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- Population dynamics based on individual size rather than age: a general model with a reef coral example. T.P. Hughes. 1984 The American Naturalist.
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- Endangered and Threatened Species; Revision of Candidate Species List Under the Endangered Species Act, Federal Register Vol 64, No. 120 6/23/99 page 33466-33467.
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Working Groups

- Status and Trends
- Biology and Ecology
- Management
- Information Acquisition

Participant list

a) Caribbean *Acropora*
Workshop: Potential
Application

of the U.S. Endangered Species Act as a Conservation Strategy

April 16-18, 2002
Rosenstiel School of Marine and Atmospheric Science
University of Miami
Key Biscayne, Florida

AGENDA

April 16, 2002, TUESDAY:

7:30-8:00AM Continental breakfast, registration

8:00-8:15 Welcome, introductions, workshop overview

8:15-8:30 Opening remarks by John McManus, Director, National Center For Caribbean Coral Reef Research (NCORE)

Session 1: *Status reports: historical extent, extent of loss, recent rate of loss, causes of mortality, and patterns of recovery*

8:30-9:30 Regional status of *Acropora palmata* and *A. cervicornis*: results of 1998-2001 Atlantic and Gulf Rapid Reef Assessment (AGRRA) surveys from 22 countries (Phil Kramer)

9:30-10:00 Threats to *Acropora* spp. in the Caribbean (Rich Aronson)

10:00-10:15 Coffee Break

10:15-11:00 Status and trends of *A. palmata* and *A. cervicornis* in the Florida Keys
A. Key Largo (Margaret Miller)
B. Recent trends throughout the Keys (Mark Chiappone and Steven Miller)
C. Historical trends 1881-2000 (Walt Jaap)

11:00-11:15 Distribution, population ecology and reproductive biology of *Acropora cervicornis* in Broward County, Florida (Bernardo Vargas-Angel/Jim Thomas)

11:15-12:00 Status and trends of *A. palmata* and *A. cervicornis* in Puerto Rico
A. Status of *Acropora* spp. populations in northern and eastern Puerto Rican coral reefs (Edwin Hernandez)
B. South and west coast populations (Ernesto Weil)
C. DNER monitoring and management (Michael Nemith/Miguel Canals)

12:00 - 1:00 Lunch

Session 1: *Status reports: historical extent, extent of loss, recent rate of loss, causes of mortality, and patterns of recovery (continued)*

1:00- 2:00 Status and trends of *A. palmata* and *A. cervicornis* in the USVI
A. Historical status, extent of decline and projection for recovery on St. Croix

- reefs. (William B. Gladfelter and Elizabeth H. Gladfelter)
- B. The Status of *Acropora* in the USVI: A wake or an awakening?
(Caroline Rogers)
- C. Status in the NE Caribbean (Anguilla, BVI, St. Croix) and changes since the
1970s (John Bythell)

2:00-2:20 The demise of *Acropora* populations in the Caribbean: a tale of two reef systems
(Bill Precht)

2:20-2:35 Status of *Acropora* species on the leeward islands of the Netherlands Antilles
(Mark Vermeij/Rolf Bak)

2:35-2:50 Acroporid populations in the Dominican Republic (Francisco Geraldès)

2:50-3:05 Acroporid populations off Mexico (Eric Jordan-Dahlgren)

3:05-3:20 Afternoon tea break

3:20-3:35 Status of Acroporid populations off Colombia (Jaime Garzon-Ferriera/Juan M.
Diaz)

Session II: *Application of research data on the biology, ecology and geology of these species
and available management tools to develop an effective conservation program*

3:35-3:50 The use of remote sensing and aerial photography for estimating the historic
distribution and abundance, extent of decline and degree of recovery of Caribbean
Acropora spp. (Barry Devine)

3:50-4:05 Unprecedented" *Acropora* Die-Offs: 6,300 & 3,000 ybp (Dennis Hubbard)

4:05-4:20 Population dynamics and life-history traits of *Acropora palmata*: costs and
benefits of fragmentation (Diego Lirman)

4:20-4:30 Genetic Status of *Acropora palmata* populations in the Caribbean (Iliana Baums)
4:30-4:45 Management measures for corals and coral reef ecosystems in the FKNMS: Are
existing and proposed regulations sufficient? (Brian Keller)

4:45-5:10 The U.S. Endangered Species Act: Application to reef-building corals (Andy
Bruckner)

5:10-5:30 Closing comments, assignments to working groups, working group tasks

7:00-9:30 **Evening reception and buffet**

8:00 Evening presentations:

- Coral Farm: the first step to restore reefs (*Antonio Ortiz and Hector Ruiz*)
- Coral Culture as a Conservation Tool for *Acropora* spp. (*Erich Mueller*)
- *Acropora palmata* and *A. cervicornis* Video Footage
 - USVI - *Zandy Hillis-Starr, Denny Hubbard*
 - *St John Acropora populations* - *Jeff Miller, Caroline Rogers*
 - *Bonaire/Curaçao* - *Mark Vermeij*

April 17, 2002, WEDNESDAY:

7:30-8:30 *Continental Breakfast*

8:30-10:00 Working group discussions

10:00-10:15 *Morning coffee*

10:15-12:00 Working group discussions

12:00-1:00 *Lunch*

1:00-2:00 Working group presentations (15 minutes each)

