shelled univalves occurs in a tolerable state of preservation, and we have found several bones of a large turtle in the coarse oolite near Key West. All the remains so found are identical with species now living on the reef.

Let us now return from this digression to the consideration of the keys themselves, under the different aspects which they present. Some have very abrupt shores, and rise like narrow ridges, with ragged edges and without a beach, from the deeper water. These were undoubtedly formed upon the narrowest parts of the old reef. Others are more spreading, have a wide beach, and dip gradually under the sea, their submarine slopes being covered with coral sand and mud. These must have been formed on the broader parts of the reef, where it slopes gently on both sides. In still others, the shores have been rendered abrupt by the denudation of some of their earlier deposits. Such denudations may have been filled again by more recent deposits, thus giving to a formation of the present geological era a diversity usually characteristic rather of unconformable deposits belonging to different geological ages. The northernmost keys, which converge toward the main-land, are covered by silicious sand. Their beaches are of like character, and slope towards the Atlantic, while their mud flats spread along the western shores. South of Cape Florida no more silicious sand is to be seen, and even in the immediate vicinity of Cape Biscayne there is a mud shoal, laid partly bare at low water, over which grow branching Millepora, with small tufts of Oculina and Caryophyllia rising between them, and here and there a few Porites furcata. Such flats are very soft,

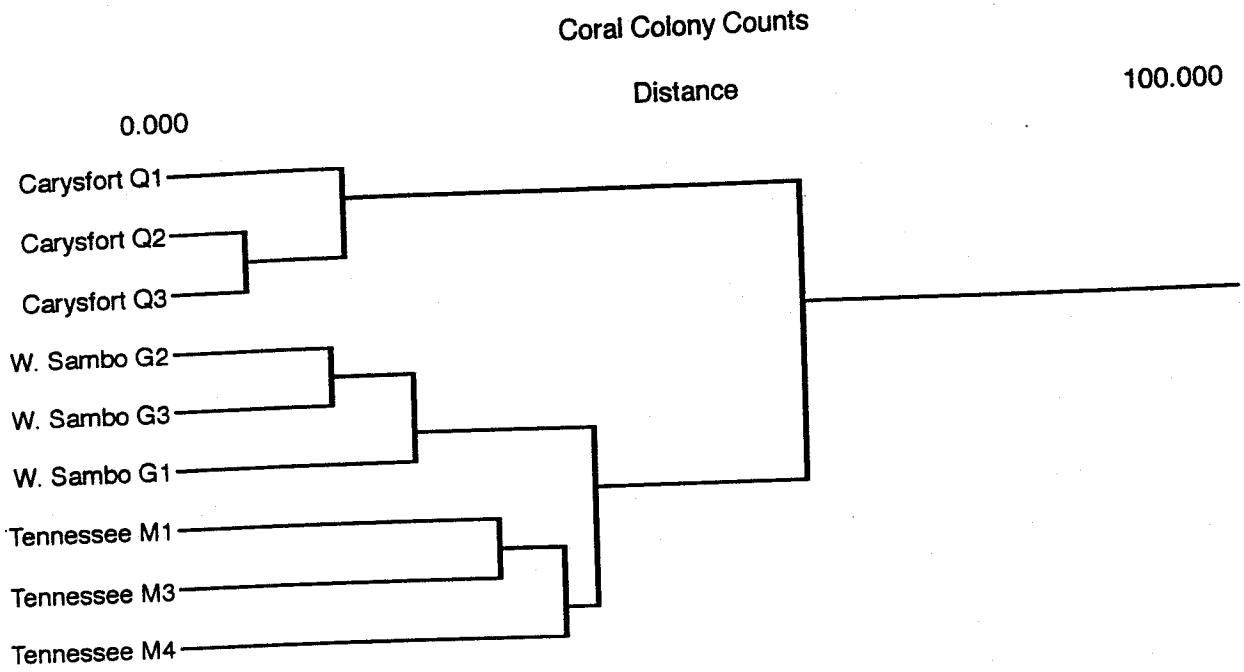


Fig. 7. Dendrogram showing relationships among the 9 subreefs, based on multivariate coral colony counts. Euclidean distances were calculated from the coral colony count data, and sites were clustered using the average linkage method.

with concentric layers, like true oolite, but of rounded, minute fragments of corals cemented together. These rocks are generally of a pure white color, though occasionally tinged with gray or brown, — the coloring matter derived, no doubt, from decomposed organic matter. At higher levels a fine-grained oolite usually comes in with more distinct traces of stratification. Even here, however, the oolitic grains are also mostly comminuted fragments of coral, as the microscope readily shows. Only here and there the most minute oolites seem to be formed by several concentric coatings of amorphous limestone. Alternating with these different layers of oolite are found small seams, varying from a line to half an inch in thickness, of compact, homogeneous limestone, so uniform as to ring under the hammer. An important fact — inasmuch as it may help to explain the formation of this compact limestone — is that a layer of it constantly occurs upon the surface of all other rocks forming the keys. It forms a last surface, as it were, even upon the highest points of the most elevated keys, a crust following all the external sinuosities and irregularities. Evidently, therefore, it cannot have been formed under the level of the water, but merely by the action of the spray; and the successive seams of similar compact limestone, intervening between the layers of oolite, would indicate the successive surfaces of the keys during the progress of their formation.

A careful survey of the character of the rocks in the keys affords satisfactory evidence that they have been formed, at whatever height they may rise, by the same action which is now going on upon the reef, — that is, by the accumulation of loose materials above the water-level. That part of the keys which rises above the level of the water is, therefore, a subaerial and not a submarine accumulation of floating matter, thrown above high-water mark by the tempestuous action of the water. We insist upon the fact that the keys furnish in themselves, by the internal structure of their rock, the fullest evidence that they have been formed above high-water mark by the action of gales and hurricanes, instead of having grown as a reef up to the water-level, and been subsequently raised to their present height. The evidence of this statement rests upon certain facts obtained from observation of the reef itself, at Sand Key and the Sambos.

These facts are as follows: First, that their stratification has all the character of a tidal shore stratification; secondly, that their different layers are separated by crusts of compact limestone similar to that now found

Table 5. Results of one-way nested ANOVAs on arcsine-transformed coral cover.

A. Regions as defined by Klein and Orlando (1994), including the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	0.799	4	0.1997	4.0051	0.0304
Reef{Region}	0.549	11	0.0498	20.589	< 0.0005
Error	0.346	143	0.0024		

B. Regions as defined by Klein and Orlando (1994), omitting the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	0.253	3	0.0843	1.5598	0.25965
Reef{Region}	0.541	10	0.0541	22.226	< 0.0005
Error	0.304	125	0.0024		

C. Regions as defined by Shinn et al. (1989), including the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	0.6521	3	0.2174	3.7723	0.0407
Reef{Region}	0.6915	12	0.0576	23.439	< 0.0005
Error	0.3516	143	0.0025		

D. Regions as defined by Shinn et al. (1989), omitting the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	0.1041	2	0.05203	0.8372	0.4587
Reef{Region}	0.6836	11	0.06214	25.1179	< 0.0005
Error	0.3093	125	0.0025		

lying each other in such a manner as to present the same irregularity which is found in all drift stratification. Layers upon layers are seen resting unconformably, dipping in different directions so as to present all the modifications which may be observed in torrential stratification, each layer following, with more or less regularity, the course of the flood under which it has been accumulated.

This dip varies for several degrees, but rarely exceeds 7 to 8 degrees upon any extensive surface where the sea has had full play. In enclosed bays or narrow channels, however, the materials accumulate at much steeper angles. In sheltered places, slopes of coral sand are formed at angles of 20 or even 30 degrees. At the Tortugas, Lieutenant Wright pointed out to us accumulations of coral sand sloping at an angle of more than 33 degrees, exceeding decidedly, therefore, the steepest slopes of silicious sand-banks. This circumstance corroborates the assertion of Mr. Darwin, that coral sand possesses an adhesive property which enables it to accumulate at higher angles than other loose materials, owing, perhaps, to the viscosity of the animal matter still pervading the coral fragments.

By a process not yet fully understood, but to which we shall return hereafter, these loose collections are gradually cemented into solid rock, presenting the most diversified appearance, according to the substances of which it is composed. Then we find a coarse breccia, consisting of larger fragments of corals and shells, enclosing sometimes coral boulders; and this is the sort of rock which generally overlies the immediate surface of that portion of the keys which has been formed by the progress of the reef, growing *in situ*. Such rock was seen among the foundations of the new lighthouse at Sand Key, where the large boulders are very numerous, and seem almost as fresh as if they had been lying on the spot but for a few years. It may be, indeed, that during the hurricane of 1846, the whole cap of the reef was renewed at that spot.

Similar rock, but of more breccia-form character, containing remains of shells in greater quantity than I have seen elsewhere in the coral rock, was brought up from excavations made in twelve feet water, when the foundations of Fort Taylor were laid in Key West. The same coarse-grained rock is observed, at low water, in many places where the tidal action has worn away parts of the primitive rock of the keys. Above these materials are generally found layers of what seems, at first sight, a coarse-grained oolite, but upon closer examination it is seen to consist, not of grains of limestone

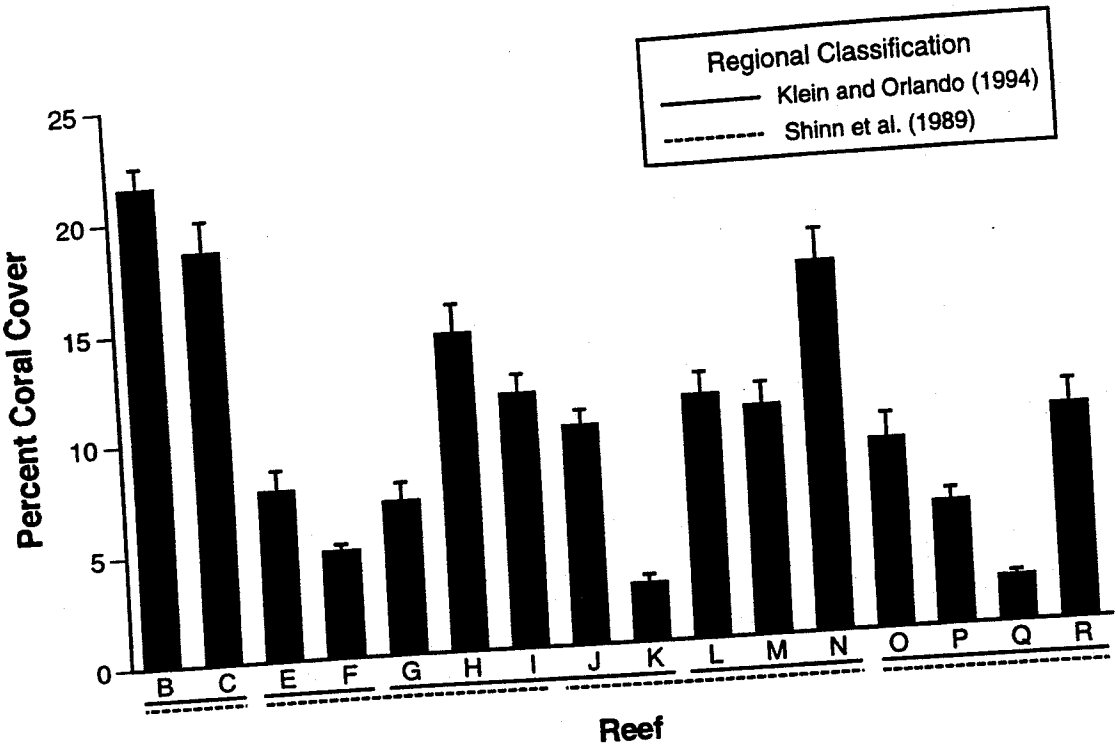


Fig. 8. Mean coral cover at the 16 reef sites that were spur-and-groove habitats. Error bars represent standard errors.

We cannot therefore infer from the absence of organized beings in ancient formations of this character, that they were deposited in a pelagic sea, destitute of life. This has already been pointed out by Mr. Dana,* in his Report on the Coral Reefs of the Pacific. It must not, however, be supposed that organic remains are wholly wanting in coral formations. There are, on the contrary, localities where they are found in considerable numbers. In such cases the action of the sea has probably been less violent, or in some instances shells may have accumulated in such quantity, before being cemented together, as to offer a certain resistance to destructive influences. Occasionally also, delicate shells or sea-urchins may be lodged in the cavities of coral stems, afterwards filled in with sand, and thus protected.

We see everywhere that the larger boulders and the coarser fragments have been the first to find a resting-place upon the dead reef; the minuter particles and coral sand, which are periodically washed away from its crest during heavy gales, never accumulating upon it till large boulders and more solid materials have collected to such an extent as to form sufficient protection for the more movable looser fragments. This fact is beautifully illustrated by an accurate survey of Sand Key, where a wide field of large boulders is partially laid bare at low water, presenting the appearance of an extensive key, with a low hill of minute materials, the product of some heavy gale, heaped upon the summit, against which the sea plays without disturbing it materially, even at high water, when it leaves in sight only a nucleus, as it were, for a greater accumulation of such loose materials which may in time cover the whole surface of the larger boulders. We have here in reality the same phenomenon which is observed upon all beaches, where larger materials have first accumulated on a shoal shore, being followed, in the course of time, by more minute fragments which have found a resting-place upon levels where the sea was powerless to increase the collection of coarser matter. In attempting to understand these formations, it must be remembered that the accumulation of the larger materials, collected at a certain level, may modify the action of the water at a subsequent period, thus producing a combination of substances, heaped unconformably upon each other. This is, in reality, the case throughout the whole main range of keys, which have been raised to their present level by the action of the tides and gales for ages past; the fragments of which they are composed having been thrown up at different periods, and over-

* Geology of the United States Exploring Expedition.

Table 6. Results of one-way nested ANOVAs on square root-transformed coral diversity (H').

A. Regions as defined by Klein and Orlando (1994), including the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	2.1296	4	0.5324	3.3399	0.05068
Reef{Region}	1.7535	11	0.1594	29.2681	< 0.0005
Error	0.7789	143	0.0054		

B. Regions as defined by Klein and Orlando (1994), omitting the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	0.9449	3	0.315	1.8051	0.2098
Reef{Region}	1.7445	10	0.1745	29.8948	< 0.0005
Error	0.7296	125	0.0058		

C. Regions as defined by Shinn et al. (1989), including the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	1.6973	3	0.5658	3.1196	0.06627
Reef{Region}	2.1763	12	0.1814	32.8307	< 0.0005
Error	0.7899	143	0.0055		

D. Regions as defined by Shinn et al. (1989), omitting the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	0.508	2	0.254	1.2888	0.31415
Reef{Region}	2.1677	11	0.1971	33.2568	< 0.0005
Error	0.7407	125	0.0059		

reef and down its slope on either side, and we have keys corresponding in essential features to those forming the main range. The difference, however, is not simply one of greater or less accumulation. There is a regular gradation in the character of the materials. All these loose materials, in proportion to their size and the violence of the waves, are now acted upon by the sea. The smaller fragments, even under the gentle flow of the ordinary tides, are constantly moved to and fro, while heavier winds and storms break away the larger masses and split them into smaller bits, and may in the end grind them to rounded pebbles, and finally to sand or to an almost impalpable coral powder. This powder is stirred up from the bottom by the waves, and often remains suspended in the water for days, giving it a milky hue. Of course a great portion of these débris, both large and small, will be thrown upon the reef, and find a resting-place there. Of such materials the Florida keys are made. It is worth our while to study the mode of formation of these deposits, since it may throw some light on the extensive accumulations, always a puzzle to geologists. The nature of the larger boulders, and even of the pebbles, cannot be mistaken, since the organic structure of the coral stocks is perceptible in them all, and yields but slowly to decomposition or attrition. Such changes as they undergo may be observed in coral stems the summits of which are still alive and growing. Meantime the lower parts are gradually dying or filling with amorphous limestone. This limestone often has within the very centre of the coral stem a crystalline structure as perfect as any crystalline limestone. When so acted upon, these corals resemble the corals of the Paleozoic rocks. From such well-preserved specimens to the smaller fragments, where only some traces of organic characters remain, and from these again to the still finer pebbles, particles, or powder from which all signs of organization have disappeared, the transition is so gradual as to leave no doubt that even the sand is of coral origin. Here and there the stronger shells, such as Strombus gigas, Fusus giganticus, Fasciolaria Rhinoceros, and others, may be preserved among the coral fragments; but the more delicate shells, as well as the carcasses of crabs and lobsters, the solid parts of sea-urchins and starfishes, are very soon ground to powder. This explains the rarity of well-preserved organic remains in coral rock. Seeing the profusion of animal life on the reef, one is at first surprised at this; but a little observation shows that the hard parts of both animals and plants, about the reef, are transformed by long-continued attrition into coral breccia, coral oolites or compact limestone.

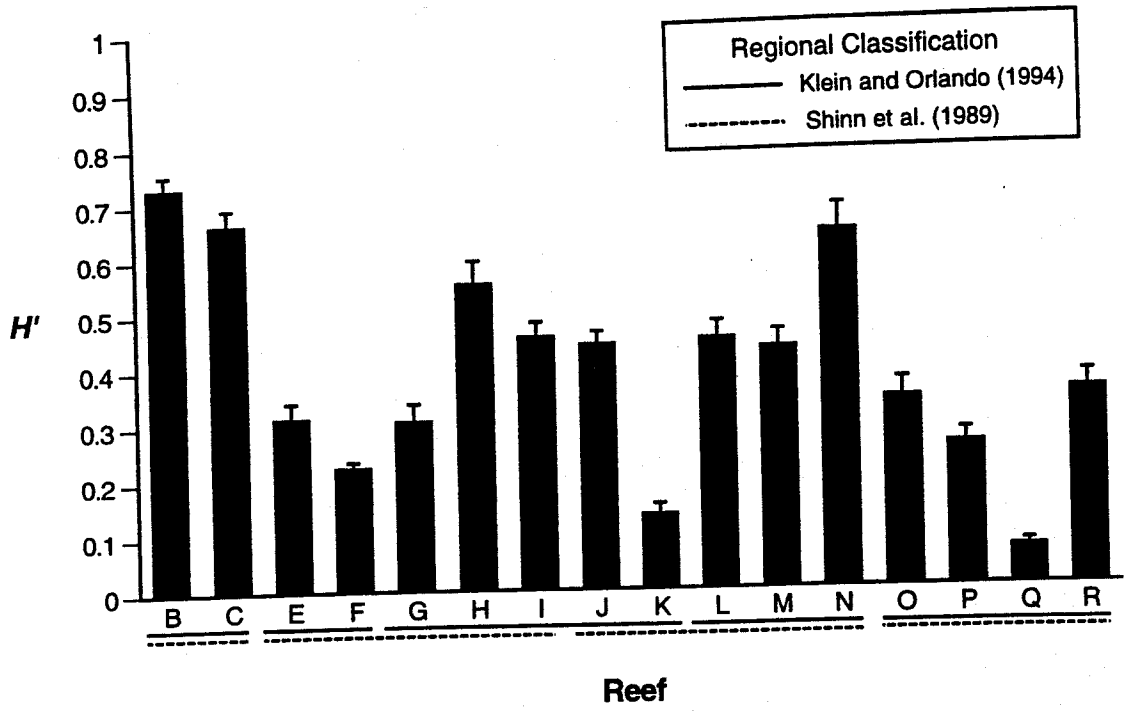


Fig. 9. Mean coral diversity at the 16 reef sites. Error bars represent standard errors.

Among the creatures mentioned above are many which bore deeply into the stems of the corals, or into the mass of the coral rock.

Such are different species of Arca, the date-fish among the Mollusca, and many worms, especially Serpula among articulates, the agency of which in the formation of the keys will be described hereafter. All these animals and plants contribute, more or less, to augment the mass of solid materials which is accumulating upon the reef, and increase its size. Not only are the hard parts of shells, echinoderms, worms, or their broken fragments, heaped among the detritus of the corals, but occasionally even the bones of fishes and turtles, which are very numerous along the reef, may be found in the coral formations.

The decaying soft parts of all these animals undoubtedly have their influence upon the chemical process by which the limestone particles of their solid frame are cemented together in the formation of compact rocks. Upon this point we may expect further information from Professor Horsford, who is now submitting to chemical analysis all the variety of rocks and the solid stems of the different corals obtained in Florida. Respecting the relations of the solid and soft parts of the living coral, and their mode of growth, we would refer to a paper of ours now in press, to appear in the next volume of the "Smithsonian Contributions to Knowledge."

The Keys.

The main range of keys has a very uniform character; the separate keys differing from each other chiefly in their more or less advanced formation. We need only, therefore, describe in detail a certain number which may serve as illustrative of various steps toward completion. Some consist simply of accumulated coral boulders heaped upon an old coral reef rising more or less above the sea-level. Upon this foundation fragments of the more brittle kinds of coral, shells, coral sand, are heaped as they are upon the dry rocks west of Sand Key or upon Rock Key, east of Sand Key, a formation resembling, indeed, that of Sand Key itself, or the Sambos or Looe Key. Such a comparison shows at once the connection between these larger keys and the incipient keys upon the reef. We have only to imagine the accumulation of coral boulders, corals, shells, and coral sand upon the small keys of the reef to be continued and increased till this cap of loose materials should extend several miles along the rising crest of the

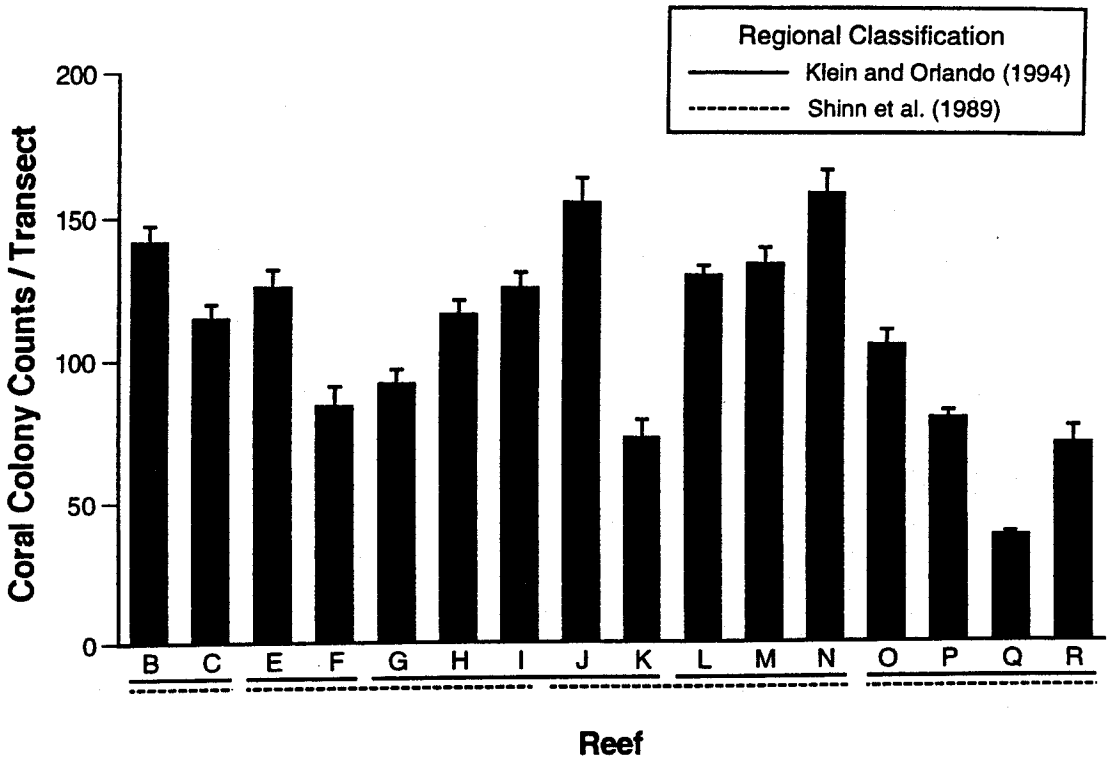


Fig. 11. Mean coral colony counts at the 16 reef sites. Error bars represent standard errors.

An endless variety of Gorgonias, for the most part too little known yet to be fully characterized, grow in tufts between the coral heads or upon the coral sands and in the mud flats. Among them are the Halcyonia growing in clusters, the branching Gorgonias forming dense bushes, and the beautiful sea-fans, a kind of Gorgonia, the branches of which spread in flat expansions forming a network of anastomoses, the meshes of which are covered with distinct animals. Again, innumerable polyps, like mollusks belonging to the lower families of that class, spread over the same ground, frequently aping, in their manifold combinations, the diversity of corals on which they rest. So similar are some of them to the true corals that they have only recently been recognized as mollusks, and referred to that type under the name of Bryozoa. Among them is one species of particular interest for the geologist, because it is the first living analogue ever found of that curious extinct family, the Graptolites, so common among the oldest fossiliferous rocks. Its modern representative was discovered in the shoal waters of Key West.

The Echini are more numerous here than upon any other part of the American coast. They belong to the genera Echinus, Tripneustes, Diadema, Cidaris, Clypeaster, and Encope. We found no Spatangoids, though they are known to occur on the West India Islands. The Diademas are found among the coral boulders, generally in nests together, frequently concealed in the larger excavations of the coral heads. The Clypeasters and Encopes on the contrary, live upon the coral sand flats, while the Cidaris prefer the shoal grounds of the Corallines and Nullipores. Holothuria swarm in myriads upon the mud flats; suggesting by their numbers the feasibility of collecting them for sale as Trepang. This is an important article of commerce in China and the East Indies, and their edible species resembles ours so closely that I believe the latter might be used in the same way and furnish a profitable industry. So may the sponges of Florida, for which there is already considerable demand. Beside this wealth of animal life, the reef abounds in tropical sea-weeds. Of these the well-known Gulf-weed is the most striking. It seems strange that the origin of these floating weeds should be doubted when they are found growing so abundantly. Even a brief description of the immense number of shells, worms, crabs, lobsters, shrimps, craw-fishes, and fishes, seen everywhere upon the reef, would be out of place here. In variety, in brilliancy of color, in elegance of movement, the fishes may well compare with the most beautiful assemblage of birds in tropical climates.

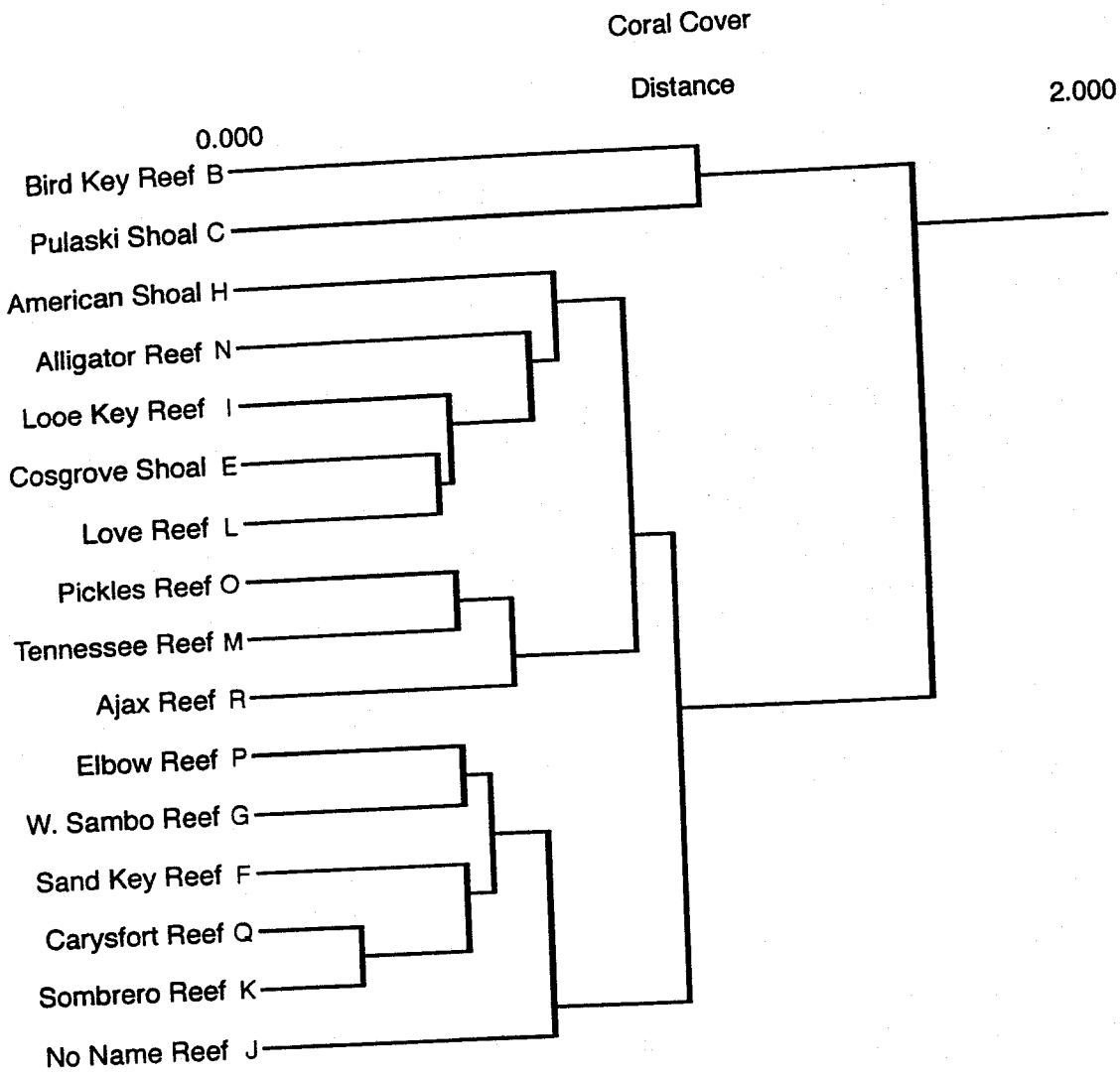


Fig. 10. Dendrogram showing relationships among 16 reefs. Euclidean distances were calculated from point count data, pooled by species for each reef. Reefs were clustered using the average linkage method.

It had been stated that the reefs consisted solely of living corals; and, indeed, this report is true of the outer reef, which is called by all the inhabitants of Florida "*the reef*" *par excellence*, and is unfounded only with regard to those few islands which rise above the surface of the sea at Sand Key and the Sambos. Others, who had noticed only the larger accumulations of coral fragments which occur on the shores of some of the islands forming part of the Florida Reef, had reported the islands to be formed of coral rocks; while some who had perhaps observed the extensive excavations made around Key West have told us only of the existence of oolitic and compact rocks, almost destitute of corals or other remains of animal life; and from still other localities comes the opinion, that the rocks consist of nothing but more or less disintegrated shells, cemented together.

Animal Life.

This fulness and variety of animal life is particularly obvious within the boundaries of coral fields, the natural limits assigned to the growth of these animals being those in which animals of other classes range in greater profusion, and the coral reefs themselves also affording very favorable circumstances for the display of numerous living forms. Hence the extraordinary assemblage of all classes of animals upon the reef, where, besides those particular kinds of corals which contribute largely to its formation, we find upon it, or on the foundation from which it rises, a great variety of other corals, which, though too insignificant in size to take a conspicuous part in building up these extensive accumulations of organic lime-rock, add none the less their small share in the work, contributing especially to fill up the vacant spaces left by the more rapid and durable growth of the larger kinds. They are to the giants of the reef what the more slender plants are to the lords of the forest, adding the elegance and delicacy of slighter forms to the strength, power, and durability of their loftier companions.

But besides the stony corals, we find in the reef a great variety of soft polyps, either attached to the surface of dead corals, dead shells, or of the naked rock, or boring into the coral sand and mud.

A variety of Medusa nurses arise everywhere, either as delicately branching tufts or as permanently attached Medusæ from the same foundation. Their free progeny may be seen floating quietly in myriads in the waters above.

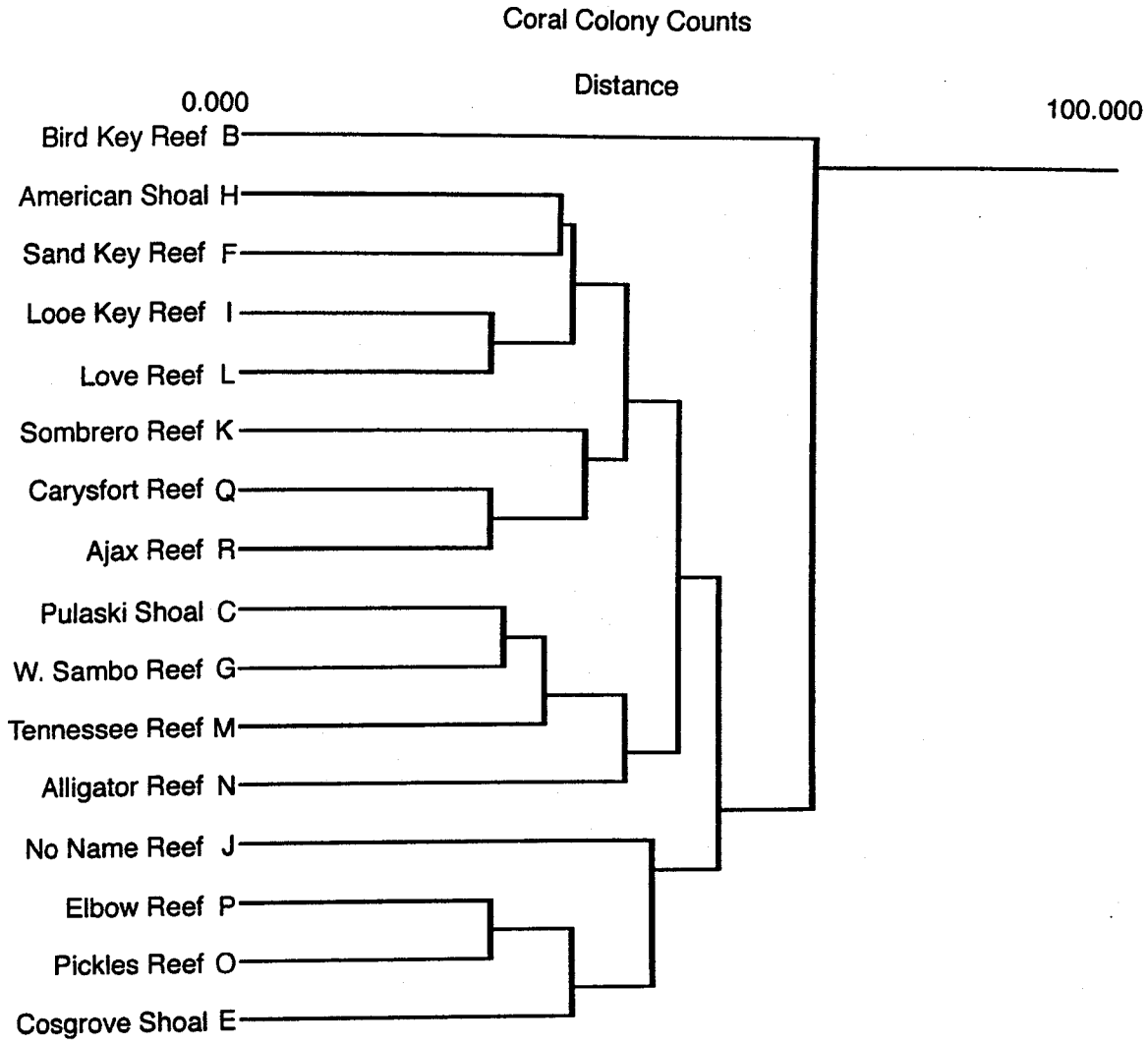


Fig. 12. Dendrogram showing relationships among the 16 spur-and-groove reefs. Euclidean distances were calculated based on the coral colony counts, pooled by species for each reef. Reefs were clustered using the average linkage method.

ble depth, and forming isolated, disconnected patches, the first rudiments, as it were, of an extensive new reef. There we have a continuous range of similar corals in unbroken continuity for miles, or even hundreds of miles, rising at unequal heights nearly to the surface.

Here and there a few heads or large patches, or even extensive flats of corals, reach the level of low-water mark, and may occasionally be seen above the surface of the waters, when the sea is more agitated than by the simple action of the tides. In other places coral sands or loose fragments of corals, larger or smaller boulders, detached from lower parts of the living reef, are thrown upon its dying summits, and thus form the first accumulation of solid materials, rising permanently above low-water mark; collected sometimes in such quantities and at such heights as to remain dry, stretching their naked heads above high water.

In other places these accumulations of loose, dead materials have entirely covered the once living corals, as far as the eye can reach into the depth of the ocean: no sign of life is left, except perhaps here and there an isolated bunch of some of those species of corals which naturally grow scattered, or of those other organisms which congregate around or upon coral reefs; but the increase of the reef by the natural growth of the reef-building corals is at an end. Again, in other places, by the further accumulation of such loose materials, and the peculiar mode of aggregation which results from the action of the sea upon them, and which will be more fully explained hereafter, extensive islands are formed, ranging in the direction of the main-land, which support them. Elsewhere we may find the whole extent of the reef thus covered, which, after a still more protracted accumulation, perhaps becomes united with some continental shore.

Now it must be obvious, that from a comparison of so many separate stages of the growth of a coral reef, a correct insight may be obtained into the process of its formation; and, indeed, in thus alluding to the different localities which came under our own observation, we have already given a general history of its progress, which we now proceed to illustrate more in detail.

We would, however, first remark, that the extraordinary varieties which exist in the natural condition of different parts of the same reef, or of different reefs, when compared with each other, fully explain the discrepancies between the reports which have been obtained, respecting the reefs of Florida, prior to our investigations.

Table 7. Results of one-way nested ANOVAs on square root-transformed coral colony counts.

A. Regions as defined by Klein and Orlando (1994), including the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	232.979	4	58.244	3.2235	0.0557
Reef{Region}	198.754	11	18.0686	25.335	< 0.0005
Error	101.985	143	0.7132		

B. Regions as defined by Klein and Orlando (1994), omitting the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	213.751	3	71.2503	3.7187	0.0497
Reef{Region}	191.598	10	19.1598	25.9669	< 0.0005
Error	92.232	125	0.7379		

C. Regions as defined by Shinn et al. (1989), including the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	208.117	3	69.372	3.7228	0.04216
Reef{Region}	223.615	12	18.635	26.1414	< 0.0005
Error	101.936	143	0.7128		

D. Regions as defined by Shinn et al. (1989), omitting the Dry Tortugas region.

Source	Sum of Squares	*df*	Mean Square	*F* -ratio	*P*
Region	188.848	2	94.424	4.7984	0.03175
Reef{Region}	216.459	11	19.678	26.684	< 0.0005
Error	92.183	125	0.7375		

prior to the formation of the outer reef the rising of which, as an external barrier, must have modified greatly the course of the currents north of the keys at a later period, leaving between them only a few narrow but navigable channels, such as exist now between the Marquesas and the Mangrove Islands, between these and Key West, and between the Pine Islands and the group of Bahia Honda.

When describing in detail the different parts of the general reef, we shall occasionally touch again upon different theoretical points only alluded to thus far, and illustrate them more fully in their connection with the facts. For the present a general idea of the topography will suffice.

We would only add that the absence of corals along the western shore of the peninsula, at present, is probably owing to the character which that shore has assumed in the progress of time; for the peninsula itself has once been a reef, at least as far as the 28th degree of north latitude, as is shown by the investigation of the everglades, and by the examination of the rocks at St. Augustine.

This latitude is the natural northern limit of the formation of coral reefs, as also of the extensive growth of stony corals, though on the southern shores of the North American continent, these formations seem to have extended far beyond their usual bounds, probably under the influence of the high temperature of the Gulf Stream; for not only do the narrow longitudinal islands which extend along the eastern shore, and their direct connection with the small keys north of Cape Florida, indicate their coralline origin, but we have even under the 32d degree of north latitude extensive coral formations at the Bermudas, still flourishing in the present day. If the growth of corals has been stopped along the eastern shore, it must be ascribed to the invasion of drift sand, which extends over the everglades, as well as along the eastern shores as far south as the Miami, Key Biscayne, and the bay of the Miami.

Mode of Formation of the Reefs.

The reefs of Florida, as they have been described in the foregoing sketch of the topography of that State, and, indeed, the separate parts of each of these reefs, in their extensive range from northeast to southwest, present such varieties as will afford, when judiciously combined, a complete history of the whole process of their formation.

Here we have groups of living corals, beginning to expand at considera-

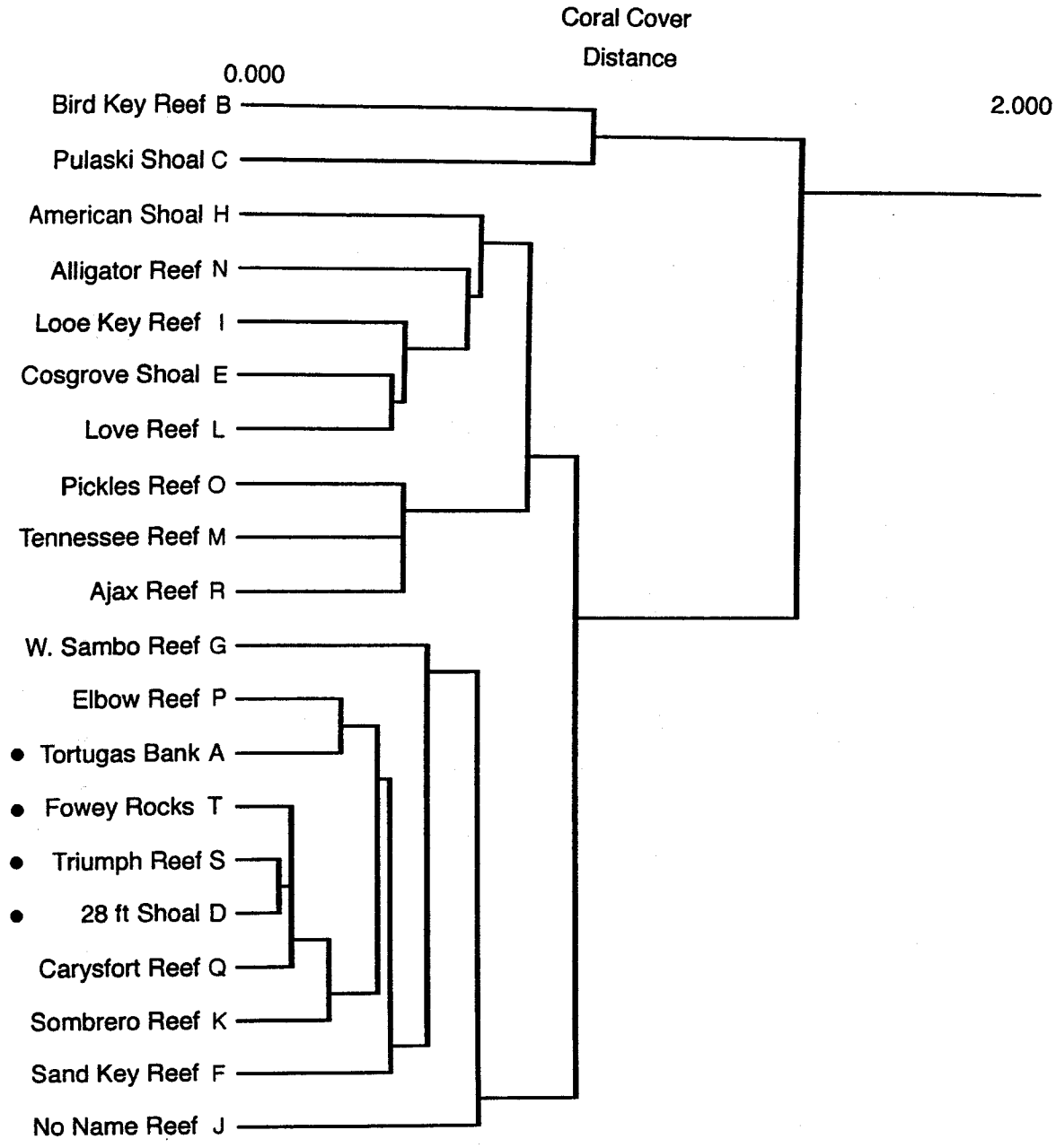


Fig. 14. Dendrogram showing relationships among all 20 reefs. Euclidean distances were calculated based on the point count data, and reefs were clustered using the average linkage method. Solid circles denote hardground sites.

even an extensive interruption in the succession of the keys before we reach the Tortugas. These last, however, as well as the bank west of these keys, belong none the less to the main range of keys, from which they are only separated by a more extensive and deeper depression. West of Sand Key the reef itself becomes gradually less elevated, until it is finally lost where the ship channel, south of the Marquesas, expands into the broad depression, separating that group of keys and shoals from the Tortugas.

In order to understand fully not only the topography, but also the mode of formation of all these keys and reefs, it must be remembered that the rising reefs, which form more or less continuous walls, reaching at unequal heights nearly to the surface, or above the level of the waters, are only a particular modification of those formations growing upon coral grounds under special circumstances. It has been ascertained, whenever similar investigations have been made, that living corals do not occur in depths exceeding twenty fathoms, that the reef-building species prosper from a depth of about twelve fathoms nearly to the surface, and that different species follow each other at successive heights. Now, if we keep in mind these facts, we shall see that all the coral-bound islands of the West Indies, as well as of the main-land of Central America, constitute an extensive coral field, divided by broad, deep channels, over which the coral reefs extend, with different features, according to the depths in which they occur and the changes which their own growth has gradually introduced upon the localities where they are found, influenced and modified to some extent also by the direction of the prevailing currents and the action of the tides.

The formation of the main range of keys in their primitive condition as a reef, — for, as we shall see hereafter, they have been a submarine reef before they rose as islands above the level of the ocean, — the formation of this range, we repeat, at gradually greater distances from the main-land, as we follow their course from east to west, has been simply owing to the depth of the bottom from which the reef has risen. It has followed the line of ten or twelve fathoms' depth; and if there is so wide an interruption between the Marquesas and the Tortugas, it is because the ground is deeper over that space. Again, if the Pine Islands have a northwesterly direction, while the main range runs more from east to west, it is no doubt because the body of water emptying from the northern part of the gulf, along the western shores of the peninsula, has, for a time, run chiefly over that field, while the tract of mud flats between the keys and the main-land was filling

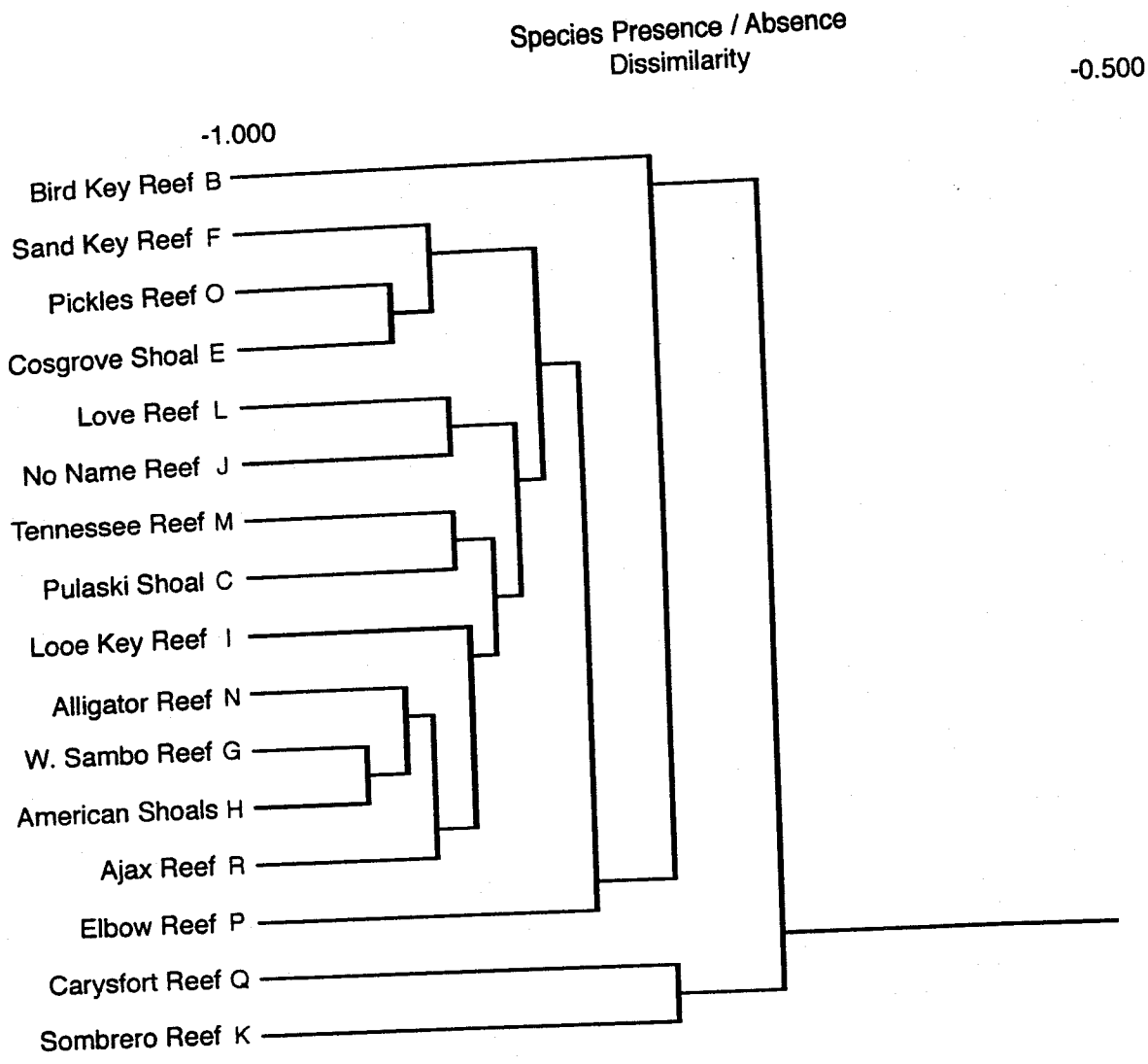


Fig. 13. Dendrogram showing relationships among the 16 spur-and-groove reefs. Jaccard dissimilarities were calculated based on the species presence/absence data for each reef. Reefs were clustered using the average linkage method.

main range of keys from Cape Florida to the western extremity of the Marquesas, where it is lost in the deep. It follows in its whole extent the same curve as the keys, encircling to the seaward the ship-channel already mentioned. This is properly the region of living corals.

Throughout its whole range it does not reach the surface of the sea except in a few points where it comes almost within the level of low-water mark, giving rise to heavy breakers, such as Carysfort, Alligator Reef, Tennessee Reef, and a few other shoals of less extent, but perhaps not less dangerous. In a few localities fragments of dead coral and coral sand begin to accumulate upon the edges of the reef, forming small keys, which vary in form and position according to the influence of gales blowing from different directions, — sometimes in the direction of the Gulf Stream from southwest to northeast, but more frequently in the opposite direction, the prevailing winds blowing from the northeast. Such are Sombrero Key, Looe Key, the Sambos, and Sand Key. Here and there are isolated coral boulders, which present projecting masses above water, such as the Dry Rocks, west of Sand Key; Pelican Reef, east of it; with many others, more isolated. Though continuous, the outer reef is, however, not so uniform as not to present many broad passages over its crest, dividing it, as it were, into many submarine elongated hillocks, similar in form to the main keys, but not rising above water, and in which the depressions alluded to correspond to the channels intersecting the keys. These broad passages leading into the ship channel, which may be available as entrances into the safe anchorage within the reef, are chiefly the inlet in front of Key Largo and to the west of Carysfort Reef, with nine feet of water; a passage between French Reef and Pickle's Reef, with ten feet; another between Conch Reef and Crocker's Reef, also with ten feet; another between Crocker's Reef and Alligator Reef, with two fathoms; another between Alligator Reef and Tennessee Reef, with two fathoms and a half; and a sixth to the west of Tennessee Reef, varying in depth from two and a half to three fathoms.

The remark which has been made respecting the mud flats and their gradual deepening from east to west applies equally to the general features of the main reef, as well as to the intervening channel. To the eastward the channel is shallower, the ground around the keys and reef becomes shoaler, and there is a gradual dip towards the west, which makes the connection less marked between the keys west of Key West, in the large groups of the so-called Mangrove Islands, and the Marquesas, beyond which there is

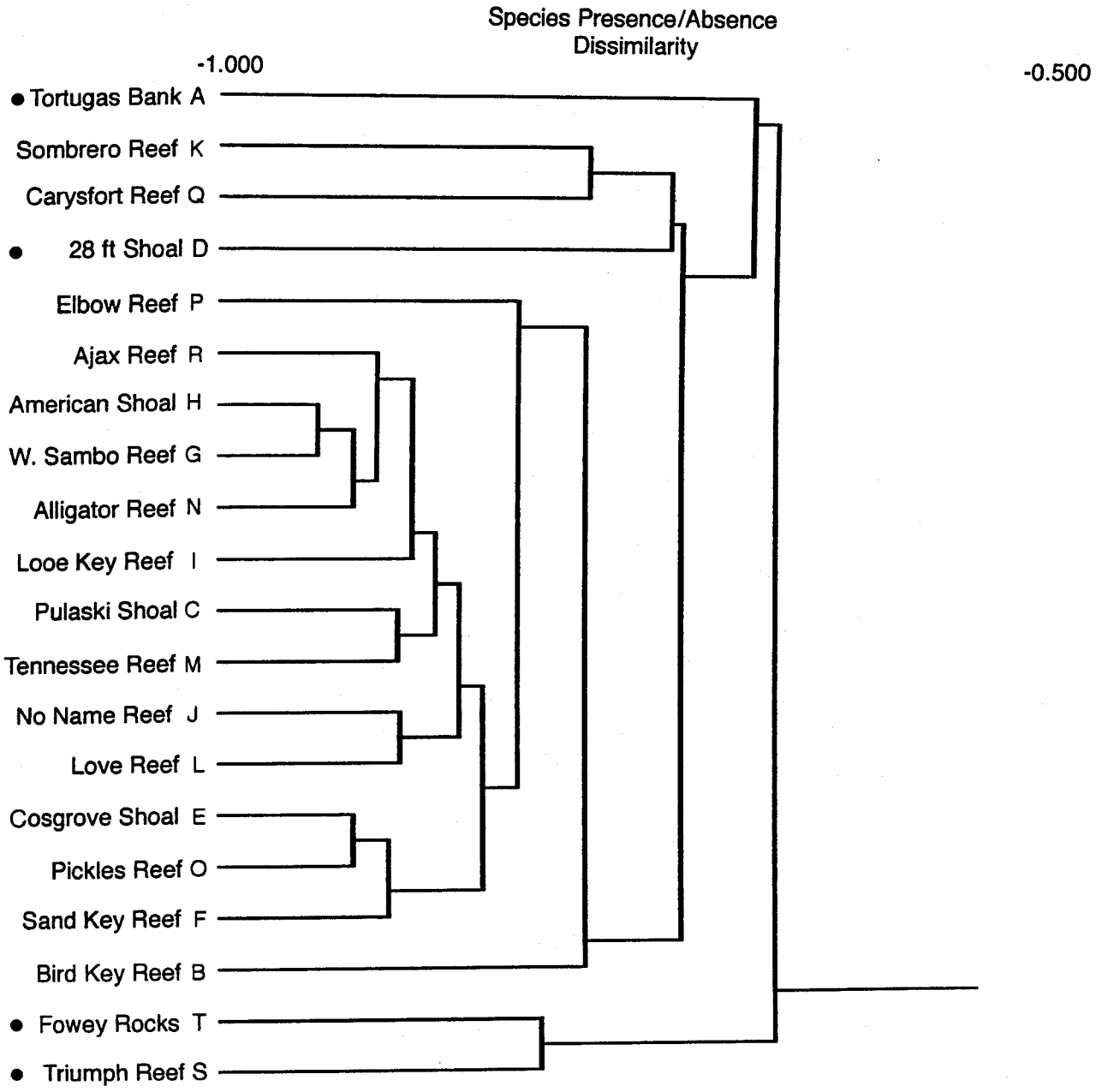


Fig. 16. Dendrogram showing relationships among all 20 reefs. Jaccard dissimilarities were calculated based on the species presence/absence data, and reefs were clustered using the average linkage method. Solid circles denote hardground sites.

their steepest shore is turned towards the Gulf Stream, while their more gradual slope inclines towards the mud flats which they encircle.

This is a point which it is important to notice, as it will assist us in our comparison between the keys and the shore bluffs of the main-land, as well as with the outer reef and the reefs of other seas, in all of which we find that the seaward shore is steeper than that turned towards the main-land, or, in the case of circular reefs enclosing basins (atolls), than that which borders the lagoon.

The reef proper extends parallel to the main range of keys for a few miles south or southeast of it, following the same curve, and never receding many miles from it. The distance between the reef and the main range of keys varies usually from six to two or three miles, the widest separation being south of Key West and east of the Ragged Keys, where the space is about seven miles. Between this reef, upon which a few small keys rise at distant intervals, and the main range of keys already described, there is a broad, navigable channel, extending the whole length of the reef, from the Marquesas to Cape Florida, varying in depth from three to six and seven fathoms, and, except off Looe Key, where the passage is not more than fourteen feet deep at low water, averaging from three to four fathoms.

Farther east the average depth is again the same as at Looe Key; but it becomes gradually more and more shoal towards the east, measuring usually about two fathoms, or even less, to the east of Long Key and Key Largo, but deepening again somewhat towards Cape Florida, where the reef converges towards the main keys and the main-land. Protected by the outer reef, this channel affords a very safe navigation to vessels of medium size, and would allow a secure anchorage almost everywhere throughout the whole length of the reef, were the numerous deep channels which intersect the outer reef well known to navigators, and marked by a regular system of signals. As it is, however, the reef seems to present an unbroken range of most dangerous shoal grounds, upon which thousands of vessels, as well as millions of property, have already been wrecked. These facts have a stronger claim upon the attention of the government, since there are, as already remarked, numerous passages across the reef which might enable even the largest vessels to find shelter and safe anchorage behind this threatening shallow barrier.

The reef proper, as we have remarked above, runs almost parallel to the

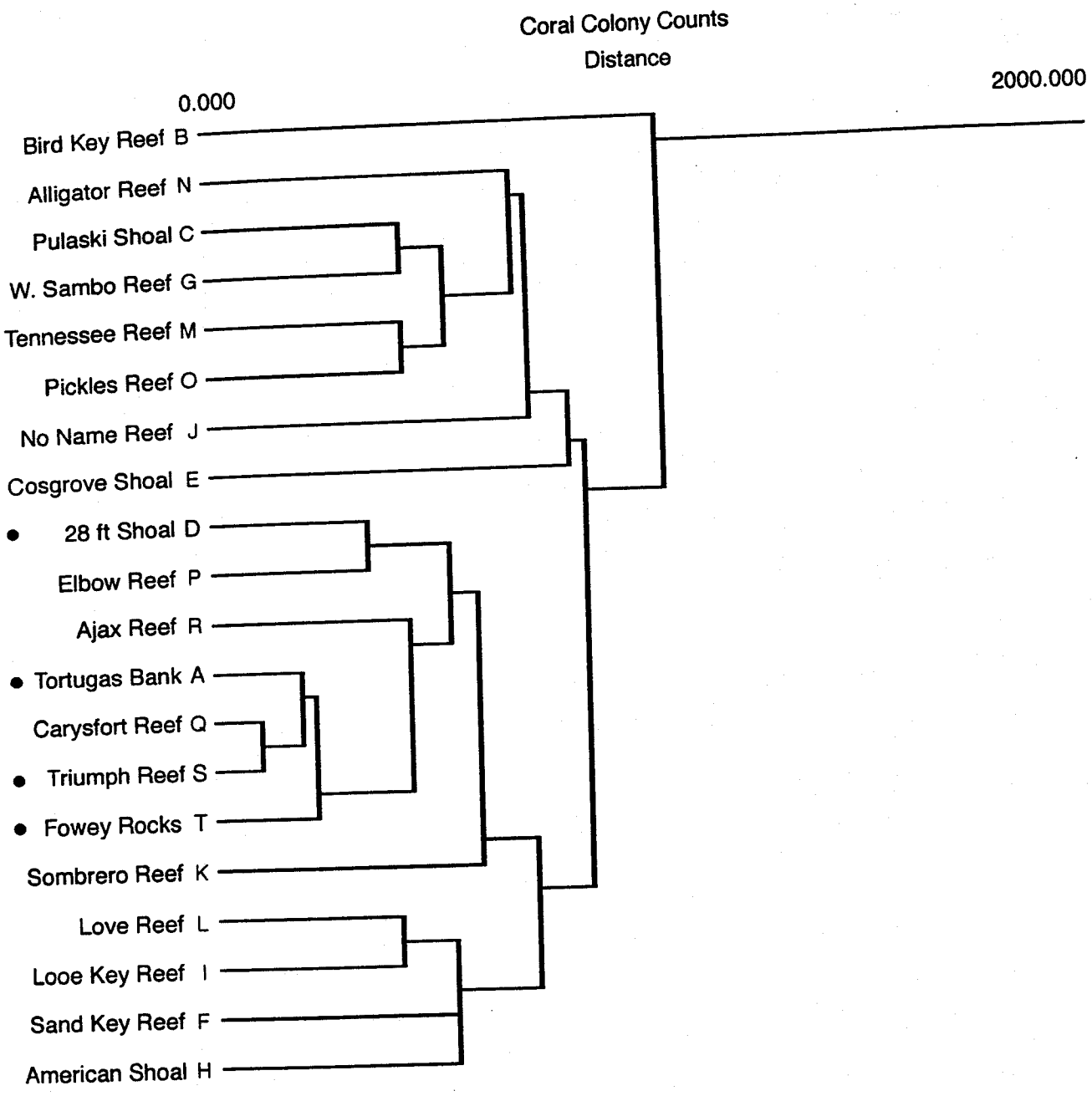


Fig. 15. Dendrogram showing relationships among all 20 reefs. Euclidean distances were calculated based on the coral colony count data, and reefs were clustered using the average linkage method. Solid circles denote hardground sites.

keys are literally studded with these Mangrove Islands. Sometimes they are distributed without apparent regularity; sometimes, as to the north of Key Largo, they form a continuous range between the main-land and the keys. They are also very numerous along the main keys, or at least along that side of them which is turned towards the most extensive mud flats. Sometimes these Mangrove Islands form little archipelagoes of innumerable small islets, so intimately interwoven, and separated by such narrow and shallow channels, as to be almost impenetrable. Such archipelagoes occur chiefly to the north of Bahia Honda and the Pine Islands, as well as to the northwest of Key West. The luxuriant vegetation which rises from these low islands, consisting chiefly of mangroves, gives them a very peculiar appearance. We shall have occasion to return to this subject when we attempt to explain the formation of the different islands connected with the Florida Reef and the main-land. The whole tract between Cape Sable and the keys, east of Bahia Honda, as far as Cape Florida, or at least as far as Soldier Key, is so shoal that it will forever remain inaccessible, except to very small vessels.

The keys consist of an extensive range of low islands, rising but a few feet, perhaps from six to eight or ten, or at the utmost to twelve or thirteen feet, above the level of the sea. They begin to the north of Cape Florida, where they converge towards the main-land, extending in the form of a flat crescent in a southwesterly direction, gradually receding from the main-land until, opposite Cape Sable, they have so far retreated as to be separated from it by a shallow sheet of water forty miles wide. Farther to the west they project in a more westerly course, with occasional interruptions, as far as the Tortugas, which form the most western group. They consist either of accumulated dead corals, of coral rocks, or of coral sand, cemented together with more or less compactness. Their form varies, but is usually elongated and narrow, their greatest longitudinal extent following the direction of the main range, except in the group of the Pine Islands, where their course is almost at right angles with the main range, — a circumstance which we shall attempt hereafter to explain.

Most of these islands are small, the largest of them, such as Key West and Key Largo, not exceeding ten or fifteen miles in length; others only two or three, and many scarcely a mile. Their width varies from a quarter to a third or half a mile, the largest barely measuring a mile across; but whatever the difference in their size, they all agree in one respect, — that

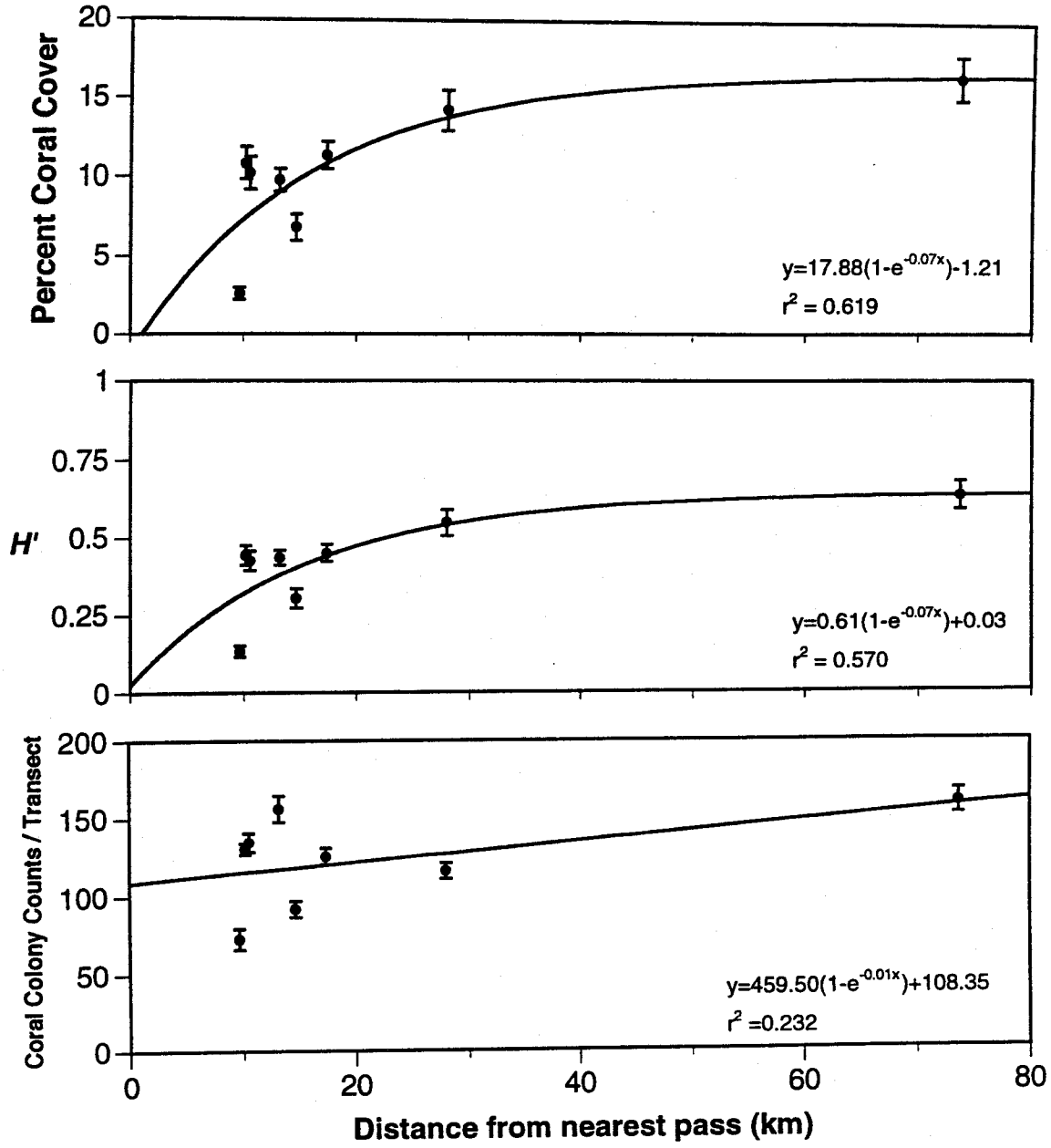


Fig. 17. Changes in univariate parameters with distance from the nearest upstream pass to Florida Bay. Reefs of the Middle and Lower Keys are plotted, as only they are exposed to Florida Bay water through passes. Error bars represent standard errors.

whole length of the eastern shore, are probably a direct continuation of the keys, covered with drifted sand.* This is certainly the case with the range of keys extending from the main-land to Cape Florida, which limits to the east the bay of Miami, their formation being of coral rock, but covered by silicious drift-sand.

As to the southernmost extremity of the main-land proper, it is very difficult to determine its outlines, as it consists of innumerable islands, sometimes separated by narrow channels, and sometimes assuming the character of real islands only at high water, being mostly connected with the main-land by very shallow flats. This is especially the case along the southwestern extremity of the peninsula. The outline of the southern shore, however, between Cape Florida and Cape Sable, is better defined,— presenting, in almost unbroken continuity, steep bluffs of the same coral limestone which forms the bottom of the everglades, and may be traced, without interruption, along the Miami from the seashore to the everglades.

South of the main-land, between it and the range of keys, there are extensive flats, which, even at high water, are but slightly covered, and which the retreat of the tide lays bare, leaving only narrow and shallow channels between the dry flats, with occasional depressions of greater depth. These mud flats extend not only between the main-land and the keys as far as Cape Sable, but may be traced to the north along the western shores of the continent, and to the west along the northern shores of the keys, not only as far as Key West and the Marquesas, but even to the Tortugas.

There is, however, this remark to be made, — that to the west the mud flats become covered, by degrees, with deeper and deeper water; or, in other words, that these low grounds, extending between the main-land and the main range of keys, dip slightly to the west, being gradually lost in the shoals extending north of the Marquesas and the Tortugas, along the western shore of the peninsula. These flats are interspersed with innumerable low islands, known in the country by the generic appellation of the Mangrove Islands, respecting which we shall give further details hereafter.

The shoals between Cape Sable, Cape Florida, and the main range of

* A direct investigation of this point, which did not come within the limits of my survey, would be of considerable practical importance, inasmuch as it may lead to the discovery of a basis of coral rock, affording a far more solid foundation for the construction of the lighthouses wanted along that coast, than the loose shore-detritus.

Based on coral cover and colony counts, the hardground sites also clustered with Carysfort Reef (Q). The spur-and-groove of the Carysfort Reef site is characterized by extremely low relief, which makes it quite similar to the hardground sites in terms of geomorphology. It thus appears that substratum characteristics influence the composition of coral assemblages. Similar results were obtained in comparisons of hardground habitats with spur-and-groove habitats at shallower depths (Aronson and Swanson in press).

Environmental Hypotheses

This study detected no geographic gradients in coral cover or assemblage composition. Instead, variation among reefs outweighed variation among regions of the reef tract. The only region that was substantially different from the rest was the Dry Tortugas. This region is isolated from the rest of the reef tract and is subject to far less human influence. While reefs of the Florida Keys are influenced by both ocean currents and lagoonal waters, the reefs of the Dry Tortugas receive oceanic water only. Therefore, it is not surprising that their coral assemblages differed.

It has long been suggested that exposure to Florida Bay water influences reef development in the Middle Keys (Ginsburg and Shinn 1964, 1994; Walker et al. 1982; Shinn et al. 1989; Lidz and Shinn 1991; Szmant and Forrester 1996; Hallock 1997; Ogden 1997). According to this scenario, reefs opposite passes between Keys are directly exposed to inimical Bay waters, which may be nutrient-enriched, hyper- or hyposaline, and/or too hot or cold. As a result, these reefs are poorly developed. Reefs opposite Keys are sheltered from Bay water and are correspondingly better developed.

In order to test this hypothesis, we regressed coral cover, H', and colony counts per transect on distance from the nearest upstream pass for reefs of the Middle and Lower Keys. We fit saturation functions of the form $y=a(1-e^{-bx})+c$, where a, b, and c are constants, to the three relationships. Distance from the nearest pass explained a maximum of 62% of the variation among reefs (Fig. 17). It is therefore possible that Florida Bay influences reef community structure in the 13-19 m depth range.

CONCLUSION

Coral reef surveys are almost always limited by time and money, necessitating short, "snapshot" visits to individual reefs. The results presented here suggest that a 10-transect sample from a small area within a reef, taken during the course of a day or less, is an adequate representation of that reef, at least for univariate and multivariate comparisons of coral cover and diversity. Somewhat less confidence can be placed on the representativeness of subreefs for univariate comparisons of coral colony counts, judging from the results for one of the 9 subreefs. Nevertheless, a multivariate cluster analysis of colony counts showed close similarity of subreefs within reefs.

Comparisons among reefs and among regions were the principal goals of the Keyswide Coral Reef Expedition. The data revealed significant differences among reefs with spur-and-groove

REPORT ON THE FLORIDA REEFS.

REPORT OF PROFESSOR AGASSIZ TO THE SUPERINTENDENT OF THE COAST SURVEY, ON THE EXAMINATION OF THE FLORIDA REEFS, KEYS, AND COAST.

CAMBRIDGE, August, 1851.

SIR,— The following report of the examination made by me of the Florida reefs, keys, and coast is prepared in compliance with your request.

Topography of Florida.

To form a correct idea of the Florida reefs, it is of paramount importance to keep in mind the topographical features of the whole country. The peninsula of Florida projects between the Gulf of Mexico and the Atlantic, from the 30th degree of northern latitude nearly to the 24th, as a broad, flat, low promontory, which has generally been considered a continuation of the low lands of the Southern States. But, as we shall see hereafter, this is not the case, or, at least, not with respect to the southern extremity of the peninsula, which consists of the same formations as the reef itself. Again, in a physical point of view, Florida is not limited to those tracts of land, forming the peninsula, which rise above the level of the sea, for the extensive shoals along its southern extremity, between the main-land and the keys and reefs, as well as those extending to the west as far as the Tortugas, whence they stretch along the western coast, in fact belong to it, and are intimately connected with it, by their physical character. There is a similar tract of flats along the eastern shore, but it is not so extensive as on the southern and western shores, nor does it partake as largely of the peculiar character of the peninsula, being chiefly formed of the alluvial sand, drifted ashore by the waters of the Atlantic.

We shall have occasion, however, to show hereafter that the narrow longitudinal islands, which extend close to the main-land almost for the

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PREFACE.

THE greater number of the Plates which accompany this Report were originally prepared for the final Report of Professor Louis Agassiz on the Coral Reefs of Florida, which for various reasons was never published. In order to make known the beautiful drawings of corals lithographed by the late Mr. Sonrel, it was my intention to publish these plates, as "Illustrations of Florida Corals,"[1] with an explanation kindly supplied by Mr. Pourtalès. He has also selected a few additional species, which have been lithographed and added to the original plates in order to make these illustrations as far as possible characteristic of the prominent Florida species, both the reef-builders and those found within the reef area.[2]

On consultation with the Superintendent of the Coast Survey, the Hon. Carlile P. Patterson, it was deemed advisable to publish at the same time, as far as it could be found, the Report of Professor Agassiz on the Florida Reefs, extracts of which were published in the Annual Report of the Superintendent of the Coast Survey for 1851, — a publication but little known to naturalists before the days of deep-sea dredging. To this Report I have appended, with the permission of the publishers, Messrs. Houghton, Osgood, & Co., the sketch of Florida found in Professor Agassiz's "Methods of Study," and based entirely upon his investigations of the Florida Reefs under the auspices of the Coast Survey. I have added a sketch map of southern Florida, with the Keys, compiled from Coast Survey maps, to facilitate the reading of this Report.[3]

[1] During his frequent visits to all parts of our sea-coast, a number of drawings of polyps and of other marine animals which can only be drawn directly from life, were made under the direction of Professor Agassiz; these I hope from time to time to publish in the Museum Memoirs, with the necessary explanations, and the Florida corals form the first part of these illustrations.

[2] For the deep-sea corals see Pourtalès, No. IV. Illust. Cat. M. C. Z. Mem. Mus. Comp. Zoöl., Vol. II.

[3] For further details see the large Coast Survey charts Nos. 166, 167, 168, 169, issued since the date of Professor Agassiz's report.

CAMBRIDGE, MASS., March, 1880.

ALEXANDER AGASSIZ.

31034

habitats in the 13-19 m depth range. The variation among reefs outweighed variation among regions, suggesting that the differences observed among reefs were caused by physical and biological parameters that varied at the scale of kilometers. Differences between the hardground sites and the spur-and-groove sites are at least partly due to the control of assemblage composition exerted by the physical structure of the substratum. The hypothesis that exposure to Florida Bay water influences coral cover was supported.

Single factors rarely provide sufficient explanations in ecology. The goal of ecological analysis should be to understand the relative contributions of multiple processes to observed patterns (Quinn and Dunham 1983). Thus, although Florida Bay may influence reef development in the Middle and Lower Keys, it is certainly not the only influence. Multiple factors apparently combine to determine patterns of community composition along the Florida reef tract.

ACKNOWLEDGEMENTS

We thank John Ogden and Steven Miller for organizing the Keyswide Coral Reef Expedition, and Ken Johns and Otto Rutten for running a program of continuous nitrox diving during the cruises. They, Dennis Hanisak, and Laura Seimon participated in the field work that formed the basis of this report. We are particularly indebted to Dione Swanson for assistance with all aspects of the project. Robert Ginsburg, Eugene Shinn, and William Precht shared their knowledge of the geology of the Florida reef tract.

The Expedition was funded by NOAA's National Undersea Research Center at the University of North Carolina, Wilmington; NOAA's Sanctuaries and Reserves Division; The U.S. National Park Service, Biscayne National Park; The Munson Foundation; The Florida Institute of Oceanography; and Harbor Branch Oceanographic Institution. This project was carried out under permits from the Florida Keys National Marine Sanctuary, the U.S. National Park Service, and the State of Florida.

Memoirs of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
VOL. VII. No. 1.

REPORT

ON THE

FLORIDA REEFS

BY LOUIS AGASSIZ.

ACCOMPANIED BY ILLUSTRATIONS OF FLORIDA CORALS,

FROM DRAWINGS BY A. SONREL, BURKHARDT, A. AGASSIZ, AND ROETTER.

WITH AN EXPLANATION OF THE PLATES BY L. F. POURTALÈS.

PUBLISHED BY PERMISSION OF A. D. BACHE AND CARLILE P. PATTERSON,
SUPERINTENDENTS OF THE U. S. COAST SURVEY.

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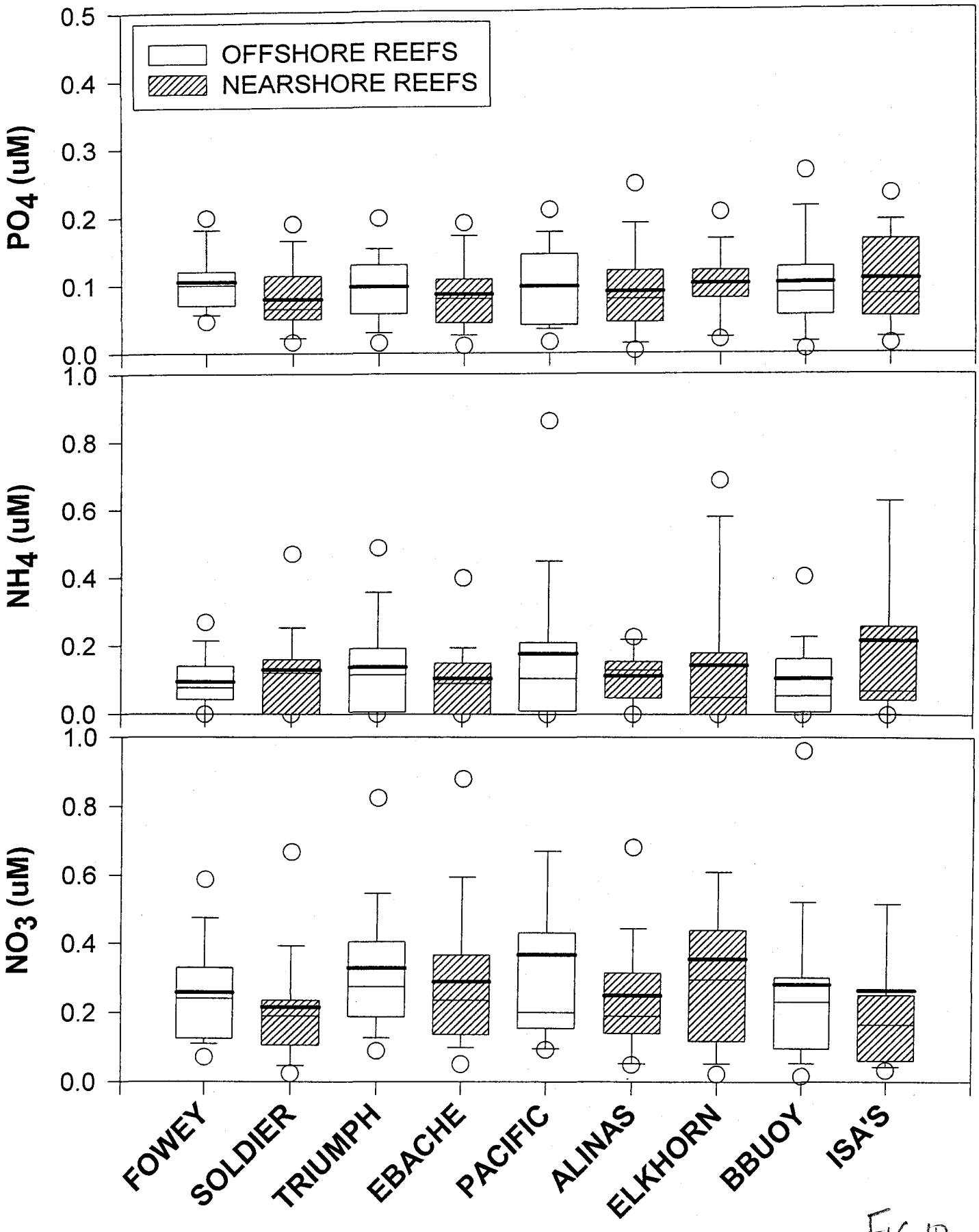

OFFSHORE REEFS
NEARSHORE REEFS
PO4 (uM)
NH4 (uM)
NO3 (uM)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.8
1.0
FOWEY
SOLDIER
TRIUMPH
EBACHE
PACIFIC
ALINAS
ELKHORN
BBUOY
ISA'S

FIG. 1D

ABUNDANCE OF SHALLOW-WATER CORALS (ORDER SCLERACTINIA) IN THE SAFETY VALVE REGION OF BISCAYNE BAY, FLORIDA

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ABSTRACT

The Safety Valve region of Biscayne Bay, Florida is an area of shallow seagrass and sand communities. Many organisms inhabit this area, among which are scleractinian corals. This region and the corals there have received little attention thus far. In this study, the abundance of corals in four areas within the Safety Valve region was examined. The number of corals ranged from 1 to 26 per square meter and averaged at 10.8 per square meter, up to 96% of which were Porites divaricata Lesueur.

INTRODUCTION

To some, the mention of scleractinian corals will bring to mind thoughts of grand reefs in the Pacific and Caribbean teeming with a diversity of life. Few though, would think of seagrass flats as important communities for corals, yet many species can be found there. The shallow seagrass beds of Biscayne Bay in Florida are a good example.

Biscayne Bay, located south of downtown Miami, is an oval body of water approximately 45 kilometers in length, 15 kilometers in width, and 4.5 meters in depth at its maximums. The bay is bordered to the west by the Florida mainland and to the east by a chain of islands,

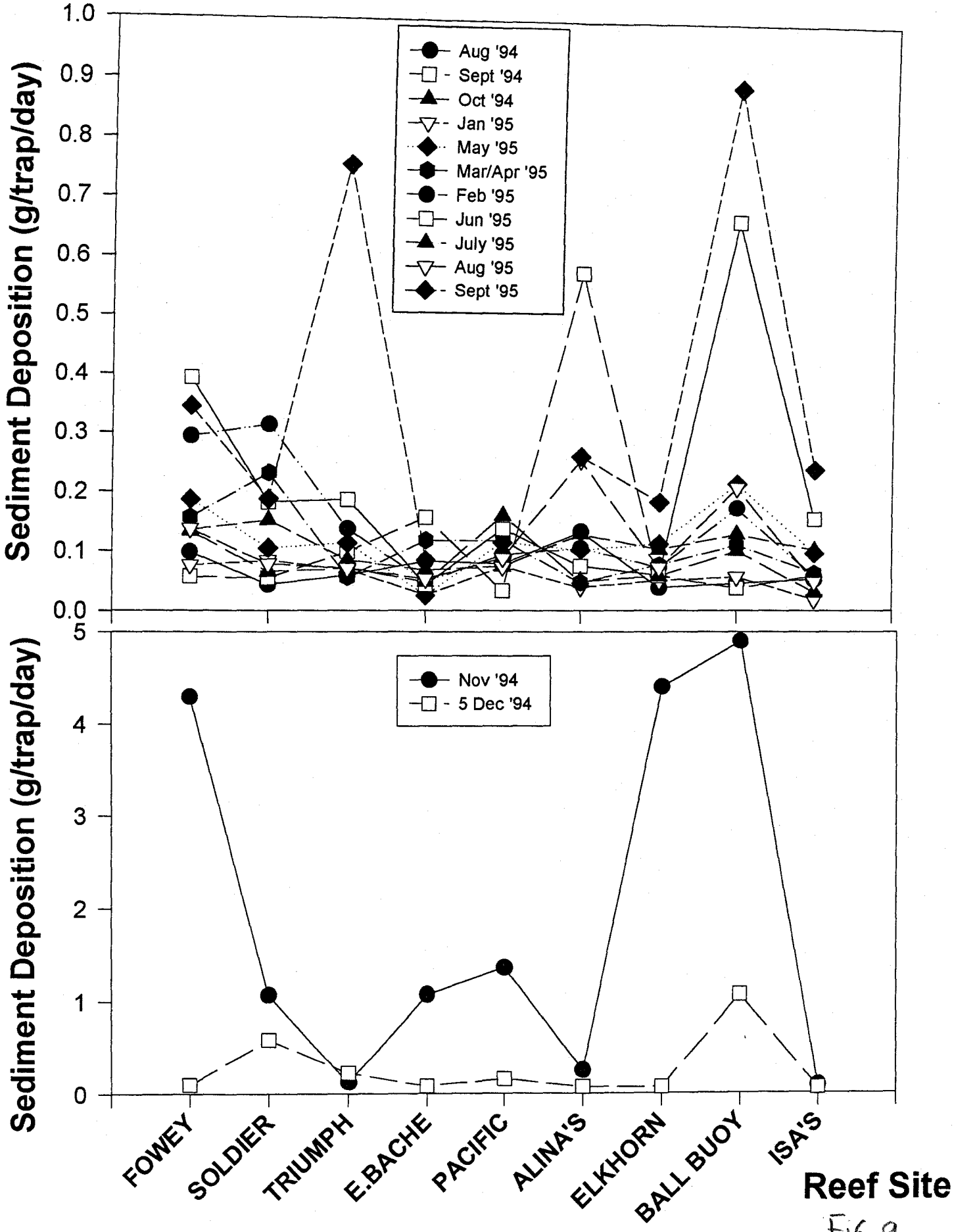

Sediment Deposition (g/trap/day)
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Aug '94
Sept '94
Oct '94
Jan '95
May '95
Mar/Apr '95
Feb '95
Jun '95
July '95
Aug '95
Sept '95
Sediment Deposition (g/trap/day)
5
4
3
2
1
0
Nov '94
5 Dec '94
FOWEY
SOLDIER
TRIUMPH
E.BACHE
PACIFIC
ALINA'S
ELKHORN
BALL BUOY
ISA'S
Reef Site

Fig. 9

lying upon the Key Largo limestone ridge (Hoffmeister 1974, Wanless 1976), most of which are the northernmost islands of the Florida Keys. The bay is mostly enclosed except for a few passages, the largest of which is an area between Key Biscayne and Soldier Key called the Safety Valve as seen in Figure 1.

The Safety Valve is located on the bay side of an area where the Key Largo limestone ridge is submerged a few meters (Wanless 1976). Sediments have accumulated to form a band of parallel east-west oriented shallow bars, each separated by deeper channels about 100 meters in width (Wanless 1976). The bars are composed of calcareous muds and sands, the majority of which are plates from the calcareous green alga Halimeda (Wanless 1976). A cross-section of the Safety Valve region and the relationship between the muds and sands can be seen in Figure 2. The thickness of the sediments throughout Biscayne Bay varies from none in parts (Voss et al. 1969) to its thickest, approximately seven meters, in the Safety Valve (Wanless 1976). The sediment thickness, among other factors, influences the type of community that inhabits the bottom (Voss et al. 1969). Seagrass communities favor thicker sediments and tend to dominate much of the Biscayne Bay bottom (Voss et al. 1969), including the bars of the Safety Valve (Wanless 1976).

Seagrass communities are complex webs of many infaunal and epifaunal populations. The typical seagrasses of Biscayne Bay are turtle grass (Thalassia testudinum Koenig), manatee grass (Syringodium filiforme Kutzing), and shoal grass (Halodule wrightii Ascherson). The extensive rhizome network of the grasses plays an important role in stabilizing the sediments of the bay (Wanless 1976). More details

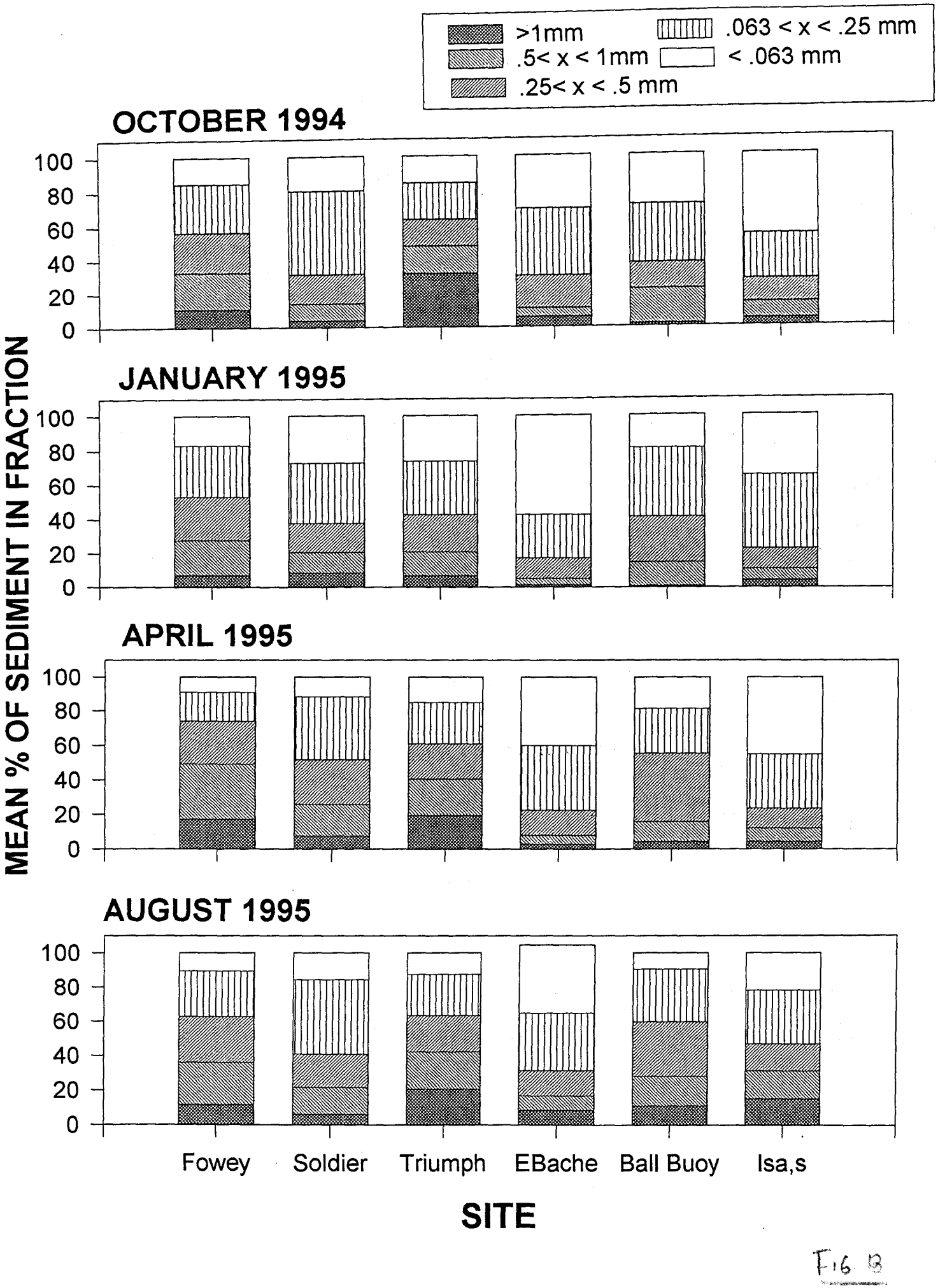

>1mm
.5< x < 1mm
.25< x < .5 mm
.063 < x < .25 mm
< .063 mm
OCTOBER 1994
JANUARY 1995
APRIL 1995
AUGUST 1995
MEAN % OF SEDIMENT IN FRACTION
100
80
60
40
20
0
Fowey
Soldier
Triumph
EBache
Ball Buoy
Isa,s
SITE

Fig B

on the grasses can be found in Thorhaug (1976). Other organisms that inhabit the seagrass communities are algae, especially calcareous green algae such as Penicillus spp. and Halimeda spp. (see Humm 1976), sponges, corals, polychaetes, bryozoans, gastropods, bivalves, cephalopods, crustaceans, and echinoderms (Voss et al. 1969).

A moderate amount of work has been done to study the abundance and distribution of organisms in Biscayne Bay. McNulty, Work, and Moore (1962) surveyed the infauna of the bay, but only in non-grass areas. O'Gower & Wacasy (1967) limited their work to the infauna of Virginia Key and Key Biscayne. Moore et al. (1968) worked only on the tidal flats of Virginia Key. Voss et al. (1969) produced species lists for taxa from alga to fish for the entire area of Biscayne National Monument which, at the time, was only proposed and did not include the Safety Valve region. Unfortunately, their work was only qualitative and not quantitative. Detailed studies have been done on southern Biscayne Bay and Card Sound by Bader (1969), Bader and Roessler (1971, 1972), and Iversen and Roessler (1973) due to the specific interest of Florida Power and Light Co. and their Turkey Point nuclear power plant. More recent studies, such as McLaughlin, Treat, and Thorhaug (1983), deal predominantly with the replanting of seagrasses and restoration of their communities due to damage from thermal discharges from the same power plant. Very little to no work has been done in the Safety Valve region or on the corals of Biscayne Bay. This study, conducted on September 29, 1990 by Dr. Peter Glynn and his Tropical Marine Ecology class, looked at the abundance of corals in the seagrass communities of the Safety Valve.

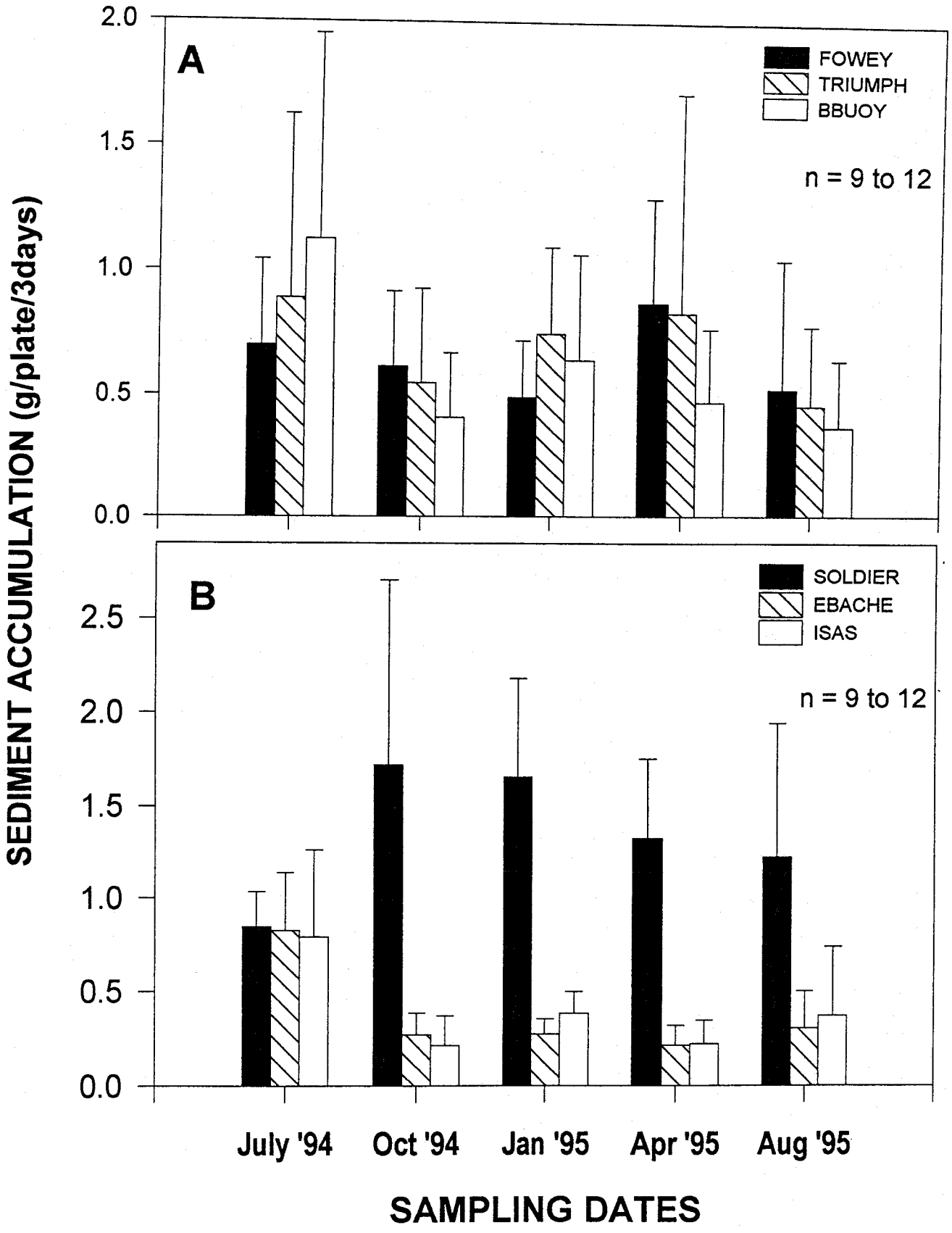

A
FOWEY
TRIUMPH
BBUOY
n = 9 to 12
2.0
1.5
1.0
0.5
0.0
B
SOLDIER
EBACHE
ISAS
n = 9 to 12
2.5
2.0
1.5
1.0
0.5
0.0
SEDIMENT ACCUMULATION (g/plate/3days)
July '94
Oct '94
Jan '95
Apr '95
Aug '95
SAMPLING DATES

Fig. 7

METHODS AND MATERIALS

The primary study site was located in the northern portion of the Safety Valve, near the center of one of the bars just south of the "Stiltsville" area south of Key Biscayne and just east of Marker 1. The depth of the area was approximately one meter near low tide. Two 70 meter transect lines were aligned, one north-south and the other east-west, in a cross such that each of the four arms was 35 meters in length. On each transect arm, a team of two students was equipped with a 1 m X 1 m square hollow PVC quadrat with holes or openings so that water could fill and keep the quadrat flat on the bottom. Thirteen stations were chosen by computer-generated random numbers. Stations were the same distances from the center for each of the four arms. The quadrats were placed at each station and the number of colonies of each species found were counted. The definition of a colony, for counting purposes, was any individual unattached to others. When all 52 stations had been counted, the four teams of students each surveyed station #13 on each arm to determine the consistency of their surveys.

At three other sites, each progressively farther north such that the last site was in the "Stiltsville" area, surveys were done for a comparison with our primary site. At each, the quadrat was arbitrarily thrown, submerged, and the corals within counted. At the first of the three sites, seven quadrats were sampled. At each of the other two sites, four quadrats were surveyed.

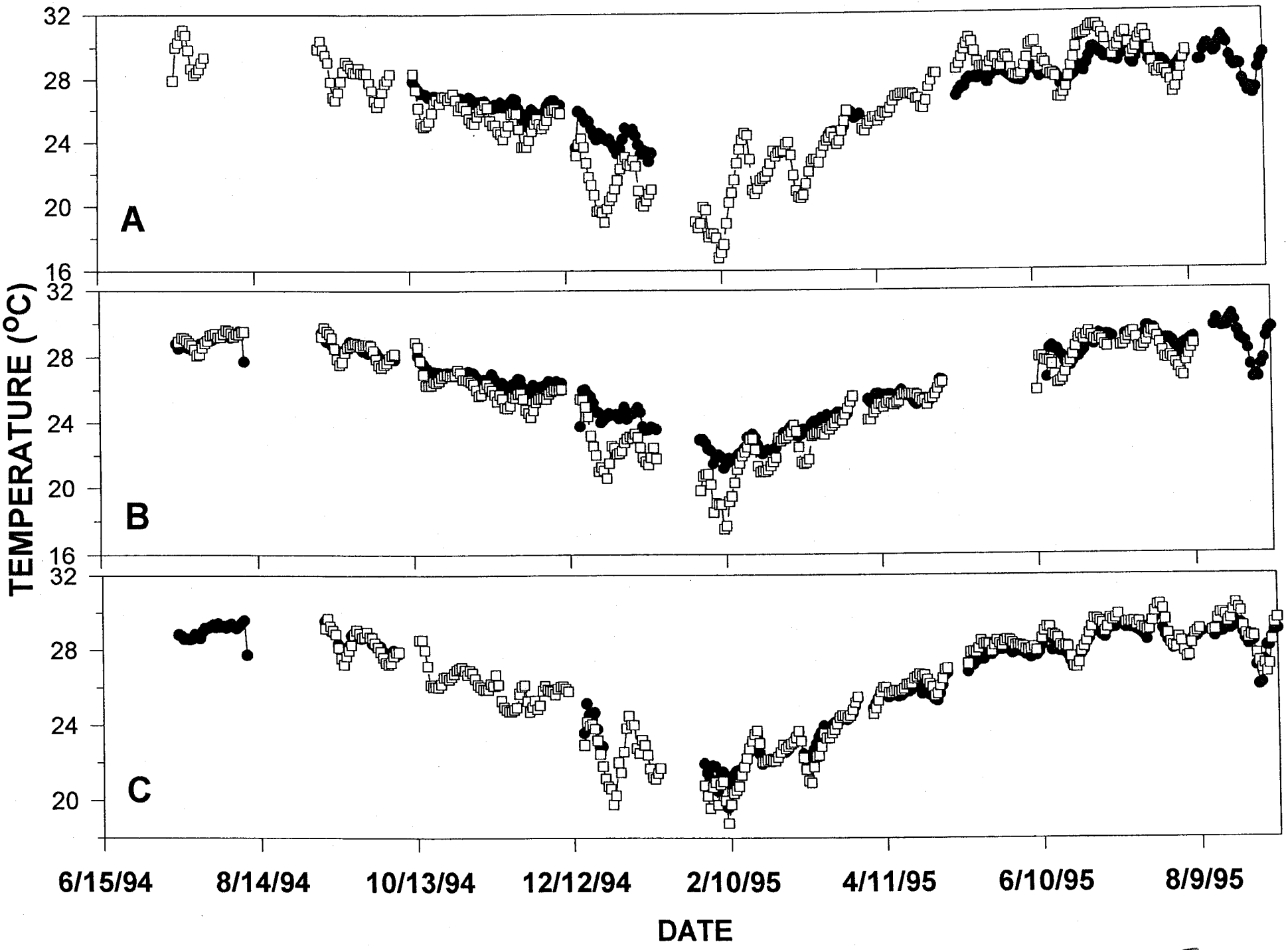

TEMPERATURE (°C)
32
28
24
20
16
A
B
C
6/15/94
8/14/94
10/13/94
12/12/94
2/10/95
4/11/95
6/10/95
8/9/95
DATE

Fig. 6

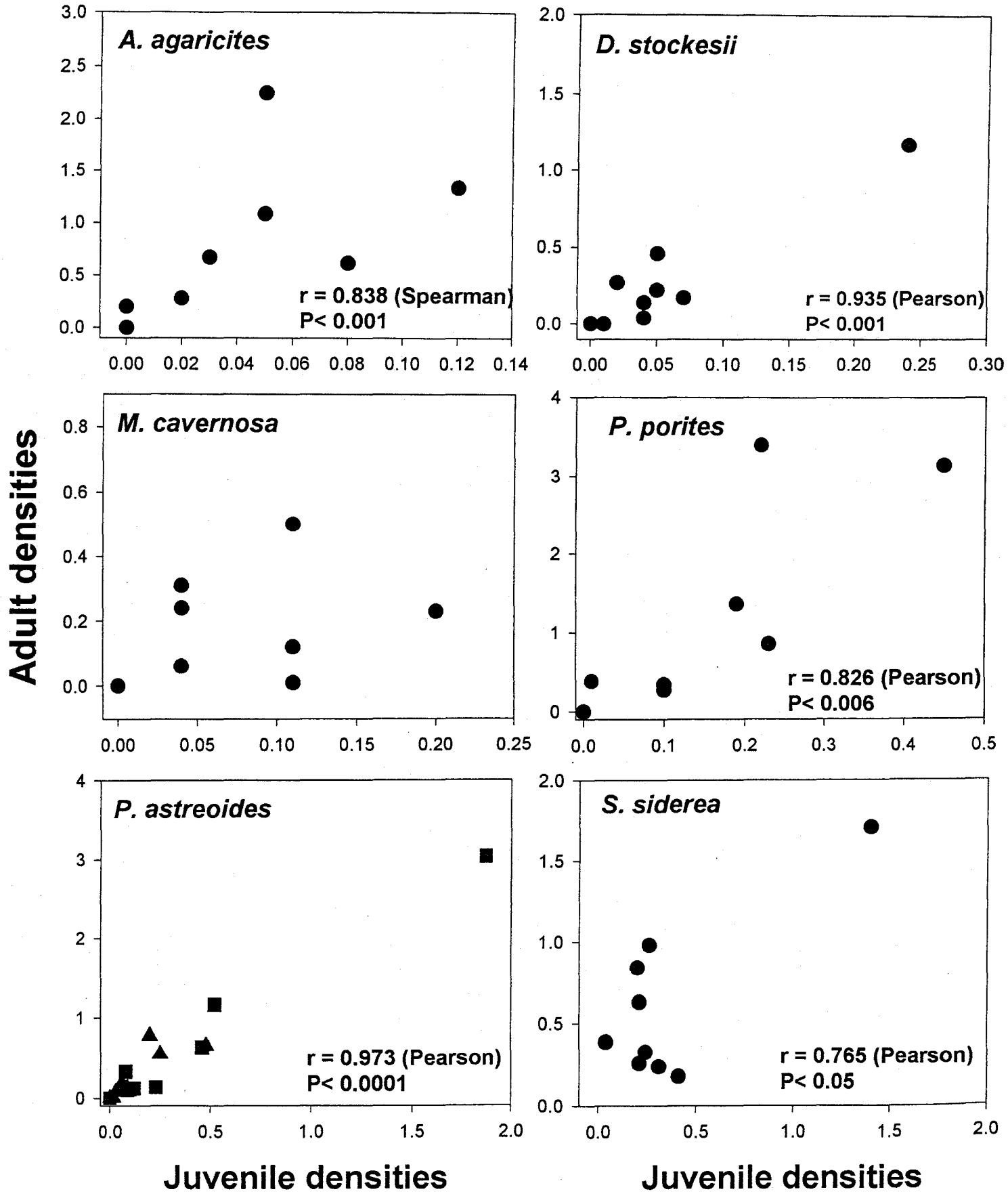
RESULTS

The results of the quadrats for each of the transect arms can be seen in Tables 1 and 2. The cumulative results of species frequencies are in Table 3. The coral species found in the primary survey, in order of their abundance (mean number of individuals, range (min.-max.) per square meter), were Porites divericata Lesueur (10.38, 1-25, N=540), Cladocora arbuscula Lesueur (0.25, 0-3, N=13), Porites furcata Lammarck (0.06, 0-1, N=3), Siderastrea radians Pallas (0.06, 0-1, N=3), Manicina areoloata Linnaeus (0.04, 0-1, N=2), Favia fragum Esper (0.02, 0-1, N=1), and Isophyllia spp. (0.02, 0-1, N=1). Oculina spp. was also seen in the area, but was not found in any of the quadrats. In the consistency test, shown in Table 4, a Chi-square goodness-of-fit test was performed. The only significant differences in group counting were found in the north arm for Porites divericata and Porites furcata (0.025<P<0.01 and 0.05<P<0.025, respectively).