2:00-3:15 Working group begin drafting recommendations

3:15-3:30 *Afternoon break*

3:30-5:30 Working groups continue drafting recommendations

April 18, 2002, THURSDAY:

7:30-8:30 *Continental Breakfast*

8:30-10:00 Working groups finish write-ups

10:00-10:15 *Morning coffee*

10:15-12:00 Working group presentations and discussion

12:00-1:00 *Box Lunch*

1:00-2:00 Final discussion and wrap-up



BACKGROUND

NMFS Coral Species and Ecosystem Conservation Project

In 1998, NMFS began an initial analysis of the major reef-building coral species to determine whether environmental or anthropogenic factors were threatening the survival of certain species in U.S. waters of the western Atlantic. Corals selected in this review were analyzed based on 1) their role in coral reef structure and function (e.g., reef growth, essential fish and invertebrate habitats, biodiversity and coastal protection); 2) species potentially threatened by anthropogenic and natural factors identified as criteria for the Endangered Species Act (ESA); and 3) species previously placed on the candidate species list for the ESA. This review includes nine species identified in 1991 as candidates for listing under the ESA that were removed in 1997. Although the 9 corals listed as candidates in 1991 had declined in some locations, they were removed from the candidate list because NMFS was not able to obtain sufficient information on their biological status and threats to the species to meet the higher scientific documentation required for inclusion on the 1997 candidates list (62 F.R. 37560).

For each species included in the 1998 review, information on the life history characteristics, habitat and distribution, historical abundance and extent of decline, threats, and existing management mechanisms was compiled using available scientific literature, grey literature and personal communications. This project identified two Caribbean species, *Acropora cervicornis* and *A. palmata* that were of immediate concern.

Addition of *Acropora palmata* and *A. cervicornis* to the Candidate Species List of the ESA

Using information collected through Phase I of the 1998 project, as well as information obtained during a public comment period, NMFS added two coral species, elkhorn coral (*Acropora palmata*) and staghorn coral (*Acropora cervicornis*) to the candidate species list of the Endangered Species Act in 1999 (Federal Register Vol. 64, No. 120, June 23, 1999 pp. 33466-33467). These species were determined to qualify for listing on the candidate species list because they had exhibited a significant decline in abundance or range from historical levels, and this decline was due to one or more of the threats used to list a species on the ESA, specifically disease outbreaks, predation, natural climatic conditions, and habitat degradation. Extensive, dense thickets of staghorn coral and elkhorn coral were a common feature of Caribbean reefs until the late 1970s or early 1980s, depending on the location. These species have progressively declined in abundance throughout their range over the last 25 years, beginning with the first reports of white-band disease from the USVI in 1977. Disturbances that contributed to the decline include disease outbreaks, storms and hurricanes, temperature extremes, bleaching, predation by snails, sedimentation, and other factors. The two major sources of mortality most commonly cited as the main cause of their demise are white band disease and physical disturbance caused by storms and hurricanes. A summary of the initial biological assessment completed during the preliminary review of *Acropora cervicornis* and *A. palmata* for the purpose of determining whether these species should be added to the NMFS Candidate Species List is annotated at the end of this document.

Addressing information gaps

The preliminary status review used to justify listing these corals as candidate species for

the ESA revealed large gaps in available information. Extensive occurrences of “standing dead” *Acropora palmata* have been reported along the Yucatan peninsula of Mexico, San Andreas, the Turks and Caicos and other locations, but often the cause of mortality or timing of the event is not known. Quantitative data documenting a widespread loss of *A. cervicornis* is available for Belize, Jamaica, the Netherland Antilles, Florida, and Colombia, but in many cases data are available for a small number of locations, often one or a few reefs. Extensive quantitative data for *A. palmata* is also available for Florida, USVI, Jamaica, and a few other locations; in most other locations the available information is largely anecdotal. This has hindered our ability to list these species on the ESA, primarily because a marine invertebrate listing has more stringent information requirements than that needed to justify a vertebrate species for listing.

1) Atlantic and Gulf Rapid Reef Assessment

In order to collect needed information on a regional scale, NMFS Office of Protected Resources is collaborating with the Atlantic and Gulf Rapid Reef Assessment (AGGRA) program to compile regional information on the status of these species using coral reef assessment data for 1998-2000. The AGGRA protocol has been applied to over 400 reefs in the western Atlantic including Bahamas, Brazil, Bonaire, Caymen, Cuba, Curacao, Dutch Antilles, Flower Gardens, Honduras, Jamaica, Mexico, St. Vincent, Turks and Caicos, USVI and Venezuela. The objective of AGGRA is to develop a comprehensive database of the condition of reefs throughout the Atlantic and Gulf of Mexico, including the condition of reefs near population centers versus those in remote locations and the identification of luxurious reefs with high coral cover, an abundance of rare or threatened invertebrates or fishes, or an unusual morphology which makes them important candidates for conservation efforts. The benthic component of the protocol characterizes corals by species and records data on abundance, percent partial mortality, size frequency, condition, and recruitment. The AGGRA program and database represent the most comprehensive large scale assessment to date, with information that is essential to understanding the extent of decline and patterns of recovery for western Atlantic acroporid corals from throughout the region.