The results of the arbitrary sampling at the other three sites is shown in Table 5. A few species; Porites furcata, Favia fragum, and Isophyllia spp.; were not seen at these other sites and one species, Solenastrea spp., was only seen at the third ("Yellow house") site. When the data from the three sites is combined, the species abundance is smaller than that from the primary site for Porites divaricata (5.53, 0-13, N=83), but greater for the other corals.

Porites divaricata was the dominant species as it constituted 96% of the primary site species and 84% of the species at other sites. The dominance of this species can also be seen in the primary site's lack of diversity (D = 0.08, Simpson's Diversity, N = 563). Cladocora

FIG 5


A. agaricites
r = 0.838 (Spearman)
P< 0.001
D. stockesii
r = 0.935 (Pearson)
P< 0.001
M. cavernosa
P. porites
r = 0.826 (Pearson)
P< 0.006
P. astreoides
r = 0.973 (Pearson)
P< 0.0001
S. siderea
r = 0.765 (Pearson)
P< 0.05
Adult densities
Juvenile densities
Juvenile densities

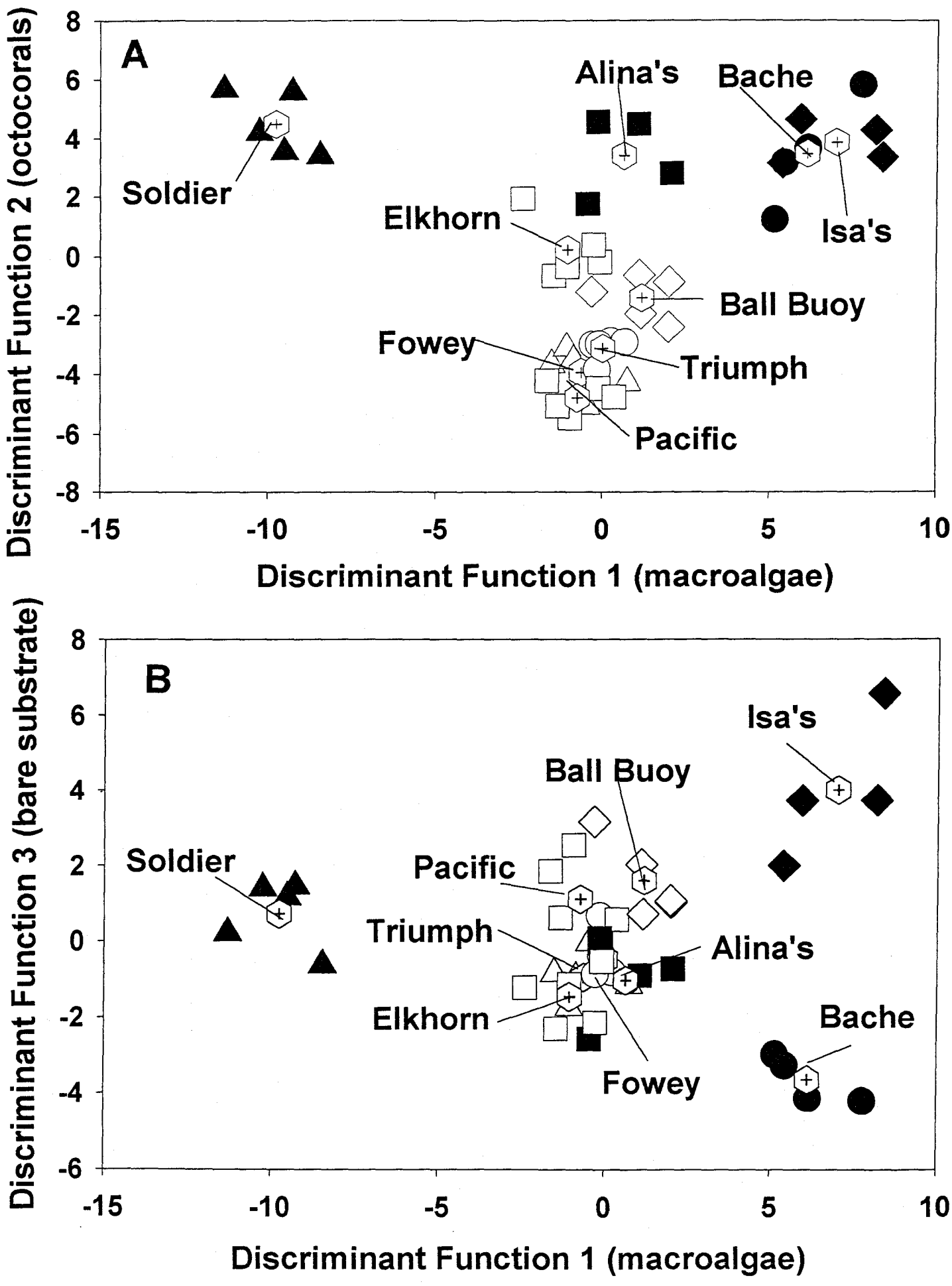
arbuscula, the second in abundance, constituted 2% and 11%, respectively.

The results of this study show that corals on the Safety Valve can vary in abundance, from 1 to 26 per square meter in any one quadrat and averaged at 10.8 corals per square meter, 10.4 of which would be of the species Porites divaricata. If one were to extrapolate these results to an area in the grassbeds in the shape of a circle with a 70 meter diameter, as in the primary study site, there would be approximately 41500 coral colonies, almost 40000 of which would be Porites divaricata.

DISCUSSION

Corals are moderately abundant in the seagrass beds of the Safety Valve. Their density can vary from place to place over the seagrass flat, as was seen in Tables 1 and 2. In the north transect arm (Table 1), for example, the numbers of corals found seemed to vary according to seagrass type and density. In quadrats N1 through N4 and N13, dense seagrass, primarily Thalassia testudinum with some Halodule wrightii, was found. In quadrats N5 through N9, the seagrass was less dense in varying degrees. The seagrass in N10 through N12 had thinned out and only Halodule wrightii in low densities remained. The abundance of corals seems to be greatest in high density seagrass and lowest in less dense areas. This was also seen in the study done at the "yellow house" site where we must have been on the edge of one of the channels between bars because most of the substrate was coarse sand and bivalve shells. Few corals were found there except in one

Fig 4


A
Alina's
Bache
Soldier
Elkhorn
Isa's
Ball Buoy
Fowey
Triumph
Pacific
Discriminant Function 2 (octocorals)
Discriminant Function 1 (macroalgae)
B
Isa's
Ball Buoy
Soldier
Pacific
Triumph
Alina's
Elkhorn
Bache
Fowey
Discriminant Function 3 (bare substrate)
Discriminant Function 1 (macroalgae)

quadrat which I would speculate (since I did not personally sample it) to have fallen in a grass area. Seagrass density might also explain the differences in abundance between the primary study site and the other three. More studies should be done to test this correlation between coral and seagrass density.

In the consistency test, our counts varied from team to team, although only significantly at the north station. The variation could be due to deviations from the colony definition in counting or possibly due to the accidental fragmention of colonies during the surveys, thereby making one "colony" into two. Both of these are reasonable since the most abundant species are branching types. This inconsistency should be considered when reviewing the data.

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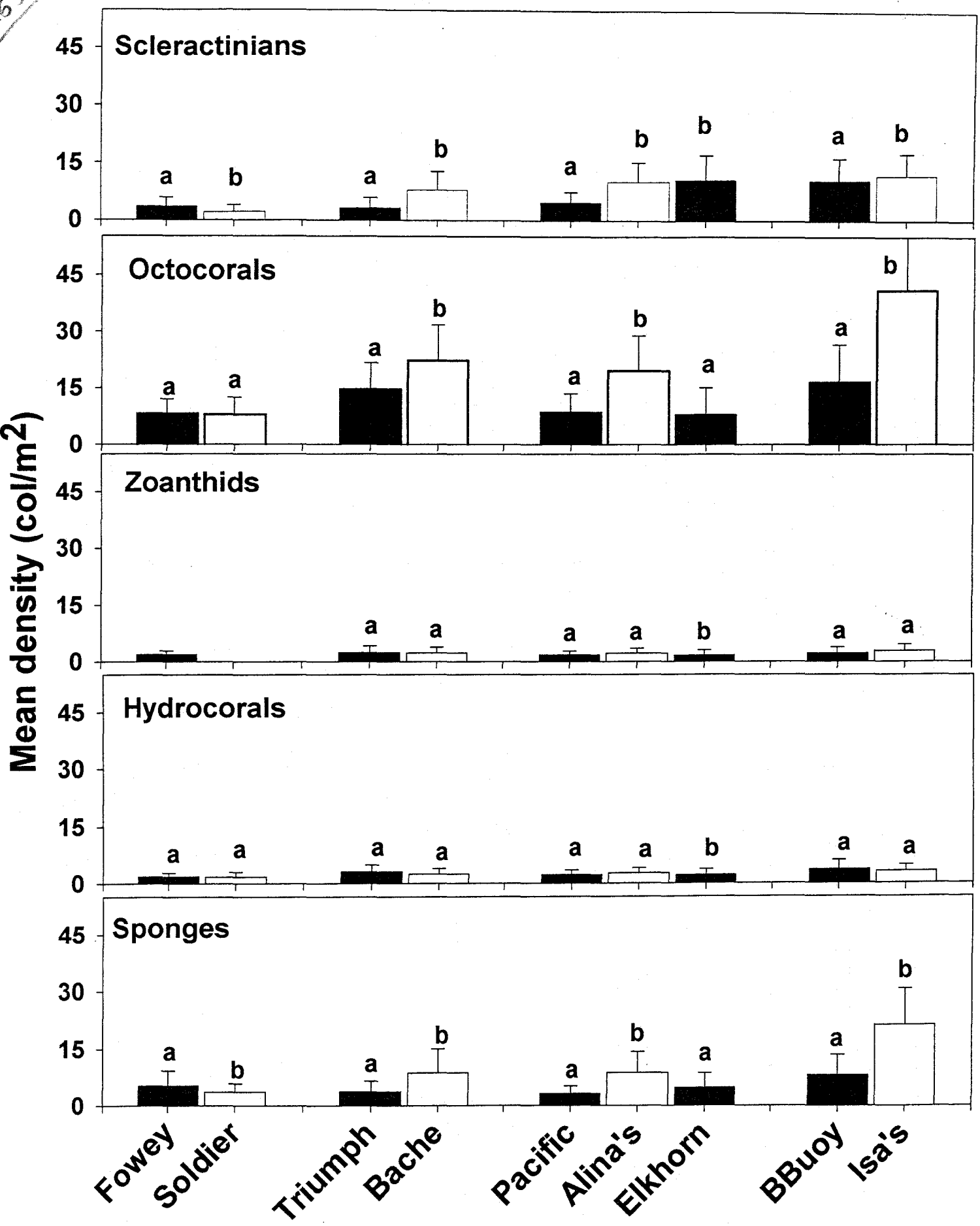
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F63


Scleractinians
Octocorals
Zoanthids
Hydrocorals
Sponges
Mean density (col/m2)
45
30
15
0
Fowey
Soldier
Triumph
Bache
Pacific
Alina's
Elkhorn
BBuoy
Isa's

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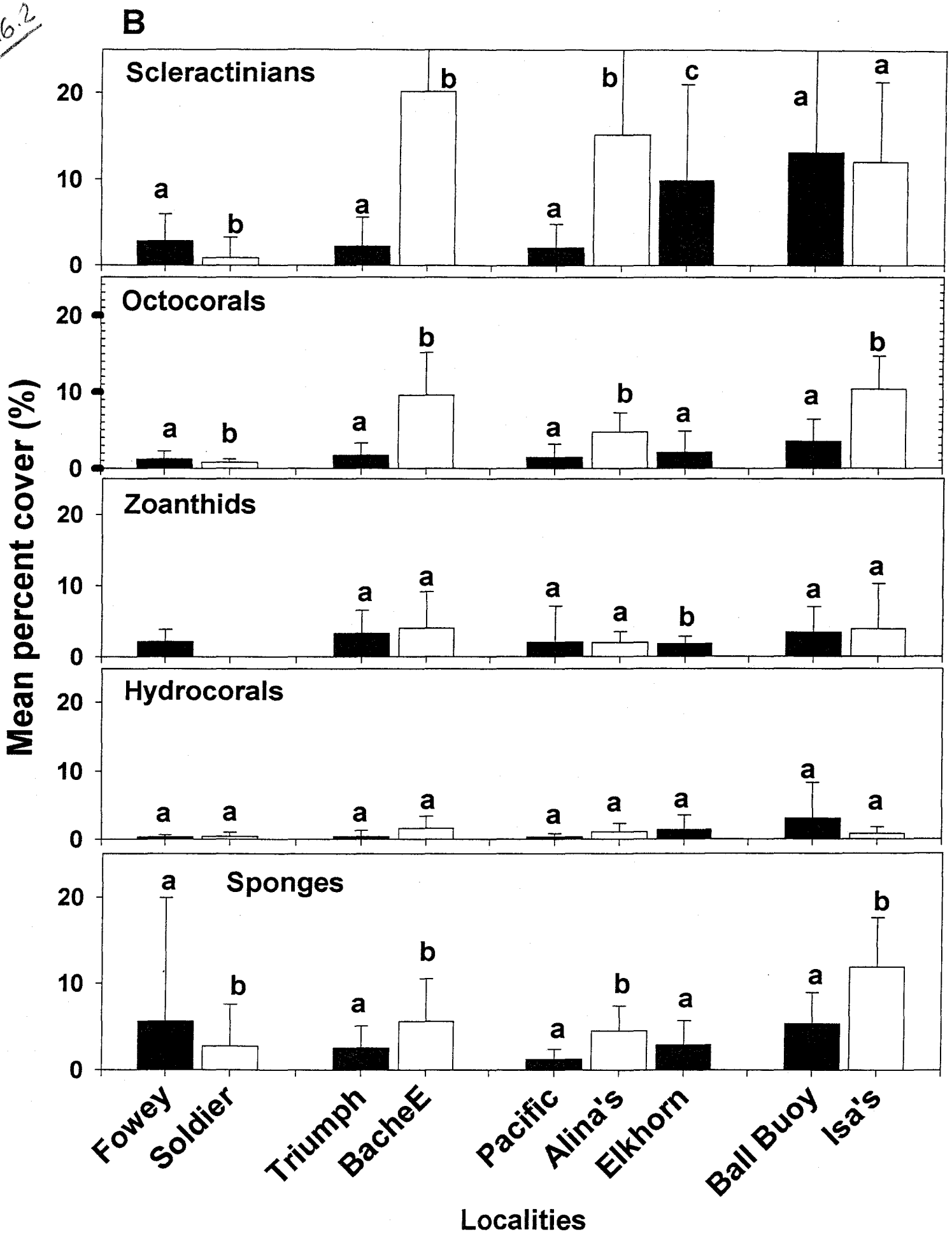
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Fig. 2


B
Scleractinians
Octocorals
Zoanthids
Hydrocorals
Sponges
Mean percent cover (%)
0
10
20
a
b
c
Fowey
Soldier
Triumph
BacheE
Pacific
Alina's
Elkhorn
Ball Buoy
Isa's
Localities

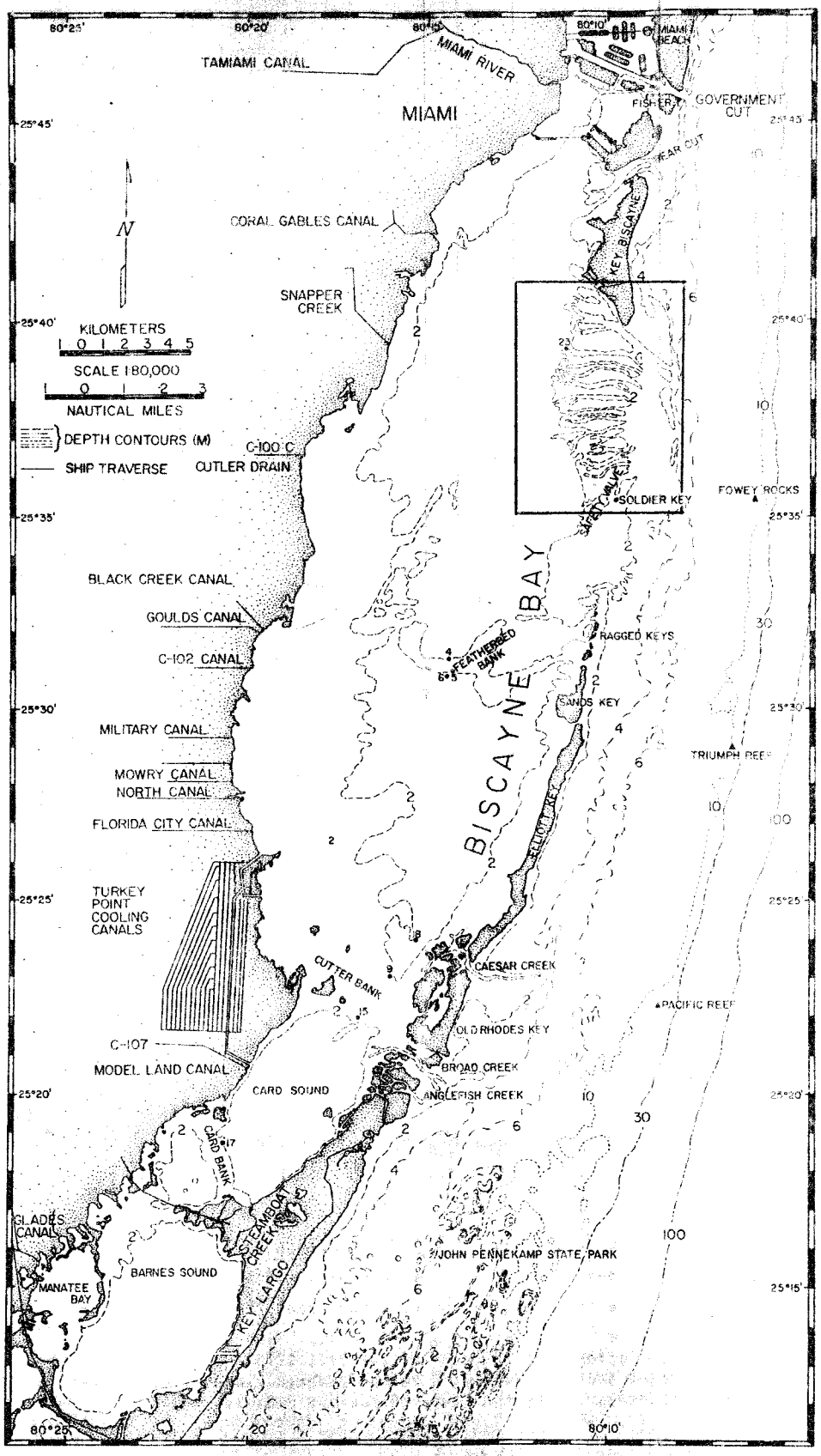
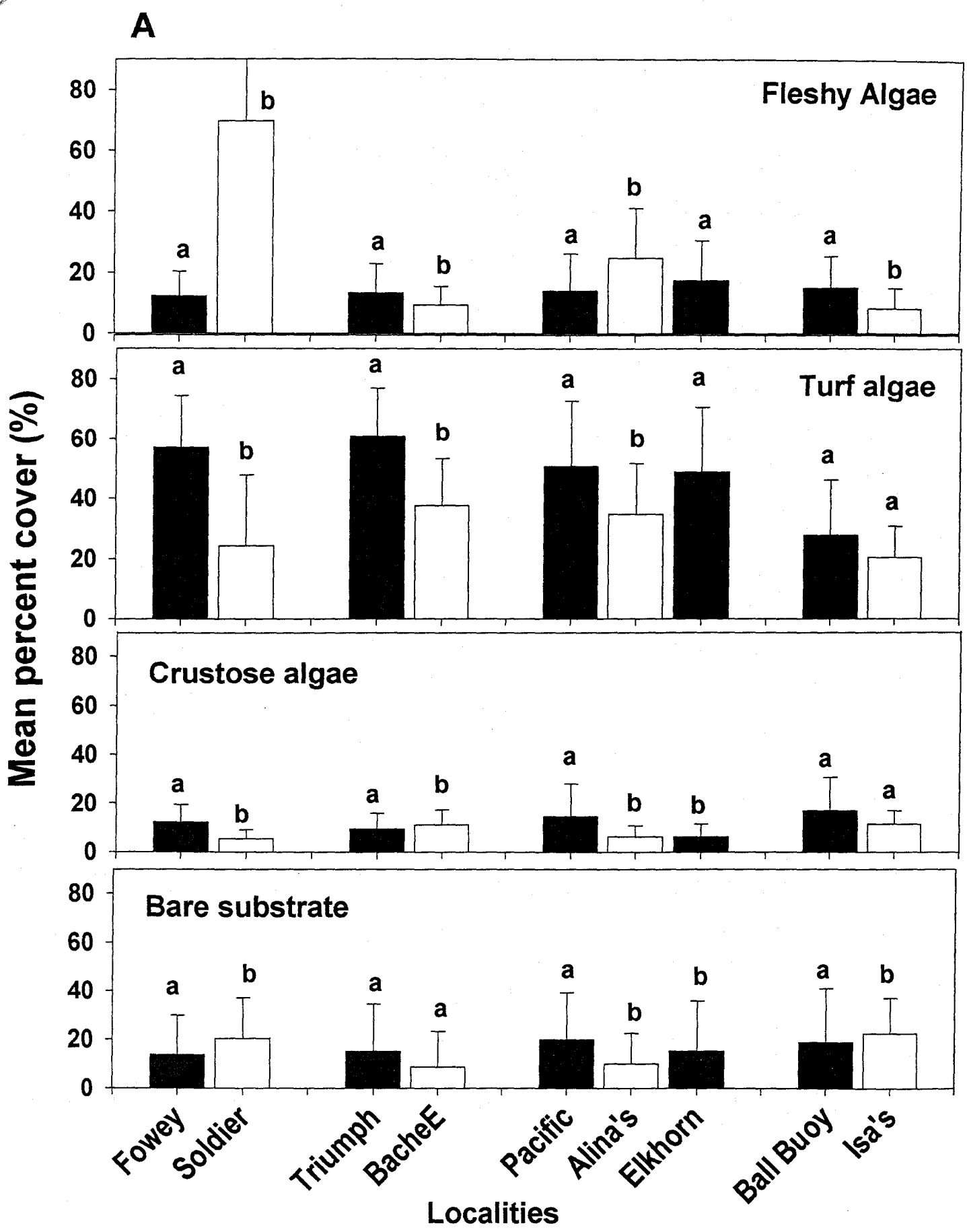


Figure 1. Location map of Biscayne Bay and connecting lagoons. The Safety Valve region is in the box. (From Rooth, C.G.H. 1976.)

Fig. 2


A
Fleshy Algae
Turf algae
Crustose algae
Bare substrate
Mean percent cover (%)
0
20
40
60
80
a
b
Fowey
Soldier
Triumph
BacheE
Pacific
Alina's
Elkhorn
Ball Buoy
Isa's
Localities

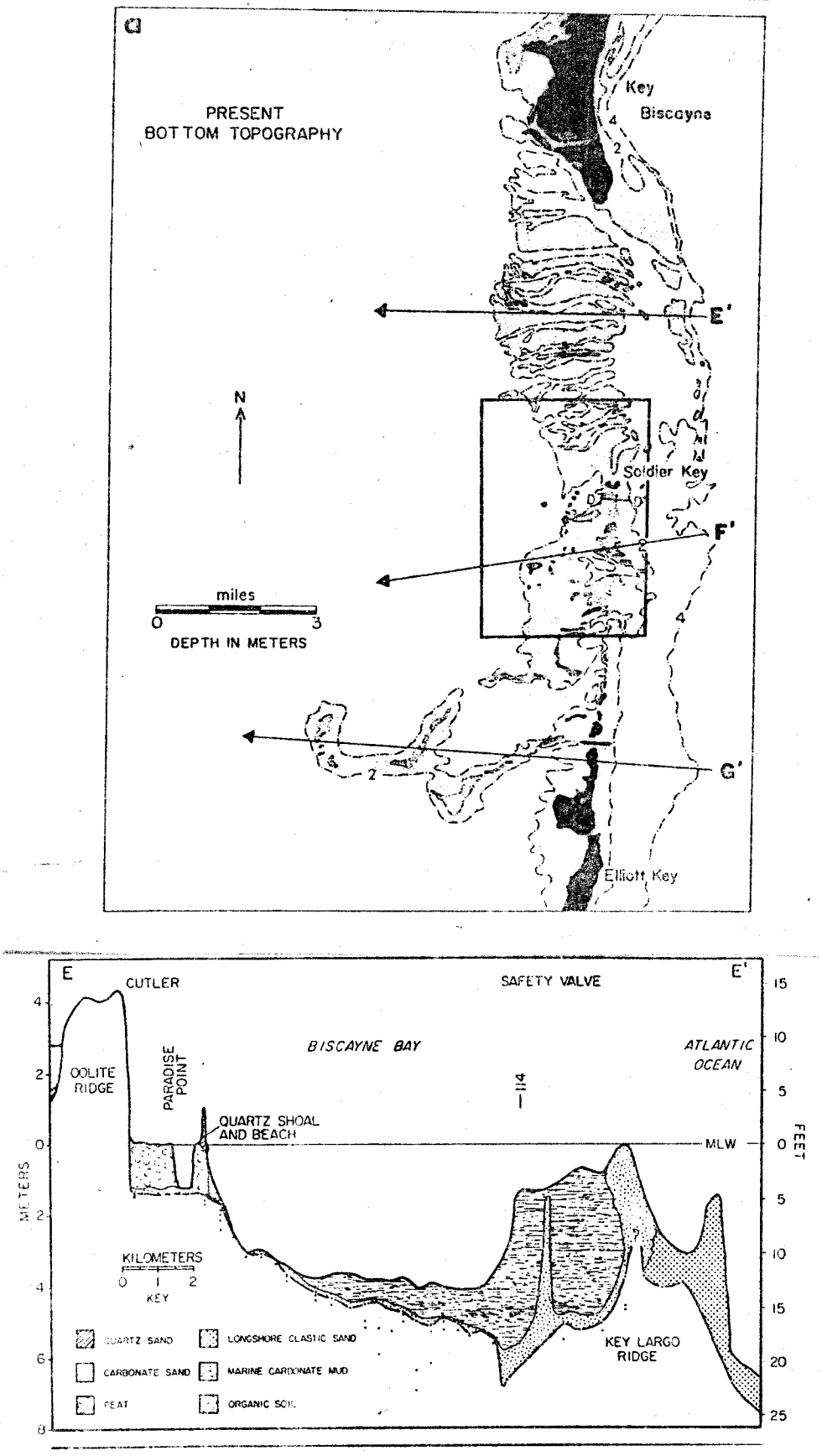


Figure 2. (top) Magnified view of the Safety Valve region and location of the cross-section. (bottom) Cross-section of Biscayne Bay through the Safety Valve. (From Wanless, H.R. 1976)

Fig 1

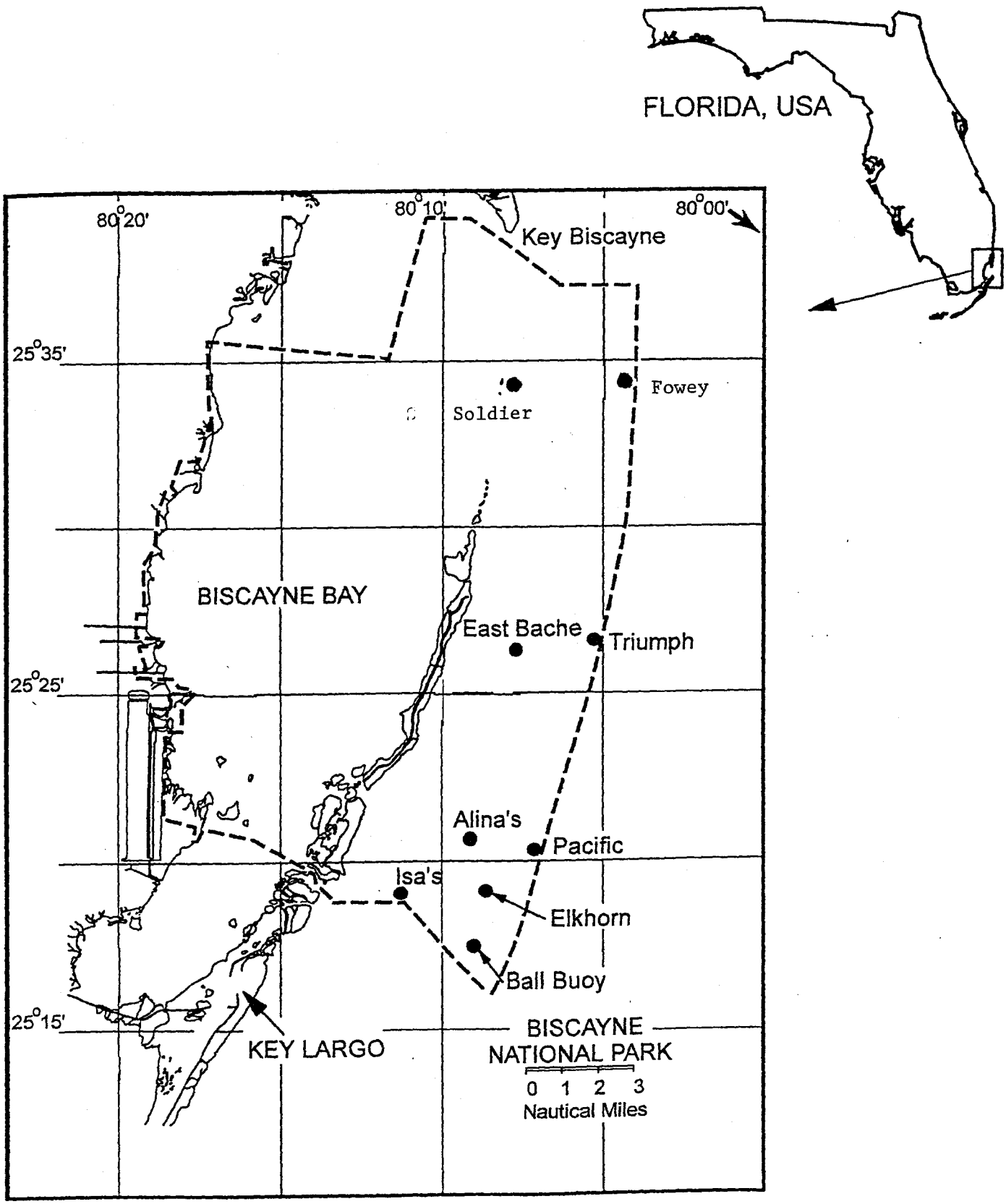

FLORIDA, USA
80°20'
80°10'
80°00'
Key Biscayne
25°35'
Soldier
Fowey
BISCAYNE BAY
East Bache
Triumph
25°25'
Alina's
Pacific
Isa's
Elkhorn
Ball Buoy
25°15'
KEY LARGO
BISCAYNE
NATIONAL PARK
0 1 2 3
Nautical Miles

Table 1. Results of the surveys from the north and south transect arms, including the sum of the coral species frequencies, mean, and standard deviation. PD = Porites divaricata Lesueur, PF = Porites furcata Lammarck, CA = Cladocora arbuscula Lesueur, SR = Siderastrea radians Pallas, MA = Manicina areolata Linnaeus, FF = Favia fragum Esper, and I = Isophyllia spp.

NORTH

	SPECIES FREQUENCY						
QUADRAT	PD	PF	CA	SR	MA	FF	I
1	12	0	0	0	0	0	0
2	11	0	0	0	0	0	0
3	13	0	0	0	0	0	0
4	9	0	0	0	0	0	0
5	7	0	1	0	0	1	0
6	4	0	0	0	0	0	0
7	6	0	3	0	0	0	0
8	9	0	0	0	1	0	0
9	8	0	0	0	0	0	0
10	1	0	0	0	0	0	0
11	3	0	0	0	0	0	0
12	2	0	0	1	0	0	0
13	13	0	3	0	0	0	0
TOTAL	98	0	7	1	1	1	0
MEAN(QUAD)	7.54	0.00	0.54	0.08	0.08	0.08	0.00
STD DEV	4.14	0.00	1.13	0.28	0.28	0.28	0.00

SOUTH

QUADRAT	PD	PF	CA	SR	MA	FF	I
1	6	0	0	0	0	0	0
2	16	0	1	0	0	0	1
3	22	0	0	0	0	0	0
4	21	0	0	1	0	0	0
5	24	0	0	0	0	0	0
6	14	0	0	0	0	0	0
7	12	0	0	0	0	0	0
8	4	0	0	0	1	0	0
9	9	0	0	0	0	0	0
10	6	0	0	0	0	0	0
11	9	0	0	0	0	0	0
12	10	0	0	0	0	0	0
13	8	0	0	0	0	0	0
TOTAL	161	0	1	1	1	0	1
MEAN(QUAD)	12.38	0.00	0.08	0.08	0.08	0.00	0.08
STD DEV	6.56	0.00	0.28	0.28	0.28	0.00	0.28

value is the mean (±1SD) of three short and three tall traps (see text). Results of eleven deployments are depicted in the upper panel, and those of two deployments during winter 1994 (following Tropical Storm Gordon) are plotted in the lower panel on a larger scale.

Figure 10. Box plots summarizing water column nutrient data for each site. Upper panel, ortho-phosphate; middle panel, nitrate+ nitrite; lower panel, ammonium. The darker horizontal bar within each box is the mean and the lighter bar the median. Upper and lower limits of each box indicate the 25th to 75th percentiles, and the error bars indicate the 5th and 95th percentiles. Circles represent maximum and minimum values for each site.

Table 2. Results of the surveys from the east and west transect arms, including the sum of the coral species frequencies, mean, and standard deviation. PD = Porites divaricata Lesueur, PF = Porites furcata Lammarck, CA = Cladocora arbuscula Lesueur, SR = Siderastrea radians Pallas, MA = Manicina areolata Linnaeus, FF = Favia fragum Esper, and I = Isophyllia spp.

EAST

		SPECIES FREQUENCY					
QUADRAT	PD	PF	CA	SR	MA	FF	I
1	16	0	2	0	0	0	0
2	16	0	0	0	0	0	0
3	18	0	0	0	0	0	0
4	5	0	0	0	0	0	0
5	12	1	0	0	0	0	0
6	13	0	1	0	0	0	0
7	3	0	0	0	0	0	0
8	5	0	0	0	0	0	0
9	9	0	0	0	0	0	0
10	6	0	0	0	0	0	0
11	5	0	0	0	0	0	0
12	2	0	0	0	0	0	0
13	3	1	1	0	0	0	0
TOTAL	113	2	4	0	0	0	0
MEAN(QUAD)	8.69	0.15	0.31	0.00	0.00	0.00	0.00
STD DEV	5.63	0.38	0.63	0.00	0.00	0.00	0.00

WEST

QUADRAT	PD	PF	CA	SR	MA	FF	I
1	11	0	0	0	0	0	0
2	7	0	0	0	0	0	0
3	8	0	0	0	0	0	0
4	4	0	0	1	0	0	0
5	7	0	0	0	0	0	0
6	19	0	0	0	0	0	0
7	14	0	0	0	0	0	0
8	25	1	0	0	0	0	0
9	15	0	1	0	0	0	0
10	18	0	0	0	0	0	0
11	13	0	0	0	0	0	0
12	8	0	0	0	0	0	0
13	19	0	0	0	0	0	0
TOTAL	168	1	1	1	0	0	0
MEAN(QUAD)	12.92	0.08	0.08	0.08	0.00	0.00	0.00
STD DEV	6.14	0.28	0.28	0.28	0.00	0.00	0.00

LIST OF FIGURES

Figure 1. Map of Biscayne National Park showing study localities.

Figure 2. Spatial variability for mean percent cover (%) of the (A) different algal groups and bare substrate and (B) cnidarians groups and sponges. Bare substrate includes sand, substrate with no live cover and rubble. Localities are distributed in offshore-inshore pairs in a north-south direction. Different letters on error lines indicate significant differences (Mann-Whitney Rank Test) in percent cover of the particular group between offshore-inshore locality pairs.

Figure 3. Spatial variation in colony densities for cnidarian groups and sponges. Different letters indicate significant differences Mann-Whitney Rank Test) in density (col/m^2) of the different groups between offshore-inshore locality pairs.

Figure 4. Classification of the different localities (communities) based on the first two discriminant functions (A) and the first and third discriminant functions (B) using transect averages for coverage of main groups and densities of cnidarians and sponges. CV1 was most heavily weighted by macroalgal cover, CV2 was most heavily weighted by octocoral coverage and CV3 was most heavily weighted by bare substrate and octocoral densities. Filled symbols are inshore localities. Hexagons with sign are the centroid for the cluster of each locality.

Figure 5. Relationship between juvenile and adult densities (col/m^2) of the most common scleractinian species with juveniles colonies in the localities sampled. *P. astreoides* includes both the brown morph (squares) and the yellow morph (triangles). There was no significant correlation between juveniles and adults in *M. cavernosa*.

Figure 6. Temperature records obtained using Hobo-Temp loggers for six sites in BNP. Values represent means of all measurements recorded (every 24 minutes) between 8pm and 6am of each day. Panels depict records for inshore/offshore reef pairs in the A) northern, B) central, and C) southern region of the Park. Periods of missing data were due to loss of malfunction of instruments.

Figure 7. Mean (± 1SD) sediment accumulation observed during each three day sediment accumulation plate deployment at three offshore (A) and inshore (B) pairs of reef sites from north to south within BNP. Sites with the same hatching in the two panels have similar latitudingal position. n= number of plates per deployment per site.

Figure 8. Grain size distribution of sediments collected with the sediment accumulation plates during the last four deployments (which utilized comparable seive sizes). The various size fractions are shown as percent of total sediment dry mass. n= 9-12 samples per deployment per site.

Figure 9. Sediment deposition collected in sediment tube traps at nine sites. Each

Table 3. Cummulative results for the primary site transects. Cummulative species frequency, mean number of individuals per 13 quadrats, and mean number of individuals per quadrat are given.

	SPECIES FREQUENCY						
	PD	PF	CA	SR	MA	FF	I
TOTAL N	98	0	7	1	1	1	0
TOTAL E	113	2	4	0	0	0	0
TOTAL S	161	0	1	1	1	0	1
TOTAL W	168	1	1	1	0	0	0
SUM	540	3	13	3	2	1	1
MEAN(ARM)	135.0	0.75	3.25	0.75	0.50	0.25	0.25
STD DEV	34.73	0.96	2.87	0.50	0.58	0.50	0.50
MEAN(QUAD)	10.38	0.06	0.25	0.06	0.04	0.02	0.02
STD DEV	2.67	0.07	0.22	0.04	0.04	0.04	0.04
95% CONF.	0.23	0.17	0.13	0.10	0.36	----	----

Table 4. Results of the consistancy test performed on the thirteenth station on each transect arm. A chi-square test was performed to test the significance of the differences (df = 3).

	N13			E15		
	PD	PF	CA	PD	PF	CA
NG	13	0	3	3	1	0
EG	31	0	1	3	1	1
SG	18	0	2	5	0	0
WG	30	3	0	4	0	0
MEAN	23.00	0.75	1.50	3.75	0.50	0.25
STD DEV	8.91	1.50	1.29	0.96	0.58	0.50
CHI-SQ.	10.35	9.00	3.34	0.74	2.00	3.00
SIGNIF.	P<.01	P<.025	NS	NS	NS	NS

	S13			W13		
	PD	PF	CA	PD	PF	CA
NG	11	0	0	15	0	0
EG	10	0	0	19	0	0
SG	8	0	0	16	0	0
WG	9	0	0	19	0	0
MEAN	9.50	0.00	0.00	17.25	0.00	0.00
STD DEV	1.29	0.00	0.00	2.06	0.00	0.00
CHI-SQ.	0.54	0.00	0.00	0.74	0.00	0.00
SIGNIF.	NS	NS	NS	NS	NS	NS

Appendix 6 con List of species of Porifera observed in 9 reefs of Biscayne National Park, Florida. [1] = Offshore sites; [2] = Inshore sites. Sites oriented in a north-south gradient from left to right.

GENUS	SPP / REEF	Fowey[1]	Soldier[2]	Triumph[1]	EBache[2]	Pacific[1]	Alina's[2]	Elkhorn[1]	Ball Buoy[1]	Isa's[2]
Siphonodictyon	*S.coralliphagum*							1		
Spheciospongia	*S.vesparium*	1	1		1					1
Spirastella	*S.coccinea*									1
Spongia	*S.obtusa*	1	1	1	1	1	1	1	1	1
	S.pertusa						1	1		1
Strongylacidon	*S. sp*				1			1	1	1
Tedania	*T.ignis*		1		1		1			1
Tethya	*T.crypta*	1								
Ulosa	*U.ruetzleri*	1	1	1	1	1	1	1	1	1
Verongula	*V.gigantea*									1
	V.rigida	1		1	1	1	1	1	1	1
Xetospongia	*X.muta*	1		1						
	X.proxima	1								
# of species	66	37	21	31	31	30	34	34	36	48
# of genera	41	25	16	21	23	19	25	23	29	35

*= dark gray, rope sponge with spine-like protrusions

Table 5. Results for the "pole", "wreck", and "yellow house" sites, including totals for the three sites, mean individuals per quadrat, and standard deviation.

	PD	CA	SR	MA	SOL.
POLE/CAGES	7	3	0	0	0
	3	0	0	0	0
	3	1	0	0	0
	4	1	0	0	0
	11	0	1	0	0
	7	2	0	0	0
	5	0	0	0	0
WRECK	5	1	0	0	0
	12	2	0	1	0
	4	1	0	0	0
	9	0	0	0	0
YELLOW	0	0	0	0	1
HOUSE	13	0	0	0	1
	0	0	0	0	0
	0	0	1	0	0
TOTALS	83	11	2	1	2
MEAN(QUAD)	5.53	0.73	0.13	0.07	0.13
STD DEV	4.26	0.96	0.35	0.26	0.35

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Appendix 6 : List of species of Porifera observed in 9 reefs of Biscayne National Park, Florida. [1] = Offshore sites; [2] = Inshore sites. Sites oriented in a north-south gradient from left to right.

GENUS	SPP / REEF	Fowey[1]	Soldier[2]	Triumph[1]	EBache[2]	Pacific[1]	Alina's[2]	Elkhorn[1]	Ball Buoy[1]	Isa's[2]
Amphimedon	*A.compressa*	1		1	1	1	1	1	1	1
	A.erina			1						
Anthosigmella	*A.varians*	1		1		1			1	1
Aplysina	*A.fulva*	1	1		1		1	1		1
	A.fistularis	1	1		1		1	1	1	1
	A.cauliformis	1	1	1	1	1	1	1	1	1
	A.archeri	1								
Agelas	*A.conifera*		1	1		1		1		
	A.wiedenmyeri			1	1	1	1	1		
	A.clathrodes			1		1				
	A.dispar			1				1		
Calix	*C.podatypa*		1	1			1		1	1
Callyspongia	*C.vaginalis*	1	1	1		1	1	1	1	1
	*C.vaginalis2**	1	1			1	1		1	1
	C.plicifera	1				1		1	1	1
	C.armigera	1								1
Clathria	*C. sp*			1	1				1	
Cliona	*C. sp*	1		1	1	1	1	1	1	1
	C.aprica			1		1	1	1		1
	C.delitrix	1			1					
	C.lampa	1		1	1	1	1			
	C.langae	1								
Cribochalina	*C.vasculum*								1	1
Cynachira	*C. sp*				1					1
Desmapsamma	*D.anchorata*	1						1	1	1
Diplastrella	*D.megastellata*				1	1	1		1	
	Diplastrella sp.	1		1	1			1	1	1
Dysidea	*D.janiae*									1
	D.etheria	1	1	1					1	
Ectyoplasia	*E.ferox*	1	1	1	1	1	1	1	1	1
Geodia	*G.neptuni*									1
Halisarca	*H. sp*									1
Holpsamma	*H.intestinalis*							1		1
	H.helwigi	1	1		1	1	1	1	1	1
Hyrtios	*H.proteous*					1		1	1	1
Iotrochota	*I.birotulata*	1	1	1	1	1	1	1	1	1
Ircina	*I.felix*	1	1	1	1	1	1	1	1	1
	I.strobilina	1	1	1	1	1	1	1	1	1
	I.campana			1		1				
Monachora	*M.unguifera*	1		1	1	1	1	1	1	1
	M.barbadensis			1	1	1	1	1	1	1
Mycale	*M.laevis*				1	1	1		1	1
Neofibularia	*N.nolitangere*	1					1	1	1	1
Niphates	*N.alba*						1			1
	N.erecta	1	1	1	1	1	1	1	1	1
	N.digitalis	1	1	1	1	1	1		1	1
Oceanapia	*O.bartsi*						1			
Pellina	*P.carbonaria*		1						1	1
Petrosia	*P.weinbergi*	1		1	1	1	1	1	1	1
Phorbas	*P.amaranthus*	1	1	1	1	1	1	1	1	1
Plesiastrea	*P. sp*									1
Pseudaxinella	*P.luneacarta*	1			1		1	1	1	1
Pseudoceratina	*P.crassa*	1					1	1	1	1

Appendix 5: List of octocoral species observed in 9 reefal sites of Biscayne National Park, Florida. [1] = Offshore sites; [2] = inshore sites. Sites oriented in a north-south gradient from left to right.

GENUS	SITE SPECIES	Fowey[1]	Soldier[2]	Triumph[1]	EBache[2]	Pacific[1]	Alina's[2]	Elkhorn[1]	Ball Buoy[1]	Isa's[2]
Briaerum	*B.asbestinum1* *	1	1	1	1	1	1	1	1	1
	B.asbestinum2 **	1		1	1	1	1		1	1
Erythropodium	*E.caribaeorum*	1		1	1	1	1	1	1	1
Eunicea	*E.laxispica*	1				1	1		1	1
	E.succineaS	1	1	1	1	1	1	1	1	1
	E.succineaP ***	1	1	1	1	1	1	1	1	1
	E.lascinata			1	1	1	1	1	1	1
	E.asperula				1		1	1	1	1
	E.fusca	1	1	1	1	1	1	1	1	1
	E.mammosa	1		1	1		1	1	1	1
	E.laxa									1
	E.clavigera		1		1		1	1	1	1
	E.tourneforti1	1	1	1	1	1	1	1	1	1
	E.tourneforti2 ****	1		1						1
	E.calyculata	1		1	1	1	1	1		1
	E.palmieri	1	1	1	1	1	1	1	1	1
	E.knighty				1	1	1		1	1
	E. sp		1		1	1	1	1	1	1
Gorgonia	*G.ventalina*	1		1	1	1	1	1	1	1
	G.flabellum	1		1	1		1	1	1	
	G.mariae	1		1	1	1	1	1	1	1
Iciligorgia	*I.schrammi*	1		1	1		1	1	1	1
Muricea	*M.muricata*	1	1	1	1	1	1	1	1	1
	M.laxa			1	1	1	1		1	1
	M.elongata				1		1	1	1	1
	M.flavida	1	1	1	1	1	1	1	1	1
Plexaura	*P.homomalla*	1	1	1	1		1	1	1	1
	P.flexuosa	1	1	1	1	1	1	1	1	1
	P.kuna		1	1	1	1	1	1	1	1
Plexaurella	*P.dichotoma*	1	1	1	1	1	1	1	1	1
	P.grisea				1		1		1	1
	P.nutans		1	1	1		1	1	1	1
Pseudoplexaura	*P.flagellosa*	1	1		1	1	1	1	1	1
	P.porosa	1	1	1	1	1	1	1	1	1
	P.crucis				1		1	1	1	1
	P.wagenaari		1	1	1		1	1	1	1
Pseudoterogorgia	*P.americana*	1	1	1	1	1	1	1	1	1
	P.kallos	1		1	1	1	1	1	1	1
	P.acerosa	1	1	1	1	1	1	1	1	1
	P.bipinnata			1	1	1				
	P. sp				1			1	1	1
Pterogorgia	*P.citrina*	1	1	1		1	1	1	1	1
	P.anceps	1	1		1					1
	P.guadalupensis		1	1	1	1	1		1	
Number of species	44	28	23	32	40	29	39	34	39	41
Number of genera	11	11	8	11	11	11	11	11	11	11

*= B. asbestinum1 = is the crustose form; ** = B. asbestinum2 = is the erect form; *** = E. succineaP = forma plantaginea; **** = E.tourneforti2 = is forma atra.

Appendix 4: List of scleractinian and hydrocoral species observed in 9 sites of Biscayne National Park, Florida. [1] = Offshore sites, [2] = Inshore sites. Sites ordered in a north-south direction from left to right.

GENUS	SPP / REEF	Fowey[1]	Soldier[2]	Triumph[1]	EBache[2]	Pacific[1]	Alina's[2]	Elkhorn[1]	Ball Buoy[1]	Isa's[2]
Stephanocoenia	*S.intersepta*	1	1	1	1	1	1	1	1	1
Madracis	*M.decactis*	1		1	1	1	1	1	1	1
	*M.senaria**					1				
	*M.pharensisL***	1			1	1	1		1	
Acropora	*A.palmata*	1					1	1	1	
	A.cervicornis				1		1	1	1	1
Agaricia	*A.agaricites*	1		1	1	1	1	1	1	1
	A.humilis	1		1	1			1	1	1
	A.purpurea	1		1	1	1	1	1	1	1
	A.danae						1	1	1	1
	A.carinata				1				1	
	A.tenuifolia				1		1	1	1	1
	A.fragilis			1	1	1				
Leptoseris	*L.cucullata*	1		1	1	1	1		1	1
Siderastrea	*S.siderea*	1	1	1	1	1	1	1	1	1
	S.radians	1	1	1	1		1	1	1	1
Porites	*P.porites*	1	1	1	1	1	1	1	1	1
	P.furcata					1		1		1
	P.divaricata		1							
	P.astreoides	1	1	1	1	1	1	1	1	1
Favia	*F.fragum*	1	1	1	1	1	1	1	1	1
Diploria	*D.strigosa*	1		1	1	1	1	1	1	1
	D.clivosa	1	1	1	1	1	1	1	1	1
	D.labyrinthiformis	1		1	1	1	1	1	1	1
	D.clivosa sp.	1				1	1			
Colpophyllia	*C.natans*				1	1	1	1	1	1
Manicina	*M.aerolata*				1					1
	M.mayori						1		1	1
Montastraea	*M.annularis*			1	1	1	1	1	1	1
	M.faveolata	1		1	1	1	1	1	1	1
	M.franksi	1		1	1	1	1		1	1
	M.cavernosa1	1		1	1	1	1	1	1	1
	*M.cavernosa2****	1			1	1	1	1	1	1
Solenastrea	*S.bournoni*	1	1	1	1	1	1		1	1
	S.hyades	1	1							1
Meandrina	*M.meandrites*	1		1	1	1	1	1	1	1
	*M.memorialis*****	1		1	1	1			1	1
Dichocoenia	*D.stockesii*	1	1	1	1	1	1	1	1	1
	D.stellaris				1	1	1	1	1	1
Eusmilia	*E.fastigiata*	1		1	1		1		1	1
Mycetophyllia	*M.aliciae*				1	1	1	1	1	1
	M.lamarckiana				1		1		1	1
	M.danaana				1		1	1	1	1
	M.ferox				1		1		1	1
	M.reesi				1					
Mussa	*M.angulosa*						1			1
Scolymia	*S.cubensis*				1		1		1	1
Isophyllastrea	*I.rigida*							1	1	
Isophyllia	*I.sinuosa*	1			1	1				1
Oculina	*O.diffusa*				1		1		1	1
	O.varicosa									1
Cladocora	*C.arbuscula*		1				1			1
Millepora	*M.alcicornis*	1	1	1	1	1	1	1	1	1
	M.complanata	1		1	1	1	1	1	1	1
Number of species	52	28	12	24	40	30	39	29	40	43
Number of genera	23	15	8	13	18	15	21	14	20	22
Hydrozoans	2	2	1	2	2	2	2	2	2	2

* = New report for the Florida area; ** = forma luciphogous; *** = form with large, less integrated calices;
**** = form with wide colines and thick septa.