2) Caribbean *Acropora* Workshop: Potential Application of the U.S. Endangered Species Act as a Conservation Strategy

Information from recent monitoring and assessment programs like AGGRA will be supplemented with data compiled during this International Caribbean Acropora workshop, with contributions from coral reef ecologists, biologists and geologists, as well as resource managers with expertise in corals. Participants have been tasked with presenting an up-to-date review on the status and trends of these corals from reefs in the U.S. and the wider Caribbean, including threats, patterns of recovery, existing management actions designed to protect remaining “healthy” populations and restore/rehabilitate degraded populations, and additional conservation actions necessary to enhance recovery of these corals.

The bulk of the workshop will involve four concurrent working groups that have been tasked with:

- 1) evaluating the risk of extinction and whether either species qualifies as threatened or endangered based on five primary factors used to evaluate an ESA listing and other

criteria;

- 2) various demographic and genetic parameters that are available to assist in making a determination of the risk these species face and their potential for recovery;
- 3) existing international and domestic regulations and their adequacy and effectiveness at protecting and restoring these species;
- 4) an evaluation of the benefits/costs of a threatened or endangered ESA listing for *Acropora* spp., including the effect this would have on associated species and coral reef ecosystems;
- 5) critical habitat designation essential to the conservation of these species;
- 6) possible conservation strategies for degraded populations, including specific criteria that would be needed in a recovery plan; and
- 7) uncertainty regarding the status, abundance and trends; the level of precaution necessary to reduce extinction risk; and research needs to fill information gaps.

3) New information

Although populations have declined by 95% or more in many locations, some degraded areas are showing positive signs of recovery. In the U.S. Virgin Islands, for example, some of the *Acropora palmata* reefs decimated by white band disease (WBD) during the 1970's and 80's appear to be recovering through continued growth and fragmentation of remaining colonies, and through new recruitment. Other areas, such as Andros Island, Bahamas appear to have avoided a major decline of *Acropora palmata* altogether and still contain extensive and healthy stands. Although many anecdotal reports indicate that there are still a number of elkhorn or staghorn coral thickets in excellent condition, major storm events or other disturbances can lead to the sudden demise of these corals, such as that which occurred in southwest Cuba in the fall of 2001.

It is impossible to appreciate the significance of reported acroporid declines or comebacks without placing them into a larger spatial and temporal context. Studies focusing on geological time scales are increasingly attempting to determine how the taphonomic signatures of fossil reefs differs from modern reefs. Future studies hold promise at extending our understanding of ecological changes to coral reefs, and specifically acroporid populations, on geologically relevant time scales. However, few studies are presently focusing on addressing questions over large spatial scales (i.e. 1000 km) regarding the distribution, abundance and connectivity of populations, causes and extent of mortality, and patterns of recruitment and recovery. This is partly because of the time and effort required to carry out an effective sampling design and the difficulty at obtaining financial support for these types of projects.

New or ongoing research programs with relevance to an ESA listing for *Acropora cervicornis* and *A. palmata* may help address how much coral has been lost on a regional scale, the potential for recovery, and possible human interventions that may reduce the time required for natural recovery. This includes:

- 1) recent monitoring programs focusing on particular reefs for which there is historic information; new regional monitoring or assessment programs; and detailed monitoring of individual colonies and recruits to evaluate their potential survivorship and causes of mortality.
- 2) geological research to characterize the historic range and abundance of populations; to determine whether the recent decline is a unique occurrence over the last 10,000 years or whether there are gaps in the *Acropora* record that would indicate that these species have been extirpated at some earlier period; and to determine whether the threats affecting coral populations today were present in the past.
- 3) genetic studies to establish linkages within and among populations; the degree of reproductive

isolation; and the importance of sexual reproduction as a possible strategy to enhance species persistence and promote recovery through recruitment from distant locations.

4) mapping efforts to characterize the extent of *Acropora* habitat and the current and historical abundance of these corals.

5) models to help evaluate relationships between life history characteristics, storm events and other disturbances on the resilience and persistence of these species.

6) novel techniques to propagate and transplant fragments into degraded areas; to improve habitat quality; to enhance sexual recruitment; and to address threats (i.e. predators).

Do these species qualify for listing as threatened or endangered on the ESA?

The working groups have been tasked with evaluating existing information on the biology, status and trends and threats, and application of new tools, to determine whether these species have declined to an extent where listing on the ESA is warranted. The groups will also evaluate whether an ESA listing would help promote recovery, or whether other actions may be more effective. There are four specific items that need to be evaluated with regards to a possible listing decision:

A. Are the species at risk of extinction or likely to become threatened with extinction in the foreseeable future?

- life history traits that increase the likelihood of extinction
- recent and projected trends in abundance and range
- current population size and composition
- range size and distribution
- reproductive capacity and recruitment potential
- high degree of threat from disease and/or predation
- other biological or environmental parameters
- models to predict the likelihood of extinction that incorporate demography, threats and life history parameters for a sessile, colonial organism.

B. Would a listing action reduce the risk of extinction?

- minimize imminent extinction of these species and possibility of long-term extinction
- choose species that are most likely to benefit from protection under the ESA
- likelihood that a species will respond to management regime proposed under a recovery plan
- ease of completing required management actions

C. Are there other management mechanisms that are sufficient to protect these corals?

- existing tools resource managers have to protect and restore coral populations
- new mechanisms being considered, developed or applied that will benefit these corals
- local, national and international (regional) mechanisms

D. Does the species exhibit ecological characteristics that benefit other species, the ecosystem or associated ecosystems?