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REPORT

D. Lirman

Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth

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Abstract Recent declines in coral abundance accompanied by increases in macroalgal cover on Florida reefs highlight the importance of competition for space between these groups. This paper documents the frequency of coral–algal interactions on the Northern Florida Reef Tract and evaluates the effects of grazer exclusions and experimental algal addition on growth and tissue mortality of three coral species, *Siderastrea siderea*, *Porites astreoides*, and *Montastraea faveolata*. The frequency of interactions between corals and macroalgae was high as more than 50% of the basal perimeter of colonies was in contact with macroalgae; turf forms, *Halimeda* spp., and *Dictyota* spp. were the most common groups in contact with corals. Decreased grazing pressure resulted in significant increases in algal biomass within cages, and caged corals showed species-specific susceptibility to increased algal biomass. While no effects were detected for *S. siderea*, significant decreases in growth rates were documented for caged *P. astreoides* which had growth rates three to four times lower than uncaged colonies. When an algal addition treatment was included to duplicate maximum algal biomass levels documented for reefs in the area, colonies of *P. astreoides* in the algal addition treatment had growth rates up to ten times lower than uncaged colonies. High susceptibility to algal overgrowth was also found for the reef-building coral *M. faveolata*, which experienced significant tissue mortality under both uncaged (5.2% decrease in live tissue area per month) and caged (10.2% per month) conditions. The documented effects of increased algal biomass on coral growth and tissue mortality suggest a potential threat for the long-term survivorship and growth of corals in the Florida Reef Tract if present rates of algal growth and space utilization are maintained.

Key words Coral–algal competition · Caging · Grazer exclusion · Algal overgrowth · Florida Reef Tract

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Introduction

In the recent past, reports of rapidly declining reef health and localized phase shifts towards macroalgal-dominated systems have highlighted the importance of competition for space between corals and macroalgae, the outcome of which can have significant implications for the long-term survivorship and growth of corals (e.g., Smith et al. 1981; Lessios 1988; Hughes 1989, 1994; Done 1992; Knowlton 1992; Lapointe et al. 1997; McClanahan and Muthiga 1998). The main objective of the present study was to document the intensity of coral–algal interactions on the Northern Florida Reef Tract and to evaluate the effects of reduced herbivory and algal competition on coral growth and tissue mortality.

Several studies have reported decreases in coral cover and diversity along the Florida Reef Tract in the recent past (Dustan and Halas 1987; Jaap et al. 1988). Just as in many other places in the Caribbean, declines in coral cover in Florida have been accompanied by corresponding increases in the percent cover of macroalgae (Porter and Meier 1992). Although the actual causes of coral decline are being debated, changes in water quality and trophic structure linked to human activities as well as natural stressors such as elevated temperatures, storms, and epizootic diseases have all been proposed as potential causal agents (Hughes 1994; Lapointe 1997; Lirman and Fong 1997; Hughes et al. 1999; Porter et al. 1999).

Even though macroalgae are important components of Florida reef communities, only limited information is available on their abundance, distribution, and community dynamics (Chiappone and Sullivan 1997; Lapointe 1997). In the Northern Florida Reef Tract, the study

Appendix 3. Sponge species with more than 5% of the total cover of sponges in each site studied in Biscayne National Park. Mean cover is in cm^2/m^2, total cover is in cm^2, density is in colonies/m^2.

REEF	SPECIES	Percent cover	Mean cover	Total cover	Mean density
FOWEY	*Callyspongia vaginalis*	23.69	6.73	121.16	0.24
	Niphates digitalis	19.52	5.55	99.85	0.20
	Amphimedon compressa	12.48	2.37	63.86	0.80
	Aplysina fistularis	8.57	1.02	43.82	1.33
	Niphates erecta	7.65	1.19	39.15	0.60
	Cliona spp.	6.46	1.94	33.02	0.27
	Xetospongia muta	5.10	8.7	26.1	0.06
SOLDIER	*Spheciospongia vesparium*	57.41	3.38	128.35	0.78
	Aplysina fistularis	14.37	0.76	32.12	0.91
	Aplysina fulva	8.27	0.84	18.49	0.60
	Ircina felix	7.96	1.11	17.8	0.30
TRIUMPH	*Callyspongia vaginalis*	22.66	1.95	50.6	0.33
	Agelas wiedenmyeri	15.96	1.98	35.64	0.37
	Ulosa ruetzleri	10.18	0.45	22.74	0.93
	Amphimedon compressa	10.12	1.61	22.6	0.35
	Ircina strobilina	6.81	1.52	15.2	0.18
	Niphates erecta	6.72	1	15	0.19
	Petrosia weinbergi	0.76	0.57	1.7	0.03
BACHE EAST	*Petrosia weinbergi*	30.71	2.31	133.7	2.23
	Amphimedon compressa	18.31	1.99	79.7	1.74
	Iotrochota birotulata	10.98	2.39	47.8	0.71
	Ulosa ruetzleri	6.91	1.11	30.1	0.93
	Niphates erecta	6.34	1.2	27.6	0.83
PACIFIC	*Ulosa ruetzleri*	17.06	0.34	17.24	0.91
	Niphates erecta	15.74	0.76	15.9	0.38
	Amphimedon compressa	12.57	1.59	12.7	0.11
	Cliona aprica	12.27	1.38	12.4	0.09
	Niphates digitalis	6.63	0.39	6.7	0.21
	Callyspongia vaginalis	5.74	1.45	5.8	0.04
ALINA'S	*Amphimedon compressa*	31.36	1.91	124.1	3.21
	Petrosia weinbergi	21.49	1.52	85.05	1.44
	Niphates erecta	7.50	0.99	29.7	0.71
	Ircina felix	7.48	1.97	29.6	0.25
	Iotrochota birotulata	5.69	0.9	22.5	0.37
ELKHORN	*Amphimedon compressa*	36.16	1.65	82.75	1.44
	Ircina felix	11.97	1.52	27.4	0.20
	Petrosia weinbergi	8.00	1.08	18.3	0.23
BALL BUOY	*Niphates erecta*	12.49	1.48	62.35	1.58
	Amphimedon compressa	11.96	1.87	59.7	1.07
	Ircina felix	10.67	1.33	53.3	0.54
	Iotrochota birotulata	8.19	1.57	40.9	0.53
	Ircina strobilina	5.77	1.69	28.8	0.19
	Callyspongia vaginalis	5.72	1.1	28.55	0.33
	Ectyoplasia ferox	5.37	2.23	26.8	0.26
	Verongula rigida	0.10	0.5	0.5	0.01
ISA'S	*Amphimedon compressa*	16.17	2.28	143.5	3.91
	Niphates erecta	13.64	1.86	121.1	4.60
	Iotrochota birotulata	11.90	1.92	105.6	2.68
	Ircina strobilina	8.39	2.26	74.5	0.59
	Petrosia weinbergi	6.58	1.95	58.4	0.61
	Callyspongia vaginalis	5.97	1.77	53	0.47
	Aplysina cauliformis	5.08	0.94	45.11	2.71

area for this project, macroalgal cover fluctuates seasonally, reaching up to 56% during the summer (Lirman and Biber 2000). During the time of peak algal abundance, small coral colonies can become completely covered by dense macroalgal mats. Similarly, large massive colonies can experience intense competition from algae growing along colony margins or on dead portions of colonies.

A limited number of studies have examined experimentally the effects of coral–algal competition on coral growth and survivorship. These studies have shown consistently that coral colonies in direct contact with macroalgae can experience reduced growth and fecundity, as well as increased tissue mortality (Potts 1977; Lewis 1986; Hughes 1989; Coyer et al. 1993; Tanner 1995; Miller and Hay 1996, 1998). The present study quantifies the frequency of interactions between corals and macroalgae at the peak time of algal abundance and determines experimentally the effects of reduced herbivory and increased algal biomass on the growth and tissue mortality of three common coral species on Florida reefs, *Siderastrea siderea*, *Porites astreoides*, and *Montastraea faveolata*.

Methods

Coral–algal contact interaction surveys

Photographic surveys were performed on reefs within Biscayne National Park, Florida (Fig. 1) to document the frequency of contact interactions between corals and macroalgae. These surveys were carried out on two inshore patch reefs, Bache Shoals (25°29.187′N, 80°08.880′W, depth = 4 m) and Elkhorn Reef (25°21.782′N, 80°09.841′W, depth = 4 m), and two offshore bank reefs, Triumph Reef (25°28.333′N, 80°06.704′W, depth = 6 m) and Pacific Reef (25°22.186′N, 80°08.360′W, depth = 6 m) during July–August 1998, at the seasonal peak of algal abundance when mean percent cover of macroalgae on these reefs was 56.7% (Lirman and Biber 2000). A belt transect (25 × 2 m) was haphazardly placed at each site, and all coral colonies (5–50 cm in diameter) found within the transect were photographed. The resulting images were scanned and the percentage of each colony's basal perimeter in direct contact with macroalgae was determined using NIH Image. Smaller colonies were not detected by this photographic method.

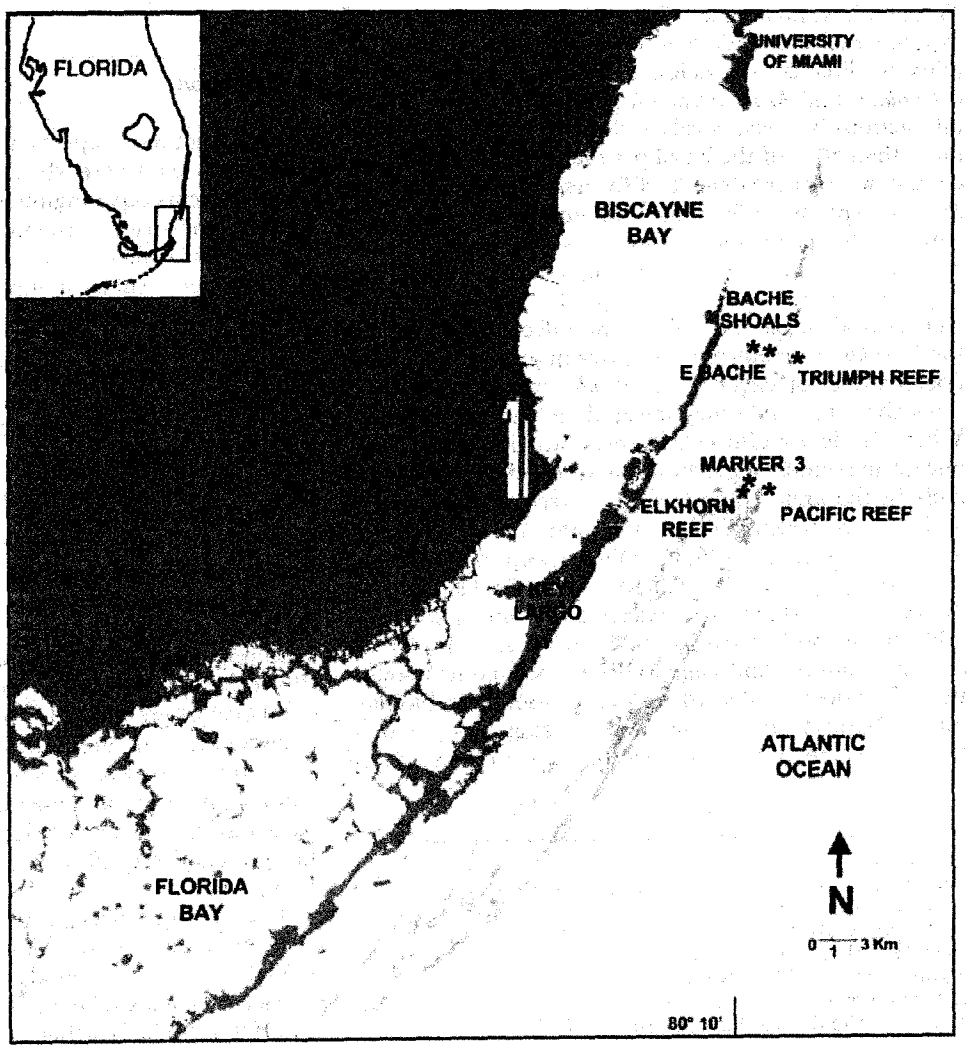


Fig. 1 Map of South Florida and the study area including location of study sites

Appendix 2. Octocoral species with more than 5 % of the octocoral cover in each site studied in Biscayne National Park. Mean cover is in cm^2/m^2, total cover is in cm^2, density is in colonies/m^2.

SITE	SPECIES	Percent cover	Mean cover	Total cover	Mean density
FOWEY	*Pseudoterogorgia americana*	35.362	0.47	4225	4.57
	Erythropodium caribaeroum	26.214	1.49	3132	0.75
	Eunicea tourneforti	10.880	0.36	1300	0.74
	Briareum asbestinum 1 *	10.462	0.89	1250	0.36
SOLDIER	*Plexaurella dichotoma*	35.758	0.35	2701	2.47
	Pterogorgia anceps	17.343	0.23	1310	1.44
	Plexaurella nutans	12.312	0.29	930	0.50
	Pseudoterogorgia acerosa	6.659	0.14	503	0.61
	Eunicea palmieri	6.302	0.14	476	0.85
	Pseudoterogorgia americana	6.262	0.21	473	0.46
TRIUMPH	*Pseudoterogorgia americana*	22.785	0.44	3868	4.69
	Gorgonia ventalina	20.405	0.63	3464	1.40
	Erythropodium caribaeroum	16.258	2.76	2760	0.32
	Pseudoterogorgia acerosa	15.051	0.32	2555	3.93
	Pseudoterogorgia kallos	6.515	0.24	1106	2.15
	Briareum asbestinum 1	5.067	0.72	860.1	0.15
BACHE EAST	*Erythropodium caribaeroum*	33.301	5.02	24620	1.41
	Briareum asbestinum 1	32.516	3.76	24040	5.35
	Plexaura homomalla	5.674	0.63	4195	2.93
	Pseudoplexaura porosa	5.394	0.74	3988	1.80
PACIFIC	*Gorgonia ventalina*	37.595	2	5001	0.82
	Erythropodium caribaeroum	26.913	2.24	3580	0.31
	Pseudoterogorgia americana	21.418	0.32	2849	5.26
ALINA'S	*Erythropodium caribaeroum*	29.277	2.47	12580	1.49
	Briareum asbestinum 1	12.197	0.92	5241	1.99
	Pseudoterogorgia americana	8.986	0.56	3861	3.73
	Gorgonia ventalina	8.429	0.66	3622	1.53
	Briareum asbestinum 2	8.308	1.98	3570	0.38
	Plexaura homomalla	5.848	0.42	2513	2.38
ELKHORN	*Gorgonia ventalina*	22.642	0.97	4458	1.31
	Erythropodium caribaeroum	16.811	3.68	3310	0.25
	Pseudoterogorgia americana	12.814	0.4	2523	2.06
	Briareum asbestinum 1	12.647	2.26	2490	0.35
	Plexaura homomalla	9.244	0.42	1820	0.93
BALL BUOY	*Erythropodium caribaeroum*	30.120	3.48	10425	0.65
	Gorgonia ventalina	17.341	0.88	6002	2.10
	Pseudoterogorgia americana	12.995	0.62	4498	4.23
	Briareum asbestinum 1	11.600	1.54	4015	0.76
	Pseudoterogorgia kallos	6.584	0.38	2279	3.91
ISA'S	*Erythropodium caribaeroum*	36.429	4.73	28375	2.83
	Briareum asbestinum 1	9.520	1.45	7415	3.01
	Pseudoterogorgia americana	8.100	0.9	6309	7.04
	Plexaura homomalla	6.061	0.7	4721	4.43
	Briareum asbestinum 2	5.639	1.76	4392	0.56
	Pseudoplexaura porosa	5.171	0.62	4028	2.80

* The erect form of the species complex.

Algae were grouped by genus if abundant (e.g., *Halimeda* and *Dictyota*) or by functional group (Steneck and Dethier 1994). The functional groups used here are: filaments (e.g., *Polysiphonia* spp., *Cladophora* spp.), corticated terete algae (CTA, e.g., *Laurencia* spp., *Acanthophora* spp.), articulated calcareous algae (ACA, e.g., *Amphiroa* spp., *Jania* spp.), and crustose coralline algae (CCA).

Herbivore exclusion experiments

Porites astreoides and *Siderastrea siderea*

In 1998, a caging study was carried out on two reefs, Triumph Reef (offshore bank reef, depth = 6 m) and East Bache Shoals (inshore patch reef, 25°29.002′N, 80°08.388′W, depth = 5 m) from 1 July–20 September (Fig. 1) to test the effects of herbivore exclusion on coral survivorship and growth. On each reef, colonies (5–15 cm in diameter) of *Porites astreoides* and *Siderastrea siderea* were labeled with metal tags and assigned to one of four treatments: caged ($n = 8$ per reef), caged-open top controls ($n = 4$), caged-open side controls ($n = 4$), and uncaged controls ($n = 8$). Cages built of galvanized steel mesh (22 cm in diameter, 15 cm in height, 1 × 1 cm opening size, Fig. 2A) were placed over colonies and secured to nails hammered onto the bottom. Cages were brushed free of colonizing organisms at bi-weekly intervals. Photographs of the coral colonies were taken at the start and at the end of the study with a Nikonos V camera equipped with a 28-mm lens and close-up lens outfit. The resulting prints were scanned and analyzed with NIH Image. Growth was estimated as the percent change in projected surface area of live coral tissue. At the end of the experiment, all algal tissue was collected by hand from caged and uncaged plots, identified, and dry weights compared among treatments.

In 1999, a second caging experiment was carried out with *P. astreoides* on Marker 3 Reef (25°22.408′N, 80°09.667′W, depth = 2–3 m, Fig. 1) from 14 May–10 September. Although grazer exclusion resulted in increased biomass within cages in 1998 (Fig. 3), algal biomass did not reach maximum levels observed for other reefs in the Northern Florida Reef Tract where mean biomass of *Dictyota* exceeded 20 g m^{-2} and small colonies of *P. astreoides* and other species were totally covered by macroalgae (Lirman and Biber 2000). Therefore, an algal addition treatment was added to duplicate observed maximum algal biomass levels. Caged corals were divided into two groups, and algal tissue was added as loose clumps to one group at bi-weekly intervals. Clumps of *Dictyota* spp. (1.5–2.5 g dry weight) were collected and introduced into the cages. The treatments used in this experiment were caged ($n = 10$), caged with algal addition ($n = 10$), caged-open top controls ($n = 10$), caged-open side controls ($n = 10$), and uncaged controls ($n = 10$). The amount of algal biomass introduced into cages approximated the maximum macroalgal biomass values recorded on reefs of the Northern Florida Reef Tract (Lirman and Biber 2000).

Montastraea faveolata

Rectangular cages were placed on large *M. faveolata* colonies (diameter > 1 m) on Elkhorn Reef (depth = 6 m, Fig. 1) from 19 May–10 September 1999. Cages (15 cm in length, 10 cm in width, 6 cm in height, 1 × 1 cm opening size, Fig. 2B) were placed so that roughly one half of the surface area enclosed was occupied by live coral tissue and the other half by macroalgae growing on dead coral skeleton. Cages were also placed over live coral tissue to document coral survivorship in the absence of direct algal competition and to determine whether algae could colonize live coral surfaces in the absence of grazing. Uncaged plots were established on coral–algal interfaces and live coral tissue without algal interaction. Each *M. faveolata* colony ($n = 10$) received one set of treatments (caged interface, caged live coral tissue without algal interaction, uncaged interface, and uncaged live coral tissue). Cages were brushed free of colonizing organisms at bi-weekly intervals and changes in percent live tissue were determined from digitized photographs of the experimental plots. In addition, the retreat rate of the live coral tissue margin was estimated by tracing the initial and final positions of the coral margin within each plot and estimating the distance between them. Distance estimates between the margins were measured at 2-cm intervals and averaged within plots. All algal tissue was collected from each plot at the end of the experiment, identified, and dry weights compared among treatments.

Statistics

The data were examined for conformity to the assumptions of each statistical test prior to analysis. Normality was tested with the Shapiro-Wilk test and homoscedasticity was tested with the Bartlett's test. As the normality assumptions were not met for percent growth of *P. astreoides* and *S. siderea*, an arcsine transformation (arcsine $\sqrt{x}$) was successfully applied prior to analysis. To evaluate potential caging artifacts, algal biomass and coral growth were compared for caged open-top controls, cage open-side controls and uncaged controls within reefs using ANOVA. Since no significant differences or patterns in algal biomass or coral growth were found

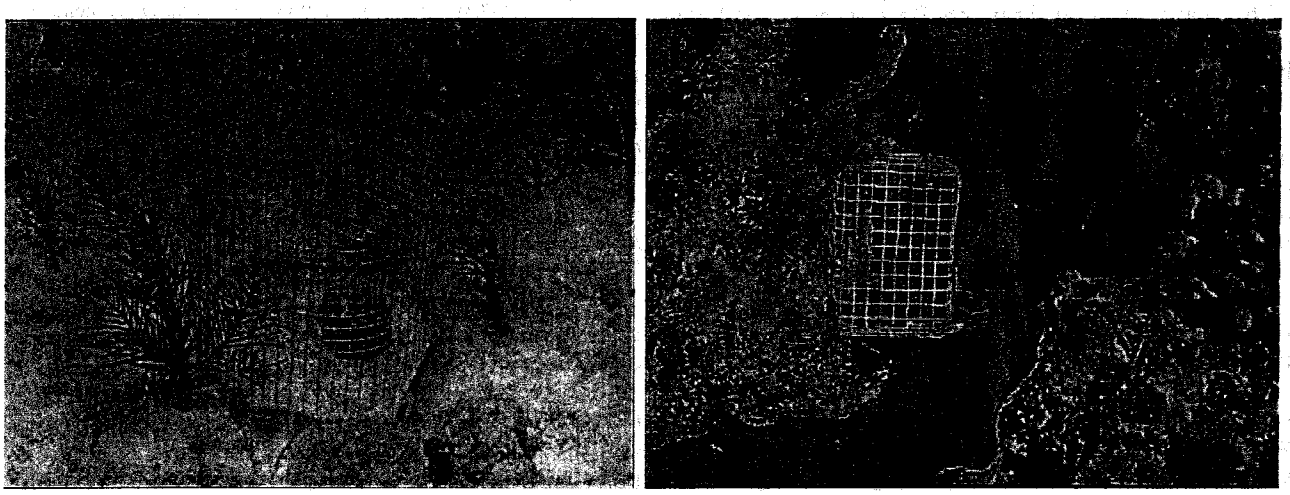


Fig. 2 Two types of herbivore exclusion cages used in this study: **A** circular cages (22 cm in diameter, 15 cm in height, 1 × 1 cm opening size) were placed over colonies of *Siderastrea siderea* and *Porites astreoides* and **B** rectangular cages (15 × 10 × 6 cm, 1 × 1 cm opening size) were placed over coral–algal interfaces on *Montastraea faveolata* colonies

(ANOVA, $p > 0.05$ for all experiments), data from these plots were pooled into a single control group for each coral species (*P. astreoides* and *S. siderea*) from each reef (Triumph Reef, East Bache, and Marker 3 Reef). Data from the 1998 caging experiment with *P. astreoides* and *S. siderea* were analyzed using a two-way ANOVA with grazing (ambient grazing–grazer exclusion cages) and reef location (inshore–offshore) as factors.

Results

Coral–algal interaction surveys

The frequency of interactions, estimated as the percentage of the basal perimeter of colonies ($n = 273$) that was in direct contact with macroalgae, was high, exceeding 50% on all four sites surveyed, reaching up to 85% on Pacific Reef (Fig. 4). Although the relative percentage of interactions varied for algal groups among sites, turf forms, *Halimeda* spp., and *Dictyota* spp. were the groups most commonly in contact with coral colonies. Cross-shelf patterns in the frequency of interactions were detected, with *Halimeda* spp. being more commonly in contact with corals at East Bache Shoals, and *Dictyota* spp. on offshore reefs (Fig. 3).

Herbivore exclusion experiments

Porites astreoides and *Siderastrea siderea*

The exclusion of grazers had significant effects on macroalgal biomass at Triumph Reef, East Bache Shoals, and Marker 3 Reef (Fig. 3). Although all groups accumulated higher biomass within cages, significant differences were not detected for all of these. Biomasses of *Dictyota* spp. and articulated calcareous algae (ACA) were significantly higher within caged plots ($n = 16$ for Triumph Reef and East Bache Shoals and 10 for Marker 3 Reef) compared to control plots ($n = 32$ for Triumph Reef and East Bache Shoals and 30 for Marker 3 Reef; t-tests, $p < 0.01$) at all three reefs. In contrast, corticated terete algae (CTA) had significantly higher biomass within cages only at Triumph Reef (t-tests, $p < 0.01$), and filamentous algae accumulated significantly higher biomass within caged plots only at East Bache Shoals (t-tests, $p < 0.01$).

In 1998, the caging experiment showed patterns of decreased coral growth rates under grazer exclusion for both *Porites astreoides* and *Siderastrea siderea* (Fig. 5); however, only the difference for *P. astreoides* was statistically significant ($n = 8$ for caged; $n = 16$ for uncaged; $p < 0.05$). No reef location or interaction effects were detected ($p > 0.1$) for either species. Colony appearance remained unchanged throughout these studies and no polyp retraction was detected.

In 1999, the loose clumps of *Dictyota* added to the cages at bi-weekly intervals remained free-floating within the cages for the first 2–3 days, but attached to the sides of the cages and to existing macroalgae after

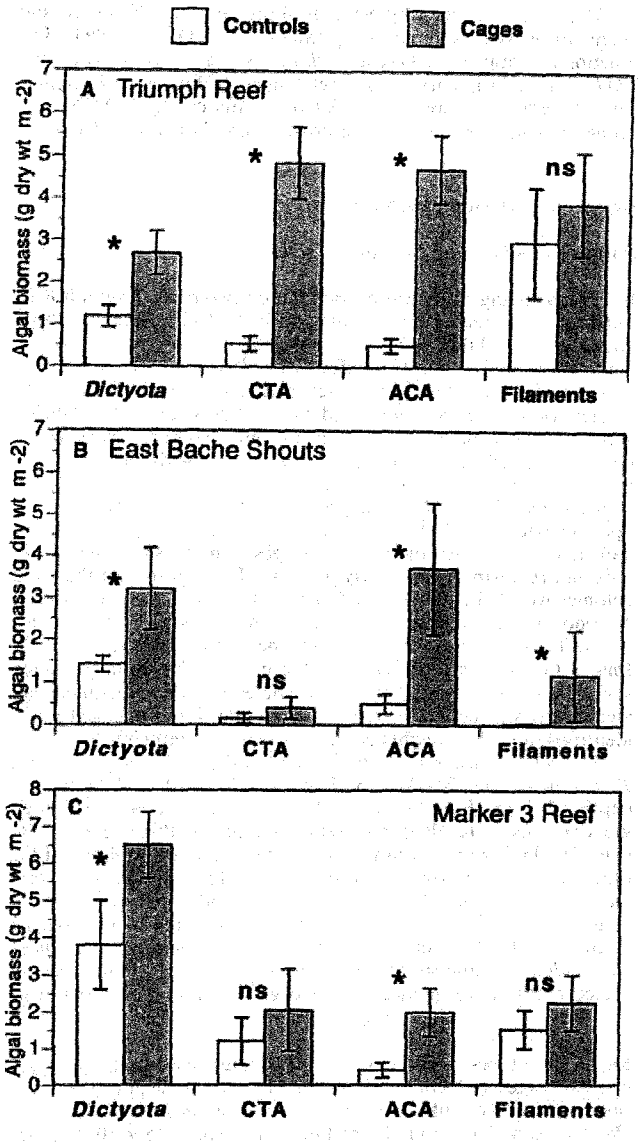


Fig. 3 Mean biomass (±1 SEM) of macroalgae (g dry wt m^{-2}) within caged ($n = 16$ for **A** and **B**, $n = 10$ for **C**) and control plots ($n = 32$ for **A** and **B**, $n = 30$ for **C**) at end of caging experiments at: **A** Triumph Reef (1 July–20 Sept 1998); **B** East Bache Shoals (1 July–20 Sept 1998); **C** Marker 3 Reef (14 May–10 Sept 1999). Functional groups represented here are: filaments (e.g., *Polysiphonia* spp., *Cladophora* spp.), corticated terete algae (*CTA*, e.g., *Laurencia* spp., *Acanthophora* spp.), and articulated calcareous algae (*ACA*, e.g., *Halimeda* spp., *Amphiroa* spp., *Jania* spp.). Data from Marker 3 do not include biomass from algal addition treatment. * Significant differences between groups (t-test, $p < 0.05$); *ns* no significant differences between groups (t-test, $p > 0.05$). Control plots combine data for caged open-top controls, caged open-side controls, and uncaged controls

this, mimicking more natural conditions. Significant differences in the growth of *P. astreoides* were found among caged, algal addition, and control treatments (ANOVA, $p < 0.01$; Fig. 6). Although corals within cages ($n = 10$) had reduced growth rates compared to controls ($n = 30$), Tukey pairwise comparisons showed that only

Appendix 1. Scleractinian species with more than 5 % of coral cover in each reef site. Mean cover is in cm²/m², total cover is in cm², mean density is in colonies/m². Percent cover within the scleractinian group only.

SITE	SPECIES	Percent cover	Mean cover	Total cover	Mean density
FOWEY	*Meandrina meandrites*	19.29	3.82	4963	0.13
	Dichocoenia stockesii	16.79	1.2	4320	0.51
	Siderastrea siderea	9.98	0.76	2569	0.47
	Agaricia agaricites	9.86	0.67	2536	0.70
	Diploria clivosa	9.52	2.23	2450	0.12
	Montastraea faveolata	6.45	5.53	1660	0.04
	Porites porites	5.98	0.57	1538	0.37
	Montastraea cavernosa	5.44	1.56	1401	0.10
SOLDIER	*Diploria clivosa*	53.45	10.38	2075	0.02
	Porites astreoidesY	17.52	3.4	680	0.02
	Siderastrea siderea	13.99	0.18	543	0.55
	Favia fragum	6.88	0.27	267	0.20
TRIUMPH	*Meandrina meandrites*	30.13	6.6	5940	0.09
	Siderastrea siderea	16.29	0.85	3211	0.57
	Agaricia agaricites	14.26	0.7	2811	0.70
	Dichocoenia stockesii	8.78	0.75	1731	0.24
	Montastraea cavernosa	8.53	0.84	1682	0.23
	Porites porites	7.39	0.61	1456	0.44
	Porites astreoidesY	5.31	0.7	1047	0.19
BACHE EAST	*Montastraea faveolata*	33.58	30.66	52130	0.35
	Siderastrea siderea	11.41	4.03	17720	1.24
	Montastraea cavernosa	10.12	8.27	15710	0.35
	Colpophyllia natans	7.61	13.13	11820	0.13
	Montastraea annularis	6.88	11.87	10680	0.15
PACIFIC	*Meandrina meandrites*	19.83	6.32	3790	0.06
	Agaricia agaricites	18.39	0.53	3515	1.46
	Porites porites	15.59	0.57	2980	1.08
	Siderastrea siderea	12.21	0.61	2333	0.59
ALINA'S	*Montastraea faveolata*	39.25	30.07	54130	0.40
	Siderastrea siderea	16.07	4.52	22169	1.03
	Porites porites	11.94	2.26	16472	3.62
ELKHORN	*Porites astreoidesY*	28.40	3.95	27653	4.90
	Porites porites	24.15	2.61	23516	3.59
	Siderastrea siderea	14.40	4.25	14023	0.43
	Acropora palmata	9.86	12	9600	0.12
	Diploria strigosa	7.21	7.81	7025	0.09
	Diploria clivosa	6.69	2.33	6515	0.32
BALL BUOY	*Acropora palmata*	20.34	22.08	26490	0.41
	Montastraea cavernosa	10.17	3.08	13250	0.61
	Siderastrea siderea	10.07	2.91	13115	0.84
	Porites porites	9.39	2.04	12231	1.55
	Porites astreoidesY	8.31	2.21	10818	1.68
	Agaricia agaricites	7.91	1.43	10300	2.30
	Colpophyllia natans	5.72	24.83	7450	0.04
ISA'S	*Montastraea faveolata*	22.90	12.22	20770	0.35
	Siderastrea siderea	19.88	2.91	18023	3.04
	Dichocoenia stockesii	11.55	2.33	10472	1.41
	Stephanocoenia intersepta	6.84	2.3	6200	0.49

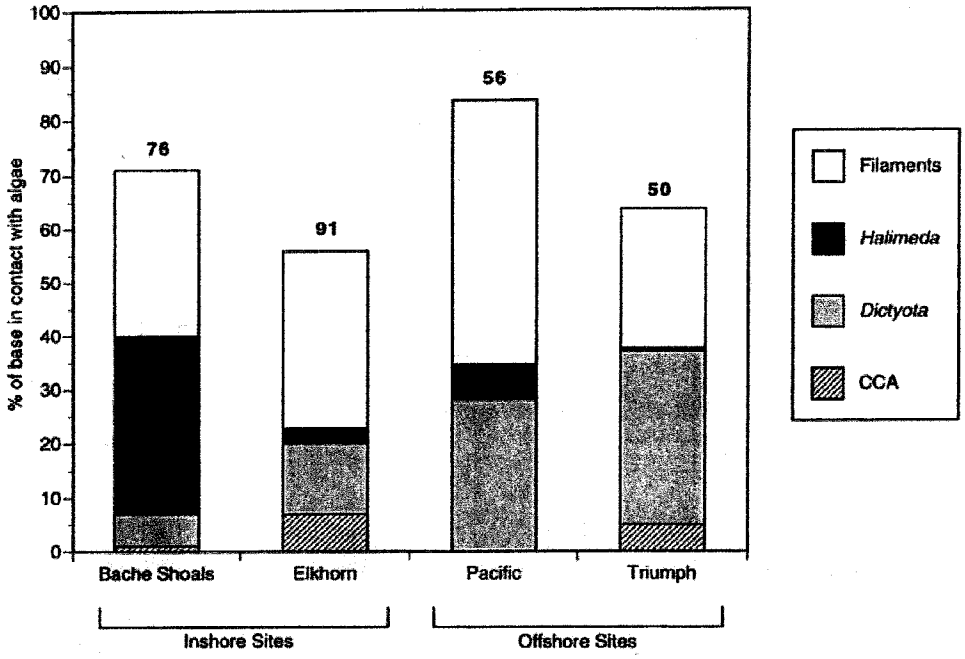


Fig. 4 Coral–algal interactions expressed as percentage of basal perimeter of colonies that was in direct contact with macroalgae on two inshore and two offshore sites within Biscayne National Park, Northern Florida Reef Tract in July–August 1998. *CCA* Crustose coralline algae. *Bold numbers* are numbers of colonies surveyed

those corals in the algal addition treatment ($n = 10$) had growth rates significantly slower than the other treatments. No net tissue losses were recorded for any of the corals, but photographic surveys showed that colonies in the algal addition treatment had retracted polyps on their upper surfaces starting 1 week after the onset of the experiment, and that this behavior was observed throughout the study.

Montastraea faveolata

Macrograzer exclusion influenced macroalgal biomass along coral–algal interfaces on *M. faveolata* colonies. Although biomass of CTA and filamentous algae was higher within caged interface plots ($n = 10$) compared to uncaged interface plots ($n = 10$), statistically significant differences were only found for *Dictyota* spp., the most abundant group along coral–algal interfaces (t-test, $p < 0.01$). Mean dry weight of *Dictyota* spp. was 16.8 g m^{-2} in caged interfaces compared to 12.7 g m^{-2} in uncaged interface plots. No macroalgae were found colonizing or growing within caged ($n = 10$) and uncaged ($n = 10$) live coral plots.

Both caged and uncaged interfaces on *M. faveolata* experienced a net loss of coral tissue in the presence of algal interaction (Fig. 7). Tissue mortality rates were significantly higher (t-test, $p < 0.05$) in caged plots where live tissue was lost at a rate of 10.2% per month (SEM = 2.4), compared to 5.2% (SEM = 2.2) in uncaged plots. Similarly, the rate of retreat of the coral tissue margin was faster on caged plots (0.43 cm $month^{-1}$, SEM = 0.09) compared to uncaged plots (0.25 cm $month^{-1}$, SEM = 0.09). No tissue mortality occurred within cages over entirely live tissue.

Discussion

Contact interactions between corals and macroalgae can be common along the margins of colonies. Along the Northern Florida Reef Tract, coral colonies had more than 50% of their basal perimeter in contact with macroalgae during the peak of algal abundance in the summer of 1998. Similarly, Tanner (1995) found algal interfaces for 92% of coral colonies surveyed at Heron Island, Great Barrier Reef. These results clearly highlight the importance of space competition between corals and algae.

Observations of coral overgrowth by macroalgae are numerous in the literature (e.g., Hughes 1989; Littler et al. 1989; Coyer et al. 1993; Tanner 1995; Anthony et al. 1997; Littler and Littler 1997; McClanahan and Muthiga 1998). In most cases, coral declines were mediated by drastic reductions in grazing due to trophic shifts, overexploitation, or massive die-offs of herbivores that resulted in uncontrolled algal growth (Carpenter 1990; Lessios 1988; Hughes 1994; Aronson and Precht 1999). The caging treatments, used here as a mechanism to increase algal biomass, showed that coral susceptibility to increased algal competition is species-specific and can be affected by the amount of algal biomass in contact with corals. Significant decreases in growth rates were documented for caged *Porites astreoides*, which had

Table 6: Wind data extracted from CMAN records for Fowey Rocks Light for the duration of each sediment accumulation plate (A) and each sediment trap (B) deployment. Mean speed and gusts are given in knots, direction is given in degress (ie. 0 to 360°).

A- Plate deployments

Date placed	Date retrieved	Mean speed	Mean max. gust	Mean direction
07/26/94	07/29/94	5.7	11.1	148
10/25/94	10/28/94	4.1	6.8	167
01/27/95	01/30/95	5.8	9.6	167
04/25/95	04/28/95	4.4	8.9	140
08/11/95	08/14/95	3.9	7	194

B- Sediment trap deployments:

Knots Knots

Date placed	Date retrieved	Mean speed	Mean max. gust	Mean direction	Direction range
7/13/94	8/8/94	4.9	14.6	137	92-235
8/9/94	9/7/94	4.9	17.6	120	83-169
9/28-29/94	10/13-14/94	4.8	13.9	141	79-258
11/9/94	11/25/94	8.4 (Gordon)	26.0	159	43-294
14/14/94	1/3/95	6.8	23.8	202	76-316
1/20/95	2/2-8/95	6.8	20.2	250	144-311
2/16/95	3/1/95	6.8	16.5	143	86-251
3/23/95	4/5/95	6.6	13.4	166	55-245
4/28/95	5/15/95	5.1	17.7	139	84-185
5/25/95	6/9/95	6.2	15.5	136	93-200
6/27/95	7/11/95	4.1	11.5	159	59-219
8/11/95	8/28/95	5.1	19.3	183	94-236
9/20/95	10/6/95	4.9	17.4	120	81-199

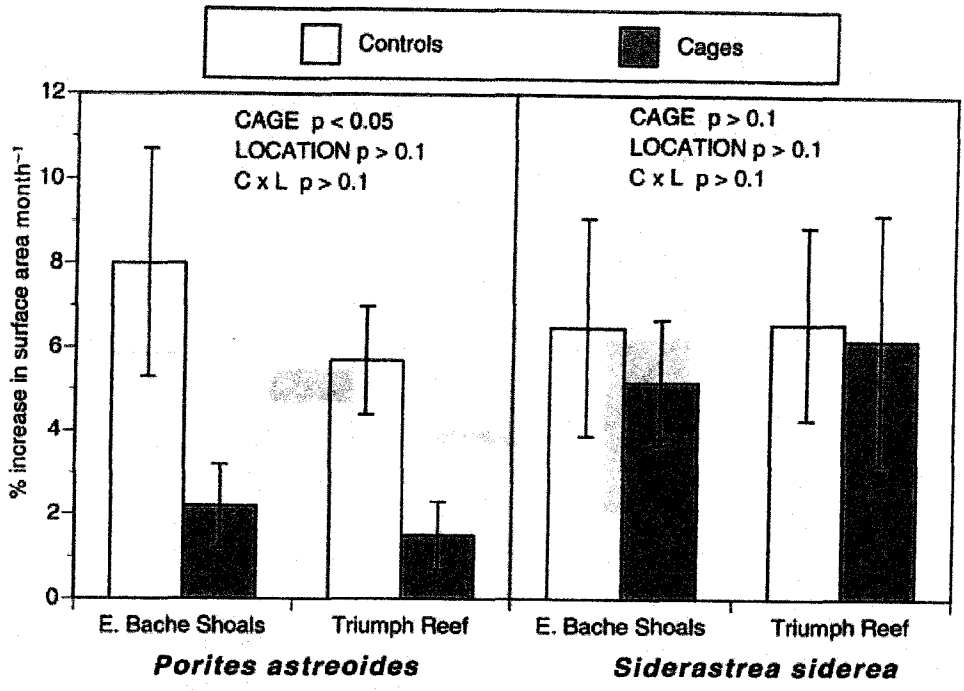


Fig. 5 Mean percent growth rates (± 1 SEM) of caged ($n = 8$) and control ($n = 16$) *Siderastrea siderea* and *Porites astreoides* during caging studies at East Bache Shoals and Triumph Reef. Study ran from 1 July–20 Sept 1998. Control plots combine data for caged open-top controls, caged open-side controls, and uncaged controls. *P* values from two-factor ANOVA

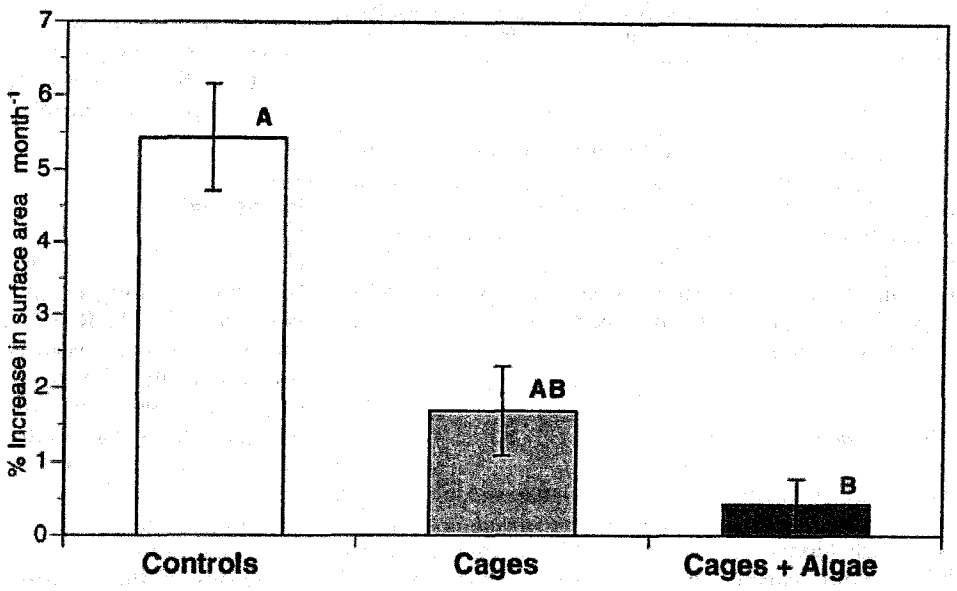


Fig. 6 Mean percent growth rates (± 1 SEM) of caged ($n = 10$), caged + algae ($n = 10$), and uncaged ($n = 30$) *Porites astreoides* during caging studies at Marker 3 Reef (14 May–10 Sept 1999). Control plots combine data for caged open-top controls, caged open-side controls, and uncaged controls. Additional algal tissue (1.5–2.5 g dry wt of *Dictyota*) was added to algal addition group at biweekly intervals. *Bars* with different *letters* are statistically different (ANOVA, Tukey pairwise comparisons)

growth rates three to four times lower than uncaged colonies. Similarly, caged coral–algal interfaces on *Montastraea faveolata* colonies had tissue mortality rates that were double those of uncaged interfaces.

Other studies have documented the negative effects of algal competition. Potts (1977) reported reduced coral growth within damselfish territories with high algal cover, and Tanner (1995) found decreased growth rates for two acroporid species in competition with macroalgae. In addition, Miller and Hay (1996) showed through manipulative experiments that algal competition can inhibit the growth of the temperate coral *Oculina arbuscula*. However, exceptions to these patterns were noted. In the present study, no effects of increased algal competition were detected for *Siderastrea siderea*. Also, Tanner (1995) noted no effects of macroalgal competition on growth rates of *Pocillopora damicornis*.

Even further decreases in growth rates were documented for *P. astreoides* when additional algal tissue was introduced into caged treatments to duplicate maximum levels of algal biomass documented for reefs of the Northern Florida Reef Tract (Lirman and Biber 2000). Colonies of *P. astreoides* in the algal addition treatment exhibited retracted polyps and had growth rates up to

Table 5. Summary table of environmental parameters measured at each site. Temperature stress indicates percent of days monitored when average temperatures were above 30 or below 20 degrees C. Sedimentation (Mean of 13 two-week deployments) in mg/cm2/day. Water column nutrient concentrations are long term means (n= 18-21) given in'uM (s.d.)

REEF SITE	FOWEY	SOLDIER	TRIUMPH	EBACHE	PACIFIC	ALINA'S	ELKHORN	BBUOY	ISA'S
Reef type	relic-bank	relic-bank	relic-bank	patch	relic-bank	patch	patch	bank-barrier	patch
Temperature stress	1.4	15.7	1.2	3.1	n.a.	2.8	n.a.	0.4	3.4
Sedimentation rate	5.4	11.2	3.7	3.3	4.7	3.7	9.3	15	1.9
WATER COLUMN									
[nitrate+nitrite]	0.25 (0.16)	0.21 (0.19)	0.31 (0.22)	0.29 (0.24)	0.43 (0.47)	0.25 (0.19)	0.35 (0.39)	0.26 (0.28)	0.26 (0.40)
[ammonium]	0.08 (0.08)	0.13 (0.16)	0.11 (0.11)	0.10 (0.14)	0.29 (0.51)	0.11 (0.07)	0.10 (0.16)	0.11 (0.13)	0.22 (0.32)
[phosphate]	0.11 (0.05)	0.08 (0.05)	0.09 (0.06)	0.10 (0.05)	0.11 (0.07)	0.09 (0.07)	0.10 (0.05)	0.10 (0.07)	0.11 (0.07)
TIN:IP	3.0	4.3	4.7	3.9	6.5	4.0	4.5	3.7	4.4

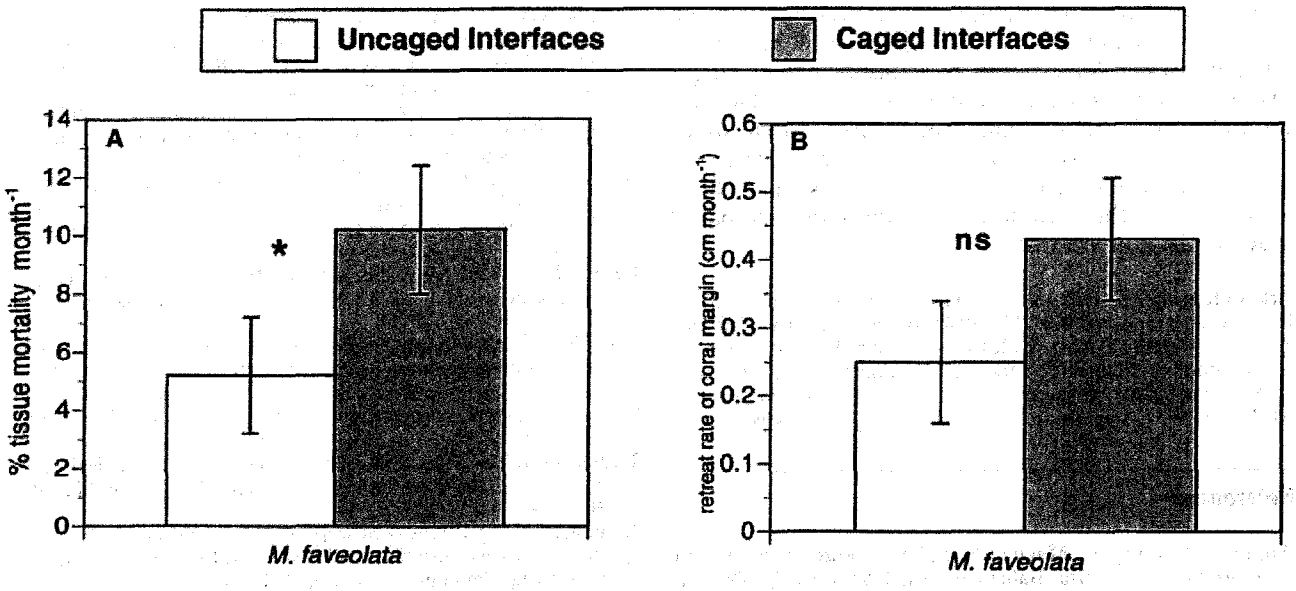


Fig. 7 A Mean percent tissue mortality rates (±1 SEM) and B mean retreat rate (±1 SEM) of coral margin of *M. faveolata* within caged ($n=10$) and uncaged ($n=10$) coral–algal interface plots at Elkhorn Reef (19 May–10 Sept 1999). * Significant differences between groups (t-test, $p<0.05$); *ns* no significant differences between groups (t-test, $p>0.05$)

ten times lower than uncaged colonies. It is important to note, however, that polyp retraction was only observed in corals in the algal addition treatments and may be a result of the potential scouring action of the clumps of algae added, which remained unattached within cages for several days. Polyp retraction and reduced growth in corals in contact with macroalgae were previously documented by Coyer et al. (1993) on a temperate rocky reef.

Coral colony morphology may have an important influence on the outcome of coral–algal competition and may partly explain the species-specific results reported here. Tanner (1995) and Hughes (1989) found encrusting colonies to be more affected by algal encroachment than branching or massive morphotypes based on the higher perimeter-to-area ratio of encrusting colonies compared to colonies with higher three-dimensionality. In agreement with these reports, growth rates of encrusting *Porites astreoides* colonies in this study were negatively affected by increased algal competition, whereas growth rates of massive *Siderastrea siderea* colonies were not affected. However, colonies of the massive *Montastraea faveolata* were found to be highly susceptible to algal overgrowth as caged tissue plots lost an average of 10% of their live tissue area per month.

For massive corals that commonly maintain live tissue cover over their whole colony surface (e.g. *Siderastrea* spp., *Diploria* spp., *Colpophyllia* spp.), algal competition would be concentrated along the colony perimeter, as few dead areas would be available for algal colonization. As colonies of these species grow, a smaller percentage of their surface area would be in direct contact with macroalgae, reducing the negative effects of competitive interactions. However, for coral species that do not normally maintain live tissue cover over their whole colony surface, dead patches provide suitable substrate where macroalgae can attach and grow. In these cases, coral–algal interfaces would be found not only along the colony base, but also at numerous points within the colony surface. Such is the case of *Montastraea annularis* where live tissue is found only at the tops of columns (Knowlton et al. 1992) or large colonies of *M. faveolata* like those surveyed in this study, which have experienced partial mortality due to the establishment of damselfish territories or other disturbances.

The present study showed that large, massive colonies like those of *M. faveolata* can experience rapid tissue losses at coral–algal interface margins. These results emphasize the importance of chronic disturbance agents such as corallivores, sedimentation, diver and boat impacts, elevated temperatures, and storms that rarely cause whole-colony mortality, but can cause numerous dead patches within coral colonies that can be subsequently colonized by algae (e.g., Bythell et al. 1993; Meesters et al. 1996; Lirman 2000). Cages placed over live tissue areas without any direct competition from algal margins experienced no tissue mortality, reinforcing the need for dead patches to be created before algae can colonize, even in the absence of grazing. Once these dead patches are colonized, the subsequent reductions in coral growth and enhanced tissue losses documented here may take place, compromising the long-term survivorship of the affected colonies.

Competition for primary space has always been considered a major structuring force within reef communities (Lang and Chornesky 1990). Increases in macroalgal cover and biomass on Caribbean reefs in response to reduced herbivory, damselfish territorial behavior, and eutrophication can result in increased

Table 4: Tally from the temperature records for each site of the number of days with stressful temperature exposure (arbitrarly set at less than 20°C or higher than 30°C). Since each site has gaps in the temperature records due to instrument loss and malfunction, the number of days of of incidence of stressful temperature is standardized to the total number of days of record for each particual reef site.

SITE	Days below 20°C	Days above 30°C	Stressful days	Total days of record	% stressful days
FOWEY	0	3	3	217	1.4
SOLDIER	19	29	48	306	15.7
TRIUMPH	0	4	4	332	1.2
BACHE E.	9	0	9	290	3.1
ALINA'S	2	6	8	287	2.8
BALL BUOY	1	0	1	271	0.4
ISA'S	5	6	11	322	3.4

rates of coral–algal interactions. Moreover, results from the present as well as previous studies show that these interactions can have significant, species-specific, negative effects on coral growth and survivorship. The susceptibility of reef-building corals like *Montastraea faveolata* to algal overgrowth under present levels of grazing suggest long-term negative effects on reef development in the area if present rates of macroalgal space utilization are maintained.

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Table 3. Summary table for juvenile/adult densities (col/m²) and reproductive patterns of the spp. in each locality sampled in BNP. ° = Hermaphrodite-broadcaster, [1] = hermaphroditic brooder; [2] = gonochoric broadcaster; [3] = gonochoric brooder;* = mixed pattern; [a] = unknown reproductive pattern and developmental mode. Total inshore and offshore numbers are the sum of juveniles and adult colonies in quadrats. P. astreoidesY and B are the two common color morphs (yellow-green and brown) and are considered as the same species. Total adult colonies and densities include all species of coral sampled in quadrats.

REEF SITES	FOWEY	SOLDIER	TRIUMPH	BACHE EAST	PACIFIC	ALINA'S	ELKHORN	BALL BUOY	ISA'S	Colonies Inshore	Colonies Offshore	Total
Acropora cervicornis °						.02/.11	.01/.01			2/11	1/1	3/12
Acropora palmata °						.02/.02				2/2	0	2/2
Agaricia agaricites [3]	.08/.62		.03/.67	.01/.20	.12/1.34		.02/.28	.05/2.25	.05/1.09	4/82	30/516	34/598
Agaricia purpurea *										1/16	0	1/16
Agaricia tenuifolia [a]						.01/.19				1/17	0	1/17
Colpophyllia natans [a]					.01/.01	.01/.01			.05/.01	5/2	1/1	6/3
Dichocoenia stockesii [a]	.05/.46	.01/0	.07/.17	.04/.14	.04/.04	.05/.22		.02/.27	.24/1.17	27/109	18/94	45/203
Dichocoenia stellaris [a]				.03/.01						2/11	0	2/11
Diploria clivosa °	.02/.10					.04/.09	.04/.28		.01/0	5/8	6/38	11/46
Diploria labyinthyformis °	.04/.01				.03/.02	.03/.01		.04/.09	.03/.04	5/4	11/12	16/16
Diploria strigosa °					.02/.03	.04/.05	.03/.06	.02/.09	.04/.15	7/16	7/18	14/34
Eusmilia fastigiata [a]									.04/.05	2/4	0	2/4
Favia fragum [1]		.09/.11				.01/.33				10/41	0	10/41
Madracis decactis [a]					.01/.10					0	1/10	1/10
Meandrina meandrites [a]	.01/.12		.01/.08		.01/.05					0	3/25	3/25
Meandrina memorialis [a]					.01/.01					0	1/1	1/1
Montastraea annularis °			.01/0	.01/.14	.01/.01	.05/.26			.01/.04	7/38	2/1	9/39
Montastraea cavernosa [2]	.04/.06		.11/.12	.04/.31	.11/.01	.04/.24		.11/.50	.20/.23	22/74	37/69	59/143
Montastraea faveolata °	.02/.02				.01/0	.01/.38		.06/.14	.07/.28	6/46	6/16	15/62
Montastraea franksi °	.01/0			.03/.11	.04/.02			.01/.08	.03/.09	4/16	6/10	10/26
Mycetophyllia aliciae [1]				.01/.31					.07/.05	6/29	0	6/29
Mycetophyllia danaana [a]									.12/.20	9/15	0	9/15
Mycetophyllia lamarckiana [a]								.06/.14	.01/.04	1/3	6/14	7/17
Porites astreoidesB [1*]	.06/.18		.09/.12	.20/.78	.02/0	.25/.55	.03/.08	.08/.11	.48/.65	161/75	28/49	189/124
Porites astreoidesY [1*]	.10/.11		.09/.10	.08/.33	.12/.12	.46/.63	1.87/3.03	.52/1.16	.23/.13	65/93	271/452	336/545
Porites divaricata [1]		.01/.04								1/4	0	1/4
Porites porites [1*]	.10/.27		.10/.34	.01/.38	.23/.85	.22/3.4	.45/3.14	.19/1.36		21/339	107/596	128/935
Scolymia cubensis [a]									.01/.33	1/25	0	1/25
Siderastrea siderea [2]	.21/.26	.31/.24	.24/.33	.26/.98	.41/.18	.20/.84	.04/.39	.21/.63	1.4/1.7	173/174	111/179	284/353
Solenastrea bournoni [a]		.01/0							.01/.07	5/2	0	2/5
Solenastrea hyades [a]		.01/0								1/0	0	1/0
Stephanocoenia intersepta [a]	.01/.03		.02/0		.05/.03				.05/.44	4/33	8/6	12/39
Number of quadrats	100	100	100	80	100	91	100	100	75	346	500	846
Juvenile colonies	75	44	77	57	125	136	249	137	235	472	663	1135
Juvenile density (col/m2)	0.75	0.44	0.77	0.71	1.25	1.49	2.49	1.37	3.13	1.36	1.33	1.34
Adult colonies	224	39	193	305	282	668	727	682	541	1553	2108	3661
Adult density (col/m2)	2.24	0.39	1.93	3.81	2.82	7.34	7.27	6.82	7.21	4.49	4.22	4.33
Total adult colonies	240	49	213	553	310	781	800	904	653	2036	2467	4503
Overall adult density (col/m²)	2.4	0.49	2.13	6.91	3.1	8.58	8	9.04	12.71	5.88	4.93	5.32
Broadcasting species	6	1	3	4	7	9	4	6	8	10	9	10
Brooding species	2	2	3	1	4	3	3	2	3	6	4	6
Mixed and unknown mode	4	3	3	6	6	3	0	3	7	12	8	15

Table 2. Results of Wilks-Lambda rank tests for paired means of percent cover of the major biological groups and the abundances of Cnidarians and Sponges between paired latitudinal localities in BNP.
* Significantly different; N= non significantly different.

Localities	ALG	CRU	TURF	BARE	SCLE	OCT	HYDR	SPO	ZOA
SOLDIER - FOWEY	*	*	*	*	*	*	N	*	N
BACHE - TRIUMPH	*	*	*	N	*	*	N	*	N
ALINA'S - PACIFIC	*	*	*	*	*	*	N	*	N
ALINA'S - ELKHORN	*	N	*	N	*	*	N	*	*
ISA'S - BALL BUOY	*	N	N	*	N	*	N	*	*

Localities	NOCT	NSCL	SPON	NHYD	NZOA
SOLDIER - FOWEY	N	*	*	*	N
BACHE - TRIUMPH	*	*	*	*	N
ALINA'S - PACIFIC	*	*	*	N	N
ALINA'S - ELKHORN	*	N	*	*	*
ISA'S - BALL BUOY	*	*	*	N	*

Table 1. Summary table of site and biotic characteristics of nine localities sampled in Biscayne National Park, Florida. Density is in colonies/m². Percent cover is relative cover in each reef.

REEF SITE	FOWEY	SOLDIER	TRIUMPH	EBACHE	PACIFIC	ALINA'S	ELKHORN	BBUOY	ISA'S
Latitude (N)	25° 35.38	25° 35.25	25° 28.31	25° 28.98	25° 22.18	25°23.20	25° 21.78	25°18.52	25° 19.91
Longitude (W)	80° 05.69	80° 09.18	80° 06.72	80° 08.44	80° 08.36	80°09.77	80° 09.94	80° 11.99	80°11.87
Depth (m)	3-10	3.5-4.5	3-7	1-5	2-10	2-6	1-5	2-9	2-6
Reef/site/ structure	relic-bank	relic-bank	relic-bank	patch	relic-bank	patch	patch	bank-barrier	patch
Number of transects	5	5	5	4	5	4	5	5	4
Number of quadrats	100	100	100	80	100	91	100	100	75
NUMBER OF SPECIES									
Hard Corals	28	12	24	40	30	39	29	40	43
Octocorals	28	23	32	40	29	39	34	39	41
Sponges	37	21	31	31	30	34	34	36	48
NUMBER OF GENERA									
Hard Corals	15	8	13	18	15	21	14	20	22
Octocorals	11	8	11	11	11	11	11	11	11
Sponges	25	16	21	23	19	25	23	29	35
PERCENT COVER									
Hard Corals	2.54	0.48	2.01	19.38	1.93	16.12	9.89	12.69	12.89
Octocorals	1.18	0.85	1.7	9.23	1.34	4.79	1.98	3.37	10.59
Sponges	5.04	2.34	2.22	6.43	1.02	4.34	2.39	4.85	11.82
Zoanthids	0.59	0	1.96	2.27	0.64	0.85	0.38	2.1	2.66
Hydrocorals	0.19	0.82	0.33	1.76	0.74	0.84	0.94	2.52	0.92
Fleshy Algae	12	70.32	13.07	9.25	13.81	24.87	18.62	14.77	8.36
Turf Algae	55.6	5.07	59.96	36.6	48.5	34.1	46.75	26.49	20.7
Crustose Algae	10.9	0.4	8.76	10.47	15.3	5.88	7.48	15.55	11
Sand	8.79	19.72	8.76	1.59	7.59	4.73	7.31	11.86	15.76
Bare substrate	3.17	0	1.14	3.02	9.13	3.48	4.26	5.8	5.3
DENSITY (col/sqm)									
Hard Corals	3.46	0.8	3.2	7.92	4.68	10.08	10.6	10.52	11.84
Octocorals	8.14	7.93	14.66	22.27	8.46	19.52	7.82	16.41	41.11
Sponges	5.36	3.77	3.84	8.68	3.29	8.77	4.84	8.04	21.25
Zoanthids	1.82	0	2.43	2.22	1.71	2.13	1.62	2.16	2.81
Hydrocorals	1.9	1.8	3.14	2.51	2.37	2.73	2.21	3.59	3.17

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Seasonal Dynamics of Macroalgal Communities of the Northern Florida Reef Tract

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Coral communities worldwide are undergoing intense degradation in response to natural and human disturbances, and many reef systems have already experienced a significant decline in live coral cover associated with an increase in macroalgae abundance. Here, we document the seasonal dynamics of the macroalgal communities of the Northern Florida Reef Tract, providing a baseline for long-term studies of coral-algal competition in the region.

Both macroalgal biomass and percent cover on reefs showed an increasing trend from January to July, when both light and temperature conditions were favorable for growth. Maximum percent cover (56.7%) was found in July and minimum levels in December (25.8%). During these peaks in algal cover, many corals were completely covered by dense mats of algae. Two genera, *Halimeda* and *Dictyota*, represented the largest proportion (77–99%) of the total algal biomass. In the summer, *Dictyota* spp. dominated the algal community, occupying up to 40% of the reef bottom with a dry biomass of up to 20 $g.m^{-2}$. In addition, two species, *Stypopodium zonale* and *Trichogloea requienii* , showed a significant bloom in April 1998, covering a significant percentage of the bottom (up to 25%) at an inshore reef. The species that exhibited rapid space monopolization on Florida reefs, such as *Dictyota* spp. and *Stypopodium zonale*, also showed rapid growth in microcosm and field growth studies.

No correlations were found between fish grazer abundance and algal biomass or percent cover, indicating that present grazer population abundance and composition are not adequate to prevent space monopolization and coral overgrowth by algae such as *Dictyota* spp. and *Halimeda* spp. Only a continued monitoring effort will determine whether the seasonal dynamics of the algal community may result in the decline of coral populations in the Northern Florida Reef Tract.

Introduction

Coral reef communities worldwide face serious threats from a combination of both natural and human-induced disturbances. Long-term ecological studies coincide in reporting general declines in live coral cover and a correlative increase in macroalgal abundance (Ginsburg 1993, Birkeland 1997). Thus, the fate of coral communities appears to be closely tied to that of macroalgal communities. Although macroalgae are conspicuous components of reefs within the Florida Reef Tract, only limited information is available on their growth and community dynamics. The purpose of this research is to document patterns of algal abundance, diversity, and growth, thereby providing a baseline to study the outcome of competition between corals and macroalgae.

Competition between corals and algae can be direct (i. e., overgrowth) or indirect (i. e., through the pre-emption of primary space). The presence of macroalgae has been shown to reduce coral growth (Tanner 1995, Miller and Hay 1996), as well as limit coral recruitment and juvenile survivorship (Birkeland 1977, Hughes 1989; Tomascik 1991, Wittenberg and Hunte 1992). Algae can also cause coral tissue mortality due to shading, sediment accumulation, abrasion, and allelopathy (Potts 1977, Sammarco 1982, Lewis 1986, Chadwick 1988, Coen 1988, Coles 1988, Keats *et al.* 1997, Littler and Littler 1997 a).

Examples of drastic ecosystem degradation resulting in the replacement of coral-dominated systems by macroalgal-dominated ones are plentiful (Smith *et al.* 1981, Sheppard 1988, Bell and Tomascik 1993, Steneck 1993, Hughes 1994, Littler and Littler 1997 b). These studies showed that factors that favor algal growth, such as increased nutrient inputs and reduced grazing intensity, can produce long-lasting phase shifts within coral communities as corals are outcompeted by macroalgae (Done 1992).

In the recent past, considerable controversy has arisen over factors controlling algal abundance on coral reefs. Top-down (i. e., consumption) and bottom-up (i. e., resource availability) controls of algal community dynamics have been proposed as opposing hypotheses, and the relative importance of herbivory and nutrient levels is currently being debated for reefs of the Florida Keys and elsewhere (Littler and Littler 1984, Hughes 1994, Szmant and Forrester

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1996, Lapointe 1997, 1999, Lapointe *et al.* 1997, Hughes *et al.* 1999). In the present study, we evaluate the relationships between the abundance of the dominant grazers, parrotfishes and surgeonfishes, and the abundance and composition of macroalgal communities on inshore patch reefs and offshore bank reefs of the Northern Florida Reef Tract.

Given their fast growth and turnover rates compared to other reef benthic components, it has been suggested that algae could be used as early-warning indicators of reef degradation (McCook *et al.* 1997). However, as with any environmental indicator, a knowledge of its distribution and variability is needed before its application (Ward 1990). To provide such baseline information for the algal communities of the Northern Florida Reef Tract, we documented: 1) the physical environment, and 2) seasonal distribution, abundances, biomass, percent cover, diversity, and growth of the dominant macroalgal groups.

Methods

Macroalgal communities were surveyed at four reefs within Biscayne National Park, on the Northern Florida Reef Tract (Fig. 1). Two inshore sites, Bache Shoals (25°29.187′ N, 80°08.880′ W) and Elkhorn Reef (25°21.782′ N, 80°09.841′ W), and two offshore sites, Triumph Reef (25°28.333′ N, 80°06.704′ W) and Pacific Reef (25°22.186′ N, 80°08.360′ W) were sampled. All surveys were done at depths of 3–5 m.

Macroalgae in this study were identified using keys by Taylor (1960) and Littler and Littler (1997c). Abundant algae were grouped by genus (e. g., *Halimeda* and *Dictyota*) or by functional group (Littler and Littler 1980, Steneck and Dethier 1994). The functional groups used are: turf algae (filamentous forms of algae with canopy < 1 cm), filaments (FIL, canopy > 1 cm), corticated terete algae (CTA, e. g., *Laurencia* spp., *Acanthophora* spp.), articulated calcareous algae (ACA, e. g., *Amphiroa* spp., *Jania* spp.), and crustose coralline algae (CCA).

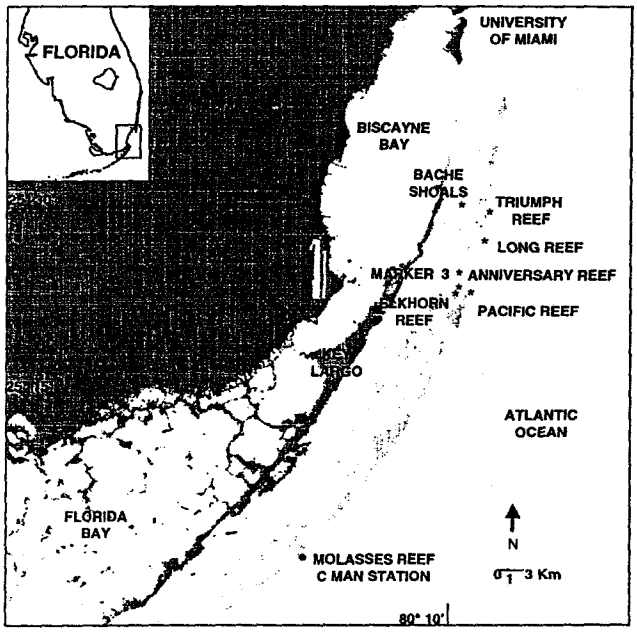


Fig. 1. Map of the Northern Florida Reef Tract with the location of study sites. Map created by S. Tosini (CMEA).

Physical Environment

Temperature and surface irradiance values for 1998 were obtained from the NOAA C-MAN weather station at Molasses Reef (Fig. 1). Hourly readings of water temperature were averaged to obtain a daily mean value. Light readings in the 400 to 700 nm wave band were recorded at hourly intervals at 35 m above sea level by LI-COR sensors. Values from 10:00 and 17:00 were averaged to obtain daily means.

Algal Biomass and Species Composition

Macroalgae were collected in May and August 1998 within 0.25 m^2 PVC quadrats placed haphazardly over the bottom. Within each quadrat, all visible macroalgae were collected by hand during a 5-minute interval. A total of 15 such quadrats were sampled per reef and returned to the laboratory. Algal biomass was also collected in the back-reef area of Elkhorn Reef to provide a within-reef comparison. Samples were sorted by species or functional group. Algal tissue was dried to constant weight at 70 °C. Sample specimens were preserved to determine species composition within sites.

Percent Cover and Relative Algal Abundance

Close-up photographs of the reef benthos were taken haphazardly to estimate the percent cover and seasonal composition of the algal community. Each photo-quadrat encompassed an area of 15 × 20 cm and 35 such quadrats were surveyed per reef. Percent cover of the different algal groups was determined by the point-quadrat method (Stoddart and Johannes 1978). A piece of acetate paper with randomly-placed dots was placed over each photograph and the identity of the algal group directly under each dot was determined. A preliminary analysis of photographs using 25 and 50 random points showed that percent cover estimates did not change significantly when the number of random points was doubled. Accordingly, a total of 25 points were surveyed for each photograph.

Given the limitations of the hand collection method used here which precludes the collection of small filaments and encrusting species, the seasonal composition of the algal community was also assessed from photographs. The relative cover of each species was determined as the number of points occupied by a given group divided by the total number of points within each photograph occupied by macroal-

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gae. Values for each group were averaged for all photographs taken at the same site.

Algal Growth

Microcosm and field studies were performed to determine the growth rates of abundant macroalgal species. In June–July 1998, tissue from 12 species of abundant macroalgae were collected from Bache Shoals and Triumph Reef and transported back to the outdoor microcosm facilities at the University of Miami within 3 hours of collection. For each species, 15 thalli (2–3 gr, wet weights) were placed inside 9.4-L aquaria filled with seawater collected at the same time as the algal tissue to provide water quality parameters similar to those found in the field. The aquaria (used as static growth chambers) were placed inside 120-L tanks set up in a flow-through system for temperature control. Air stones were placed inside each aquarium for aeration. Temperature was maintained between 28 and 30 °C for the duration of the growth study. Thalli were weighed initially and at the end of the growth study (2–3 days).

In July–August 1999, growth rates were estimated *in situ* for four macroalgal species, *Dictyota pulchella* Hörning *et* Schnetter, *D. cervicornis* Kützing, *Laurencia poiteaui* Lamouroux, and *Halimeda goreauii* Taylor. Algal tissue was collected and placed inside 1-L clear plastic containers. The plastic containers, which had holes punched through the sides to allow for water circulation, were attached to a mooring line at a distance of 50 cm from the bottom. For each species, 15 thalli were placed at one inshore (Bache Shoals) and one offshore (Triumph Reef) site. Thalli were weighed initially and at the end of the growth study (5 days).

For the growth studies, growth was recorded as percent weight change per day using the following formula:

$$\%change = [(wt_{t1} - wt_{t0})/wt_{t0}]/t,$$

where

w_{t0} = initial weight
w_{t1} = final weight
t = time

Grazer Abundance and Grazing Rates

Swimming surveys of the main fish grazers, parrotfishes (Scaridae) and surgeonfishes (Acanthuridae), were performed within 50 m^2 belt transects in July 1998 (n = 6 transects per site). Moving at a slow pace, each transect (2 × 25 m) was surveyed in approximately 3 minutes. All parrotfishes and surgeonfishes found immediately ahead of the moving diver were counted.

In July 1999, fish surveys were carried out in the four initial study sites (Bache Shoals, Elkhorn Reef, Pacific Reef, and Triumph Reef) as well as in three additional sites:

Marker 3 Reef (25°22.408′ N 80°09.667′ W),
Anniversary Reef (25°23.306′ N 80°09.913′ W), and
Long Reef (25°26.690′ N 80°07.150′ W) (Fig. 1).

Grazing assays using the seagrass *Thalassia testudinum* Banks ex König and the macrophyte *Laurencia poiteaui* were done to compare the intensity of fish grazing among sites (Hay 1981). Freshly collected blades of *Thalassia* were cut into 5 cm-long sections and woven into one end of 3-strand nylon rope sections (30 cm long). Pre-weighed sections of *Laurencia poiteaui* were woven into the opposite end of the ropes. Thirty such ropes were placed on the bottom and were collected after 2 hours. The remaining seagrass blades were measured and the ungrazed algal tissue was weighed. Control ropes were also placed on the reefs at the same time to determine the potential changes in algal or seagrass biomass due exclusively to growth or handling. Five control ropes, similar to those ropes used for determining grazing rates, were placed on the bottom inside clear plastic bags to prevent grazing during the assays. Grazing assays were performed in April and August 1998.

The data were examined for conformity to the assumptions of each statistical test prior to analysis. Normality was tested with the Shapiro-Wilk test and homoscedasticity was tested with the Bartlett's test. When assumptions were not met, non-parametric tests were used instead (Sokal and Rohlf 1981).

Results

Physical Environment

Seasonal trends in light and temperature are shown in Figure 2. Mean daily temperatures in the Northern Florida Reef Tract commonly reach minimum values between February and March and maximum values between July and September. In 1998, mean water temperatures exceeded 30 °C on 57 days between July and September, and the maximum water temperature

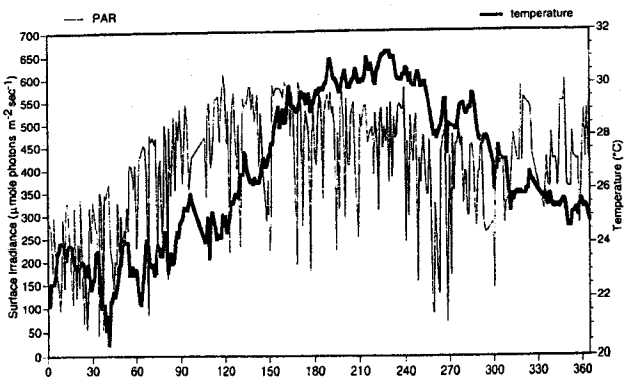


Fig. 2. Mean daily surface irradiance and sea temperatures from the NOAA C-MAN weather station at Molasses Reef, Florida for 1998.

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was 31.3 °C. Maximum values of surface irradiance were recorded between May and August, while lowest values were obtained in January and February.

Algal Biomass and Species Composition

Two genera, *Halimeda* and *Dictyota*, represented the largest proportion (77–99%) of the algal biomass within the reefs sampled (Table I). An exception to this pattern was seen at Elkhorn Reef on May 1998 when two species, *Stypopodium zonale* (Lamouroux) Papenfuss and *Trichogloea requienii* (Montagne) Kützing, underwent a significant bloom. The presence of these species was detected in April 1998 and within a short period of time they monopolized a significant percentage of the bottom (up to 25% cover in May 1998), and represented up to 70% of the total algal biomass within Elkhorn Reef. These species had disappeared by the time of the following biomass survey in August 1998. Similar blooms of *Stypopodium zonale* have been observed on a yearly basis on this reef since 1993 (Lirman, per. obs.).

A general increase in biomass for most algal groups was observed between May and August 1998. However, differences between dates were only significant for a few groups (Table I, Mann Whitney U-test, $p < 0.05$). No significant differences in total algal biomass were found among reefs in May 1998 (Kruskal-Wallis, $p > 0.1$). In August 1998, Pacific Reef had a significantly lower algal biomass compared to the other reefs (Kruskal-Wallis, $p < 0.05$). A power analysis revealed very low power (0.1–0.3) for those comparisons that were not significantly different.

Significant differences in biomass between offshore and inshore reefs were detected only for *Dictyota* spp. in May (higher biomass in offshore reefs), and CTA, ACA and filaments in both May and August (higher biomass in inshore reefs, Kruskal-Wallis, $p < 0.05$, Tukey-Kramer comparisons).

Although there was a general increase in the number of species between the January-May and August surveys, species composition did not differ considerably among sites or season, and no clear inshore-offshore patterns were detected. Species in several genera (i. e., *Halimeda*, *Dictyota*, *Amphiroa*, *Gelidiella*, *Gelidiopsis*, and *Galaxaura*) showed seasonal persistence, and more than half of the species found in the initial surveys were found in subsequent surveys (Table II).

Percent Cover

The percent cover of macroalgae showed an increasing trend from January to July, followed by a subsequent decrease (Fig. 3). Maximum cover for all reefs was observed in July (56.7%, S. E. = 4.6) and minimum levels were observed in December (25.8%, S. E. = 2.6). Significant differences in algal cover were detected between July-October and December (ANOVA, $p > 0.1$, Tukey-Kramer comparisons). When data were grouped by reef type, inshore reefs showed higher, non-significant, percent cover of algae at all times (t-tests, $p > 0.1$).

Macroalgal communities were dominated by turf forms, *Dictyota* spp., *Halimeda* spp, and CCA but the relative cover of algal groups varied throughout the year (Fig. 4). Both turf forms and *Halimeda* spp. showed an inverse relationship with *Dictyota* spp. On all four reefs, the algal community was dominated by turf forms throughout the year, except during the summer, when *Dictyota* spp. became dominant. Filaments, CTA, and ACA groups were minor components of the algal communities in terms of relative bottom cover throughout the year.

Algal Growth

The growth rates of 12 species of macroalgae collected from the Northern Florida Reef Tract and kept

Table I. Mean biomass (gr dry weight/m^2 ± 1 S. E.) of the most abundant macroalgal species or groups within the northern Florida Reef Tract. BS = Bache Schoals, ER = Elkhorn Reef, ER (BR) = Back Reef area on Elkhorn Reef, TR = Triumph Reef, PR = Pacific Reef. CTA = Corticated Terete Algae, ACA = Articulated Calcareous Algae. * = signifcant differences in main biomass between dates with the same reef (Mann-Whitney U-tests, $p < 0.05$). n = 15.

Reef	Date	*Halimeda* spp.	*Dictyota* spp.	CTA	ACA	Filaments	*Stypopodium zonale*	*Trichogloea requienii*	Total
BS	Jan	47.4 (9.7)	0.3 (0.1)	0.64 (0.16)	0.37 (0.16)	0.24 (0.15)	0	0	47.3 (8.6)
BS	Aug	194.7 (89.6)*	12.2 (2.2)*	0.78 (0.26)	0.64 (0.25)	0.03 (0.01)	0	0	206.3 (99.2)*
ER	May	35.3 (7.3)	7.5 (2.3)	0.21 (0.05)	2.30 (9.75)	1.25 (0.63)	46.8 (20.0)	0	90.3 (22.2)
ER	Aug	33.9 (14.8)	8.2 (2.6)	1.99 (1.03)	2.74 (0.78)	0.53 (0.50)	0	0	44.2 (13.1)*
ER(BR)	May	33.9 (15.3)	5.1 (1.6)	0.37 (0.20)	0.07 (0.07)	0.14 (0.05)	13.0 (6.3)	23.7 (9.4)	43.2 (24.3)
ER(BR)	Aug	185.1 (32.5)*	2.4 (2.0)	0.20 (0.10)	0.18 (0.14)	0.68 (0.55)	0	0	186.7 (32.6)
TR	May	142.4 (59.6)	8.3 (1.3)	0.33 (0.20)	0.12 (0.05)	0.21 (0.07)	0	0	153.4 (59.1)
TR	Aug	258.6 (92.9)	19.7 (5.2)*	0.41 (0.12)	0.34 (0.12)	0	0	0	284.3 (95.3)
PR	May	47.2 (16.0)	9.7 (1.9)	0.33 (0.05)	0.23 (0.04)	0.09 (0.05)	0	0	56.3 (17.5)
PR	Aug	17.5 (17.5)	20.4 (1.4)*	0.10 (0.05)*	0.45 (0.34)	0.02 (0.02)	0	0	38.2 (18.2)

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in 9.4-L aquaria at the microcosm facility at the University of Miami ranged from 0.6% to 5.6% (% daily change in biomass, Table III). Brown algae, including *Stypopodium zonale* (5.65%) and *Dictyota* spp. (3.1–4.9%) had the fastest growth rates. Among the red algae, *Champia parvula* (Agardh) Harvey had the fastest growth rates (5.0%).

The growth rates measured *in situ* for *Dictyota pulchella*, *D. cervicornis*, *Laurencia poiteaui*, and *Halimeda goreauii* compared favorably with those measured for the same species in the microcosm growth studies as no significant differences between growth rates were found (t-tests, $p > 0.05$, Table III). Moreover, no significant differences in growth rates were found between thalli of the same species placed at inshore and offshore reefs (t-tests, $p > 0.1$).

Table II. Macroalgal species present within 0.25 m^2 quadrats sampled on four Florida reefs at two different times of the year (n = 15 quadrats per site). Bache Shoals was sampled in February 1998 and all other reefs in May 1998. All reefs were sampled in August 1998. • = present in survey.

Marcroalgal Species	Feb–May	August
Green algae		
Halimeda goreauii Taylor	•	•
Halimeda tuna (Ellis and Solander) Lamouroux	•	•
Halimeda opuntia (Linnaeus) Lamouroux	•	•
Halimeda opuntia f. triloba (Decaisne) Barton	•	•
Halimeda discoidea Decaisne		•
Halimeda simulans Howe		•
Caulerpa sp.		•
Cladophora sp.	•	
Red algae		
Amphiroa fragilissima (Linnaeus) Lamouroux	•	•
Amphiroa tribulus (Ellis ans Solander) Lamouroux	•	•
Amphiroa rigida f. antillana Børgesen	•	•
Gelidiopsis intricata (Agardh) Vickers	•	•
Gelidiopsis variabilis (Agardh) Schmitz		•
Gelidiella acerosa (Forsskål) Feldmann and Hamel	•	•
Gelidium floridanum Taylor	•	
Laurencia poiteaui (Lamouroux) Howe	•	•
Laurencia corallopsis (Montagne) Howe		•
Laurencia sp.		•
Hypnea spinella (Agardh) Kützing	•	•
Botrycladia pyriformis (Børgesen) Kylin	•	
Champia parvula (Agardh) Harvey	•	•
Jania adhaerens Lamouroux	•	•
Trichogloea requienii (Montagne) Kützing	•	•
Acanthophora spicifera (Vahl) Børgesen		•
Polysiphonia sp.		•
Galaxaura obtusata (Ellis and Solander) Lamouroux		•
Liagora farinosa Lamouroux		•
Murrayella periclados (Agardh) Schmitz		•
Centrocerus sp.		•
Brown algae		
Dictyota pulchella Hörning and Schnetter	•	•
Dictyota bartayresiana Lamouroux	•	•
Dictyopteris deliculata Lamouroux	•	
Dictyota cervicornis Kützing	•	
Stypopodium zonale (Lamouroux) Papenfuss		•

Grazer Abundance

Significant differences in the mean abundance of herbivorous fishes were detected (Table IV). In 1998 and 1999, offshore reefs had a significantly higher abundance of surgeonfishes compared to inshore reefs (ANOVA, $p < 0.05$, Tukey-Kramer comparisons). In 1999, the mean abundance of parrotfishes was significantly higher on inshore reefs compared to offshore reefs (ANOVA, $p < 0.05$, Tukey-Kramer comparisons). Whereas the mean abundance of surgeonfishes did not show any significant changes between 1998 and 1999, the mean abundance of parrotfishes showed significant increases between 1998 and 1999, reaching a maximum mean abundance of 72 individuals.m^{-1} on Bache Shoals (Table IV). The abundance of the sea urchin *Diadema antillarum* Philippi was extremely low in the area surveyed. Only 2 juveniles (< 3 cm in test diameter) were found on Elkhorn Reef in 1998, and no other individuals were found on any of the other reefs.

No significant correlations were found between percent cover of macroalgae and mean fish grazer abundance in 1998 ($r = -0.03$, $p > 0.1$) or 1999 ($r = -0.3$, $p > 0.1$). Moreover, in reefs such as Bache Shoals and Elkhorn Reef, no significant changes in mean algal cover were detected between 1998 and 1999 (t-test, $p > 0.1$) even when the mean abundance of herbivorous fishes in 1999 was more than what was recorded in 1998 (Table IV).

Grazing Rates

A comparison of the biomass of *Thalassia* and *Laurencia* on control ropes before and after the graz-

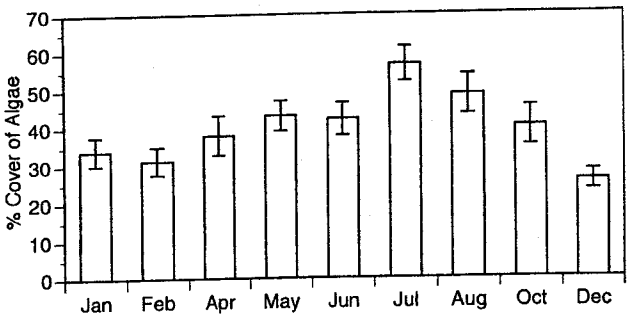


Fig. 3. Mean percent cover of macroalgae (± S. E.) on reefs of the Northern Florida Reef Tract. Only Bache Shoals was sampled in January and February. Only Triumph and Elkhorn Reefs were sampled in April and October. All four reefs were sampled in all remaining times. n = 35 photo-quadrats per site.

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ing assays showed that changes due to handling or growth were not significant (t-tests, $p > 0.1$). Grazing rates, as estimated by the grazing assays, were significantly different among reefs and between seasons (2-Way ANOVA, $p < 0.05$, Table V). Consumption of *Thalassia* and *Laurencia* was significantly higher on offshore reefs compared to inshore reefs. Although season had a significant effect on consumption rates, *Thalassia* and *Laurencia* assays exhibited different seasonal responses. Whereas consumption of *Thalassia* was significantly higher in August than in April, the opposite results where obtained for *Laurencia*, which registered higher losses due to grazing in April than in August. No significant interactions were found between reef type and season ($p > 0.05$). The highest consumption rates for both species were found on Pacific Reef in April 1998 (ANOVA, $p < 0.05$, Tukey-Kramer comparisons). No significant correlation was found between consumption rates and biomass of *L. poiteaui* on reefs in August ($r = 0.18$, $p > 0.05$). Lastly, a significant correlation was only found between *Thalassia* grazing rates and the abundance of surgeonfishes in Summer 1998 ($r = 0.95$, $p < 0.05$).

Discussion

The macroalgal communities of the Northern Florida Reef Tract showed marked seasonal dynamics; algal biomass and percent cover, which were at their lowest levels in winter, increased as both water temperature and light levels increased. Peak abundance and biomass, specially of *Dictyota* spp., were found between July and August when it reached 56.7% cover, followed by subsequent declines. The decline that took place in the later part of the year was correlated with high temperatures that exceeded 30 °C as well as a decline in light availability. Negative effects of high temperatures on Florida macrophytes were previously reported by Dawes *et al.* (1976), Josselyn (1977), and Mathieson and Dawes (1986).

Different algal groups dominated the algal communities at different times of the year. *Dictyota* spp. exhibited highest relative abundance during the summer months when they were found growing not only on the bottom but overtopping corals and other types of algae such as *Halimeda* spp. as well. Similar space monopolization was observed during the bloom of two algal species (*Stypopodium zonale* and *Trichog-*

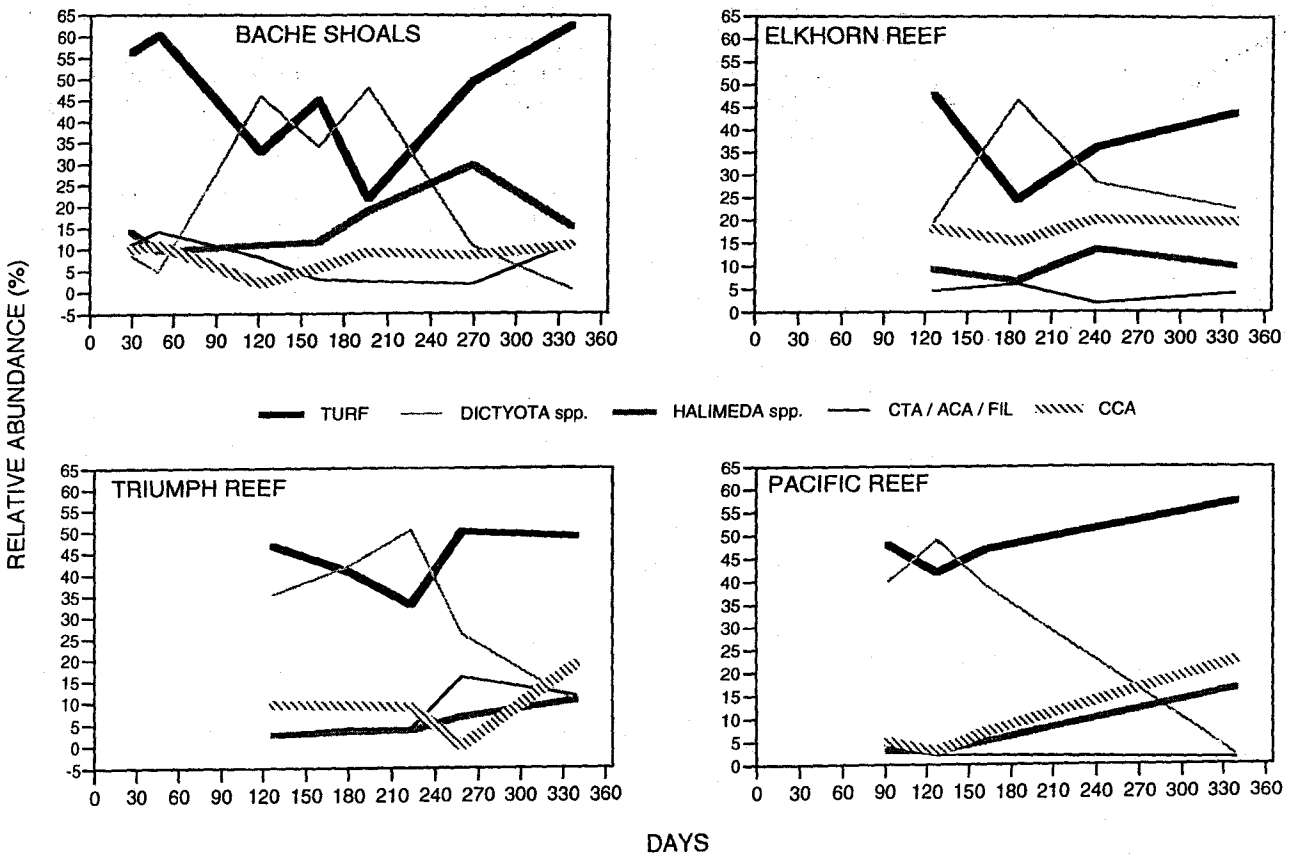


Fig. 4. Seasonal abundance of different macroalgal groups expressed as mean relative percent cover (i. e., number of points occupied by a given group divided by the total number of points within each photograph occupied by macroalgae). TURF = filamentous forms of algae with canopy < 1 cm), FIL = filaments with canopy > 1 cm, CTA = corticated terete algae (e. g., *Laurencia* spp., *Acanthophora* spp.), ACA = articulated calcareous algae (e. g., *Amphiroa* spp., *Jania* spp.), and CCA = crustose coralline algae. n = 35 photo-quadrats were surveyed from each site.

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loea requienii) that lasted three months and completely covered small corals. The species that exhibited rapid space monopolization on Florida reefs, such as *Dictyota* spp. and *Stypopodium zonale*, also showed rapid growth in microcosm and field growth studies. Summer blooms were reported previously for another species, *Codium isthmocladum* Vickers, on Florida reefs where it reached up to 100% cover over large areas (Lapointe 1997).

Table III. Growth rates (± S. E.) of dominant macroalgae from the northern Florida Reef Tract expressed as % increase in weight per day. n = 15.

Macroalgal Species	Growth (% per day)	
	Micro-cosms	Field
Brown algae		
Stypopodium zonale	5.6 (0.6)	
Dictyota pulchella	4.9 (1.5)	4.0 (1.0)
Dictyota bartayresiana	3.7 (0.9)	
Dictyota cervicornis	3.1 (0.5)	3.8 (1.1)
Sargassum platycarpum Montagne	0.8 (0.2)	
Red algae		
Champia parvula	5.0 (0.3)	
Laurencia poiteaui	2.8 (0.5)	3.4 (0.7)
Laurencia papillosa (Agardh) Greville	1.7 (0.3)	
Trichogloea requienii	1.1 (0.3)	
Hypnea spinella	0.8 (0.3)	
Galaxaura obtusata	0.6 (0.1)	
Green algae		
Halimeda goreauii	1.3 (0.4)	1.5 (0.5)

Numerous studies of herbivory on reefs have documented that macrograzers (i. e., fishes and urchins) can have an overriding influence on the abundance and composition of algal communities (Wanders 1977, Littler and Littler 1984, Hay 1985, Lewis 1986, Carpenter 1986, Lessios 1988, Morrison 1988, Hughes 1994, Hixon and Brostoff 1996). In this study, however, several lines of evidence indicate a less influential role of herbivorous fishes at the present time. These findings include: a) a general lack of correlation was found between algal community attributes (i. e., biomass and percent cover) and abundance and consumption rates of fish grazers, b) peaks in algal biomass and percent cover were observed at a time of the year when fish grazing rates are commonly highest (Schmitt 1997), and c) no significant differences in algal cover were detected between 1998 and 1999, even when the number of fish grazers nearly doubled. A similar lack of correlation between herbivorous fish abundance and percent cover of different algal groups was also reported by Schmitt (1997) for the Florida Keys.

These findings suggest that present grazing levels are insufficient to offset algal growth and prevent

Table IV. Mean abundance (± 1 S. E.) of herbivorous fishes determined by swimming visual counts within 50-m^2 belt transects. N = 6 transects per site. nd = no data vailable.

	Study sites	July 1998		July 1999	
		Parrotfishes	Surgeonfisches	Parrotfishes	Surgeonfisches
Inshore	Bache Shoals	36.0 (6.6)	9.2 (1.3)	72.0 (9.05)	6.2 (1.5)
	Anniversary Reef	nd	nd	55.2 (7.5)	7.8 (3.5)
	Marker 3 Reef	nd	nd	54.5 (1.0)	10.0 (1.4)
	Elkhorn Reef	13.2 (2.6)	9.5 (1.2)	40.0 (1.0)	8.2 (1.6)
Offshore	Triumph Reef	11.3 (2.6)	14.2 (1.3)	19.5 (3.6)	12.2 (1.9)
	Long Reef	nd	nd	13.6 (2.1)	17.2 (2.3)
	Pacific Reef	14.0 (1.6)	15.2 (1.7)	30.6 (5.3)	15.4 (3.3)

Table V. Mean proportion (± 1 S. E.) of *Thalassia testudinum* and *Laurencia poiteaui* consumed by herbivorous fishes during 2-hour assays. n = 30.

Reefs	*Thalassia*		*Laurencia*	
	Apr-98	Aug-98	Apr-98	Aug-98
Bache Shoals	0.33 (0.02)	0.61 (0.09)	0.33 (0.05)	0.12 (0.06)
Elkhorn	0.18 (0.06)	0.64 (0.15)	0.42 (0.06)	0.45 (0.10)
Triumph	0.49 (0.11)	0.98 (0.01)	0.20 (0.05)	0.41 (0.06)
Pacific	0.85 (0.07)	0.91 (0.04)	0.69 (0.05)	0.44 (0.07)
All Reefs	0.45 (0.05)	0.80 (0.07)	0.39 (0.03)	0.33 (0.06)

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macroalgal space monopolization. This space monopolization is especially evident for algae such as *Dictyota* spp., *Stypopodium zonale*, *Trichogloea requienii*, and *Halimeda* spp. that contain structural and chemical defenses documented to deter fish grazing (Littler *et al.* 1983, Hay 1992, 1997, Paul 1992). In contrast, biomass and percent cover of other algal types commonly consumed by fish grazers such as filamentous or corticated terete algae (CTA) were low throughout the year (Hay 1981, 1984, Littler *et al.* 1983, Paul and Hay 1986). Although historical data are lacking for the area, several studies have documented that, unlike parrot fishes and surgeon fishes, the sea urchin *Diadema antillarum*, which experienced a region-wide decline starting in 1983, readily consumed *Dictyota* and *Halimeda*, the two genera that now reach high abundance and biomass on Florida Reefs (Hay and Taylor 1985, Lessios 1988, Morrison 1988). Hay and Taylor (1985) also arrived to the similar conclusion that herbivorous fishes are not able to control erect macroalgal abundance in the absence of *Diadema*.

Corals are in continuous contact with macroalgae along colony margins as they grow side by side on Florida reefs. The outcome of competition between these two dissimilar groups will be determined by their growth characteristics as well as their competitive abilities. Given the fast growth rates of algae documented in this study, this group can prove a superior competitor for space on Florida reefs under favorable environmental conditions. Although grazers have controlled algal abundance historically, the major changes that have taken place over the last two decades may have limited their influence. The regional demise of the sea urchin *Diadema antillarum*, as well as potential increased nutrient inputs from human activities, may have resulted in the present conditions of algal overgrowth that may be threatening reef communities of the Florida Reef Tract (Carpenter 1990, Lapointe and Clark 1992, Hughes 1994, Szmant and Forrester 1996, Lapointe 1997, Bryant *et al.* 1998). In 1998, *Dictyota* spp. and *Halimeda* spp. exhibited a summer peak in biomass and percent cover that resulted in many corals being overtopped by dense algal mats. Given the lack of historical data for the region, it is extremely important to determine whether the documented seasonal dynamics are regular events, and to evaluate their potential effects on the long-term persistence of these reef communities.

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move across the area. Blair et al. (1994) found significantly more damage on deeper areas of the reefs after hurricane Andrew with significant movement of sediment across all reefs surveyed. This suggests that episodic storm events can have a significant impact on coral populations at a given site via sediment disturbance and abrasion without distinctness of long-term mean sedimentation.

not sure what you are saying here!

The sediment nutrient levels we reported here are somewhat higher than those reported for other reefs in the Florida Keys and around the Caribbean (Szmant and Forrester, 1996 and references therein). This may be due to a different source of sediments. The other studies analyzed sediment cores from areas of accumulated sediments on the reef. The sediments analyzed in this study were deposited in sediment traps approximately 1 m above the reef surface, and likely were composed of both resuspended reef sediments as well as some portion of imported sediment, possibly of terrestrial origin. Indeed, the nitrogen gradient in these sediments may be due to relatively greater contribution by terrigenous sediments at the nearshore sites.

good point

In any case, the only environmental factor examined in this study that we could determine to correspond with spatial patterns of reef community distribution in Biscayne National Park was sediment quality (size and nutrient content), though other physical factors that we did not measure (such as energy regime) are no doubt important. The best explanation may have to do with a combination of high energy sediment scour as well as biotic factors such as high grazing mortality (Miller et. al., in press) that prevent small corals from growing up. The factors preventing reef development at the northern offshore sites remain somewhat enigmatic.

inshore versus offshore sites might make sense in terms of the greater energy regimes offshore filtering off the fine sediments allowing them to accumulate inshore) it is not clear whether this result can help explain the depauperateness of coral populations at the offshore sites. That is, it is not clear whether or why fine sediments should be more favorable to corals than coarser sediments. It may be that the abrasive effects of larger particles in the higher energy regimes of the offshore sites are detrimental or that fine sediments (especially nitrogen-rich ones) are beneficial to corals as a food source. It should be noted that the chronic mean levels of sediment accumulation we measured at the reef sites in this study of around 1.75 to 3.5 mg/cm^2/day are substantially below the threshold of 10 mg/cm^2/day suggested by Rogers (1990) as representing stressful levels of sedimentation for reef corals.

The data from the sediment traps show ~~that there is~~ no clear spatial pattern in chronic sedimentation levels, even to distinguish Soldier Key. These chronic levels ranged up to about 400 mg/trap/day or 8.6 mg/cm^2/day which is still below the 10 mg/cm^2/day threshold proposed by Rogers (1990). However, offshore sites seem to experience greater sediment deposition during extreme storm events (and perhaps periods of more easterly winds) and these factors may represent a source of mortality for (especially juvenile) corals. We did observe partial burial and scour of coral colonies at Triumph reef after Tropical Storm Gordon. Small colonies may be more susceptible to mortality due to sediment abrasion and/or burial during storms since most of the colony surface may be affected making the probability of recovery is low.

Why? What is the potential source?

Hurricane damage to reefs can vary from severe (Rogers et al., 1982, Woodley et al., 1981) to moderate (Rogers et al., 1983; Fenner, 1991) and the degree of damage might be more of a function of the time since the previous storm (Kjerfve et al., 1986) and the length of time ~~it spends~~ over the area. For example, Tropical storm Gordon was a weak storm compared to hurricane Andrew, however, it produced far more damage over the 5 days ~~it expended~~ close to the Florida coast and BNP reefs than Andrew ~~in its fast~~

tropical storm days.

interval where storm

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Low cover and small colony sizes (Miller et al., in press) of most scleractinian species in BNP (especially offshore bank reef sites) may imply that partial mortality rates are high and/or colony growth rates are low. This suggests that corals are experiencing physiological stress (e.g., decreased photosynthesis of zooxanthellae), weakened defense mechanisms to diseases, reduced sediment-cleaning efficiency and feeding capacities) due to some environmental variable(s). However, the environmental parameters hypothesized to affect coral community structure in this study (temperature, sedimentation, nutrient regime) do not coincide with expectations based on community structure. For example, while the temperature data help explain a general lack of coral cover and of significant reef development at Soldier Key, they show the opposite pattern from that which would help explain greater coral cover, diversity and reef development on the nearshore patch reefs versus the offshore reefs. That is, temperature regimes are more, not less, stressful at these nearshore sites. Similarly, the lack of discernable spatial pattern in the water column nutrient data provide no insight into possible effects on benthic community structure. Long-term means are in the ranges expected for subtropical reef areas (Szmant & Forrester, 1996).

Stress due to winter cold temperature has been documented as impacting the Florida reef tract via plumes eminating from Florida Bay (Walker et al., 1982). It is possible that similar limitation of reef development by outflow of Biscayne Bay water occurs in the Biscayne National Park area as suggested by Burns (1985). Offshore reefs on the other hand, may be affected by the occasional cold water counter current plume coming down from Fort Lauderdale and extending as far south as Triumph or Pacific reef sites (Ginsburg, 1956).