- cover the most species possible per listing action
- target ESA listing actions to those species that have large influences on ecological processes within the ecosystem they inhabit
- choose “umbrella” species to convey benefits to associated species with shared habitats or threats

Summary of biological information on *Acropora palmata* and *Acropora cervicornis* used to justify a Candidate Species Listing for these species.

Acropora palmata

Description: Elkhorn coral is a large branching coral up to 3 m in diameter with exceptionally thick and sturdy branches. This species was formerly the dominant species on shallow, exposed reefs throughout the Caribbean and in the Florida Reef Tract, forming extensive, densely aggregated, monospecific thickets (stands) that develop during periods between storms (Adey and Burke, 1976; Woodley, 1992). The success this species has achieved is a result of its fast rate of growth, rapid wound healing by injured adults, high rate of survival of fragments, and ability of broken branches to cement to the substratum and continue growing (Gladfelter et al., 1978; Bak and Criens, 1981, Highsmith, 1982). Because of the high survivorship of fragmented branches, *A. palmata* was rapidly reestablished after a major disturbance, and colonies spread into neighboring areas not previously occupied by *A. palmata*, including sandy habitats not suitable for settlement by sexually-produced larvae (Lirman and Fong, 1997). In sheltered areas, and on reefs where storm disturbances are low, this species occurs as isolated colonies, primarily due to reduced likelihood of fragmentation, and the low recruitment success of sexually-produced larvae (Dustan, 1977; Rylaarsdam, 1983; Rosesmyth, 1984).

Preferred habitat: Elkhorn coral is found between low water level and 5-6 m depth, in wave-exposed and high surge reef zones (Adey and Burke, 1976); isolated colonies can be found to depths of 18 m, primarily in areas with low rates of sedimentation and high current. This is an environmentally sensitive species that requires clear, high saline, well circulated water with mean temperatures of 25-29°C (Jaap et al., 1989). *A. palmata* is intolerant of sedimentation; this species is not found in areas with considerable runoff, river discharge or land erosion (Lewis, 1984), and populations will disappear from coral reefs exposed to sudden changes in temperature, salinity or water quality (Davis, 1982; Dustan and Halas, 1987).

Importance: *Acropora palmata* is a major reef-building species and the dominant coral on the shallow fore reef in the "palmata zone". Few other species coexist in this environment, due to the extreme fluctuation of environmental conditions. Dense thickets of elkhorn coral reduce incoming wave energy, offering critical protection to coastlines. Loss of this species may result in increased coastal erosion and may negatively affect shorelines with mangrove and grass bed habitats which rely on calm water provided by these effective coral barriers. Of the 60+ species of coral in the Caribbean, only three dominate present day coral reefs and the Pleistocene geological record: *A. palmata*, *A. cervicornis* and the *Montastraea annularis* "complex" (Jackson, 1992). *A. palmata* colonies contribute to the reef framework, and coral thickets account for some of the greatest measured reef growth rates (Goreau, 1959). Gladfelter (1982) estimated a rate of reef accretion by this species of 10.3 kg CaCO₃/m²/yr; over 1000 years, shallow windward *A. palmata* reefs have grown upward close to 15 meters, keeping pace with rising sea level (Adey, 1975). This species also produces islands; boulder ramparts and coral cayes in exposed locations in the Caribbean islands are composed primarily of *A. palmata* skeletons (Williams et al., 1999). High structural complexity produced by the interdigitated branches of *A. palmata* colonies provide essential fish habitat; *A. palmata* thickets often contain a higher diversity of fish species than in other reefs in comparable areas (Gladfelter and Gladfelter, 1978).



Species distribution: *A. palmata* is found on reefs in southern Florida and the Bahamas, and throughout the Caribbean, including the Antilles, the West Indies, Central and South America, including Mexico, Belize, Honduras, Nicaragua, Costa Rica, Panama and Columbia, and. Isolated populations occur in the southern portion of the Gulf of Mexico, near Veracruz, Mexico; the northern limit in 1992 was the Tuxpan Reef System, approx 29°N latitude (Jordan-Dahlgreen, 1992). *A. palmata* was one of the dominant reef-builders Barbados, but has virtually disappeared (Lewis, 1984). The southern limit is Venezuela (Los Roques) and the northeastern tip of Tobago. Elkhorn coral does not occur in Bermuda, the northern Gulf of Mexico, or the east coast of South America (Guyana, Surinam or Brazil).

Acropora palmata prefers moderately high energy wave environments found along the windward sides of islands and banks generally always found within 5 m of sea level. Depending on the degree of wave energy, *A. palmata* colonies may grow either in the shallow fore reef, back reef or patch reef environments, however it usually forms either continuous or discontinuous crests. *Acropora cervicornis* prefers moderate-to-low energy environments and occurs in depths down to 20 m. It can occur in patch reef, back reef, reef crest, and fore reef habitats. Historically, populations of *A. palmata* and *A. cervicornis* populations occur throughout the greater Caribbean and have been documented as far back as the Pliocene. Northern-most populations occur in southern Florida off Broward County and the northern Bahamas region, and southern-most populations occur near Trinidad & Tobago and the offshore islands of Venezuela and Columbia.

U.S. distribution: *A. palmata* coral occurs in Biscayne National Park, on the Florida Keys Reef Tract, off Puerto Rico and offshore islands, and on fringing reefs around the U.S. Virgin Islands. This species is absent from Flower Garden Banks, Florida Middle Grounds and Southeast Florida. The northern limit on the east coast of Florida is in the Biscayne National Park (Triumph Reef 25°29' N).