Results for sediment accumulation further confirm the uniqueness of Soldier Key among the sites examined in this study, but do not provide any further distinction along spatial gradients. While the distinctive size distributions of accumulating sediments at

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NUTRIENT EFFECTS ON CORAL REEFS: A HYPOTHESIS ON THE IMPORTANCE OF TOPOGRAPHIC AND TROPHIC COMPLEXITY TO REEF NUTRIENT DYNAMICS

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ABSTRACT

Quantitative aspects of nutrient dynamics on coral reefs are poorly understood. Gaining such understanding is critical since nutrification is a main anthropogenic threat to reef health. In some areas, nutrient sources impacting reefs are obvious, but for others we lack information on natural nutrient sources and processes, and confounding factors such as over-fishing or grazer die-offs make attribution much more difficult. We are in need of a more integrative understanding of factors that regulate and affect nutrient dynamics on coral reefs. This paper presents a hypothesis regarding the importance of (1) habitat complexity and (2) intact trophic pathways to the nutrient flux rates tolerated by coral reef ecosystems without major shifts in dominance from corals to algae. It predicts that coral reef communities have the ability to utilize and benefit from higher fluxes of nutrients than are generally recognized, without changing to algal-dominated systems, if (a) there is sufficient habitat complexity to provide shelter for large numbers of grazers and a diversity of consumers, and (b) the major trophic groups of fishes and invertebrates have not been impacted by fishing, disease or other disturbance. It further predicts that alterations in community and trophic structure that result from overfishing can result in generalized coral reef deterioration, that at times may be indistinguishable from increased nutrient supply.

INTRODUCTION

Despite decades of interest and effort by coral reef scientists, functional level nutrient dynamics on coral reefs remain poorly studied. Gaining a better quantitative understanding of such aspects at this time is critical since nutrification is widely considered one of the main anthropogenic threats to reef health (Pastorok and Bilyard 1985; Birkeland 1988a,b; Wells and Roberts 1993). The dramatic case of Kaneohe Bay, Hawaii, in the late 1960's through 1970's, where sewage discharge resulted in the algal overgrowth and death of most of the coral reefs in the southern bay (Smith et al. 1981), alerted scientists and managers to the severe impact humans can have on coral reefs *via* increased nutrient inputs. In the aftermath of Kaneohe Bay, recent observations of widespread algal over-growth of corals and algal diseases are also being attributed to anthropogenic nutrification (e.g. Lapointe 1989; Shinn 1989; Hallock et al. 1993), even where significant local nutrient sources have not been demonstrated and natural nutrient sources and other processes, such as grazing dynamics, are unknown. Many of these reports ignore or fail to recognize the significance of confounding factors such as over-fishing or grazer die-offs (*e.g. Diadema;* Hughes 1994). The general concern over anthropogenic nutrients gave rise to project ENCORE on the Great Barrier Reef, a multi-disciplinary study of the effects of nutrient enrichment on coral reefs (Steven and Larkum 1993). However, after one year of daily nutrient addition to 10 times ambient concentrations, ENCORE researchers were hard-put to measure any significant response by enriched algal communities (Larkum and Steven, personal communications). Thus, we are in need of a more integrative understanding of factors that regulate and affect nutrient and algal dynamics on coral reefs.

Coral reefs are generally found in waters with much lower nutrient concentrations than those of temperate coastal systems, and have many features that we interpret as adaptations to low nutrient conditions (D'Elia 1988; Smith 1988; D'Elia and Wiebe 1990). Increasing nutrient concentrations with higher latitude have been invoked as a major factor limiting the latitudinal distribution of coral reefs (Johannes et al 1983), and persistent upwelling as a factor limiting the development of coral reefs in otherwise suitable areas (Hallock and Schlager 1986). While there is no doubt that persistent high concentrations and fluxes of nutrients will favor dominance by algae over corals, the literature reveals that coral reefs have both formed and thrived under much higher nutrient conditions than generally recognized (Table 1; also see summary for Houtman Abrolhos by Hatcher and Collins 1993). The question is, then: What are the factors that have allowed those reefs to form under what some present investigators consider nutrient-polluted water quality conditions (Tomascik and Sander 1985, Bell 1992)? I suggest that the answer to this question is the presence of both (a) sufficient habitat for consumers (high topographic complexity), and (b)intact, complex food webs. I present here a synthetic hypothesis on the functional aspects of nutrient processing by coral reef communities, that hopefully will foster more integrated studies of nutrients on coral reefs. Given the space limitations of the proceedings, I've unfortunately had to limit the number of literature citations; the ideas I present here are synthesized from a large number of published works by a large number of investigators; my contribution, I hope, is the integration across disciplines.

Table 1: Examples of areas with elevated nutrients that formed Holocene reefs. The threshold limits for eutrophication proposed by Bell (1992) are included at the bottom. DIN= dissolved inorganic N. Concentrations in µM

AREA	NO_3	NH_4	DON	PO_4
Palau	0.2-1.0			0.1-0.2
Lizard Island	0.7	0.2-0.3	4-5	0.3- 0.6
N GBR	2			
Canton	2.6	1		0.6
Tarawa	2-3	0.3	9.4	0.4
Yap	0.2-0.35	1.2-1.4	4.5	0.1- 0.2
Gulf of Panama				0.5->2
St. Croix	0.5	0.76	6.6	
Bell(1992)	≥ 1.0 DIN			0.1

PRESENT PARADIGM

One of the generally held popular paradigms regarding coral-reef nutrient dynamics is that coral reefs are adapted to "low" nutrient conditions, and that ANY increase in nutrient flux (or concentration) will result in coral reef deterioration (e.g. Hallock et al. 1993; newspaper and magazine articles too numerous to cite). One problem that surfaces in management issues is to define the upper limits of this LOW concentration range, and Bell (1992) has proposed that these are 1 µM dissolved inorganic N (DIN) and 0.1 µM soluble reactive phosphate. The origin of this popular view derives from studies of coral reef gross and net productivity, mostly from work on reef flats and lagoons of a few mid-oceanic atolls where P/R was estimated to be ≈ 1 (net P ≈ 0)(reviewed in Hatcher 1988; Smith 1988; D'Elia 1988; D'Elia and Wiebe 1990). When net production ≤ 0, efficient recycling can account for all of the nutrient requirements of a reef system, and outside nutrient sources are not needed to support high levels of gross production (Smith 1983). The problem is that such views have been generalized to whole reef systems, and to coral reefs world-wide. It is not surprising that atoll lagoons have a P/R ≤ 1, and are heterotrophically dependent on inputs from surrounding reefs or oceans, but it is not clear that forereef areas should be expected to be functionally similar to such lagoons and reef flats. Other factors to consider are that continental and high-island reefs differ significantly from atolls with regard to their potential for terrestrial nutrient inputs (Littler et al.1991), and that the nutritional input to coral reefs *via* import of particulates by planktivores has not been included in most nutrient budgets. The export of organics from coral reefs to oceanic and coastal waters is also poorly studied, and an important determinant of nutrient requirements and tolerances. Furthermore, Smith (1983) shows that even for atoll lagoons, increased nutrient supplies (e.g. upwelling) result in higher gross and net production.

Another short-coming of our present view of nutrients and coral reefs is that nutrient cycling, net production, P/R ratios and anthropogenic effects have been mostly considered from the 'production' (bottom up) end of things, even though it is well accepted that most of the primary production is normally rapidly transferred to consumer pathways (i.e. top-down control by high grazing rates; Lewis 1986; Hatcher 1988, 1990). For instance, increases in algal biomass are generally viewed as signs of increases in nutrient supply (Lapointe 1989; Shinn 1989; Hallock et al. 1993), when in fact they could just as well be symptomatic of decreases in grazing (e.g. aftermath of the *Diadema* die-off; Hughes 1994). Furthermore, estimates of nutrient requirements and sufficiency based on the scaling of elemental ratios for production have mostly considered the larger primary producers (Atkinson and Smith 1983; Atkinson 1988), primarily turf and macroalgae with high C:N:P ratios of ≥500:30:1, and not those of zooxanthellae with ratios similar to the Redfield ratio (106:16:1) or those of the consumers such as fishes, which have low C:N ratios of ca. 4:1. Studies of coral reef nutrient dynamics should consider the factors that determine how much consumption of primary production a coral reef can accommodate, and the nutrient requirements of the consumers.

NEW SYNTHESIS

The ideological foundation of the model of nutrient dynamics that I present here is that the inherently high topographic complexity [m^2 of total area/m^2 of planar area] of coral reefs is essential to their ability to acquire and retain nutrients, maintain high levels of gross production and consumption, and maintain coral dominance over algae, especially under moderately elevated nutrient fluxes. High topographic complexity provides the habitat for coral reefs to accommodate highly complex food chains that contribute to relatively low levels of net community production in spite of high levels of gross production.

The essence of habitat complexity are the massive and branching scleractinian corals. Coral skeletons, live and dead, modified by bioerosion, provide the habitat for the rest of the reef community. The amount and types of corals, and their health, will in turn be dependent on a diversity of reef consumers, especially herbivores, that keep algal biomass under control (Birkeland 1988a,b; Done 1992).

The first topic that merits revisiting is that of the nutrient conditions under which healthy coral reefs can exist. The issue of nutrient concentration vs flux is fundamental to the problem, but a difficult one to address logistically. The measurement of nutrient concentrations is relatively simple and inexpensive compared to that of estimating the hydrodynamic parameters needed to calculate fluxes. However, the common and acceptable assumption is that under any given flow regime, higher nutrient concentrations will result in higher nutrient fluxes. While coral reef nutrient concentrations are definitely low compared to temperate estuarine conditions (earlier references), they are not always as low as many people think (Table 1). Coral reefs on the Pacific coast of Panama experience both elevated nutrients (PO_4> 2 µM; D'Croz et al. 1991) as well as lowered temperatures, as do reefs off upwelling zones such as the coast of Oman, Houtman Abrolhos, Canton, Fanning and Tarawa (Smith and Jokiel 1978; Kimmerer and Walsh 1981; Hatcher and Collins 1993; and others). Mechanisms that induce upwelling are numerous and common in reef areas. Upwelling mostly occurs along the outer shelf margins, but nutrients can move onto narrow or even wider shelves (e.g. Halimeda banks behind outer ribbon reefs in GBR; Marshall and Davies 1988). Since many of these events may be episodic and of short duration, they are easily missed during expeditionary sampling programs.

Given the few reefs that have been studied, more reefs in naturally high nutrient conditions will be recognized, especially in continental and upwelling areas. Continental and high-island reefs also have higher potential nutrient inputs from terrestrial sources, including ground water percolation and runoff, and bird colonies can also enrich especially with PO_4 (Smith and Johnson 1995).

Even in areas where the dissolved inorganic nutrient concentrations are low most of the time, there are significant levels of dissolved organic and particulate nutrients (PN) in waters flowing unto reefs, that can be incorporated by reef microbes (Moriarty et al. 1985). The contribution of PN is especially under-recognized: large schools of planktivorous fishes line the forereefs day and night capturing both incoming and outgoing particles (Williams and Hatcher 1983; Hamner et al. 1988). These fishes are important prey for larger fishes, and their feces have a high trophic value for benthic feeding invertebrates and fishes (Robertson 1982; Williams and Hatcher 1983; Rothans and Miller 1991). High densities of small planktivores require the abundant shelter from predation that high-complexity coral reefs provide.

Once nutrients are 'captured' by reefs, recycling is important to their continued availability to reef primary producers. The symbiosis of invertebrates and microalgae is well studied. However, there are many other biotic and abiotic pathways of recycling, for example storm resuspension of sediment nutrients, which can make re-available both nutrients stored in forereef sediments, and nutrients in lagoonal deposits leeward of the reef (Smith 1988; Szmant and Forrester 1996). Biotic pathways include mechanisms such as upstream transport of nutrients by fish schools during feeding migrations (Meyer and Schultz 1985).

Most of reef production is by benthic turfs, pockets of macroalgae, and algal endosymbionts (Odum and Odum 1955; Adey and Steneck 1985; Hatcher 1988). When nutrient concentrations of incoming waters are moderately high, reef producers can take up nutrients directly from the water column, and new reef production results. The ability of reef algae to remove nutrients from the lowest oceanic nutrient concentrations is poorly studied, but it can be expected that little net uptake will occur, and that primary production will be (e.g. Hanisak 1983; Fig. 1a,b). Nutrient concentrations close to the benthos are higher than those in incoming oceanic waters because of efflux from sediment nutrients and excretion from benthic fauna (Szmant-Froelich 1983, Szmant and Forrester 1996), and benthic nutrients are likely the direct source of nutrients to reef producers when incoming concentrations are low (Williams 1984, McGlathery et al. 1992). Resulting production is, however, recycled, not new, production. Flow rate will affect nutrient uptake by decreasing the thickness of the diffusional boundary layer over the algal surface, and increasing the uptake rate at low and intermediate nutrient concentrations (Carpenter and Williams 1993; Fig. 1a).

Increased production with increased nutrient concentration will likely first occur by increased growth rates of normal reef algae, but eventually competitive interactions between algal groups should result in high-nutrient adapted (=nutriphilic) species replacing normal reef species, and thus shifts in algal community composition (Fig. 1b). Grazing pressure will affect these community shifts (Littler and Littler 1985, Birkeland 1988b), but there are few quantitative studies on this topic.

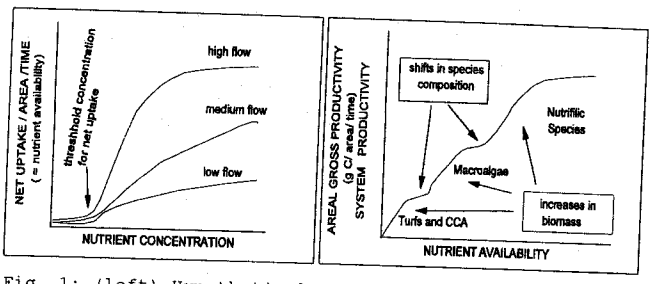


Fig. 1: (left) Hypothetical relationship between nutrient concentration, advective flow and nutrient availability. (right) Hypothetical effect of nutrient flux on primary production and algal community composition.

Re-examination of coral reef productivity data summarized by Kinsey (1985) shows that GPP (gross primary production) per area of reef or lagoon can vary by a factor of 2 to 3 (from 2.3 to 6.0). The striking feature of the data is how the consumption rates of those reef systems were able to increase in pace with the level of production, so that the estimated P/R and E (excess or net community production) was reportedly always near 1.0 and ca. 0, respectively!!!

So, how does one explain the proportional increases in primary production (P) and consumer abundances (R) on those coral reefs? Differences in nutrient fluxes are obviously partially responsible for the differences in primary production between reefs, but I suggest that the topographic complexity (=surface area) of those reefs allowed their producer communities to respond to the increased nutrient availability, and their consumer communities to respond to the increased primary production. Adey and Steneck (1985) and others have demonstrated a correlation between reef topography and GPP, and Grigg

studies (Smith, 1992; Chiappone & Sullivan, 1996; Miller et al., in press) does not support the hypothesis that recruitment limitation is a cause of the depauperateness of coral communities in certain Florida reefs and suggest that high mortality of juveniles and not low recruitment might be determinant in the development of the coral community structure in these marginal areas (Miller et. al., in press). This relatively high input of sexually produced recruits into the populations may be the result of one or two years of successful reproduction and recruitment, however. Our findings also contradict Porter and Meier (1992) report of no recruitment of broadcasting species over several years in two localities in BNP.

The diversity of zooxanthellate scleractinians and sponges compares well with more tropical coral reefs systems (i.e Puerto Rico) but are still below those observed in well developed reef areas in the southern and western Caribbean [i.e. Jamaica (Wells and Lang, 1973); Curacao (Bak, 1974); Venezuela (Weil, 1985, in press); Panama (Weil and Jackson, unpubl. data); Colombia, (Von Prahl & Erhardt; 1985; Zea, 1987). A new record for the Florida area was the crustose-massive species *Madracis senaria.* In our transects, it was found only at Pacific reef at 10 m depth but we found it to be common in deeper reef areas to the south (Key Largo Dry Rocks and Conch reef) and shallow reefal areas to the north (Ft. Lauderdale). This species was believed to be endemic to Jamaica (Wells, 1973), but it has been reported or observed all over the southern (Venezuela, Bonaire, Curacao) and western (Panama) Caribbean as well as in coral reefs of the Bahamas and Puerto Rico (Bak, 1984; Weil, 1985; Weil and Jackson, unpub. data; Weil, in press). *Porites "branneri"*, a small crustose species reported by Burns (1985) as common on some of the offshore localities in BNP, is a misidentification. *P. branneri* is likely to be endemic to Brazil and what has been reported for the southern Caribbean as *P. "branneri"* is probably a different taxon (Weil, 1992a, b). The colonies that Burns (1985) reports as *P. "branneri"* in BNP are blue crustose morphs of *P. porites* growing in exposed reef platforms. The blue coloration might be produced by a UV-light reflection from UV-protection pigments produced by the polyp.

(1994), and others have shown that fish numbers and diversity increase in proportion to complexity measures. While fish are critical contributors to reef trophodynamics, they are but one small part of a reef's consumer community. Macro- and micro- invertebrates, meiofauna and microbial populations also increase as a function of habitat complexity, and are quantitatively a greater proportion of the consumer biomass than are fishes (Johnson et al. 1995).

The major tenet of the proposed conceptual nutrient dynamics model is that nutrient and carbon cycling are dependent on how reef topographic complexity influences the relative and absolute abundances of primary producers and consumers (Fig. 2). As the complexity increases, up to some maximum, more canopies of producers (∴ more algae to take up nutrients) can co-exist, and more reef substrate is available for infaunal and epifaunal consumer groups to inhabit (∴ more trophic complexity). Therefore, GPP will be a function of both allocotonous nutrient supply and of surface area for algal growth, while consumption will be a function of primary production and of habitat for shelter.

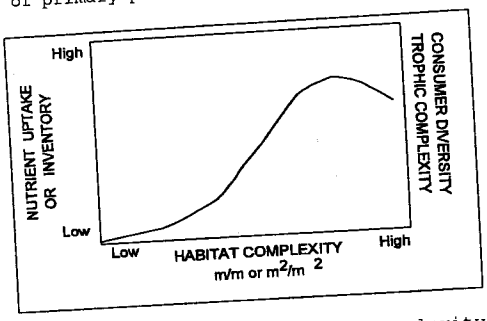


Fig. 2: Hypothesized effect of reef complexity (bottom axis) on: reef's ability to take up and store nutrients (left axis) and diversity of consumer trophic levels (right axis).

Another way to conceptualize the relationship between habitat complexity and nutrient dynamics is encompassed in the proposed 'intermediate nutrient hypothesis' (Fig. 3), explained in the figure caption. The significance of this hypothesis is that it encompasses the ability of reefs to thrive under a range of nutrient fluxes, but also to exhibit what are generally considered classic symptoms of nutrification (shifts to algal dominance) without changes in nutrient flux if either habitat complexity is reduced (loss of coral due to natural physical disturbance, coral mining, destructive fishing practices, etc.), or where there is overfishing or herbivore die-off.

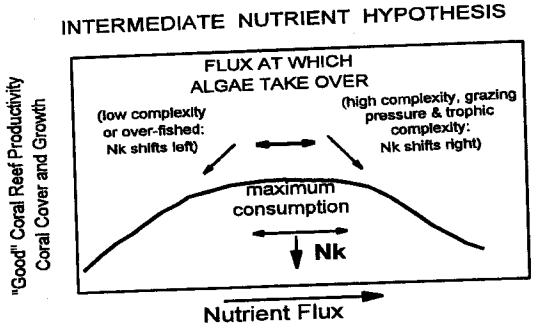


Fig.3: The intermediate nutrient hypothesis. Coral reefs respond to and benefit from increased nutrient fluxes, with increased productivity, coral cover and coral growth, until the point where consumers cannot consume all of the production, and there is a biotic shift in dominance from corals to algae (N_k). The nutrient flux at which this shift in dominance occurs is a function of habitat complexity, which determines the amount of available shelter for grazers and other consumers (as well as surface area for producers), and factors such as fishing pressure, which reduce grazer densities.

Let us consider how the progression from [low complexity/low diversity/low productivity] to [high complexity/high diversity/high productivity] may develop over the history of a reef's formation during the Holocene (Fig. 4). The diagrams illustrate that as corals were able to become established after reflooding due to sea level rise, they created habitat for other organisms, leading to opportunity for increased nutrient processing, biomass accumulation and trophic complexity. An important asset that accrues to hard-bottom systems along with higher complexity is the formation of sediment pockets that form within interstices in high complexity reliefs, and which serve as important sites of detritus entrapment and microbial remineralization (Szmant-Froelich 1983). In the absence of such "trapping" microhabitats, detrital materials are easily washed out of the system before they can contribute to reef trophodynamics.

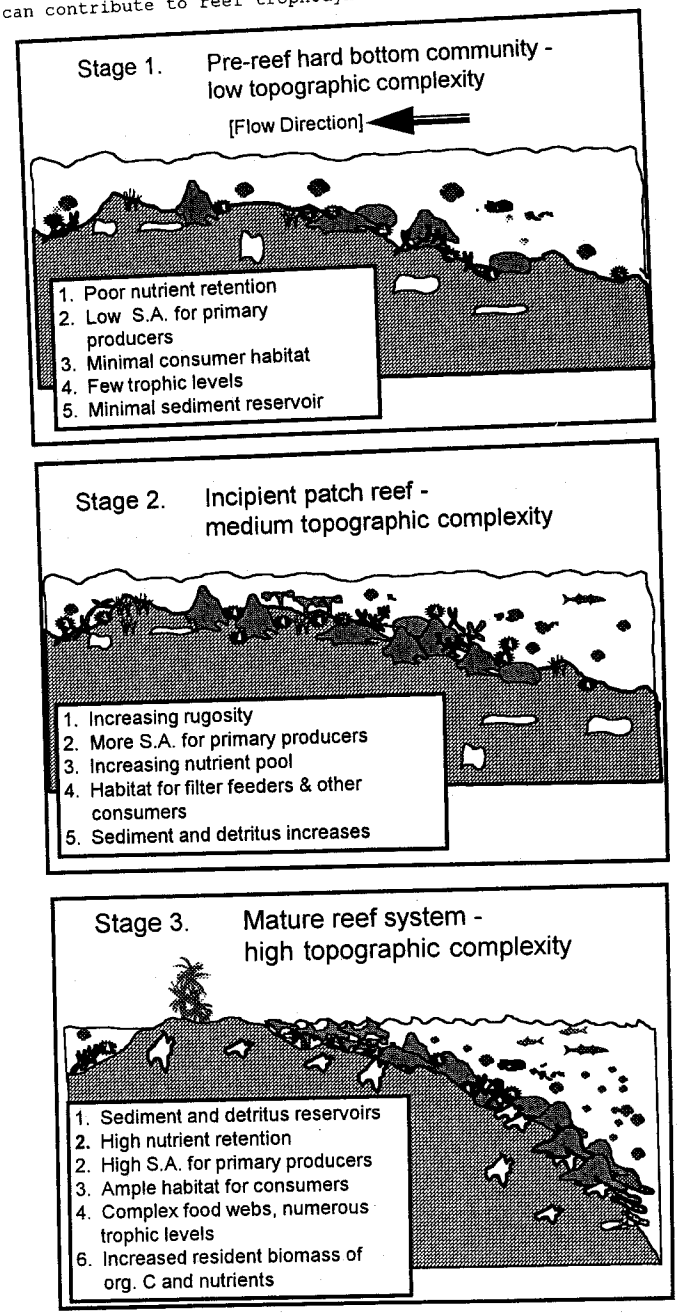


Fig. 4: Illustrations of the hypothetical increase in structural and community complexity during the development of coral reefs on low-relief hard-bottom areas during periods of sea-level rise. S.A. = surface area.

It is interesting to speculate that differences in the amount of habitat complexity created during subaerial erosion may have been one of the factors contributing to the variability in success of Holocene reef initiation. Areas with more suitable habitat for fish and sea urchin shelters might have had higher levels of grazing, and thus made it easier for corals to get established. Figure 4 summarizes how the substrate complexity of an antecedent platform might have influenced the probability of a reef

In general, patterns of community structure of reefs in BNP is characteristic of sub-tropical coral reefs influenced by cold spells, high nutrient input and high sedimentation. All reef communities studied were dominated by fleshy, turf and crustose algae with low cover of scleractinians, octocorals and sponges. The low cover of most zooxanthellate corals was comparable to that reported by Japp (1984), Dustan (1984), and Burns (1985) for the Florida reef tract and BNP. Though the current study was limited to a single survey at each site, it appears that cover of fleshy algae (including calcareous algae such as *Halimeda* spp.) changed throughout the year especially after storms that produced strong surge and currents which cleaned the algae's excess growth from the substrate and from coral colonies such as *M. annularis* (pers. obs.). Thus, storms, although detrimental in some aspects, may be important in the survival of coral colonies when they are heavily colonized by *Halimeda* spp or *Dictyota* spp. in reef communities.

Information about the reproductive biology and the associated processes of dispersion and recruitment is important for ecological studies of populations and communities (Harrison & Wallace, 1990). Reproductive studies in the Caribbean show that most of the large, cover-dominant reef building corals are broadcasters (Wyers, 1985; Szmant, 1986; Soong, 1990) and most of the small, highly abundant species are brooders (van Moorsel, 1983; Szmant, 1986; Chornesky and Peters, 1987; Soong, 1990). Brooding well developed phylopatric larvae many times a year is thought to increase recruitment and survival in coral species living in frequently disturbed habitats (Szmant, 1986), thus coral reefs in marginal areas are expected to be dominated by small, brooding species (Harriot & Banks, 1995). Recruitment patterns in Caribbean reefs have been characterized by low rates of settlement with a dominance of small brooding species and a marked lack of recruits of the large, broadcasting reef building species (Bak and Engel, 1979; Rogers et al,. 1984; Smith, 1992; Porter & Meier, 1992). Results of the current study show that recruitment rates are significantly higher than previously reported for southern Caribbean reefs and that offshore and inshore reef systems had a higher number of broadcasting species with recruits and juveniles than brooding species. Similar evidence from other

forming under differing nutrient regimes. Hallock and Schlager (1986) proposed that high nutrient fluxes precluded reef formation in areas with upwelling and/or other local high nutrient fluxes. On the other hand, there are good examples of large reef complexes forming within upwelling areas (cited above), and it is thought that many reflooded shelf areas had relatively higher nutrient regimes (Adey 1978). If habitat for sufficient grazers occurred in such areas, nutrient-tolerant corals may have been able to get a strong- hold and form reefs under somewhat elevated nutrient levels, and possibly at higher growth rates than in lower nutrient regimes.

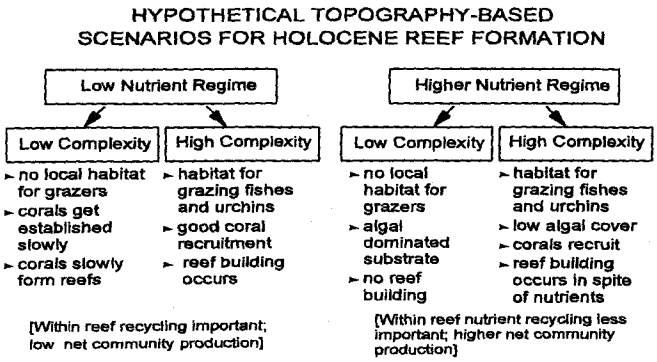


Fig. 5: Consequences of topographic complexity on the formation of coral reefs under low and high nutrient levels.

TROPHIC ASPECTS OF NUTRIENT DYNAMICS

New nutrients can enter coral reef food webs as either dissolved inorganic and organic nutrients, or in particulate form. Once new nutrients, regardless of source (natural or anthropogenic, chronic or episodic), are assimilated by reef primary producers or suspended particulate feeders, they move through the food web to other biotic/trophic groups either through direct consumption of the producers or planktivores by herbivores and piscivores, or by detrital pathways. Coral reefs are estimated to have at least 6 major consumer levels, each with transfer efficiencies of ca. 17 % (Grigg et al. 1984). These diverse consumer organisms release unassimilated N and P as ammonium, phosphate or feces. Feces can either re-enter the food web via coprophagy, or settle into the sediments, where together with other detrital material (e.g. algal fragments) they are remineralized by detritivores and microbes (Hatcher 1983; Moriarty et al. 1985). In order to truly understand biogeochemical cycles of coral reefs, we need to know the biomass of each of these biotic/trophic groups, the flux rates of each of the transfers, and their rate controlling processes.

Reflecting on this conceptual summary of coral reef nutrient dynamics, some special features and linkages are worthy of re-visiting:

1) The enormously high rates of GPP reported for coral reefs are a function of the large number and diversity of primary producers, but, under balanced trophic flow the producer biomass doesn't accumulate (except for symbiotic cnidarians) because it is quickly passed up the food web.

2) Reef corals are the major contributors of structural complexity, but contribute less to direct trophic flow, mostly through the excretion of mucus. Few animals eat corals and much of coral energy may be used to support calcification. However, mass spawning by corals can release large amounts of potential food into reef waters (e.g. 40 % of tissue C, 25 % of tissue N each year; Szmant 1991), and fishes and invertebrates feed on the spawn.

3) The importance of nutrient import and retention to coral reefs effected by planktivorous fishes has been under-appreciated. Dense schools of planktivores feed in the water column on both windward and leeward sides of reefs, and intercept nutrient-rich particles before they can reach benthic filter feeders or be washed away from the reef. At abundances of 0.1 to 1.0 g AFDW per m^3 (Hamner et al. 1988), zooplankton could be the source of 1 to 10 mmol of N per m^3 of water passing over the reef. Williams and Hatcher (1983) found that planktivores numerically dominate some GBR reef fish communities (> 80 % of individuals) and constitute up to 20 % of their biomass, and Russ (1985) reported that reef areas with high fisheries yields have a large percent of their fish communities (and catch) made up of planktivores. Planktivores are small and by virtue of their feeding mode, prone to predation, thereby providing a potentially short trophic connection between oceanic particulate nutrient inputs and higher trophic levels. Nutrients in the captured particulates become available to primary producers after they are excreted or defected and reminrealized. As planktivore density is highly dependent on substrate complexity (Eklund 1996), this is a prime example of how topographic complexity can contribute to both nutrient acquisition and processing on coral reefs.

4) If nutrient concentrations or other factors shift algal species composition towards dominance by algae with low palatability (e.g. chemically or structurally defended), then the predicted increases in trophic flow may not occur and algal biomass may build up (to the detriment of corals). In such a case, flow through detrital pathways should also increase (Johnson et al. 1995)

5) Ammonium and phosphate are excreted by all animal groups into their habitats, much of it into the benthic boundary layer where it elevates local nutrient concentrations (Szmant-Froelich 1983), and enhances uptake by benthic algae. A minimal estimate of recycled N produced by NH_4 excretion, derived from too many papers to cite here, suggests that the major groups of coral reef consumers produce ca. 13.9 mmol/m^2/d (fishes 0.5; echinoderms 4.5, molluscs 6.1; crustaceans 2.4; polychaetes 0.4). Using a C:N of 20-30 (Atkinson and Smith 1983), this excretion can support a GPP of 3-5 g C/m^2/d, or 40 to 70 % of Kinsey's (1985) standard coral reef performance (7 g C/m^2/d). The biomass estimates used were likely low and many taxa were not included, thus actual ammonium excretion rates are possibly twice these values.

6) Defecation products and algal detrital particles are either immediately consumed (Robertson 1982; Rothans and Miller 1991), or fall into the sediments where microbial groups and macro-detritivores will feed off them (Hatcher 1983; Moriarty et al. 1985), and in the process, remineralize nutrients. Reef sediments are typically low in nutrient content (Szmant and Forrester 1996), but they cover extensive areas of the reef, including the lagoon, sand channels on fore reefs, and trapped within topographic irregularities (Szmant-Froelich 1983). They can produce ca. 70 to 100 µmol NH_4/m^2/day. Furnas et al. (1993) estimated that on the Great Barrier Reef, benthic remineralization is the largest component of the total gross nutrient supply.

7) Coral reefs, by virtue of their existence, must have a long-term net positive community production. Over geological time, as reefs grow, they accrete a biomass of 'living' nutrients in the biomass of their fauna and flora. In addition, reefs have small amounts of organic C (0.5-0.8 %) and nutrients (0.07% N and 0.02% P) in their carbonate accumulations. For example, Carrie Bow Cay, on the Belize barrier reef, has accumulated ca. 8 x 10^6 m^3 of carbonate under ca. 0.7 km^2 of reef area over a 6-7,000 year time frame. This amounts to burial of 17.6 g organic C/m^2/yr (0.7 % of the Kinsey standard for GPP), 0.11 mol N/m^2/yr, and 0.014 mol P/m^2/yr. It is interesting to note that the C:N:P of the buried material as estimated is 105:8:1.

8) Coral reefs are reported capable of sustained fisheries yields of 5-15 mton/km^2/year, and this also represents a form of net production. By comparison with sediment burial, fisheries production [3.4 g C/m^2/yr, 0.05 mol N/m^2/yr and 0.002 mol P/m^2/yr] is small.

CONSEQUENCES/PREDICTIONS OF THESE HYPOTHESES

Johnson et al. (1995) produced a numerical model of carbon flow through a coral reef system, with two alternative pathways for C flow if algal cover increases. While their approach and objectives were different from the present one, they reached an important conclusion that is relevant to the present discussion: changes in relative abundance of major trophic groups can cause changes in trophic pathways and efficiencies at many different levels. Similar statements have been made by others (e.g. Birkeland 1988a; McClanahan and Shafir 1990; Done 1992; Hughes 1994).

Nutrification is blamed for many incidences of reef deterioration world-wide. However, most coral reefs have suffered from moderate or intense harvesting for longer than they have suffered from significant nutrification. Because fishermen travel far from home, over-harvesting can and has occurred in uninhabitable reef areas distant from human habitation (Roberts and Polunin 1994). Coral reefs in isolated or sparsely populated areas that are in poor health or deteriorated may be suffering from ecological

content from north to south (Fig. 10A). Sediment phosphate levels were temporally variable and no spatial pattern was evident (Fig. 10B). Thus, N:P shows a similar spatial pattern to total N.

not clear - variability in Phosphorus not large enough to mask biological pattern?

Water column inorganic nutrients

Table six (6) relates to bird characteristic not nutrients.

Overall, inorganic nutrient concentrations were quite variable in space and time with long term means around 0.1 uM for phosphate, 0.1-0.2 uM for ammonia, and 0.2-0.3 uM for nitrate+nitrite (Table 6). Marked temporal spikes occurred in the time series, though the only one of identifiable origin is following Tropical Storm Gordon in November 1994 (up to 1.7 uM nitrate+nitrite in a surface water sample). No clear spatial patterns were present, though nitrate+nitrite was consistently marginally higher in overall mean if the offshore component of each inshore/offshore pair (i.e. mean for Fowey marginally higher than Soldier, for Triumph marginally higher than Bache East, Pacific than Alinas, and Ball Buoy very marginally higher than Isa's; Table 6).

DISCUSSION

Coral reef community structure is influenced by processes occuring on different ranges of temporal and spatial scales (Jackson, 1991). Generally, some biological and environmental processes (i.e. predation, disease, bleaching) may happen rapidly on relatively small scales of space and time (Antonius, 1981; Glynn, 1990; Knowlton et al., 1990), whereas others such as hurricanes, epidemic diseases, mass mortalities and sea level change occur less frequently over larger spatial scales (Gladfelter, 1982; Porter et al., 1981, Woodley et al., 1981; Porter and Meier, 1992; Rogers, 1993). The purpose of this study was to characterize and quantify gradients in benthic community structure and in various physico-chemical factors that might help explain variations observed in reef benthic community structure along north/south and nearshore/offshore gradients in Biscayne National Park.

imbalance due to the removal of important trophic groups, and not from water quality deterioration.

Conequences of overfishing are most obvious when herbivorous fishes or sea urchins are harvested. Such harvesting may eventually lead to a change of benthic community structure (i.e. algal over-growth of corals). Natural mortality of herbivores can have the same effect (Hughes 1994). Herbivore loss will also affect the transfer of nutrients to other trophic groups that eat the herbivores, or the detrital materials they produce. It will also affect nutrient cycling since most of the nutrients that normally re-enter the coral reef food web as excretory and fecal products of these animals may remain on the reef as algae.

Harvesting of higher level consumers (piscivorous fishes, predatory molluscs and crustaceans) are predicted to also have important cascading effects on coral reef community structure and nutrient dynamics. Their exact manifestations are less simple to predict given the complexity of the feeding habits of these animals. Some estimates are that many reefs have <<50 % of their natural fish biomass (Clark et al. 1989; McClanahan and Shafir 1990; Roberts and Polunin 1994; Russ and Alcala 1996). An example of possible secondary effects of fishing is the increase in damsel fish abundance on Puerto Rican reefs over the past decade. These fishes have killed a large number of massive corals with their algal lawns (unpubl. observ.). I suspect that overharvesting of predatory fishes from these reefs has allowed damsel fish populations to explode. On Florida reefs we see large numbers of large-sized individuals of the coral eating gastropod, *Corallophila*, actively feeding on their preferred food, acroporid corals: Could a snail population explosion be related to overharvesting of spiny lobster, which used to be abundant in *Acropora palmata* thickets? I am sure that readers can think of other such examples of potential cascading effects of fishing that impact corals other than *via* algal overgrowth. The nutrient dynamics consequences of these cases will be difficult to recognize without detailed studies of the trophodynamics and nutrient balances for each such example.

I must caution that the objective of proposing this hypothesis is not to minimize in any way the idea that excess nutrients are harmful to coral reefs. There are coral reefs located in areas receiving intolerably high inputs of anthropogenic nutrients that could not be absorbed even with high topographic complexity and intact community structure. On the other hand, we should not be too quick to blame every 'sick' coral reef on sewage pollution while ignoring or over-looking the effects of fishing and habitat destruction. The management consequences of such an attitude will be the expenditure of large sums of money to manage the sewage, with little to no benefit to the reefs in question.

Finally, from an academic point of view, nutrients as an agent of deterioration should be differentiated from the sediments and/or organics with which they are often associated. "Clean" nutrients, such as those from upwelling, have the potential to enter through the algal community and from there transfer through the food web in a balanced fashion. Nutrients associated with high organic loads will stimulate bacterial production, result in lower dissolved oxygen, increased growth of filter feeders and boring borers, and cause major changes in trophic flow (Birkeland 1988a; Done 1992). In such cases, the organics are the major problem, not the N or P. Sediments usually have an associated nutrient (and organic) component, but again, the abrasive and smothering properties of the particles can have negative effects separate from those of the nutrients. While measures to control sediment and organic inputs to coral reef waters usually simultaneously reduce nutrient inputs, the mechanism of any resulting benefit should not be misunderstood.

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sediments.

Sediment traps

The most striking aspect of these data is, again, extreme temporal variability. The traps were deployed during Tropical Storm Gordon (November 1994) and this sample was up to an order of magnitude greater than those of any other deployment, but the extreme levels of deposition were predominantly at offshore reefs (Fig. 9). Aside from the high deposition during Gordon (and perhaps the Dec. 94 deployment) which were associated with greatest magnitude of winds, the other occasions when anomalously high depositions were recorded, at least at some sites (Sept 95, June 95, and Sept 94), were associated with more easterly wind directions whereas the rest of the deployments had a greater occurrence of southerly winds based on C-MAN data from Fowey Rocks tower (Table 6A).

A one way ANOVA on ranks (normality test failed) indicated that there was significant variation in overall sediment deposition among sites ($p=.0153$, $n=13$), but the less powerful post-hoc tests did not yield any pairwise comparisons which were significant at $p < 0.05$ level. When the samples from four inshore sites and from 5 offshore sites were pooled, a Mann-Whitney test indicated the offshore sites as a group had significantly higher rates of deposition than the inshore sites ($p=.0145$, $n=51$, Elkhorn reef excluded), but this is probably attributable to the differentially high deposition at most offshore sites during the anomalous tropical storm sample (Nov. 1994).

Sediment nutrients

Nutrient analysis of the deposited sediments from the tall traps did show some clear spatial pattern. Total nitrogen content of these sediments was significantly higher at inshore (versus offshore) sites (one-way ANOVA $p<0.0001$ followed by SNK pairwise comparisons). Also, within the inshore sites there was a trend of decreasing nitrogen

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SEDIMENTATION

Sediment accumulation plates

Results for total accumulation are given in Figure 7. Again, these data reveal Soldier Key to be qualitatively different from all the other sites in terms of total sediment accumulation. One-way ANOVA on total accumulation (six levels of the factor Site) shows significant variation among sites ($p<0.0001$, n=5 deployments), and post-hoc tests (SNK - $p<.05$) indicate that Soldier Key has significantly higher sedimentation than each of the other sites. The consistently high accumulation in the July 1994 deployment corresponded with the strongest gust winds of the five deployments and a high average wind speed (Fig. 7 and Table 6). The January 1995 deployment had highest average wind speed, but a lower gust, and showed typical levels of sediment accumulation.

The average distributions of size fractions for sediments accumulated at each site are given in Figure 8 for the last four deployments. For each deployment, Chi-square tests showed that the percentage distribution of sediment size fractions varied significantly from site to site ($p<.0001$ for each deployment). Also, ANOVA on each individual size fraction showed significant variation among sites, especially between inshore and offshore sites. That is, sediment accumulation at the offshore sites (especially Triumph) had greater incidence of the larger size fractions (>1mm and .25-1mm) while the inshore sites had greater incidence of the smallest fractions (.063-.25 mm and <.063mm).

Thus, while the total accumulation data shows substantial temporal variation, and similar levels of accumulation at all sites except Soldier Key, this accumulation is qualitatively different at inshore patch reefs versus offshore bank reefs. At the inshore sites, the sediment accumulated is consistently 60-85% composed of size fractions <.25mm while the offshore sites have a significantly greater component of coarser

adult colonies of same species and 28% if we consider all the adult colonies) compared to inshore reef sites (31% of adult colonies of same species and 23% of all adult colonies) (Table 3). With the exception of *M. cavernosa,* juvenile and adult densities (col/m^2) for the more common species were positively and significantly (Pearson) correlated accross reef sites (Fig. 5). Juveniles of mostly large, broadcasting species were more common in seven of the nine localities (3 of 4 inshore localities and 4 of 5 offshore localities) compared to brooding species. Overall, juveniles of 10 broadcasting vs. 6 brooding species were found in inshore sites compared to 9 broadcasting vs. 4 brooding species in the offshore localitiess (Table 3). More detailed results on juvenile dynamics and mortality is presented by Miller et.al., (Coral Reefs, in press).

Temperature

In general, the inshore patch reef sites showed higher variability and greater extremes of temperature, both cold in winter and warm in summer (Table 4, 5 and Fig. 6). This was most pronounced for Soldier Key which is closest to the Safety Valve, a large pass from Biscayne Bay between Key Biscayne and the the lower barrier islands. Means in temperature are not really useful in determining influence on corals, but rather the extremes. Table 3 shows the number of days that the nightly average temperature was below 20 °C or above 30 °C (limits of stressful cold and warm temperatures for corals). Soldier Key is qualitatively distinct from all the other sites with an order of magnitude greater exposure to extreme temperatures (Table 4). The other three inshore patch reef sites (Bache East, Alina's and Isa's) also show approximately triple the exposure to extreme temperatures (mean = 3.1% of recorded days) as the outer shelf reef sites (mean = 1.0%).

increase from north to south in both inshore and offshore reefs with the higher diversity of all three groups found in Isa's patch reef in the southern edge of the Park (Table 1, appendices 4-6).. The sponges were the most diverse group at both the generic and species level (66 species in 41 genera) compared with the scleractinians (52 species in 23 genera) and the octocorals (44 species in 11 genera) (Table 1, appendices 4-6). *Madracis senaria*, a crustose-massive, dark brown or green scleractinian species is a new record for the Florida area. Within BMP this species was observed only in Pacific, however, survey dives showed it as a common species in reefs off Key Largo (Key Largo Dry Rocks and Conch reef) and coral communities off Ft. Lauderdale. *Montastraea faveolata* and *M. franksi* (Weil and Knowlton, 1994) have been traditionally pooled as the same species *M. annularis.*

Juvenile colonies

Juveniles colonies belonging to 31 species of scleractinian zooxanthellate corals were identified in the quadrats (Table 3). Juvenile densities (col/m^2) increased from north to south. In the northern half of the Park, higher juvenile densities were found in offshore than in nearshore reefs while in the south, juvenile densities were higher on nearshore reefs, especially at Isa's patch reef (Table 3). *S.siderea* showed the highest abundances of juveniles in inshore localities followed by *P. astreoides, D. stockesii, M. cavernosa* and *P. porites*. In the offshore localities, *P. astreoides* had the highest densities of juveniles followed by *P. porites*, *M. cavernosa* and *A. agaricites*. With the exception of *S. Siderea*, neither one of the other species was a dominant coral in terms of cover and densities in any of the localities.

In general, juveniles colonies represented a significant proportion of the coral population in BNP (32 % of the total number of coral colonies of the species with juveniles and 26% considering all species of corals). Juveniles represented a proportionally higher component of the coral populations of offshore reefs (34% of population considering only

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With our Compliments

Rich + Bill

9

Evolutionary Paleoecology of Caribbean Coral Reefs

Richard B. Aronson and William F. Precht

ECOLOGISTS HAVE RADICALLY ALTERED their thinking about coral reefs, and those views continue to evolve. Coral reefs, formerly viewed as stable, equilibrial systems (Newell 1971), are now interpreted as nonequilibrial on ecologically relevant scales of time (years to decades) and space (landscapes to reef systems) (Grigg and Dollar 1990; Karlson and Hurd 1993; Edmunds and Bruno 1996; Brown 1997). Increasing awareness of this variability is motivating a strategic shift in coral reef research. Paleontologists are taking up the quest for predictability, searching for large-scale patterns in the fossil record (Jackson, Budd, and Pandolfi 1996).

The nonequilibrial view of reef ecology gained initial support when the intermediate disturbance hypothesis was formulated for coral reefs in the 1970s (Grassle 1973; Connell 1978). This hypothesis predicts maximum diversity at intermediate levels of disturbance. At low disturbance levels the competitive dominants exclude other species, whereas at high disturbance levels good colonizers, which are poor competitors, are the only ones able to persist. Intermediate disturbance levels strike a balance between the slowly recruiting competitive dominants and the rapidly recruiting competitive subordinates, leading to coexistence and higher diversity than at the extremes of the disturbance

later also showing the highest densities.

Twelve species of octocorals had a percent cover higher than 5% of the total octocoral cover at any given reef site (Appendix 2). *Pseudoterogorgia americana*, *Erythropodium caribaeroum*, *Briareum asbestinum* (morphs 1 and 2) and *Gorgonia ventalina* showed the highest mean percent cover and densities in both offshore and inshore reef sites. *Pseudoterogorgia kallos* and *Plexaura homomalla* were very abundant in two offshore and two inshore reefs but overall, had lower mean cover than the other species mentioned above. Soldier was very different from the other reef sites in species composition and abundances with *Plexaurella dichotoma*, *P. nutans* and *Pterogorgia anceps* dominating this area. Isa's and East Bache had similar mean cover of octocorals but densities were significantly higher (Kruskal-Wallis, Dunn's post-hoc tests, $P<0.001$) at Isa's reef.

Each of eighteen species of sponges had greater than 5% of the total sponge cover at any given reef site (Appendix 3). *Amphimedon compressa*, *Callispongia vaginalis, Niphates erecta, Ulosa ruetzleri* and *Petrosia weinbergi* were the dominant and most abundant species in offshore sites. *Iotrochota birotulata* and three of the dominant offshore species, *A. compressa, N. erecta, and P. weimbergi,* were also dominant in the inshore reefs. Soldier was again very different from the other reef sites in the composition of species and the dominant species were *Spheciospongia vesparium* and *Aplysina fistularis*.

Species Richness

With the exception of Soldier-Fowey, coral, octocoral and sponge diversity was higher in all the other inshore sites compared to their offshore pairs (Table 1). The number of species and genera (biological richness) of scleractinians (range from 12 to 43 spp.), octocorals (range from 23 to 41 spp.) and sponges (range from 21 to 48 spp.) tends to

continuum. In 1980, Hurricane Allen further promoted the idea of nonequilibrium on coral reefs by devastating the best-studied reef in the Caribbean: Discovery Bay, on the north coast of Jamaica (Woodley et al. 1981). Attempts to fit the effects of Hurricane Allen into an intermediate disturbance scenario of increasing coral diversity (Porter et al. 1981) helped convince many ecologists that hurricanes are an important structuring force in coral reef communities.

Although intermediate disturbance effects occur on coral reefs under certain conditions (Rogers 1993a; Aronson and Precht 1995), serious doubts persist over the explanatory value of the hypothesis (Huston 1985a; Jackson 1991). Hurricane Allen and its indirect effects (Knowlton et al. 1981; Knowlton, Lang, and Keller 1990) caused such massive destruction at Discovery Bay that diversity ultimately decreased, a result that neither supports nor falsifies the intermediate disturbance hypothesis (Hughes 1994; Hughes and Connell 1999). Despite the enormity of its consequences in Jamaica, even Hurricane Allen, which is arguably the most famous disturbance in the literature on coral reefs, could not have prepared ecologists for what followed throughout the Caribbean region.

Many coral reefs worldwide have changed dramatically since the 1970s. Coral cover has typically declined, and the cover of noncoralline, fleshy and filamentous macroalgae (henceforth "macroalgae") has increased (Done 1992a; Wilkinson 1993; Ginsburg 1994; Cortés 1997). This transition has been particularly pronounced in the Caribbean region, including the Florida Keys and the Bahamas (Rogers 1985; Porter and Meier 1992; Ginsburg 1994; Hughes 1994; Connell 1997).

Corals are, of course, the principal framework builders of coral reefs. Bioeroders, including fish and invertebrates, break down that framework (Hutchings 1986). Crustose coralline algae are thought to play a role in reef cementation, but their importance has recently been questioned (Macintyre 1997). From the 1950s through the 1970s, living communities on the open surfaces of Caribbean reefs were dominated by corals, crustose coralline algae, and algal turfs. Today, macroalgae are the dominant space-occupiers on most Caribbean reefs.

Disturbances of various types have been invoked to explain the changing face of Caribbean reefs. These include hurricanes, coral bleaching, diseases of corals and sea urchins, overfishing, nutrient loading, sedimentation, and pollution (Tomascik and Sander 1987; Lessios 1988; Bythell et al. 1989; Hatcher, Johannes, and Robertson 1989; Rogers 1990; Glynn 1993; Liddell and Ohlhorst 1993; Hughes 1994; Shulman and Robertson 1996; Peters et al. 1997; and many others). Whether the coral-to-macroalgal transition is due primarily to natural or anthropogenic impacts remains controversial (Grigg and Dollar 1990).

Macroalgal dominance of Caribbean reef communities may not be unusual. On the contrary, Discovery Bay prior to 1980, from which the ecology of Caribbean reefs was originally described, may represent an atypical condition (Precht 1990; Woodley 1992). On average, hurricanes pass close enough to Discovery Bay to do significant damage more often than once per decade (Kjerfve et al. 1986; Woodley 1992). It just happened that the now-classic studies of zonation on Jamaican reefs (Goreau 1959; Goreau and Wells 1967; Goreau and Goreau 1973; Kinzie 1973) were conducted following several decades without a hurricane. This is a problem of scale and variance; the unusual lack of physical disturbance prior to Hurricane Allen may explain the "typically" high coral cover observed earlier.

Before the 1980s, living bank/barrier reefs of the Caribbean displayed a generalized zonation pattern of three common species that were the primary builders of reef framework (Goreau 1959; Graus and Macintyre 1989). The thickly branching elkhorn coral, *Acropora palmata*, was dominant at the reef crest and the shallowest depths of the fore reef (0–5 m depth). The more thinly branching staghorn coral, *A. cervicornis*, was dominant at intermediate depths (~5–25 m) on exposed reefs, and it ranged into shallower habitats on more protected reefs (Adey and Burke 1977; Geister 1977; Hubbard 1988). The massive corals of the *Montastraea annularis* species complex (Knowlton et al. 1992, 1997) were common in reef habitats from approximately 5 m to greater than 30 m.

Woodley (1992) suggested that Discovery Bay, and by extension other Caribbean reefs, which currently have low coral cover and high macroalgal cover, may be that way much or most of the time. Because most study reefs were initially chosen for their luxuriant coral growth, it is perhaps not surprising that the predominant direction of change has been toward declining coral cover (Hughes 1992). The alternative interpretation is that high coral cover is the usual condition. By this reasoning, current dominance by macroalgae is the result of a novel combination of circumstances (Hughes, Reed, and Boyle 1987; Jackson 1991, 1992; Knowlton 1992; Liddell and Ohlhorst 1993; Hughes 1994).

The fossil record has the potential to discriminate these two possibilities. Reef zonation patterns similar to Jamaica before 1980 have been recognized in Pleistocene and Holocene reef deposits throughout the region (Mesolella 1967; Macintyre, Burke, and Stuckenrath 1977; Geister 1980, 1983; Lighty, Macintyre, and Stuckenrath 1982; James and Macintyre 1985; Boss and Liddell 1987; Macintyre 1988; Fairbanks 1989; Stemann and Johnson 1992). Thick deposits that display this zonation have been taken as prima facie evidence that (1) corals dominated Caribbean reef communities for most of Pleistocene-

(col/m²) of corals, zoanthids, and sponges. Scleractinians showed significantly higher densities of individual colonies in all inshore localities compared to offshore localities with the exception of Fowey and Soldier (Mann-Whitney $P < 0.01$) (Fig.3). Hydrocoral densities were similar between all localities except Alina's and Elkhorn. All cnidarians showed a general trend to increase densities from north to south in both offshore and inshore localities (Fig. 3). Sponges also showed significant higher densities in all inshore sites from Bache to Isa's compared with their offshore counterparts (Mann-Whitney $P < 0.01$). A general trend towards an increase in density from the north to the south is also clear (Fig. 3).

The discriminant analysis readily separated 6 distinct groups with the first canonical function accounting for 52 % of the variance and the first three canonical functions explaining 93 % of the variation. CV1 weighted cover of macroalgae (ALG) most heavily and was strongly correlated with it. It separated Soldier, Ball Buoy, Elkhorn and the cluster of ofshore localities (Triumph, Pacific, and Fowey). CV2 weighted octocoral cover (OCT) and crustose cover (CRU) most heavily and further separated Alina's and a cluster with Isa's and Bache Shoals (Fig. 4A). CV3 weighted cover of bare substrate (BARE) and density of octocorals (NOCT) more heavily and further separated Isa's from Bache shoals (Fig. 4B). Overall, 92.9 % of all original grouped cases were correctly classified by the analysis.

Fourteen species of scleractinians had more than 5% of the total coral cover in at least one reef site (Appendix 1). Of these, *Meandrina meandrites*, *Siderastrea siderea, Agaricia agaricites. Porites porites, P. astreoidesY* and *Montastraea cavernosa* were the most *important* species in the offshore reef sites. *M. meandrites* has a low density but is the dominant species in terms of cover in all offshore sites except Ball Buoy, where *Acropora palmata* and *M. faveolata* dominate. *A. agaricites, S. siderea, P. astreoides* and *P. porites* had the highest densities. *Montastraea faveolata* and *S. Siderea* were the dominant coral species in the inshore reef sites (with the exception of Soldier), with the

Holocene time, and (2) macroalgae dominated rarely if at all (Jackson 1991, 1992; see also Stemann and Johnson 1995). Thus, despite nonequilibrial dynamics on small spatio-temporal scales, corals are thought to have persisted in interspecific associations that are predictable on larger scales, forming long-lived communities.

Knowlton (1992) hypothesized that the coral- and macroalgal-dominated situations represent alternative community states, each of which is resistant to conversion to the other (see also Lighty 1981; Hatcher 1984; Precht 1990; McClanahan et al. 1999). The conjunction of recent disturbances has disrupted associations of coral species, shifting many Caribbean reefs to the macroalgal state (Jackson 1991, 1992, 1994b). The implication is that reef communities display emergent properties based on direct or indirect interspecific interactions, which influence their response to disturbance at various scales. The structure of coral reef communities may therefore differ fundamentally from that of other Neogene marine communities, which are interpreted as assemblages of independently distributed species (Jablonski and Sepkoski 1996).

This chapter critically reviews our current understanding of changes to Caribbean reefs on ecological and geological–evolutionary scales. We first examine causes of the recent shift to macroalgal dominance. Reduced herbivory and nutrient loading each played a role. We argue, however, that coral mortality, especially from disease, was a major driving force in the transition. Rates of recovery on Caribbean reefs are strongly influenced by the life history strategies of the corals. Second, we review work on the historical forces that have shaped the Caribbean coral fauna since the early Miocene. The evolutionary history of the fauna explains a great deal about the current state of Caribbean reefs. Third, we discuss the implications of that history for the hypothesis of whole-community responses to disturbance. The "community integration" hypothesis, an explanation based on emergent properties of biological systems, is pitted against an individualistic, "independent species distribution" hypothesis. These alternative models of community structure can be tested by considering the variability of coral reefs at multiple scales, connecting living reef communities to their fossil record. Finally, we suggest avenues of future research on coral reefs in the emerging field of evolutionary paleoecology.

Much of our knowledge of the coral-to-macroalgal shift comes from research at Discovery Bay and environs over the past 30 years. It will come as no surprise that generalizing those results to the rest of the Caribbean has often proved erroneous. Nevertheless, Discovery Bay provides a convenient point of departure for our discussion.

Herbivory and Its Consequences

If they are present in sufficient numbers, herbivores limit the rapid accumulation of macroalgal biomass, thereby promoting the growth and recruitment of corals (Hay 1981; Sammarco 1982; Hay and Goertemiller 1983; Carpenter 1986; Lewis 1986; Steneck 1988; Knowlton 1992). The most influential herbivores on Caribbean reefs are parrotfish (Scaridae; placed in the Labridae by Kaufman and Liem 1982), surgeonfish (Acanthuridae), and sea urchins (Echinoidea) (Ogden and Lobel 1978; Glynn 1990a; Choat 1991; Carpenter 1997; Hixon 1997).

Damselfish (Pomacentridae) are also herbivores, but they are ecologically quite different from scarids, acanthurids, and echinoids. Some pomacentrids kill living coral tissue and cultivate algal lawns on the dead surfaces for feeding and breeding purposes. They have had significant negative effects on coral cover in Recent and Pleistocene reef communities of the Caribbean (Kaufman 1977, 1981; Potts 1977; Lobel 1980). Because they promote algal growth rather than inhibiting it, pomacentrids will not be considered functional herbivores in this discussion.

The blackspined urchin, *Diadema antillarum*, was an important herbivore on many Caribbean reefs, including Discovery Bay and nearby areas (Sammarco 1982; Hay 1984; Carpenter 1986, 1997; Liddell and Ohlhorst 1986; Hughes, Reed, and Boyle 1987). Where it was abundant, this sea urchin competed strongly with other herbivores. *Diadema* negatively affected population densities of herbivorous fishes, although there was no evidence of a converse effect (Hay and Taylor 1985; Carpenter 1988, 1990b; Morrison 1988; Robertson 1991). *Diadema* severely limited the growth of macroalgae on the north coast of Jamaica before and for several years after Hurricane Allen (Hughes, Reed, and Boyle 1987). At high densities, *Diadema* also suppressed coral recruitment by grazing small colonies (Sammarco 1980).

A water-borne pathogen of unknown origin caused mass mortality of *Diadema* throughout the region in 1983–1984 (Lessios, Robertson, and Cubit 1984; Lessios 1988; Peters 1997). In the absence of *Diadema*, macroalgae flourished on heavily fished reefs like the one at Discovery Bay, because scarids and acanthurids had been largely eliminated by humans over the previous decades (Liddell and Ohlhorst 1986; Hughes, Reed, and Boyle 1987). Macroalgae are capable of overgrowing and shading small, recently settled corals (Birkeland 1977; Sammarco 1980, 1982), and, in extreme situations like Discovery Bay, even adult corals, including massive colonies of the *M. annularis* complex, were overgrown (Hughes 1994). The cover of crustose coralline algae declined as well (Steneck 1997).

this area (Table 2). Soldier was qualitatively and quantitatively very different from the other reef sites in species composition, mean percent cover and abundances of algae, cnidarians and sponges. It had significantly (Kruskal-Wallis, Dunn's post-hoc tests, $P<0.001$) higher mean percent cover of fleshy algae and lower mean percent cover and mean densities (col/m^2) of all cnidarian groups compared to the other reef sites towards the south.

Excluding Soldier Key, mean percent cover and mean densities of scleractinians were significantly higher (Mann-Whitney, $P<0.001$)in all other inshore reef sites compared to their offshore pairs with the exception of Isa's s which showed no significant differences with Ball Buoy in coral mean percent cover (Fig. 2B). Mean percent cover of corals had opposite spatial trends between offshore and inshore sites in the north-south direction with offshore sites showing a trend to increase in percent cover of corals and inshore sites a trend to decrease (Fig. 2B). Octocoral cover was significantly higher (Mann-Whitney, $P<0.001$) in inshore localities compared to their offshore pairs. Hydrocoral cover was similar in all localities (Table 2). Percent cover of octocorals and hydrocorals showed a trend to increase towards the south. Cover of zoanthids was generally low and showed no spatial pattern between pairs of localities and in the north to south direction. Sponges had significantly higher cover in all the inshore localities compared to their offshore pairs and showed a trend to increase in cover from north to south in both offshore and inshore localities (Fig. 2B).

Octocorals were significantly more abundant (K-W & Dunn's test, $P<0.001$) than all other cnidarians and sponges in all reef sites except in Elkhorn, where scleractinians showed a higher density due to high numbers of juveniles of *Porites astreoides* and ramets of *P. porites* (Table 1, Fig. 3, appendix 1). With the exception of the north pair (Fowey-Soldier), all inshore reef sites had a significantly (Mann-Whitney, $P<0.001$) higher octocoral density compared to their offshore counterparts with Isa's patch reef showing the highest (41 col/m^2, Table 1) abundance. Isa's also showed the highest abundances

This scenario is widely accepted as a model for the recent dynamics of Caribbean reefs. It was inferred largely from events of the past several decades at Discovery Bay and nearby sites, and it emphasizes the role of herbivory by *Diadema* in community turnover (e.g., Glynn 1990a; Steneck 1994; Carpenter 1997). In contrast, Hay (1984) argued that Discovery Bay and many other reefs had artificially elevated densities of *Diadema* because of fishing pressure, whereas scarids and acanthurids were more important on less fished reefs (see also Lewis and Wainwright 1985; Lewis 1986; Rogers, Garrison, and Grober-Dunsmore 1997). *Diadema* populations were released from predation by human exploitation of their predators, particularly the queen triggerfish, *Balistes vetula*, and the hogfish, *Lachnolaimus maximus* (Munro 1983; Hay 1984; Reinthal, Kensley, and Lewis 1984; Hughes, Reed, and Boyle 1987; Roberts 1995). The negative influence of *Diadema* on scarids and acanthurids, combined with overfishing of those herbivorous fishes, made *Diadema* by far the most important herbivore, at least down to 10 m depth (Liddell and Ohlhorst 1986; Jackson 1991). The mass mortality of *Diadema* then resulted in high macroalgal cover, a condition that persisted for more than a decade (for Discovery Bay: Liddell and Ohlhorst 1993; Aronson et al. 1994; Hughes 1994; Steneck 1994; Andres and Witman 1995; Edmunds and Bruno 1996; Aronson and Precht 2000; figure 9.1). Similar effects of fishing pressure on sea urchin abundance, sea urchin grazing on macroalgal abundance, and macroalgal abundance on coral cover have been observed on coral reefs of the Indo-Pacific (Muthiga and McClanahan 1987; McClanahan and Muthiga 1988, 1989; Tanner 1995; McClanahan et al. 1999).

Levitan (1992) uncovered a positive relationship between *Diadema* population density in the Caribbean and inferred levels of human exploitation pressure through time. Increasing ratios of jaw size to test size in museum specimens collected over the century before 1983 implied that *Diadema* density increased as human population density increased. This finding supported Hay's (1984) contention that *Diadema* density was related to fishing pressure. Levitan pointed out, however, that this result may have been confounded by the proximity of many less populated, less fished sites to continental landmasses.

One problem with generalizing the herbivory scenario beyond Discovery Bay is that macroalgal cover has increased on protected and moderately fished reefs, as well as on heavily fished ones, although to a lesser degree (e.g., Levitan 1988 for St. John, U.S. Virgin Islands; Carpenter 1990a for St. Croix, U.S. Virgin Islands ; McClanahan and Muthiga 1998 for Belize). Carpenter (1986 for St. Croix; see also Foster 1987 for Panama) explained these observations with evidence that *Diadema* were the most important herbivores even on lightly fished reefs, contradicting Hay (1984). By Carpenter's reasoning, the 1983–

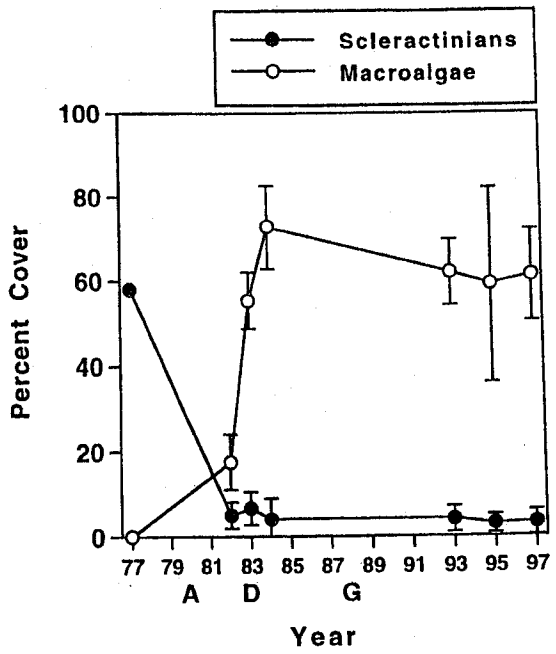


FIGURE 9.1. Changes in scleractinian coral and macroalgal cover at 5–6 m depth on the West Fore Reef at Discovery Bay, Jamaica. Letters beneath the *x*-axis mark significant events in the history of the site: A, Hurricane Allen (1980); D, *Diadema* mass mortality (1983); G, Hurricane Gilbert (1988). Data for 1977 are from visual transects by M. A. Huston, reported in Liddell and Ohlhorst (1987); data for 1982–84 are from visual transects by Liddell and Ohlhorst (1986); data for 1993–97 are from transects videotaped by the authors and analyzed by M. L. Kellogg, per Aronson et al. (1994). Error bars represent standard deviations, which are not available for 1977 data.

1984 *Diadema* mass mortality significantly decreased herbivory at both unfished and fished sites.

Carpenter's hypothesis, however, does not explain the response of Belizean reefs to damage from Hurricane Hattie in the early 1960s, two decades before the *Diadema* mass mortality. After Hurricane Hattie, macroalgae dominated for more than ten years before corals recovered on those unfished reefs (Stoddart 1963, 1969, 1974). Likewise, as coral cover declined in the 1980s, macroalgal cover increased from less than 5% to greater than 60% on the fore reef at Carrie Bow Cay, Belize (12–15 m depth; Littler et al. 1987; Aronson et al. 1994). Carrie Bow Cay was lightly fished at the time, and *Diadema* were virtually absent below 6 m depth before, as well as after, their mass mortality (Lewis and Wainwright 1985).

resulting solution using an autoanalyzer.

Water column inorganic nutrients

Water samples were taken haphazardly, but approximately bi-weekly over the reefs in all 9 sites. Dedicated water sample bottles were rinsed 3 times with surface water before samples were taken. Samples before May, 1995 were taken from surface water and after this, the rinsed bottle was taken down on the dive and filled at the reef level. One sample was collected per site per date, transported back to the lab in a dark cooler, and frozen until analysis. Samples were then thawed and duplicates of each sample were analyzed for ammonia, nitrate+nitrite, and phosphate on a Technicon AutoAnalyzer II.

RESULTS

Benthic community structure

Algae (fleshy, turf, and crustose groups) make up a substantial biological component of all reefs sites (Table 1, Fig. 2A). Turf algae shows the highest mean percent cover of all substrate groups in all the localities studied except for Soldier. Mean percent cover was significantly higher (Mann-Whitney, $P<0.001$) in offshore versus adjacent nearshore sites except for Ball Buoy and Isa's at the southern edge of the Park (Table 2). There was a general decrease in mean percent cover of turf algae from north to south for offshore reef sites and no clear spatial pattern for inshore localities (Fig. 2A). Fleshy macro algae was most abundant in Soldier where it covered 70 % of the substrate. Coverage showed no clear spatial pattern between offshore/inshore pairs and had a general trend to increase towards the south in the offshore localities. Cover of Crustose algae was higher in the southernmost sites (Ball Buoy and Isa's) but showed no clear spatial pattern (Fig. 2A) and no significant differences between offshore/inshore pairs in

Knowlton (1992) proposed a hypothesis to explain macroalgal dominance in areas with high densities of herbivorous fishes, such as Carrie Bow Cay. Scarids and acanthurids are selective herbivores, whereas *Diadema* are less selective (but see Ogden, Abbott, and Abbott 1973; Carpenter 1981, 1997; and Hay, Kappel, and Fenical 1994 on selective feeding by *Diadema*). Where *Diadema* were abundant, macroalgal cover was low because the urchins ate algae more or less indiscriminately. The *Diadema* mass mortality removed the single most important nonselective herbivore from Caribbean reefs. Following space-clearing disturbances, macroalgal cover increased, because the algae grew faster than the corals and because herbivorous fishes avoided physically and chemically defended algal species (Hay 1985, 1991, 1997; Hay and Goertemiller 1983; Knowlton 1992). The cover of unpalatable macroalgae increased even on some reefs and in some reef habitats where fish density was high and *Diadema* density was low prior to the mass mortality. In those places, coral mortality led to macroalgal dominance precisely because *Diadema* were historically rare. In other cases, high densities of herbivorous fishes were able to maintain low algal cover.

In St. Croix, microherbivores (amphipods, tanaids, polychaetes, and gastropods) had a negligible effect on algal biomass and productivity (Carpenter 1986). On the other hand, microherbivores (gastropods and hermit crabs) were important in preventing macroalgae from dominating a site in Bermuda disturbed by a ship grounding (Smith 1988). From this and the foregoing observations, we can only conclude that although herbivory influences the distribution, abundance, and productivity of algae, it is sometimes difficult to predict specific effects.

Arguments about the ecological effects of herbivores on "pristine" versus "disturbed" reefs may well be moot, because pristine reefs probably have not existed in the Caribbean for a very long time. Megaherbivores such as sea turtles and manatees most likely had important effects on algal dynamics until their near-extermination in the eighteenth century (Jackson 1997). The loss of megaherbivores, along with the subsequent exploitation of reef fishes, is evidence that Caribbean reefs have been disturbed for centuries.

Of course, it is still important to understand the dynamics of change in modern reef ecosystems, and many ambiguities remain. Jackson (1997), citing historical descriptions, argued that *Diadema* were naturally abundant on at least some Caribbean reefs. Historically, *Diadema* may have exerted a generally greater influence on the (oceanically influenced) islands of the eastern Caribbean than along the (terrestrially influenced) Central American coast (Levitan 1992; Jackson 1997). Perhaps this biogeographical pattern was erroneously attributed to recent differences in fishing pressure; from the literature cited previously, *Diadema* appear to have been less important in Belize (less fished) and more important in the Antilles (more heavily fished).

Nutrient loading has increased macroalgal cover on some Caribbean reefs (Tomascik and Sander 1987; Tomascik 1991; Knowlton 1992). In addition to increasing algal growth rates, dissolved nutrients disrupt the coral-zooxanthellae symbiosis, poison the calcification process, and promote bioerosion (Highsmith 1980; Barnes and Chalker 1990; Jokiel, Dubinsky, and Stambler 1994; Dubinsky and Stambler 1996; Marubini and Davies 1996). Consequently, reef development is poor in areas influenced by upwelling, terrestrial runoff, or other nutrient sources (Neumann and Macintyre 1985; Hallock and Schlager 1986; Hallock 1988; Wood 1993; Burke 1994; Ginsburg and Shinn 1994). Temporary, nutrient-induced algal blooms often occur in fore-reef habitats following storms (e.g., Hughes 1994; Rogers, Garrison, and Grober-Dunsmore 1997). These blooms probably result from the sudden resuspension of nutrients stored in sediments, as well as from the outflow of nutrient-rich lagoonal waters and terrestrial runoff (Szmant and Forrester 1996; Szmant 1997). Debate continues over the importance of natural and anthropogenic nutrient input to the balance between corals and macroalgae on coral reefs (Lewis 1984; Hunte and Wittenberg 1992; Rougerie, Fagerstrom, and Andrie 1992; Wittenberg and Hunte 1992; Hunter and Evans 1995; McCook 1996; Szmant and Forrester 1996; Lapointe 1997; McCook, Price, and Klumpp 1997; McClanahan and Muthiga 1998; McCook 1999; Miller et al. 1999).

Szmant (1997) suggested that the level of topographic complexity on a reef indirectly influences the effects of nutrient input and uptake. In the absence of overfishing or mass mortalities of herbivores, topographic complexity determines the availability of shelter for herbivores, thereby mediating rates of consumption of algae in the face of pulsed or chronic nutrification. Nutrients and herbivory clearly interact in complex ways to determine the outcome of competition between corals and macroalgae (Meyer, Schultz, and Helfman 1983; Littler and Littler 1985; Littler, Littler, and Titlyanov 1991; McClanahan 1997; Miller 1998).

Attention to herbivory and nutrient loading de-emphasizes the pivotal role of coral mortality in the transition to macroalgal dominance. Some authors have explicitly acknowledged the importance of coral mortality (Adey et al. 1977; Hughes, Reed, and Boyle 1987; Done 1992a; Knowlton 1992; Rogers, Garrison, and Grober-Dunsmore 1997; Hughes and Connell 1999; McCook 1999), but others advocate a primary role for herbivory (Steneck 1994; McClanahan 1995; Hay 1997) or nutrient enrichment (Lapointe 1997). Although algae have higher growth rates and are capable of outcompeting corals, they must recruit to the reef in order to do so (Umar, McCook, and Price 1998). Discovery Bay

recommended 3:1 height-diameter ratio were deployed at about .75 m above the reef; additional shorter traps (~12cm tall) were deployed as close to reef level as possible. Though these traps of different heights are not directly comparable, and even though the shorter traps may have been subject to greater loss of deposited sediments due to resuspension, they should provide a conservative measure of sediment deposition. Upon collection, traps were capped underwater and then drained through the Nitex bottom, brought back to the lab, and frozen until processing within one week. Thawed sediments were rinsed from the traps into a pre-weighed dish with de-ionized water, dried, and weighed. These dried sediments were then stored for later nutrient analysis (see below). One tall and one short trap were deployed at each of three stations in each of six pairs of offshore/inshore reef sites. There were 13 deployments of approximately two weeks duration. However, weather and other problems caused slight variation in the length of each deployment. Thus, data are expressed as deposition per day for the mean of 6 traps (3 short and 3 tall) for each deployment for each site.

Wind data (speed, maximum gust, and direction) was extracted from the record of the CMAN station at Fowey Rocks to help explain temporal variation in sedimentation rates.

Sediment nutrients

Samples collected from the sediment traps were analyzed in duplicate for total carbon and total nitrogen content on a Carlo-Erba 1108 elemental analyzer. For the initial deployment, all tall and short trap samples were analyzed and nitrogen content was generally higher in the tall trap samples. For subsequent samplings, only the samples from tall traps were analyzed, thus data presented represent means of $\leq$ 3 duplicated samples per date. Total phosphorus content of the sediments was determined by ashing the dried sediments in duplicate samples for at least 5 hours at 485°C, dissolving in .5N HCl, filtering out the residue, and determining the concentration of dissolved phosphate in the

had been heavily fished for decades to centuries (Munro 1983; Jackson 1997) but supported high coral cover prior to 1980, even in intermediate to deeper habitats in which *Diadema* were less common (Morrison 1988; Jackson 1991). Before 1980, the corals apparently pre-empted space (Ohlhorst 1984; Littler and Littler 1985). Had Hurricane Allen not occurred and had coral cover remained high at Discovery Bay, the *Diadema* die-off probably would not have had such a rapid and dramatic effect, because there would have been far less free space available on which *Diadema* grazing was suddenly alleviated.

Even in situations where herbivores are abundant and nutrient concentrations are low, coral mortality can result in macroalgal dominance if the amount of empty space created exceeds the feeding capacity of consumer populations. The potential of herbivores to respond numerically to the availability of algae will be limited by the loss of topographic heterogeneity that accompanies coral mortality from hurricanes and other disturbances (e.g., Adey et al. 1977; Kaufman 1983; Szmant 1997). Furthermore, in the absence of *Diadema*, the scarids and acanthurids, which are selective feeders, may be unable to control physically and chemically defended macroalgae (Knowlton 1992).

Differential Coral Mortality

Observations of interspecific differences in coral mortality support the contention that mortality is a precondition for macroalgal dominance. Branching corals, including the two *Acropora* species, are particularly susceptible to hurricane damage. Both species were devastated in Discovery Bay by Hurricane Allen (Woodley et al. 1981).

Edmunds and Bruno (1996) compared the West Fore Reef at Discovery Bay to other reef sites along the north coast of Jamaica in 1995. Fishing pressure was historically heavy throughout the area studied, and *Diadema* had been absent for more than a decade. One comparison site was located at Dairy Bull, a few kilometers east of Discovery Bay. At the intermediate depth of 10 m, coral cover was considerably higher at Dairy Bull than at Discovery Bay (table 9.1), and macroalgal cover was lower (40% macroalgal cover at Dairy Bull versus 62% at Discovery Bay; Edmunds and Bruno 1996). A principal reason for the difference between sites was that the cover of *M. annularis* complex was much higher at Dairy Bull than at Discovery Bay. In fact, the cover of *M. annularis* was higher at Dairy Bull in 1995 than it was at Discovery Bay prior to Hurricane Allen (table 9.1).

The maximum skeletal growth rate measured for *M. annularis* is ~1.5 cm linear extension per year (Hudson 1981a,b). The average growth rate is lower: a 50 cm tall colony is approximately 50 yr old under good conditions (Dodge,

TABLE 9.1. Comparison of Coral Cover at 10 m Depth Between the West Fore Reef at Discovery Bay (WFR) and Dairy Bull, Jamaica.[a]

Category	*WFR 1977*	*WFR 1995*	*Dairy Bull 1995*
Total coral cover	42%	2%	23%
M. annularis complex	7%	1%[b]	13%
A. cervicornis	12%	0%	0%

[a]The 1977 data for Discovery Bay are from Huston (1985b). The 1995 data for Discovery Bay and Dairy Bull are from Edmunds and Bruno (1996 and unpubl. data).
[b]Value for *M. annularis* cover at Discovery Bay in 1995 agrees with values for the same depth in 1993 reported by Hughes (1994).

Aller, and Thomson 1974; Dustan 1975; Graus and Macintyre 1982; Highsmith, Lueptow, and Schonberg 1983; Shinn et al. 1989). Because most of the *M. annularis* colonies at Discovery Bay and Dairy Bull were considerably taller than 50 cm in 1995, they must have predated Hurricane Allen and the *Diadema* mass mortality. This suggests that much of the difference between the sites in 1995 was due to the mortality and subsequent macroalgal overgrowth of corals more susceptible to hurricane damage than *M. annularis*.

Prior to 1980, the most common coral at the two sites other than *M. annularis* was *A. cervicornis*, judging from (1) surveys conducted at Discovery Bay in the 1970s (Porter et al. 1981; Huston 1985b), and (2) the enormous quantity of *A. cervicornis* rubble at 10 m depth at both sites in the 1990s. Hurricane Allen had the main effect of subtracting *A. cervicornis* from Discovery Bay and (presumably) Dairy Bull, leaving *M. annularis* more or less intact (Woodley et al. 1981; Hughes 1989; Steneck 1994; see also Bak and Luckhurst 1980). Hurricane Gilbert in 1988 had less dramatic effects on corals at Discovery Bay and (presumably) Dairy Bull, because *A. cervicornis* and other corals had only begun to recover from Hurricane Allen (Woodley 1989). *M. annularis* colonies again were largely unaffected (Hughes and Connell 1999).

This pattern was repeated elsewhere. Stoddart (1963) reported the nearly complete destruction of *A. cervicornis* but only moderate to minimal destruction of *M. annularis* following Hurricane Hattie in Belize (see also Glynn, Almodóvar, and González 1964 on Hurricane Edith's impact in Puerto Rico). Shinn (1976; Shinn et al. 1989) commented on the volatility of *A. cervicornis* populations in the Florida Keys, and Curran et al. (1994) noted that *A. cervicornis* died but *M. annularis* remained intact in the Bahamas. Macroalgal overgrowth subsequent to the *Diadema* mass mortality reduced the cover of *M. annularis* in Jamaica (Hughes 1994), but this did not happen in Belize, the Florida Keys, or the Bahamas.

Sedimentation

We used two methods to assess sedimentation stress on BNP reefs. (1) Sediment accumulation plates (Baynes 1993) were used in short-term deployments (3 days). These devices (11 cm diameter astroturf surfaces with a rigid pvc backing) are intended to mimic benthic surfaces and provide an assessment of the sediment accumulation experienced by reef substrates. We performed five quarterly three-day deployments at each of six reefs (three inshore/offshore pairs). The plates (n=9-12 per reef) were attached even with the substrate to washers glued at fixed sites on the reef. At collection, lids with o-ring seals were carefully placed over the plates and brought back to the lab in an upside-down position. Accumulated sediments were rinsed out of the lids and astroturf and then washed through a series of sieves (1mm - .063 mm) to determine their size fractionation. Effluent from the smallest sieve was poured into 60 ml centrifuge tubes and centrifuged to concentrate the very fine sediments. Supernatant water was siphoned from these tubes and the concentrated fine sediments rinsed into pre-weighed drying dishes. All size fractions were dried to constant weight and weighed. Data presented are both total accumulation and percent of total accumulation in each size fraction for each deployment. The exception is that the size fractionation for the first deployment is not shown, since a different set of seives (of uncomparable sizes) was used. One-way ANOVA was used to detect significant variation in total accumulation across sites. Size fraction data for each deployment was subjected to a Chi-squared test to determine if the distribution of sediments into size fractions varied by site. Individual fractions were tested to determine if there was variation over sites (n=5 deployments) by one-way ANOVA. Lastly, for each fraction, data for inshore and for offshore sites were pooled and T-tests (or Mann-Whitney rank sum tests, n=15) were used to detect significant differences in the percent of that fraction present at inshore versus offshore reef samples. (2) Sediment tube traps were used at nine sites in approximately monthly two week deployments. Sediment traps were constructed from 3 inch (~7.5 cm) diameter pvc pipe with a Nitex mesh bottom (so that water would drain out upon collection) and were of two heights: tall traps (~20cm) of the

In extreme cases of herbivore removal, macroalgae will overgrow massive corals (Hay and Taylor 1985; Lewis 1986; but see de Ruyter van Steveninck, van Mulekom, and Breeman 1988). Although the absence of herbivores may have been largely responsible, the mortality of *M. annularis* at Discovery Bay can also be linked to the activities of pomacentrids. L. S. Kaufman (personal communication, 1998) noted an increase in the number of three-spot damselfish (*Stegastes planifrons*) territories on *M. annularis* after Hurricane Allen. *S. planifrons* apparently moved their territories to head corals after the hurricane eliminated their preferred microhabitat, *A. cervicornis* thickets. *M. annularis* heads were less preferred before the demise of *A. cervicornis* (Kaufman 1977; see also Williams 1978; Ebersole 1985), but those coral heads are currently the microhabitat of choice for *S. planifrons* in St. Croix (Tolimieri 1998). Eakin (1989) also observed that, in the absence of live branching corals, juvenile *S. planifrons* occupied living *M. annularis* colonies in Florida. By partially killing head corals, *S. planifrons* probably contributed to macroalgal overgrowth. Qualitative observations over the past few years indicate increasing numbers of *S. planifrons* territories on massive corals in Belize and the Florida Keys, again causing partial mortality (W. F. Precht, unpublished observations, 1998; S. L. Miller and A. M. Szmant, personal communications, 1998).

Differential coral mortality has also occurred between reef zones. For example, fore-reef zones at Carrie Bow Cay, Belize, experienced differential mortality in the 1980s. The shallow spur-and-groove zone (3–6 m depth) had high coral cover in the 1970s to early 1980s, dominated by the blade-shaped lettuce coral, *Agaricia tenuifolia*. Even though *Diadema* were present in this shallow zone at that time, scarids and acanthurids were the most important herbivores (Lewis and Wainwright 1985). The deeper spur-and-groove zone at intermediate depths (9–15 m) also had high coral cover, dominated by *A. cervicornis* (Burke 1982; Rützler and Macintyre 1982). *Diadema* were rare in this deeper zone, herbivorous fishes were more abundant in the deeper zone, and herbivory was intense and macroalgal cover was low in both zones (Lewis and Wainwright 1985; Littler et al. 1987). In the 1990s, *Diadema* were absent from both zones, and scarids and acanthurids were abundant and not subject to fishing pressure. Coral cover remained variable but high in the shallow spur-and-groove (Aronson and Precht 1995), while the deeper spur-and-groove was largely covered by macroalgae (Aronson et al. 1994). The difference in macroalgal cover between zones in the 1990s arose because most of the *A. cervicornis* in the deeper zone died in the early 1980s.

These observations highlight the importance of coral mortality, specifically the mortality of *A. cervicornis*, as a prerequisite to macroalgal dominance at intermediate depths. Presumably the mortality of *A. palmata* is equally necessary for coral-to-macroalgal transitions in reef crest and shallow fore-reef habitats. What are the important causes of coral mortality in the Caribbean?

Causes of Coral Mortality

Like the herbivory scenario, much of what reef ecologists believe about coral mortality is influenced by the experience at Discovery Bay. The devastation of *A. cervicornis* from Hurricane Allen and collateral mortality from pomacentrids and corallivorous invertebrates (Porter et al. 1981; Woodley et al. 1981; Knowlton et al. 1981; Knowlton, Lang, and Keller 1990) was followed by some damage from Hurricane Gilbert in 1988 (Woodley 1989; Hughes 1994). In 1989 Hurricane Hugo damaged reefs in the U.S. Virgin Islands (Edmunds and Witman 1991; Hubbard et al. 1991; Rogers, McLain, and Tobias 1991; Bythell, Bythell, and Gladfelter 1993; Aronson, Ebersole, and Sebens 1994). These studies and other ecological and geological work (e.g., Ball, Shinn, and Stockman 1967; Perkins and Enos 1968; Stoddart 1974; Rogers, Suchanek, and Pecora 1982; Mah and Stearn 1986; Fenner 1991; Kobluk and Lysenko 1992; Blair, McIntosh, and Mostkoff 1994; Blanchon 1997; Blanchon, Jones, and Kalbfleisch 1997) led to the prevailing opinion that hurricanes are a primary cause of present and past coral mortality in the Caribbean.

Hurricanes have been important at some localities, but they do not explain recent patterns of coral mortality in much of the region. Damage from hurricanes is patchy on many spatial scales (Hubbard et al. 1991; Rogers 1993b; Steneck 1994). Some areas of the Caribbean, such as Trinidad, Costa Rica, and Panama, receive virtually no hurricanes, while others, including Jamaica, are struck frequently (Neumann et al. 1987; Woodley 1992; Tremel, Colgan, and Keevican 1997). Coral populations often suffer more extensive damage from chronic disturbances (Rogers 1993b). In Belize, for example, the deeper, *A. cervicornis*-dominated spur-and-groove zone lost cover beginning in the 1980s, as described previously. Hurricane Greta is known to have damaged the fore reef in 1978 (Rützler and Macintyre 1982; Kjerfve and Dinnel 1983); however, Hurricane Greta was not responsible for the mass destruction of *A. cervicornis* populations in the 1980s. White-band disease (WBD) was the principal cause of *A. cervicornis* mortality.

WBD is a presumed bacterial infection that is specific to *Acropora* spp. (Antonius 1981; Gladfelter 1982; Peters 1993). Cases of WBD are recognizable as segments of bare skeleton, sometimes bordered by narrow bands of disintegrating, necrotic coral tissue, on otherwise healthy-looking, brown *Acropora* branches. The "bands" of disease spread along the branches, generally from base to tip, and eventually kill entire colonies. The etiology of WBD and the causes of outbreaks

substrates such as sand, bare substrate, and rubble was also measured. For scleractinian corals, juvenile and adult colonies were distinguished and counted. The criteria used was that all colonies measuring less than 1-5 cm in diameter (depending on the species) with no evidence of being reattached, asexual fragments or ramets of older colonies were considered juveniles. Data for each group was tested for normality (Bartlet's test) and homogeneity of variance. Mean percent cover and densities (col/m^2) were then estimated for each reef site and significant differences between pairs of offshore and inshore sites tested with Student t-test and/or Mann-Whitney Rank Sum Test when the data failed to comply with normality and equality of variances. Percent cover data was transformed with the arcsin ($\sqrt{}$cover) function for univariate statistic analyses. ONEWAY ANOVAS were used to compare coverage and abundances of the major groups across the different reef within each of the offshore and inshore series. Recurrent communities (groupings) were explored with stepwise canonical discriminat function analysis using average data for all coverage and abundance variables each major group in each transect per locality.

Physico-chemical parameters

Temperature

Temperature was monitored more or less continually at several reef sites using Hobo-Temp temperature loggers (Onset Instruments, Pocasset, MA) anchored to the reef substrate in Ikelite clear plastic housings. The loggers were set to record approximately every 20 minutes, and were downloaded approximately monthly. It was determined that the housings provided some artifactual warming due to a "greenhouse effect" during daylight hours, so data reported are based on daily means of readings taken before 6 am and after 8 pm to avoid solar heating. Gaps in the data are due to dislodgement and loss of instruments, or instrument malfunction.

are poorly understood, and recent reports suggest that there are several varieties of the disease with different symptoms (Peters 1993, 1997; Antonius 1995; Peters and McCarty 1996; Santavy and Peters 1997; Richardson 1998).

Despite the difference in appearance upon careful examination, WBD in Caribbean *Acropora* spp. has often been mistaken for coral bleaching, which has received considerably more attention in the literature. Dramatic bleaching events at times of elevated sea temperature and ultraviolet radiation have caused mass mortalities of corals in the Indo-Pacific, although bleaching-related mortality has until recently been more limited in the Caribbean (Jaap 1979; Brown 1987, 1997; Ogden and Wicklund 1988; Glynn 1990b, 1993; Williams and Bunkley-Williams 1990; D'Elia, Buddemeier, and Smith 1991; Glynn and Colgan 1992; Lang et al. 1992; Fitt et al. 1993; Shick, Lesser, and Jokiel 1996; Aronson et al. 2000). An important reason for the current interest in bleaching is that global warming may increase its frequency and extent (Smith and Buddemeier 1992; Glynn 1996).

Acropora spp. will bleach under thermal stress (Cortés 1994). Other sources of *Acropora* mortality include predation by corallivores (Knowlton et al. 1981; Knowlton, Lang, and Keller 1990; Tunnicliffe 1983), nutrient loading (Weiss and Goddard 1977; Lewis 1984; Bell and Tomascik 1994), sedimentation (Rogers 1990; Cortés 1994), and, in Florida and the Bahamas, cold water stress (Davis 1982; Porter, Battey, and Smith 1982; Roberts et al. 1982; Burns 1985). Although quantitative data are generally lacking, it is becoming apparent that WBD epizootics have been the primary cause of the recent mortality of *A. cervicornis* and *A. palmata* over wide areas of the Caribbean (Rogers 1985; Wells 1988; Sheppard 1993; table 9.2).

Stands of *A. cervicornis* killed by WBD generally collapse due to weakening of the skeletons by bioerosion, and the result is large fields of *A. cervicornis* rubble. *A. palmata* is more robust, and stands of this species remain in growth position for longer periods after they have been killed, as has been observed in Anguilla, Belize, the Florida Keys, St. Croix, and elsewhere. Dead stands of *A. palmata* are then leveled by storms (Bythell et al. 1989; Hubbard et al. 1991). Hurricane damage has clearly been a more localized cause of *Acropora* mortality over the past few decades (table 9.3).

Compared with *Acropora* spp., the mortality of massive corals has been more variable. Colonies of *M. annularis* complex have been affected by hurricanes, bleaching, and disease (Rützler, Santavy, and Antonius 1983; Porter et al. 1989; Edmunds 1991; Edmunds and Witman 1991; Fitt et al. 1993; Meesters and Bak 1993; Kuta and Richardson 1996), but large stands of *M. annularis* can still be observed throughout the region (e.g., Shinn et al. 1989; Precht 1993; Curran et al. 1994; Edmunds and Bruno 1996; Burke et al. 1998; McClanahan and Muthiga 1998).

TABLE 9.2. Reports of White-Band Disease as the Primary Cause or an Important Cause of *Acropora* Mortality on Caribbean Reefs over the Past Few Decades[a]

Location (habitat)	*Species Affected*	*Time Period*	*Source*
Anguilla			
(rc)	*A. palmata*[b]	1980s–90s	Sheppard et al. 1995
Bahamas			
Andros Barrier Reef			
(br)	*A. cervicornis*	1980s	S. Cove, personal communication
(rc)	*A. palmata*[c]	1980s	S. Cove, personal communication
(fr)	*A. cervicornis*	1980s	S. Cove, personal communication
New Providence Island			
(br)	*A. cervicornis*	1980s	S. Cove, personal communication
(rc)	*A. palmata*[c]	1980s	S. Cove, personal communication
(fr)	*A. cervicornis*	1980s	S. Cove, personal communication
San Salvador Island			
(rc)	*A. palmata*	1980s	Shinn 1989
(pr)	*A. cervicornis*	1980s	Shinn 1989; Curran et al. 1994
Lee Stocking Island, Exumas			
(pr)	*A. cervicornis*[c]	1980s–90s	J. C. Lang, personal communication
Belize			
Ambergris Cay			
(pr)	*A. cervicornis*	1980s–90s	Precht, unpublished observation
(rc)	*A. palmata*	1980s–90s	Precht, unpublished observation
(fr)	*A. cervicornis*	1980s–90s	Precht, unpublished observation
Carrie Bow Cay			
(pr)	*A. cervicornis*	1980s–90s	Precht, unpublished observation
(rc)	*A. palmata*[c]	1980s–90s	Aronson and Precht, unpublished observation
(fr)	*A. cervicornis*	1980s	Precht, unpublished observation
Central Shelf Lagoon			
(l)	*A. cervicornis*	1986–90	Aronson and Precht 1997
Ranguana Cay			
(rc)	*A. palmata*	1980s–90s	Precht, unpublished observation
(fr)	*A. cervicornis*	1980s–90s	Precht, unpublished observation
British Virgin Islands			
(rc/fr)	*A. palmata*	1980s–90s	Bythell and Sheppard 1993
Cayman Islands			
Grand Cayman			
(fr)	*A. cervicornis*[d]	1980s	Woodley et al. 1997
Colombia			
(g)	*Acropora* ssp.[b]	1970s–90s	Garzón-Ferreira and Kielman 1994
San Andrés			
(l/pr)	*A. palmata*[b,d]	1970s–90s	Zea et al. 1998
(l)	*A. cervicornis*[b,d]	1970s–90s	Zea et al. 1998

(Continued on next page)

inshore patch reef system with large scleractinian colonies and high densities of octocorals and sponges. Triumph Reef is a low relief, relic-hard-bottom, offshore site with scattered coral, octocoral and sponge colonies and high cover of turf and crustose algae. In the south-central region, three reefs were selected; Alina's Reef is a near-shore, well developed patch reef with substantial coral development on its shoreward side and high abundances of octocorals. Pacific Reef is an offshore hard-bottom site similar to Triumph, and Elkhorn Reef is an exposed, well developed patch reef positioned further offshore compared to the other patch reefs that used to have a dense population of *Acropora palmata*. At the southern edge of the Park we selected Ball Buoy Reef, a well developed, high relief, mid-shelf bank-barrier reef with abundant populations of elkhorn coral and hydrocorals and high densities of octocorals and sponges. Isa's Reef is a low relief patch reef with a highly diverse community of octocorals, sponges and scleractinians (see Table 1). The Soldier Key site is the only one located to the west of Hawk's channel (Fig. 1).

Benthic community structure

Reef benthic community structure was carefully quantified using 1 m² quadrats along four or five parallel transect lines at each site. The transects ran parallel to the substrate contour of offshore reefal areas usually in a northeast-southwest direction. In the offshore sites, the first transect was haphazardly placed at the deep side (fore-reef area) towards the east, four more, evenly spaced (20 or 25 m) transects were placed up the slope towards the west to cover most of the different habitats within each site (front reef, slope, crest, back reef, etc). In the inshore patch reefs transects ran parallel to the longer axis placed as follows: one on the eastern, wave-exposed zone, one in the back reef zone and two on the top of the reef. A 1 m² quadrat gridded into 100 areas of 100 cm² each was moved at 2-4 m intervals along the transect line depending on the length of the reef. In each quadrat, detailed measurements were done of the live cover (to the closest cm²) and the density (number of colonies) of each species of scleractinian coral, octocoral and sponge. Cover of fleshy, crustose and turf algae, miscellaneous organisms, and other

TABLE 9.2. (*continued*)

Location (habitat)	*Species Affected*	*Time Period*	*Source*
Cuba			
(rc/fr)	*A. palmata*[c]	1980s–90s	P.M. Alcolado, personal communication
(fr)	*A. cervicornis*[c]	1980s–90s	P.M. Alcolado, personal communication
Dominican Republic			
(fr)	*A. cervicornis*[b]	1980s–90s	M. Vega, personal communication
Florida Reef Tract			
Biscayne National Park (2 reefs), Northern Keys (1 reef), and Looe Key (1 reef)			
(rc/fr)	*A. palmata*[d]	1980s	Porter and Meier 1992; Porter et al. 1993
Northern Keys (4 reefs)			
(fr)	*A. cervicornis*	1980s	Jaap, Halas and Muller 1988; Shinn, et al. 1989
Jamaica			
Discovery Bay			
(fr)	*A. cervicornis*[d]	1980–88	Knowlton, Lang, and Keller 1990; Tunnicliffe 1983
Netherlands Antilles			
(rc/fr)	*A. palmata*[c]	1970s–80s	Bak and Criens 1981
(fr)	*A. cervicornis*	1970s–80s	Bak and Criens 1981; van Duyl 1982, 1985; Wells 1988
Puerto Rico			
La Parguera			
(rc/fr, l)	*A. palmata*[d]	1990s	Bruckner et al. 1997
(pr)	*A. cervicornis*[d]	1990s	Bruckner and Bruckner 1997
Panama			
San Blas Islands			
(pr)	*Acropora* spp.[b]	1970s–80s	Ogden and Ogden 1994
Trinidad and Tobago			
Tobago			
(rc/fr)	*A. palmata*	1980s	Laydoo 1984
U.S. Virgin Islands			
St. Croix: Buck Island			
(rc/fr)	*A. palmata*	1976–85	Gladfelter 1982; Bythell et al. 1989
(fr)	*A. cervicornis*	1976–85	Bythell et al. 1989
St. John			
(rc/fr)	*A. palmata*[d]	1980s–90s	Rogers 2000

[a] Habitat abbreviations: rc, reef crest; fr, fore reef; pr, patch reef; l, lagoon; g, reef habitats in general. No superscript, WBD as principal cause of widespread mortality. See Rogers (1985) and Wells (1988) for earlier reports of the presence of WBD around the Caribbean.
[b] WBD as probable cause of widespread mortality.
[c] WBD as cause of some mortality.
[d] WBD associated with other sources of coral mortality.

TABLE 9.3. Reports of Hurricane Damage as the Primary Cause or an Important Cause of *Acropora* Mortality on Caribbean Reefs over the Past Few Decades.[a]

Location (habitat)	*Species Affected*	*Year (Storm)*	*Source*
Belize			
Turneffe Islands			
(rc)	*A. palmata*	1961 (Hattie)	Stoddart 1963
(fr)	*A. cervicornis*	1961 (Hattie)	Stoddart 1963
Barrier Reef leeward of Turneffe Islands			
(rc)	*A. palmata*	1961 (Hattie)	Stoddart 1963
(fr)	*A. cervicornis*	1961 (Hattie)	Stoddart 1963
Peter Douglas Cay			
(l)	*A. cervicornis*[c]	1961 (Hattie)	Stoddart 1963
Carrie Bow Cay			
(rc)	*A. palmata*	1978 (Greta)	Highsmith et al. 1980; Kjerfve and Dinnel 1983
(fr)	*A. cervicornis*[c]	1978 (Greta)	Highsmith et al. 1980; Kjerfve and Dinnel 1983
Cayman Islands			
Grand Cayman			
(rc/fr)	*A. palmata*[c]	1988 (Gilbert)	Blanchon et al. 1997
Colombia			
San Andrés			
(l/pr)	*A. palmata*[b?]	1988 (Joan)	Zea et al. 1998
(l)	*A. cervicornis*[c?]	1961 (Hattie)	Zea et al. 1998
Florida Reef Tract			
Biscayne National Park			
(pr)	*A. palmata*[c]	1992 (Andrew)	Rogers 1994; Lirman and Fong 1996, 1997a
(pr)	*A. palmata*[c]	1993 (Storm of the Century)	Lirman and Fong 1997b
(pr)	*A. palmata*[c]	1994 (Gordon)	Lirman and Fong 1997b
Northern Keys, off Key Largo			
(rc/fr)	*A. palmata*[c]	1960 (Donna)	Ball et al. 1967
(rc/fr)	*A. palmata*	1965 (Betsy)	Perkins and Enos 1968
(fr)	*A. cervicornis*	1965 (Betsy)	Perkins and Enos 1968
(rc/fr)	*A. palmata*[c]	1992 (Andrew)	Precht et al. 1993
Jamaica			
Port Royal Cays			
(rc)	*A. palmata*[b]	1951 (Charlie)	Goreau 1959; Woodley 1992
Discovery Bay			
(rc)	*A. palmata*	1980 (Allen)	Porter et al. 1981; Woodley et al. 1981
(fr)	*A. cervicornis*	1980 (Allen)	Woodley et al. 1981; Knowlton et al. 1990
(rc)	*A. palmata*[c]	1988 (Gilbert)	J. D. Woodley, pers. comm.
(fr)	*A. cervicornis*[c]	1988 (Gilbert)	Woodley 1989

(*Continued on next page*)

winter cold temperature has been documented as impacting the Florida reef tract via plumes emanating from Florida Bay (Walker et al., 1982). It is possible that similar limitation of reef development by outflow of Biscayne Bay water occurs in the Biscayne National Park area as suggested by Burns (1985). Offshore reefs on the other hand, may be affected by the occasional cold water counter current plume coming down from Fort Lauderdale and extending as far south as Triumph or Pacific reef sites (Ginsburg, 1956). Other factors potentially affecting BNP reefs include sediment abrasion and deposition from storms, anthropogenic effects from fishing and heavy tourism, and the extensive agricultural and urban development in South Florida (Hudson, 1981; Roberts et al., 1983; Jaap, 1984; Dustan & Halas, 1987; Glynn et al., 1989).

The goals of this study were: (1) to describe and compare the benthic community structure (including diversity, density and live cover of the major biological groups) between offshore reef sites and near-shore sites spanning the north/south extent of BNP, and (2) to characterize environmental factors such as temperature, sediment deposition, sediment composition, water column and sediment nutrient levels to examine possible correlations between the spatial patterns in benthic community structure and these environmental factors known to affect coral reef communities.

METHODS

Study Sites

Nine sites within Biscayne National Park were selected to include pairs of inshore reefs localities and offshore sites in four east-to-west transects in the northern, central, and southern regions of the Park respectively (Figure 1, Table 1). Fowey Rocks and Soldier Key in the northern region of the Park are characterized by low relief, relic Pleistocene hard-bottom substrate with scattered coral, octocoral and sponge colonies. In the north-central area, East Bache Shoals is part of the northernmost well developed,

TABLE 9.3. (*continued*)

Location (habitat)	*Species Affected*	*Year (Storm)*	*Source*
Netherlands Antilles			
Bonaire			
(rc/fr)	*A. palmata*[c]	1988 (Gilbert, Joan)	Kobluk and Lysenko 1992
(fr)	*A. cervicornis*[c]	1988 (Gilbert, Joan)	Kobluk and Lysenko 1992
Puerto Rico			
La Parguera			
(rc)	*A. palmata*	1963 (Edith)	Glynn et al. 1964
(fr)	*A. cervicornis*	1963 (Edith)	Glynn et al. 1964
(rc)	*A. palmata*	1979 (David)	Vicente 1994
(fr)	*A. cervicornis*	1979 (David)	Vicente 1994
U.S. Virgin Islands			
St. Croix: Buck Island			
(rc/fr)	*A. palmata*	1979 (David, Frederic)	Rogers et al. 1982
(rc/fr)	*A. palmata*[c,d]	1989 (Hugo)	Bythell et al. 1989; Rogers 1992

[a] Habitat abbreviations as in Table 2. No superscript, hurricanes as principal cause of widespread mortality. Note that the effects of Hurricane Gilbert (1988) in Jamaica were limited because the reef had not yet recovered from Hurricane Allen (1980). The same can be said for the effects of the Storm of the Century (1993) and Tropical Storm Gordon (1994) in Florida, both of which following Hurricane Andrew (1992).
[b] Hurricanes as probable cause of widespread mortality.
[c] Hurricanes as cause of some mortality.
[d] Hurricanes associated with other sources of coral mortality.

In summary, WBD, and to a lesser extent hurricanes, caused the mortality of *Acropora* throughout the Caribbean, reducing coral cover substantially on most reefs. Even at Discovery Bay, WBD was noted on *A. cervicornis* prior to Hurricane Allen, and the disease may have killed surviving fragments after the storm (Knowlton et al. 1981; Knowlton, Lang, and Keller 1990; Tunnicliffe 1983; Woodley et al. 1997). Hurricanes, diseases, bleaching, and probably nutrient loading have caused mortality in populations of nonacroporid corals in recent years, including massive *Montastraea* spp. and *Diploria* spp., foliose *Agaricia* spp., branching and head-forming *Porites* spp., and many others. This mortality has been highly variable: As an example, Hurricane Hugo severely damaged *M. annularis* populations in St. John, U.S. Virgin Islands (Edmunds and Witman 1991), but hurricanes had minimal impacts on *M. annularis* populations in Jamaica and Belize.