Growth: Branches increase in linear dimensions by 5-10 cm/year, depending on geographical location, temperature, horizontal position on the reef, depth, and environmental conditions. The greatest rate of growth occurs on the shallow fore reef during summer and early fall; reduced growth is reported during cold water periods, and in back reef environments (Gladfelter et al., 1978).

Life history adaptations: *Acropora palmata* has a high investment into persistence of adult colonies with modifications in growth patterns in response to wave stress and light intensity. Colonies in deep water have broad and flattened branches which are very fragile. On wave-exposed, shallow reefs, branches are fewer in number; branches become thicker, shorter and more cylindrical and are oriented at close to a 45° angle, pointing into incoming currents and waves. In the back reef, colonies have broad, flattened branch tips, although branches are thicker in cross section when compared to deep-water colonies (Gladfelter, 1982). The skeleton is less porous and stronger than most massive corals, and porosity is lower towards the base and higher in branch tips (Chamberlain, 1978). Of all Caribbean corals, *A. palmata* exhibits the most rapid and efficient ability to regenerate tissue and skeleton over injuries (Bak, 1983), allowing this species to recover quickly from storm damage. *A. palmata* is low on the aggressive hierarchy, experiencing tissue destruction if it contacts slow-growing massive corals (Lang, 1973). *Acropora palmata* outcompetes massive corals by growing above them, thereby reducing light penetration and water circulation water (Shinn, 1972).

Reproduction: Individual colonies of *A. palmata* produce both eggs and sperm which are broadcast into the water column for external fertilization. Egg and sperm bundles are positively buoyant, floating to surface and remaining viable for up to 8 hours after release. This species spawns 4-5 days after the full moon in August and/or in September. Although colonies have a high investment in gamete production, few larvae survive and sexual recruits are rare (Dustan, 1977; Bak and Engel, 1979; Rylaarsdam, 1983). Unlike Indo-Pacific acroporids, the main mode of propagation of *A. palmata* is by colony fragmentation, enabling this species to colonize areas unsuitable for sexually produced larvae, and allowing rapid recovery following minor hurricanes and tropical storms.

Threats: The major sources of mortality to *A. palmata* responsible for the virtual elimination of this coral from the Caribbean over the past two decades has been white-band disease (Gladfelter, 1991). Other causes of mortality include natural factors such as breakage by hurricanes and tropical storms, predation by invertebrates and fish, hyper- and hypothermic stress, and bleaching episodes. Anthropogenic causes of mortality include nutrient loading and overgrowth by macroalgae, sedimentation and reduced water clarity, and physical damage from boat groundings and anchors.

Although *A. palmata* has adaptations allowing it to inhabit shallow, high energy reefs, it is susceptible to breakage from physical forces associated with storms and hurricanes. Fragmentation was thought to be adaptive, with a high survivorship of hurricane-generated fragments and a rapid recovery of affected zones (Glynn et al., 1964; Highsmith, 1982). While storms may enhance the spread of *A. palmata* populations, recent observations indicate that initial mortality to colonies and fragments may be quite high, injured colonies and fragments exhibit reduced growth rates and declines in reproductive output, and damaged populations are susceptible to subsequent disturbances (Bruckner, unpubl. Data; Lirman, 1998). In Puerto Rico, populations damaged by storms have continued to decline, with a high incidence (40-60%) of fragment mortality within the first 90 days (Bruckner and Bruckner, unpubl. Data). Woodley (1992) suggested that the large monospecific stands of *A. palmata* described as a characteristic feature of Caribbean reefs (Goreau, 1959; Adey and Burke, 1976) may have developed only because of an unusually long interval (approximately 35 years in Jamaica) between major hurricanes.

Outbreaks of coral disease were first observed among *A. palmata* populations in St. Croix in the mid 1970s and disease epizootics have spread throughout the Caribbean over the past two decades. Up to 95% of the *A. palmata* disappeared over a ten year period from Tague Bay, St. Croix as a result of **white-band disease** (WBD) and storm damage (Gladfelter, 1991). Goenaga reported 20-33 % of *A. palmata* affected with WBD on one reef near La Parguera PR in the early 1980s (Davis et al., 1986); disease epizootics were also reported in Florida (Jaap, 1984). *A. palmata* populations in Puerto Rico and elsewhere in the Caribbean continue to be afflicted by WBD (Bythell, 1993; Bruckner et al., 1997; Aronson and Precht, 1998; Williams et al., 1999). In addition to WBD, new diseases have emerged on *A. palmata*, including **white pox** (Williams, 1996) and **patchy necrosis** (Bruckner and Bruckner, 1997b). Tumors or **calicoblastic neoplasms** (raised, whitened, abnormal lumps on colony surfaces with distorted polipary structures) were first noted by Squires (1965) and their affect on growth and regeneration was examined in Curacao (Bak, 1983). Calicoblastic neoplasms were reported from Carysfort Reef in Florida in 1975 and Grecian Rocks, Florida in 1982, and they are known to occur sporadically, at low levels throughout the Caribbean (Peters et al., 1986). Neoplasms are thought

to reduce the reproductive potential of coral, and they are susceptible to ulceration and invasion by filamentous algae; affected areas lack mucous secretory cells and are very porous, increasing vulnerability to sedimentation and wave stress (Peters et al., 1986).

Coral-eating **predators** including the fireworm, *Hermodice carunculata* and the corallivorous gastropod, *Coralliophila abbreviata* appear to have become more prevalent and cause more damage to *A. palmata* populations in Puerto Rico and the Florida Keys possibly as a result of overfishing of their predators, the octopus and spiny lobster (Bruckner et al., 1997b; Szmant, 1997), and possibly because their host populations have been greatly reduced, effectively concentrating predators (Knowlton et al., 1990). Territorial damselfish (*Stegastes planifrons*) bite repeatedly at the same location on *A. palmata* branches creating conspicuous lesions which are colonized by algae. Regeneration of these lesions is continually interrupted. As a result, the surrounding polyps secrete a wall of tissue and skeleton around the lesion, which extends vertically upward, resembling a chimney; this growth encloses the tufts of algae. Stoplight parrotfish (*Sparisoma viride*) also bite at elkhorn coral branches, removing tissue and underlying skeleton (Bruckner and Bruckner, 1998).

Death to large stands of *A. palmata* by **hypothermia** has been significant in the Dry Tortugas (Jaap and Sargent, 1993) and areas along the Florida Reef Tract with direct connections to the Florida Bay. *A. palmata* is vulnerable to **sedimentation** associated with increased runoff and river discharge, especially in areas with minimal wave action. Rogers (1983) found that even low doses of sediment accumulate on the flattened branch surfaces, resulting in rapid tissue necrosis; in addition, injuries regenerate more slowly at elevated sedimentation levels (Meesters and bak, 1995). In areas with heavy commercial boat traffic and recreational use, *A. palmata* thickets are vulnerable to **boat groundings** and anchor damage, primarily because these corals are restricted to shallow water (Dustan and Halas, 1987).

Acropora cervicornis

Description: *Acropora cervicornis* (staghorn coral) is a branching coral with cylindrical branches ranging from a few centimeters to over two meters in length and height (Aronson and Precht, 1997). Colonies are yellow-brown in color and have distinct, protruding tubular corallites. The tip of each branch has an enlarged apical polyp which is often pale in color and is the actively growing portion of the colony. Colonies tend to branch trichotomously once each year, expanding in diameter 12 cm or more annually. The species often forms dense, localized thickets throughout its range. In these thickets, usually only the upper portions of the branches support living polyps; the bases of the colonies are often encrusted with algae and invertebrates and provide important habitat for damselfish, juvenile grunts and other species (Tunncliffe, 1981).

Preferred habitat: Of the three Western Atlantic species of *Acropora*, this species occupies the most extensive range, occurring in back reef and fore reef environments from 0 to 30 m (Baker et al., 1997). The upper limit of *A. cervicornis* populations are defined by wave forces and the lower limit controlled possibly by suspended sediments and light availability (Dodge et al., 1974; Tunncliffe, 1981). Fore reef zones at intermediate depths (5-25 m) were dominated by extensive monotypic stands of *A. cervicornis* until the mid 1980s (Aronson et al., 1998). Although branches tend to be fragile and easily broken, colonies are often most abundant in areas of intermediate to high water turbulence (Tunncliffe, 1981).

Importance: *A. cervicornis* is one of the three most important reef building corals on Caribbean reefs today, and this species is often the dominant component in fore reef and lagoonal Pleistocene and Holocene deposits (Jackson, 1992; Stemmann and Johnson, 1992; Greenstein et al., 1998). High population density, rapid growth rates and high partial mortality results in the accumulation of large amounts of *A. cervicornis* skeletal material (Gilmore and Hall, 1976). This rubble may remain in place, compacting to form an important component of the reef-framework. It may be transported and deposited at the base of the reef, or it may be broken down into smaller fragments by dissolution and bioerosion, to contribute to clastic material which fills spaces in the rigid framework of the reef (Tunnicliffe, 1983). The most rapid accretion rate for a Holocene reef dominated by *A. cervicornis* was 12 m per 1000 years at Alacran Reef, Mexico (Macintyre et al., 1977). The open framework of densely populated *A. cervicornis* thickets provides essential habitat for motile invertebrates and fishes; back reef populations are important habitat for juvenile grunts and other reef fishes.

Species distribution: *A. cervicornis* is found throughout the Florida Keys, the Bahamas, the Caribbean islands, and Central and South America, including Mexico, Belize, Honduras, Nicaragua, Costa Rica, Panama and Columbia. This coral occurs in the western Gulf of Mexico, to the Veracruz Reef System, but is absent from U.S. waters in the Gulf of Mexico, as well as Bermuda and the west coast of South America (Guyana, Surinam and Brazil).

U.S. Distribution: In U.S. territorial waters, this species occurs throughout the Florida Keys reef tract, the Dry Tortugas, Biscayne National Park and Southeast Florida reefs, extending north to Boca Raton. It also occurs in the U.S. Virgin Islands and Puerto Rico, and the associated islands of Mona, Desecheo, Culebra and Vieques. It is absent from Flower Garden Banks and the Florida Middle Grounds.