The effects of corallivorous invertebrates on Caribbean reefs remain poorly understood, but there may be a causal link between coral diseases and outbreaks of corallivores (Knowlton, Lang, and Keller 1990; Antonius and Riegl 1997; Bruckner, Bruckner, and Williams 1997). Also, despite earlier reports to the contrary, some parrotfish species eat corals at some localities in the Caribbean, but the importance of this trophic linkage to the ecology of Caribbean reefs requires further study (Bruckner and Bruckner 1998; Miller and Hay 1998). The prospects for recovery of coral populations depend to a large extent on the nature and recurrence of disturbance and on the life-history strategies of the corals.

Coral Reproductive Strategies

Corals reproduce asexually, primarily by fragmentation. They also employ two strategies of sexual reproduction: broadcast spawning of gametes and release of brooded planula larvae (Szmant 1986; Richmond and Hunter 1990; Smith 1992; Richmond 1997). Slow recovery times of populations of *A. palmata, A. cervicornis,* and (to a lesser extent) *M. annularis* complex can be tied to their reproductive strategies.

The key to success for *A. cervicornis* prior to 1980 was rapid growth coupled with reproduction by branch fragmentation (Shinn 1966; Gilmore and Hall 1976; Tunnicliffe 1981; Highsmith 1982). The dominance of *Acropora* spp. through asexual reproduction likely resulted in low genetic variation in at least some localities, possibly increasing the susceptibility of populations to disease (Bak 1983; Neigel and Avise 1983). However successful *A. cervicornis* was formerly, a nearly exclusive dependence on asexual reproduction, with limited potential for larval recruitment (Hughes 1985; Sammarco 1985; Knowlton, Lang, and Keller 1990; Hughes, Ayre, and Connell 1992), has slowed its recovery at most localities. *A. palmata* has shown higher rates of sexual recruitment than *A. cervicornis* in some situations (Rosesmyth 1984; Jordán-Dahlgren 1992), but *M. annularis* complex, like *A. cervicornis,* has recruited poorly (Bak and Engel 1979; Hughes 1985, 1989; Szmant 1986; Smith 1992).

A. palmata, A. cervicornis, and *M. annularis* complex are all broadcast spawners. Because they are now rare, *A. palmata* and *A. cervicornis* may be experiencing an Allee effect: colonies may be too far apart for high fertilization success (Knowlton 1992; Kojis and Quinn 1994; Levitan and Petersen 1995). The same may be true for *M. annularis* complex, although the mortality of

et.al., 1998, Richardson, 1999) may play an important role in shifting coral reef comunity structure.

Sedimentation effects on coral reef communities are multi-faceted since reduced light levels (disrupting nutritional dynamics), abrasion, and smothering can all result in limiting coral reef development (Hubbard, 1986; Rogers, 1990; Wittenberg & Hunte,1992). Coral reefs under sedimentation stress generally exhibit slower coral growth rates, lower coral diversity, and lesser rates of accretion (Roy & Smith, 1971; Loya, 1976; Rogers et al., 1984; Hubbard & Scatturo, 1985; Cortés & Risk, 1985). More recently, severe sedimentation has become a matter of increasing concern especially in developing areas undergoing rapid alterations in coastal land-use patterns (Hatcher et al., 1989; Rogers, 1990; Hodgson, 1993; Richmond, 1993). While periodic hurricanes are a normal feature of the environment in South Florida, there is concern that recent declines in water quality and changes in sedimentation regimens due to the urban and agricultural development may interact with storm disturbances (Ogden, 1992) and affect the recovery process for reefs affected by big storms like Andrew and Gordon which passed through Biscayne National Park in 1992 and 1994 respectively.

Though substantial reef development occurs at some sites within BNP, many areas are depauperate in coral cover and have very low relief. It is particularly interesting that the offshore, relic limestone areas with presumably better environmental conditions for reef development most of the year (warm, clear waters from the Florida current and stable substrate) show little development of physical structure (except for the Ball Buoy area in the extreme south of the Park), low diversity, and low abundances of corals compared to the inshore patch reefs. One regional factor potentially contributing to temperature and sedimentation stress on Florida reefs is the outflow of low quality water from Florida Bay. Ginsburg and Shinn (1993) discuss the inimical effect of bay water on reef distribution inferred from the distribution of Florida reefs adjacent to islands and lack of reefs where large passes between islands allow greater outflow of Florida Bay water. Stress due to

adult colonies has not been nearly as dramatic or complete as in the *Acropora* spp. (see Bak and Meesters 1999).

At this point, brooding corals are recruiting more successfully than broadcast spawners in the Caribbean. *Ag. agaricites,* a morphologically plastic, foliose species; other *Agaricia* spp.; *Porites astreoides,* a head-forming species; and *P. porites,* a branching species, are among the first to appear on disturbed reef surfaces, including *Acropora* rubble fields (Bak and Engel 1979; Neese and Goldhammer 1981; Rylaarsdam 1983; Rogers et al. 1984; Hughes 1985, 1989; Sammarco 1985; Hunte and Wittenberg 1992; Smith 1992, 1997; Chiappone and Sullivan 1996; Aronson and Precht 1997; Edmunds et al. 1998). All Caribbean representatives of the families Agariciidae and Poritidae are brooders.

One explanation is that the flexibility of larval lifespan afforded by lecithotrophy enables brooded planulae to settle either near or far from the mother colony (Fadlallah 1983; Szmant-Froelich, Ruetter, and Riggs 1985; Richmond 1987; Sammarco and Andrews 1989; Harrison and Wallace 1990; Ward 1992; Edinger and Risk 1995; Sakai 1997). Another possibility is that brooders have some advantage over broadcasters in fertilization success. *Acropora* spp., *Montastraea* spp., *Ag. agaricites,* and *P. astreoides* are all hermaphroditic, although *P. porites* may be gonochoristic (Harrison and Wallace 1990; Szmant 1986; Richmond and Hunter 1990; Richmond 1997). Information on rates of self-fertilization in hermaphroditic brooders *versus* hermaphroditic broadcasters would be highly relevant to the issue of recruitment success; the brooding *P. astreoides* and *Favia fragum,* for example, can exhibit high rates of self-fertilization (Gleason and Brazeau 1997; Brazeau, Gleason, and Morgan 1998), whereas self-fertilization is probably rare in broadcasting *Montastraea* spp. that are hermaphroditic (Knowlton et al. 1997; Szmant et al. 1997) and in other hermaphroditic broadcasters (Hagman, Gittings, and Vize 1998).

In the Indo-Pacific, brooding and broadcasting acroporids and other brooding and broadcasting species rapidly recolonize hard substrata in the wake of crown-of-thorns starfish (*Acanthaster planci*) outbreaks, coral bleaching, and other disturbances. Post-disturbance periods of algal dominance are generally shorter than in the Caribbean (Pearson 1981; Sammarco 1985; Colgan 1987; D. Smith 1991; Done 1992b; S. Smith 1992; Kojis and Quinn 1994; Gleason 1996; Fabricius 1997; Connell, Hughes, and Wallace 1997; but see Hatcher 1984; Endean, Cameron, and DeVantier 1988). The difference is in part a function of the small size of the Caribbean, where disturbances are more likely to have regional-scale effects, limiting the availability of coral recruits from upstream reefs in the wake of coral mortality (Connell 1997; Roberts 1997). Interoceanic differences in life history strategies, including a greater emphasis on sexual reproduction in Indo-Pacific acroporids, are probably also a factor.

It may be that the successful colonists of the Caribbean, which are not important framework builders, just happen to be brooders because a high proportion of living Caribbean species are brooders (Richmond and Hunter 1990; Richmond 1997). In other words, even if recruitment success on Caribbean reefs is independent of reproductive strategy, most good recruiters could be brooders based on chance alone. The emphasis on brooding in the Caribbean is tied to the evolutionary history of the modern coral fauna, as we shall see in the next section.

Origin of the Modern Coral Fauna of the Caribbean

The present-day coral fauna of the Caribbean is very unlike that of the Indo-Pacific, although both originated from the same Eocene–Oligocene pantropical species pool. Many of these differences can be traced to two intervals of evolutionary change in the Caribbean: A regional extinction in the early Miocene and a period of accelerated turnover during the Plio-Pleistocene. These two formative episodes affected both the taxonomic composition and ecological attributes of the fauna.

Following an extinction interval in the late Eocene (Budd, Stemann, and Stewart 1992), coral reefs were well developed and the scleractinian fauna was diverse in the Caribbean by the late Oligocene (Frost and Langenheim 1974; Frost 1977b; Veron 1995). At the beginning of the Miocene, closure of the eastern end of the Tethyan Seaway and the opening of the Drake Passage increased upwelling in the Caribbean (references in Edinger and Risk 1994, 1995). Environmental changes related to upwelling, including increased nutrient loading and turbidity, and lowered sea temperatures, were apparently responsible for the regional extinction of half the genera living in the Caribbean at the time (Edinger and Risk 1994, 1995). The survivors were primarily eurytopic genera in terms of both habitat distribution and environmental tolerance (the latter surmised from the autecology of modern representatives). Genera that were tolerant of the cool, turbid water produced by upwelling survived in far greater proportion than genera tolerant of cool water only, turbid water only, or neither cool nor turbid water (Edinger and Risk 1994). Broad habitat distribution was also correlated with survival.

Taxonomically, the result of this extinction was a culling of genera in the Caribbean. Most of the genera that became extinct in the Caribbean are extant in the Indo-Pacific (Frost and Langenheim 1974; Frost 1977a). Ecologically, the early Miocene extinction may have fundamentally changed the distribution of reproductive strategies in Caribbean corals.

Edinger and Risk (1995) inferred the reproductive strategies of Miocene coral genera from the modern representatives of those genera. If such inferences

INTRODUCTION

The global distribution of coral reefs is generally restricted to lower latitude environments with less variable temperature regimes and clear, well circulated waters with relatively low standing stocks of nutrients. Such correlational observations have formed the basis of consensus that these environmental factors are the primary delimiters of coral reef development and distribution. Despite its latitudinally marginal position just south of 26°N, the Florida reef tract is the second longest barrier reef system in the western Atlantic and is the most extensive reef development in the continental United States. Biscayne National Park (BNP) lies at the northern extreme of the Florida Reef Tract (Fig.1).

Temperature is probably the oldest-acknowledged limiting factor for reef building zooxanthellate corals and for reef development (Darwin, 1842; Dana, 1843; Mayor, 1914; Hudson et al., 1976a,b; Hudson, 1981). In Florida, there is a fairly long temperature record dating back to the late 19th century and documenting temperatures below 16°C on BNP reefs as far back as 1898 (Vaughan, 1918). More recent records have documented three episodes below 14°C and four additional episodes at or below 16°C between 1977 and 1981 in BNP and Florida Bay waters (Roberts et al., 1983; Tilmant, cited in Burns 1985). Coral mortality attributed to winter cold has been reported repeateadly from many reefs in the Florida Reef Tract and the Dry Tortugas (Porter et al. 1982, Davis 1981, Walker et al. 1982). Long lasting, high water temperatures can be equally detrimental to corals. Widespread coral bleaching events in Florida in the late 1980's due to higher than normal summer water temperatures also indicate stressful conditions for corals in this area. Even though temporary recovery was usually observed, bleached and "recovered" corals may show elevated rates of mortality in subsequent years (Porter & Meier 1992). Disease outbreaks such as the white band disease that significantly reduced population levels of acroporids in the Caribbean and the white plague infestation of 1995 which killed large numbers of several zooxanthellate corals in the Florida keys (Gladfelter, 1982, Richardson

are valid (and they require caution since coral reproductive modes are evolutionarily labile; Kinzie 1997), then most genera that survived the extinction contained all or at least some brooding species. This apparent bias in survival during the Miocene contributed to the greater emphasis on brooding reproduction in the Caribbean today; most modern Indo-Pacific species are broadcasters (Smith 1992; Richmond 1997).

Edinger and Risk (1995) suggested two possible explanations for the preferential survival of brooding genera in the early Miocene, one based on dispersal and the other on recruitment. The first hypothesis was that brooded, lecithotrophic planulae dispersed further than the planktotrophic planulae produced by broadcast spawning (Richmond 1987, 1988; Richmond and Hunter 1990). The observed geographic ranges of brooding and broadcasting corals in the Indo-Pacific do not support this dispersal hypothesis. Instead, Edinger and Risk (1995:212–213) preferred a recruitment-based hypothesis in which the high proportion of brooding genera surviving the Miocene extinction event was a consequence of species sorting. In this hypothesis, brooding was associated with other features that conferred recruitment success and resultant extinction resistance:

> Brooding . . . coral genera are mostly eurytopic, tolerant of both turbid and cold conditions. . . . Onset of upwelling in the Caribbean during the Early Miocene apparently favored brooding corals, but by virtue of the ecological correlates of brooding, rather than reproductive mode per se. Rather, brooding is correlated with other traits which helped corals survive in the deteriorating habitats of the Miocene Caribbean.

This argument is based on the observed correlations among brooding, eurytopy, and survival in the Miocene.

If brooding was a consequence rather than a cause of generic survival, then we can make a testable prediction: There should be no difference in generic survival between eurytopic brooders and eurytopic broadcasters. We used Edinger and Risk's (1995) data on eurytopic Miocene coral genera from Puerto Rico to examine the relationship between survival and reproductive mode. One null hypothesis was that survival among genera tolerant of both cold water and turbidity was independent of reproductive mode. We could not falsify this null hypothesis (one-tailed Fisher's exact test, $0.20 < P < 0.50$), a result that probably reflects low sample size (figure 9.2A). Brooding genera with a wide habitat distribution, however, were significantly more likely to survive than broadcasting genera with a wide habitat distribution ($P < 0.05$; figure 9.2B). Therefore, the possibility remains that brooding itself conferred survival advantage during the Miocene crisis.

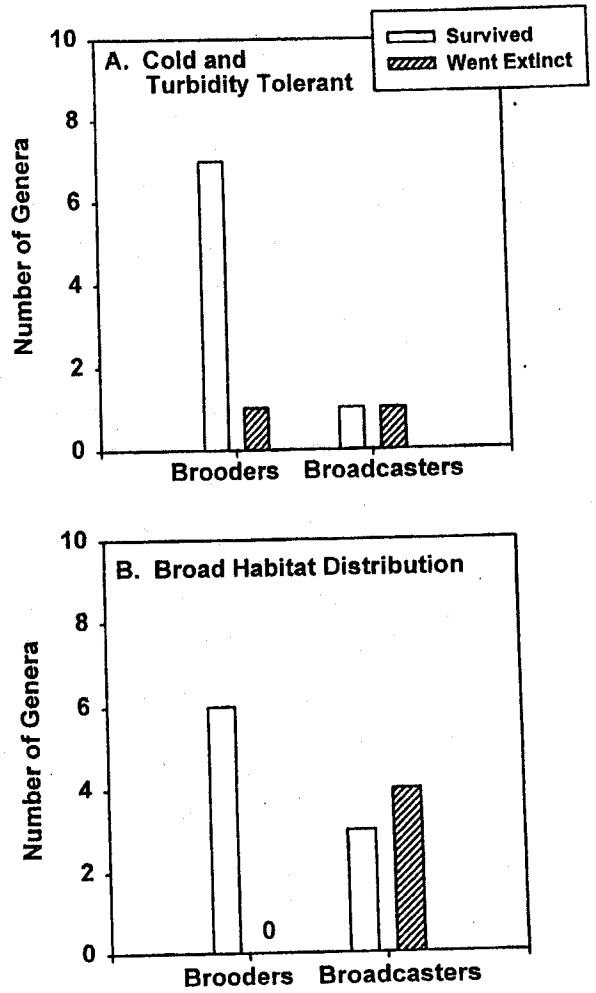


FIGURE 9.2. Relationships between generic survivorship through the early Miocene extinction interval and mode of sexual reproduction (genera in which some or all species are brooders versus genera in which all species are broadcasters) for (A) genera tolerant of cold water and turbidity, and (B) genera with a broad habitat distribution. Data are from a survey in Puerto Rico by Edinger and Risk (1995, their table 3).

Brooding genera may have survived preferentially in the Miocene because of the enhanced recruitment success of individual, brooded coral planulae, but not because of long-distance dispersal ability. The advantage of brooding in the Miocene, as well as today, may lie precisely in the potential for a short larval life. Short dispersal distances enable brooding colonies that survive a disturbance to

correlated with adult densities for six common scleractinian species. Temperature regimes were more variable in the patch reefs, a pattern opposite to what would be expected to correspond to the greater coral cover in these localities. Sediment deposition rates, water column and sediment nutrient concentrations were temporally variable and provided no clear correlation with the observed spatial patterns of benthic community structure. This suggest that other factors such as historical effects of severe cold snaps, storms, disease outbreaks, coral recruitment and juvenile survival may be the dominant structuring forces limiting the abundances of large, reef-forming species in offshore sites in Biscayne National Park.

Key Words: Community structure, coral reef, environmental correlates, Florida, coral recruits.

disperse their planulae effectively to nearby patches of substratum that have been opened by mortality of the previous incumbents (Szmant 1986; Carlon and Olson 1993). As a result, local brooders may have the advantage of priority over distant broadcasters.

After the extinctions of the early Miocene and further origination and extinction activity in the middle and late Miocene (Kauffman and Fagerstrom 1993; Budd, Stemann, and Johnson 1994; Veron 1995), the Caribbean coral fauna changed little from ~8 Ma until the Plio-Pleistocene. Increased rates of origination from 4 to 3 Ma and extinction from 2 to 1 Ma resulted in a fauna virtually identical in species composition to the modern fauna (Budd, Johnson, and Stemann 1994, 1996; Budd and Johnson 1999). It was during the interval from 2 to 1 Ma that acroporids replaced pocilloporids as the dominant corals on Caribbean reefs (Jackson 1994a; Jackson and Budd 1996; see also Frost 1977a). The environmental causes of the Plio-Pleistocene turnover are not well understood, but they may be related to the emergence of the Isthmus of Panama 3.5 Ma (Budd, Johnson, and Stemann 1994; Johnson, Budd, and Stemann 1995). Global climate change associated with the onset of prolonged glacial eustasy from 2.5 to 1 Ma (e.g., Shackleton 1985; Stanley 1986) could have played a role as well. Subsequent glaciations and deglaciations in the Pleistocene, however, did not affect the fauna appreciably. After 1 Ma, the Caribbean coral fauna persisted largely intact until the present (Budd, Stemann, and Johnson 1994; Jackson 1994b; Hunter and Jones 1996).

Like the Miocene extinctions, the Plio-Pleistocene turnover had ecological as well as taxonomic consequences. Neither mode of sexual reproduction was favored, but Johnson, Budd, and Stemann (1995) documented extinction resistance and a resulting relative increase in taxa that (1) grow as large, long-lived colonies, and (2) reproduce by fragmentation. This Plio-Pleistocene bias underlies the dominance of modern Caribbean reefs by the three primary framework builders: *A. palmata, A. cervicornis,* and *M. annularis* complex (Budd, Johnson, and Stemann 1994; Johnson, Budd, and Stemann 1995).

In summary, after passing through environmental filters in the early Miocene and the Plio-Pleistocene, the Caribbean coral fauna, and the zonation patterns that the fauna created, survived the glacial cycles of the Pleistocene. Jackson (1994a; Jackson and Budd 1996) raised the possibility that species selection or species sorting accounts for the recent dominance and subsequent demise of the three primary species. Features such as high growth rates and an emphasis on fragmentation in *Acropora* spp., acquired before the Pleistocene, may have helped these species persist through the Pleistocene glaciations to become framework builders on modern reefs (Jackson 1994a; Veron 1995; McNeill, Budd, and Borne 1997). *Acropora* spp. in particular have been decimated over the past two decades as some of those features have become less advantageous or even detrimental (Jackson and Budd 1996; Jackson, Budd, and Pandolfi 1996).

We have described a relatively static coral fauna interrupted by two historical intervals of accelerated turnover. The Recent episode of rapid transition could also have consequences beyond ecological time. We now turn to the community integration hypothesis posed in the Introduction. Does the long-term persistence of species composition on reefs imply that Caribbean corals form interactive, tightly integrated communities? The next section reviews the theory behind the community integration debate, and the two sections following apply those theoretical considerations to Caribbean reefs.

Coordinated Stasis and the Response to Disturbance

A number of studies have documented the persistence of terrestrial and marine paleocommunities through environmental fluctuations for as long as several million years. Community replacement then occurred during ecosystem reorganization in the face of more intense environmental change (e.g., Vrba 1985; Brett and Baird 1995; Morris et al. 1995; Brett, Ivany, and Schopf 1996; DiMichele, Pfefferkorn, and Phillips 1996; Holterhoff 1996; Tang and Bottjer 1996). This temporal pattern has been dubbed *coordinated stasis*, and it is viewed as the paleoecological analogue of phylogenetic punctuated equilibrium. Most observations of coordinated stasis come from Paleozoic sequences.

For paleobiologists, coordinated stasis revived a classical debate in ecology over the nature of community structure. In the Clementsian view, the community was interpreted as a superorganism. The component species were highly interactive and their distributions were strongly associated along environmental gradients (Clements 1916, 1936). The Gleasonian model rejected the idea of tight community integration. Instead, the community was seen as a collection of independently distributed species (Gleason 1926). The Gleasonian model does not exclude the possibility of succession, competition, niche partitioning, assembly rules, and other interspecific interactions. Rather, it denies interspecific interdependence as the cause of species distributions (Hoffman 1979; Allen and Hoekstra 1992; McIntosh 1995).

Few ecologists subscribe to the Clementsian superorganism concept at this point, the majority opinion being that communities conform to the Gleasonian "independent-but-interactive" model (Underwood and Denley 1984;

ABSTRACT

The coral reefs of Biscayne National Park, Florida, lie at the northern fringe of the Florida Reef Tract and of coral reef distribution in the western Atlantic. Environmental forcing of community structure is expected to be strong. Nine refal areas were quantitatively characterized within the Biscayne National Park and environmental factors such as temperature, sedimentation, and nutrient content in the sediment and water column were monitored to examine possible correlations with community structure patterns. Live cover, densities and diversity of scleractinian corals, octocorals, sponges, zoanthids and hydrocorals as well as cover of algae and other substrate types were quantified in 75-104, 1 m^2 quadrats along 4-5 transects for each of nine shallow bank and patch reefs and hard bottom communities selected along four east-west transects distributed from north to south within the Park. Benthic cover was dominated in all sites by algal turf, crustose and macro algae. Sponges were the most diverse group of macro invertebrates (66 spp. in 41 genera) followed by scleractinian corals (52 spp. in 23 genera) and octocorals (43 spp. in 11 genera). Octocorals were the most abundant group on eight of the nine localities sampled. Despite closer proximity to hypothetically detrimental terrestrial and bay influences, near-shore patch reefs had higher live cover, densities and species richness of cnidarians and sponges, a greater abundance of large scleractinian corals and of octocorals, and reduced prevalence of bare substrate and algal turf compared to latitudinally-similar offshore localities. Inshore patch reefs were more spatially variable in mean percent cover of the different bio-groups, with increases for sponges, hydrocorals and crustose algae towards the south and decreases in cover of turf algae, scleractinians and octocorals. Octocoral densities were significantly higher in all but one reef compared to other cnidarians and sponges with significantly higher densities in the patch reefs compared to the offshore sites. Decrease cover of turf algae towards the south, away from Miami, was correlated with an increase in live cover, densities and diversity of cnidarians and sponges, cover of macro-algae and bare substrate in offshore sites. Juvenile coral densities were higher in southern patch reefs and were significantly

Roughgarden 1989; McIntosh 1995; Dayton et al. 1998). Nevertheless, some studies of terrestrial ecosystems suggest a causal connection between high species diversity and "superior" ecosystem function (high productivity, stability, resistance to invasion) (Bengtsson, Jones, and Setälä 1997). Whether diversity per se is important to the function of coral reef ecosystems is an unresolved question (Done et al. 1996).

Coordinated stasis in the fossil record has been interpreted as evidence in favor of the Clementsian model of community structure: Communities persisted for geologically significant periods as tightly integrated entities, and sets of mutually dependent component species appeared and disappeared as units (DiMichele 1994). Morris et al. (1995) suggested that interspecific interactions led to "ecological locking." According to this hypothesis, interspecific dependencies enabled the living communities to resist disturbance, up to some threshold disturbance intensity that caused whole-community reorganization. Brett, Ivany, and Schopf (1996:15) stated, "Some form of internal coherency appears to be necessary to maintain the stability of assemblages (derived from either traditional notions of incumbency, or ecosystem organization e.g. ecological locking. . .)" These "autogenic" models (Miller 1996) invoke interspecific interaction or dependence as an emergent property that stabilizes community composition for long periods. "Allogenic" explanations for the persistence of communities include persistently stable environments and faunal tracking of environments when conditions vary (Brett 1998).

Ironically, even as paleobiologists considered patterns of coordinated stasis, ecologists discovered the large body of paleontological literature that supports the Gleasonian model (Walter and Paterson 1994). In contrast to the coordinated stasis observed in Paleozoic paleocommunities, species in Cenozoic paleocommunities are in general distributed independently (e.g., Davis 1986; Paulay 1990; Valentine and Jablonski 1993; Buzas and Culver 1994, 1998; Roy, Jablonski, and Valentine 1995; Bennett 1997). Some studies of Paleozoic marine faunas also support the Gleasonian model (Westrop 1996; Patzkowsky and Holland 1997).

Brett, Ivany, and Schopf (1996) attributed the apparent Paleozoic–Cenozoic difference in community structure to better stratigraphic resolution in the Cenozoic. Because variance is high at the scales of the living community and preserved paleocommunity, biotic patterns occur at and should be sought at scales and organizational levels above the community and paleocommunity: the assemblage or community type of Boucot (1983, 1990), the paleocommunity type of Bennington and Bambach (1996), or the metacommunity of Jackson, Budd, and Pandolfi (1996). A metacommunity is a set of connected communities occupying a habitat type. Ecological-scale noise of the fluctuating

component communities should be small compared to larger-scale, metacommunity signals. For example, patterns should emerge when coral reefs are studied in aggregate, over areas larger or through time intervals longer than the spans of individual reefs.

Searching for pattern at larger scales is entirely reasonable, but inferring process at those larger scales is problematic. In terms of the putative mechanisms underlying coordinated stasis, it seems unrealistic to try to reconcile individualistic distributions at ecological scales and community integration in time-averaged paleocommunities at larger scales. Species from different successional stages may interact in ecological time (through substratum conditioning, etc.), but it is far more difficult to argue for dependence among species that lived in a habitat thousands or tens of thousands of years apart (Aronson 1994). (The dynamics of coral reefs may actually be amenable to such multiscaled explanations under certain circumstances, and we will return to this possibility later.)

Community Structure of Coral Reefs

From a broad-scale, regional perspective, at least some assemblages of Cenozoic reef corals display distributional patterns that suggest coordinated stasis punctuated by community change. Does this mean that coral reefs are an exception to the Gleasonian dynamics of most Cenozoic communities (Brett, Ivany, and Schopf 1996; Jablonski and Sepkoski 1996)? While rejecting a strictly Clementsian interpretation, Jackson (1994a; Jackson, Budd, and Pandolfi 1996) proffered a version of the ecological locking hypothesis for Caribbean reefs, in which interspecific interactions or associations at some scale keep species bound up in stable communities or metacommunities.

To test for the pattern of coordinated stasis, Budd and colleagues examined the Plio-Pleistocene turnover at several Caribbean localities with good stratigraphic resolution. They found that the dynamics of faunal replacement varied with geographic location (Budd, Johnson, and Jackson 1994; Budd, Johnson, and Stemann 1996). In the Bahamas, pre- and post-turnover coral assemblages were discrete and did not overlap in species composition, favoring the coordinated stasis model. At other localities, however, the model was not supported. The turnover in Curaçao and Costa Rica was characterized by protracted, stepwise addition and removal of species rather than by whole-community collapse and reorganization (Budd and Johnson 1997; Budd, Petersen, and McNeill 1998).

What of the static coral fauna that followed during the Pleistocene–Holocene? Ecological locking, community integration, or mutual dependence

SPATIAL PATTERNS OF REEF COMMUNITY STRUCTURE AND ENVIRONMENTAL CORRELATES IN BISCAYNE NATIONAL PARK, FLORIDA.

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of species within associations may account for the observed constancy of assemblage composition. On the other hand, individualistic interpretations may have equal or greater explanatory value while requiring fewer assumptions about higher-order processes.

There is a striking concordance in species composition between Pleistocene–Holocene fossil reefs and living reefs of the Caribbean. Most impressive are fossil coral assemblages that are compositionally similar to living communities occurring in the same place (e.g., Hubbard, Gladfelter, and Bythell 1994; Hunter and Jones 1996). Observations of this sort have been tendered as evidence for the community integration hypothesis.

In Jamaica, limestone outcrops spanning 0–6 m above present sea level represent coral reefs deposited ~125 Ka, during the last major interglacial high sea stand (Liddell, Ohlhorst, and Coates 1984; Boss and Liddell 1987). The 125 Ka Pleistocene bank/barrier reef exposed along the eastern margin of Rio Bueno Harbor, on the north coast of the island, is dominated by *A. palmata, A. cervicornis, M. annularis* complex, and *Porites porites* in the fore-reef facies (Liddell, Ohlhorst, and Coates 1984). The same species characterize(d) the living fore-reef community in the waters just below at Rio Bueno and at nearby Discovery Bay (Precht and Hoyt 1991).

The living community at Negril, on Jamaica's west coast, is quite different. Here the primary habitat type is flat limestone pavement. As is typical of hardground habitats in the Caribbean, Negril is populated primarily by gorgonians and massive corals. In this case *M. annularis* complex, *Siderastrea siderea, Diploria* spp., and the pillar coral *Dendrogyra cylindrus* are among the dominant scleractinians. Examination of the emergent, 125 Ka Pleistocene deposit just above reveals the same suite of massive coral species. Gorgonians are not preserved, but flamingo tongues, *Cyphoma gibbosum* (Gastropoda), are abundant (W. F. Precht, unpublished data). Since flamingo tongues prey significantly and exclusively on gorgonians in modern Caribbean communities (Harvell and Suchanek 1987; Lasker and Coffroth 1988), their abundance in the Pleistocene of Negril signifies that gorgonians were common at the time. Thus, the difference between locations is far greater than the difference between 125 Ka and the present.

These qualitative observations agree with a detailed, quantitative study of reef coral assemblages in the Pleistocene of New Guinea. Pandolfi (1996) examined paleocommunity composition based on species presence and absence on nine sequentially uplifted, Pleistocene reef terraces on the Huon Peninsula, Papua New Guinea. The interval examined spanned 95 k.y. and included nine glacial cycles. Variation in species composition was greater across space than through time. Although there was considerable variation

through time even at a single locality, only a limited subset of the available, habitat-specific species pool constituted the metacommunity characteristic of a particular place. This suggested to Pandolfi (1996:152) that "local environmental parameters associated with riverine and terrestrial sources had a greater influence on reef coral composition than global climate and sea level changes." Pandolfi (1996), however, argued against the hypothesis that metacommunities were simply collections of species that tracked habitats and local environments. Instead he favored a community integration model to explain limited membership in coral assemblages.

Pandolfi's argument was based on the inference of interspecific competition in Caribbean corals, for which zonation patterns are better understood than Indo-Pacific corals. A few extant coral species, such as *A. palmata,* live only under a narrow range of environmental conditions. Most coral species occupy a broad range of environments, but they are common or dominant only within a subset of that range. This observation could imply present or past competitive interactions, which could in turn imply community integration.

As discussed previously, competition and other biological interactions such as niche partitioning (Hubbell 1997) can occur in reef communities even if they are collections of independently distributed species. More significant are the observations that (1) many Caribbean coral species are common over a broad range of environments (e.g., Porter et al. 1981; Aronson and Precht 1997; Bruno and Edmunds 1997), and (2) most Caribbean species are broadly distributed on a regional scale (Veron 1995; Pandolfi and Jackson 1997; Karlson and Cornell 1998). Both of these patterns are consistent with the independent distribution model. Given the clear influence of local physical conditions in Pandolfi's (1996) study, it is difficult to reject the hypothesis that the shared distributional patterns of Indo-Pacific coral species in New Guinea resulted from shared environmental preferences, which have persisted since the Pleistocene.

Coral diversity within reef communities depends on both the regional species pool and a suite of local factors (Karlson and Cornell 1998). The redundancy of ecologies observed in Indo-Pacific corals and other reef-dwelling taxa ensures that those reef communities function in essentially the same manner over a broad range of species richness values and through large variations in species composition (Roberts 1995; Paulay 1997). Because the Caribbean is dominated by only three coral species, the resilience of entire reef communities after disturbance may be more limited (Kojis and Quinn 1994; Birkeland 1996; see also Coral Reproductive Strategies). One might therefore predict that the community integration model is more likely to apply to Caribbean reefs.

Following Pandolfi's (1996) approach, Jackson, Budd, and Pandolfi (1996) presented evidence for limited membership in Caribbean fore-reef communities: Species composition varied geographically among fore-reef assemblages, but the fauna occurring in a particular environment through time was a limited subset of the available species pool. The same criticisms of proposed process apply. It is well established that Caribbean reef corals track environmental conditions through space and through changes in sea level (Goreau 1959, 1969; Lighty, Macintyre, and Stuckenrath 1982; Macintyre 1988; Fairbanks 1989; Pandolfi and Jackson 1997). In fact, one environmental signal that Jackson, Budd, and Pandolfi (1996) discovered was a difference in assemblage composition between the eastern/oceanic and western/continental areas of the Caribbean. Again, the persistence of species composition does not appear to be predicated on integrated species assemblages or interspecific associations within (meta)communities.

In many situations, small-scale variability masks large-scale pattern and higher-order process. In this case, we suggest that the small-scale variability detected among assemblages within environments is an important aspect of pattern: It reflects the independent distribution of species on coral reefs. The search for large-scale pattern has, we think, confused the issue somewhat through deliberate time-averaging.

Modern and "Postmodern" Reefs of the Caribbean

Even if community composition exhibits a pattern of stasis and punctuated change, paleontological data alone cannot eliminate one or another model of underlying causality (Miller 1997). The only hope for such a test is to combine paleontological observations of pattern with ecological observations of process. Is it possible to distinguish the independent distribution and community integration models with respect to the transition to macroalgal dominance on Caribbean reefs? Regardless of the availability of ecological data, the coral-to-macroalgal transition in the Caribbean presents a paleontological problem: Corals preserve in the fossil record, but fleshy macroalgae do not (Kauffman and Fagerstrom 1993).

Aronson and Precht (1997; Aronson, Precht, and Macintyre 1998) avoided this taphonomic pitfall when they documented a recent transition from *A. cervicornis* to *Agaricia* spp. (primarily *Ag. tenuifolia*) on reefs in the central shelf lagoon of the Belizean Barrier Reef. One lagoonal reef, Channel Cay, was studied intensively over a 10 yr period. Beginning in 1986, the *A. cervicornis* population at Channel Cay died off catastrophically from white-band disease. *Agaricia,* rather than macroalgae, recruited to the *A. cervicornis* rubble, and

subsequent *Agaricia* growth produced a thick accumulation of dead skeletal material.

Both *A. cervicornis* and *Agaricia* have high preservation potential in the lagoonal environment in Belize. By 1995 the community shift had produced a clear signal in the sedimentary record: a thin layer of heavily eroded *A. cervicornis* rubble topped by a 22 cm thick layer of imbricated *Agaricia* plates. The uncemented, uncompacted nature of the subsurface sediments made it possible to core the reef in search of previous transitions of this sort.

Cores were extracted from Channel Cay and radiocarbon dated. The 7.6 cm diameter cores revealed no significant reworking of the reef sediments and no layers of *Agaricia* rubble below the post-1986 accumulation (figure 9.3). From the age determinations, Aronson and Precht (1997) concluded that prior to 1986, a transition to *Agaricia* had not occurred since at least 3–4 Ka. We have now taken cores from reefs throughout a 375 km^2 area of the central shelf lagoon. The new cores support the conclusion of a unique transition. The unique transition, however, did not result because the incumbent, *A. cervicornis*–dominated community was tightly integrated, nor did it result because that community as a whole somehow resisted less intense disturbances.

Point-count data along replicate transects at Channel Cay showed that *Agaricia* spp. were present but rare in 1986 (figure 9.4). As the *A. cervicornis* population crashed, *Agaricia* opportunistically recruited to the *A. cervicornis* skeletal rubble and increased in percent cover. Macroalgal cover remained low (<10%) throughout the period 1986–1995. *Agaricia* increased instead of macroalgae because of (1) the brooding reproductive strategy of *Agaricia* spp., which promoted local recruitment, combined with (2) intense herbivory by the abundant sea urchin *Echinometra viridis,* which suppressed macroalgal populations. Meanwhile, the 12 other coral species that were present maintained low cover (<10%) and did not fluctuate significantly. The trajectories of percent cover of coral species and genera were thus largely independent, at least on a decadal scale. Whether the independent distribution model will still explain the dynamics of Channel Cay several decades from now is unknown.

Agaricia spp. are not the only coral species that can take advantage of WBD outbreaks. *Porites porites* opportunistically replaced *A. cervicornis* on a patch reef at San Salvador Island, Bahamas (Curran et al. 1994). This replacement sequence was also noted in backreef habitats in Belize (Macintyre and Aronson 1997). Like the Caribbean *Agaricia* spp., *P. porites* is a brooder and a good colonizing species (see Coral Reproductive Strategies). If more than one coral species can be the replacement species, it is again difficult to argue for community integration.

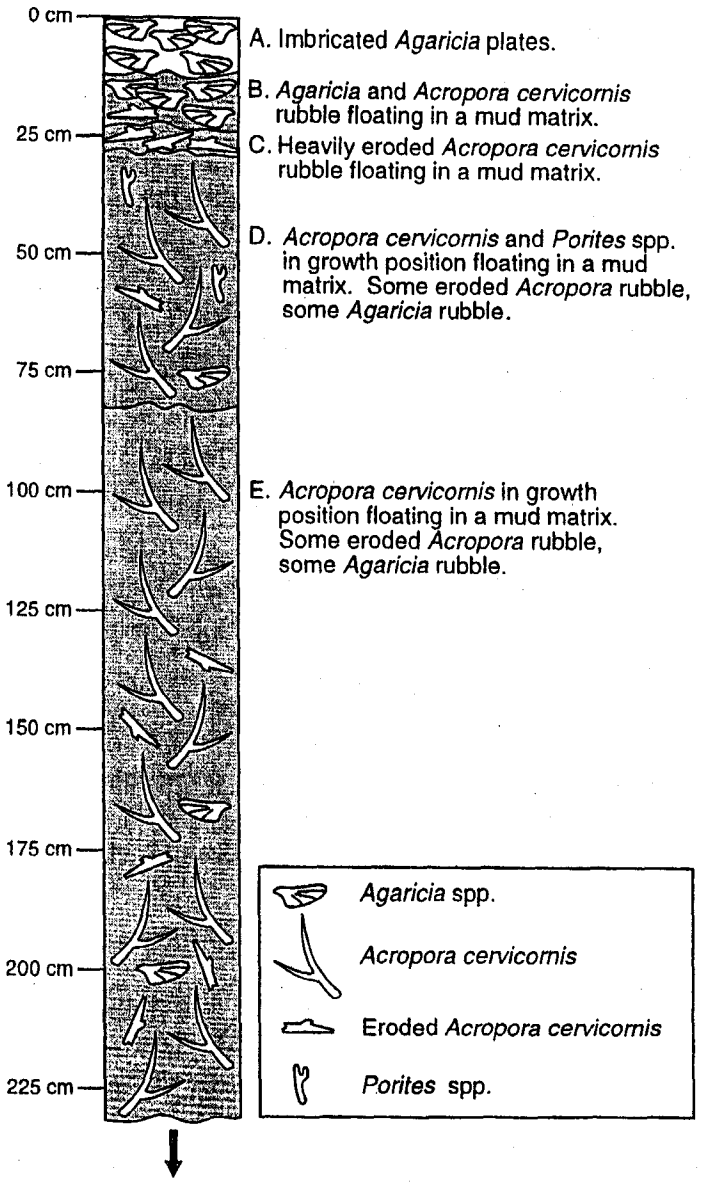


FIGURE 9.3. Schematic drawing of a generalized core from Channel Cay, a reef in the central lagoon of the Belizean Barrier Reef. The living community was removed prior to coring. Wavy, horizontal lines separate conformable variations in core composition, as a convenience to the reader. (A), (B), and (C) represent deposition during the period 1986–1995. All coral species other than those figured constituted <5% of the material. Centimeter scale shows depth within the core, and shading represents mud matrix. Redrawn from Aronson and Precht (1997).

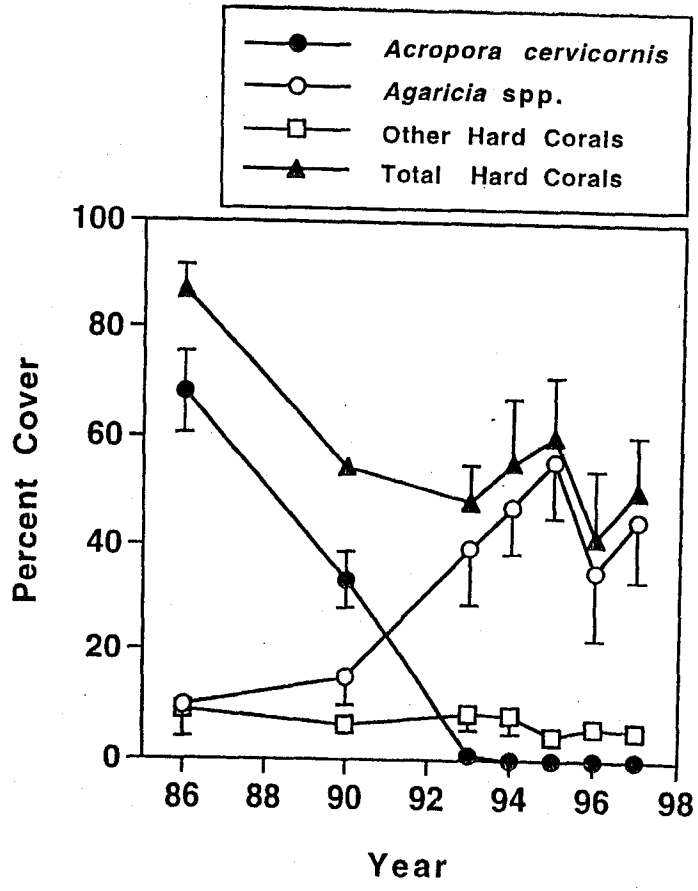
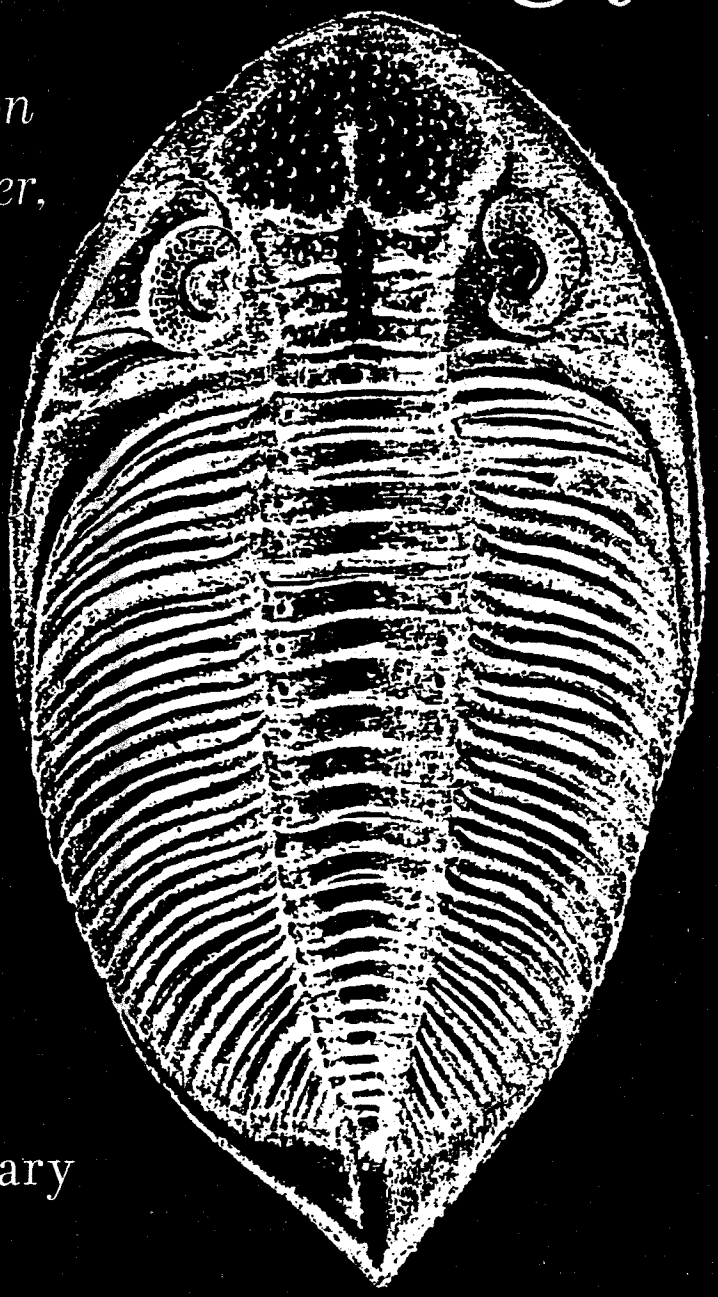


FIGURE 9.4. Changes in percent cover of living corals at Channel Cay over the period 1986–1997. Percent cover values were calculated from point counts along transects laid down the slope of the reef at two stations, perpendicular to depth contours. Data were pooled across the 3–15 m depth range of the transects. Error bars represent standard deviations; positive or negative errors are omitted for clarity.

Turning to the more widespread coral-to-macroalgal transition, even if it represents a rare or unique occurrence it would be premature to conclude that it was caused by the disruption of integrated reef communities. One could argue that the persistence of *M. annularis* depended indirectly on the presence of *A. cervicornis*. Macroalgal overgrowth of adult *M. annularis* colonies at Discovery Bay may have occurred because algal colonization was enhanced by the availability of *A. cervicornis* rubble or because pomacentrids switched their territories to *M. annularis*. In general, however, different things have happened

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Editors



The Ecological Context of Macroevolutionary Change

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to *M. annularis* in different places (see Causes of Coral Mortality). Where mortality of *M. annularis* has occurred, it has generally been a separate issue from the demise of *A. cervicornis* populations.

There is no doubt that coral species interact on Caribbean reefs, particularly when coral cover is high (Lang 1973; Porter 1974; Lang and Chornesky 1990). There is also no doubt that strong biological associations exist on Caribbean reefs; corals and zooxanthellae are mutually dependent, and flamingo tongues cannot exist without gorgonians. Nevertheless, the transition to macroalgal dominance is only the summation of coral species' independent responses to a number of contemporaneous perturbations. The excision of *Acropora* spp. from previously stable Caribbean reef communities has not dragged *M. annularis* and other coral species into a maelstrom of community disintegration, at least not yet.

Stasis and Change Reconsidered

Potts (1984) proposed an individualistic explanation for faunal stasis after the Plio-Pleistocene turnover. For Indo-Pacific corals with long generation times, continual disturbance in the Plio-Pleistocene maintained high intraspecific genetic variation. The result was low turnover of the coral fauna (see also Veron 1985, 1995). A similar individualistic hypothesis can be constructed for the Caribbean fauna, although there are some species with short generation times to which the model apparently does not apply (Potts and Garthwaite 1991). Jackson and Budd (1996) suggested as an alternative that Pleistocene stasis occurred in the Caribbean because those species that passed through the Plio-Pleistocene filter were eurytopic: Their preadaptations made them resistant to subsequent fluctuations.

The two explanations are really quite similar. In each hypothesis, the mechanisms maintaining stasis before and after the turnover event were different. Before the turnover, a long period of stasis occurred in a relatively benign environment. That stasis was shattered by environmental change during the Plio-Pleistocene. Then, after the turnover, stasis occurred despite continued environmental change because of the eurytopic (Jackson and Budd 1996) or plastic and variable (Potts 1984) nature of the coral species. Most recently, new combinations of coral diseases and other factors have overwhelmed the capacity of the eurytopic or plastic species to adjust to new conditions, hence the sudden biotic shift of the last 20 years. Ecological and evolutionary stasis and change of the Caribbean coral fauna thus becomes largely an observation of species' independent responses to the tempo and amplitude of environmental change.

Future Research

The recent transition to macroalgal dominance is a regional phenomenon. Widespread mortality of incumbent coral populations was a prerequisite, and white-band disease was probably the most important cause of *Acropora* mortality over the past decades. Paleontological data suggest that, although populations of *Acropora* spp. have died off locally in the past (Shinn et al. 1981; Lewis 1984; Shinn et al. 1989), a Caribbean-wide mass mortality of these corals has not occurred previously during the Holocene. Core data from St. Croix suggest that the WBD-induced mortality event was unique in the Holocene (Hubbard, Gladfelter, and Bythell 1994). Our studies in the shelf lagoon in Belize support the hypothesis of a unique event, if the WBD-mediated, *Acropora*-to-*Agaricia* transition can be considered a preservable proxy for the more widespread *Acropora*-to-macroalgal transition. Likewise, Greenstein, Curran, and Pandolfi (1998) argued that the WBD-mediated *Acropora*-to-*Porites* transition observed at San Salvador had not occurred previously. Mann et al. (1984; Taylor et al. 1985) described a lagoonal reef in the Dominican Republic that dated to 9–5 Ka. Judging from the excellent preservation of the corals, the shallow outer slope of this fossil reef was dominated continuously by *Acropora*, without intervening transitions to other community configurations (Stemann and Johnson 1995).

More paleontological evidence is needed to test the generality of these patterns. There is, for example, evidence of late Holocene declines of *A. palmata* populations in the Bahamas, Barbados, and Florida (Lighty 1981; Lewis 1984; Shinn et al. 1989). We agree with Jackson and Budd (1996) that ecological change in fossil reef communities is best understood from the relative abundance of species and not just from presence-absence data.

On the biological side, we know precious little about diseases on coral reefs. Do pollution and other forms of disturbance render corals more susceptible to disease (Edmunds 1991; Harvell et al. 1999)? We also must learn more about the sexual systems, fertilization, larval transport and behavior, settlement, recruitment, and post-settlement mortality of the coral species that have been displaced and those that have begun to colonize in their wake (see Bak and Meesters 1999; Mumby 1999). Reproductive processes interact in complex ways to influence the distribution of adult colonies and the ecology of reef communities. Self-fertilization, rather than brooding, could be the key to success after disturbance, and the predominance of brooding in Caribbean corals could be a nonadaptive consequence of species sorting after all.

By analogy with current models of natural selection at multiple taxonomic levels, Wilson (1997) argued that selection at the level of the community is at

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least conceivable and should not be rejected out of hand. One model of coral reef ecology holds that the persistence of reef communities turns on the positive interactions between corals and herbivorous fishes: Corals provide the structure necessary to shelter fish, and fish control the algae that would otherwise impede coral growth (e.g., Hay and Goertemiller 1983; Hay and Taylor 1985; Szmant 1997). Coral species may not be mutually dependent, but perhaps compositionally variable assemblages of coral species are dependent on compositionally variable assemblages of herbivorous fish species, and vice versa. Does this postulated "diffuse mutualism" between corals and fish represent community integration? Was it responsible for faunal stasis of Caribbean reefs during the Pleistocene–Holocene? Only by long-term monitoring can we attempt to answer these questions. We must follow the ecological dynamics of reef communities on the multidecadal scale appropriate to the turnover times of the fish and corals, while recognizing that some hypotheses will be untestable in our lifetimes.

There remains a potential link between the individualistic behavior of coral species in ecological communities and integrated dynamics of reef metacommunities, but it is highly speculative. The current decline of the three primary framework builders in the Caribbean could promote bioerosion and slow future reef accretion (cf. Glynn and Colgan 1992). As a result, reefs could drown in the face of rising sea level (Smith and Buddemeier 1992; Graus and Macintyre 1998). In such a case, the trajectory of the future community would be influenced by species in the current community. Biological interaction, interspecific interdependence, and metacommunity integration could thus occur on a geological timescale, despite independent species fluctuations within communities on an ecological scale.

Of course, the recent coral-to-macroalgal transition in the Caribbean has not yet been tied to extinction or speciation. The *Acropora* spp. appear to be surviving, and they may yet recover to their former large population sizes. What the transition portends for the diversity of corals in the Caribbean is a question for the future.

Ecology and paleobiology reciprocally illuminate each other, and they can be used in tandem to attain a broad understanding of biological systems (Gould 1981; Peterson 1984; Hubbard 1988; Jackson 1988; Bennett 1997). The most fruitful approach to the paleoecology of coral reefs is to combine paleontology with ecological observations. And just as surely, reef ecology cannot be understood without considering the historical context provided by paleoecology (e.g., Colgan 1990; Aronson and Precht 1997). Fossil reefs are time-averaged, highlighting long-term patterns; living reef communities supply

information on the mechanisms underlying those long-term trends. Our impression is that paleobiologists pay close attention to ecology, but ecologists largely ignore the fossil record. If the important questions are to be answered, the only option is to combine the two disciplines into an evolutionary paleoecology of coral reefs.

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