Growth (linear extension): Average annual growth rates for individual branches ranges from 3-15 centimeters, depending on geographical location and local environmental conditions. Under optimal conditions, growth rates of 11 cm per year are reported for Florida (Shinn, 1966), 7.1 cm for the U.S. V.I. (Gladfelter et al., 1978), and 12 cm for Jamaica, with a maximum annual growth for individual branches of over 20 cm/year (Tunnicliffe, 1983). In St Croix, Gladfelter (1984) did not observe any major changes in growth rates throughout the year; a 30-60% decline in rates of linear extension occurs during months in which water temperatures did not exceed 26°C in Florida (Shinn, 1966). A reduction in growth rates is associated with extreme turbidity (Rogers, 1990).

Morphological adaptations: Branching morphology, combined with a rapid growth rate promotes colony proliferation and dominance of large areas, but may result in high susceptibility to physical disturbance. Unlike *A. palmata*, this species may fragment completely, sacrificing adults for the production of new asexual propagules. Vegetative propagation allows for the rapid establishment of new colonies throughout the year, unlike sexual larvae which are only produced once each year. Fragmentation may also provide an effective method of inhibiting competitors (Tunnicliffe, 1981). Wave exposure and depth affect colony morphology: colonies from shallow, exposed habitats are robust and have many short branches, while colonies in protected locations are taller and have fewer slender, elongate branches (Goreau et al., 1979). In addition, back reef colonies had a higher level of branching than fore reef colonies (Tunnicliffe, 1981). Aggressive, massive coral species such as *M. annularis* can digest *A. cervicornis* tissue when in

contact, however *A. cervicornis* is able to out-compete these corals by growing above them, presumably through shading (Shinn, 1972). *A. cervicornis* populations have been found to contain two distinct algal symbionts which enables the coral host to occupy two competitively different photic habitats; at shallow depths the symbiont is similar to that found in *A. palmata*, while deep water populations contain a distantly-related symbiont (Baker et al., 1997).

Reproduction: *A. cervicornis* is a hermaphroditic broadcast (mass) spawner with an annual cycle of gametogenesis and release. In Puerto Rico, Steiner (1995) observed spawning 6 days after the August 1987 full moon. Persistence of this species appears to depend heavily on successful asexual reproduction, as larval recruitment is seldom observed (Knowlton et al., 1990; Hughes et al., 1992).

Threats: The major cause of mortality to *Acropora cervicornis* populations has been white-band disease, with synergistic effects from storm damage, predation, shading and sedimentation, mechanical abrasion, overgrowth and thermal shock (Knowlton et al., 1981; Tunnicliffe, 1981; Woodley et al., 1981; Rogers, 1983; Porter et al., 1982; Aronson and Precht, 1998). Although branching morphology and rapid growth rates allow this species to survive in areas with considerable sediment deposition, chronic elevated turbidity caused bleaching and reductions in growth (Rogers, 1983). The spread of *A. cervicornis* through asexual reproduction reduces genetic variability of populations, possibly increasing their susceptibility to disease (Bak, 1983).

In Jamaica, WBD was observed on colonies prior to Hurricane Allen; extensive hurricane damage, disease and increased predation by corallivorous invertebrates caused a large scale decline during the early 1980s, and populations have failed to recover after nearly 20 years (Woodley et al., 1981; Knowlton et al., 1990). In other Caribbean localities outbreaks of WBD are believed to be the prominent factor contributing to a widespread disappearance of this species (Aronson and Precht, 1997). A second form of WBD (type II) has recently emerged among *A. cervicornis* populations; affected colonies bleach in a band which advances up the branch, and is followed by progressive tissue necrosis (Richie and Smith, 1998). The advance of white-band disease can be up to 5 mm/day, exceeding the growth of regenerating branches, which is approximately 0.3 mm/day (Davis et al., 1986).

A Caribbean-wide demise of this species as a result of anthropogenic and natural disturbances appears to be a unique event that contrasts with the long-term persistence of this taxon during Pleistocene and Holocene periods (Greenstein et al., 1998; Aronson et al., 1998). *Acropora cervicornis* may be experiencing an Allee effect; this species is now rare, and colonies may now be too far apart to ensure fertilization success, preventing reduced populations from becoming reestablished by sexual recruits (Knowlton, 1992).



THREATS TO *ACROPORA* SPP. IN THE CARIBBEAN

Richard B. Aronson, Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, AL 36528

William F. Precht, PBS&J, 2001 Northwest 107th Avenue, Miami, FL 33172

Mass mortalities of *Acropora palmata* and *Ac. cervicornis* on Caribbean reefs over the last three decades have caused drastic declines in coral cover throughout the region. Although hurricanes and cold-water events (in Florida and the Bahamas) have killed acroporids on some reefs, white-band disease has been the single most significant source of mortality on a regional level. Paleontological work in Belize suggests that the *Acropora* kill is without precedent in at least the last 3-4 Kyr. Analysis of 36 reef cores extracted from a 375-km² area of the central shelf lagoon showed that *Ac. cervicornis* dominated continuously for at least the last 3,000 yr. The lettuce coral *Agaricia tenuifolia* occasionally grew in small patches until the late 1980s. Within a decade, *Ac. cervicornis* was virtually eliminated by white-band disease. *Ag. tenuifolia* recruited to and grew on the dead coral branches and was the dominant coral by the mid-1990s. The scale of species turnover increased from tens of square meters or less to hundreds of square kilometers or more. Paleontological data from the Dominican Republic, St. Croix and the Bahamas support the hypothesis that the current situation is unprecedented on a millennial scale.

In fore reef environments, the establishment of damselfish territories and other localized mortality were responsible for variability at the smallest spatial and temporal scales (square meters, months to years) within populations of acroporids. Hurricane damage introduced variability at larger spatial and temporal scales (kilometers to tens of kilometers, years to 1-2 decades). The spatial scale of mortality of *Acropora* spp. has increased to a regional scale, virtually eliminating variation at a range of smaller spatial and temporal scales.

Current threats to remnant populations of *Acropora* include hurricanes, disease, corallivory, hyper- and hypothermic stress, sea-level rise and pollution. These threats generally act in combination rather than individually. The life history strategies of *Ac. palmata* and *Ac. cervicornis* are not conducive to rapid recovery from regional mass mortality. At present, agariciids and poritids are the most common corals colonizing the disturbed surfaces of reefs formerly occupied by acroporids.



Focal *Acropora* spp. assessment in the Florida Keys

MW Miller

This presentation will summarize two recent assessments of *Acropora* spp. status. The first involves population surveys of elkhorn coral, *Acropora palmata*, and its predator, the corallivorous snail *Coralliophila abbreviata*, in the Key Largo area. Surveys were conducted annually in May from 1998 to 2001 at six sites in the FKNMS were surveyed in all years; three no-take zones and three reference areas. At each survey, size and condition of each sampled coral colony was estimated as well as the number and size of its resident snails. A drastic decline in *A. palmata* populations was observed between May 1998 and May 1999, coinciding with a severe bleaching event and Hurricane Georges during summer/fall of 1998. All colonies in three patches (out of 10, ~200 colonies) sampled in 1998 suffered complete mortality by May 1999. Sampling at two sites in October 1998, after Hurricane Georges, confirmed that average sizes of standing colonies and of loose fragments had decreased while the abundance of fragments had increased. The total amount of live *A. palmata* (as measured by total # of colonies or by total "live area index") extant at three sites where all colonies were sampled declined drastically from 1998 to 1999 and has shown only marginal recovery from 1999 to 2001. The incidence of white band disease (WBD) in these *A. palmata* patches has been consistently low throughout the study, below 6% for any given site survey with zero incidence observed in many site surveys. The average incidence of WBD observed in 2001 was 2% of colonies (n=6 sites). The average density of corallivorous snails on *A. palmata* (#/*A. palmata* colony surveyed, n=6 sites) more than doubled from 1998-2000 but declined slightly between 2000 and 2001 (overall mean ~0.8 for 2001). Sites with low-density *A. palmata* stands (LD sites) had consistently more snails colony⁻¹ (0.8-2.5) than sites with thickets (0.4-1.0). Meanwhile, the average size of snails on *A. palmata* declined between 1998 - 1999 and has rebounded somewhat by 2001. Published measurements of average snail consumption rate are ~1-2 (cm²live *A. palmata* tissue)snail⁻¹d⁻¹ with individual measurements ranging up to 6.5 (cm²live *A. palmata* tissue)snail⁻¹d⁻¹.

The second assessment evaluated change in total *Acropora* spp. cover at Looe Key (lower Keys) over a longer time frame. In 2000 the occurrence and approximate size of all *A. palmata* and *A. cervicornis* colonies was recorded on scaled base maps of the spur and groove structure at Looe Key and compared to archival maps made with the same scaled base maps in 1983. Total areal loss for the mapped area was estimated at 93% for *A. palmata* and 98% for *A. cervicornis*. It is likely that considerable *Acropora* spp. loss had occurred prior to 1983, and is thus not included in these estimates.

Lastly, recent attempts at larval culture of *A. palmata* for restoration will be described.



Distribution and Status of Acroporid (scleractinia) Populations in Puerto Rico

(Draft 1)

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Potential Application of the US Endangered Species Act (ESA)
as a Conservation Strategy
NOAA-NMFS and NCORE - RSMAS
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By

Ernesto Weil¹, Edwin A. Hernández-Delgado², Andy Bruckner³
Antonio L. Ortiz⁴, Michael Nemeth⁵, and Héctor Ruiz¹

¹ Dept. of Marine Sciences, U. of Puerto Rico, PO Box 908, Lajas PR 00667

² Dept. of Biology, U. of Puerto Rico, PO Box 23360, San Juan, P.R. 00931-3360

⁵ NOAA/NMFS 1315 East West Hwy. Silver Spring, MD 20910

³ Dept. of Natural Sciences, U. of Puerto Rico, Aguadilla, PO Box 250160, Aguadilla, 00604-0160

⁴ Dept. of Natural and Environmental Resources, San Juan, P.R. 00906-6600

Abstract

Acroporid corals were important components of shallow fore reef and lagoonal habitats in coral reefs of the tropical western An epizootic event of white band disease (WBD) in the early 80's, produced extensive mass mortality of both species throughout their distribution range in the wider Caribbean. As a result, there were significant changes in community structure, loss of habitat and biodiversity. In the late 70's, dense and extensive thickets of elkhorn coral *A. palmata* were present in 40 % of 35 reef localities surveyed around the island. Another 20 % of these reefs had dense patches and abundant colonies. *A. cervicornis* was also abundant, in some cases forming thickets in 20 % of the reefs. Surveys of over 100 reef localities around the island and in the offshore islands indicate a significant decline in populations of both species. Most of the high profile, dense thickets that formed the *Acropora* "zones" have disappeared, and only a few reefs localities, mostly in the southwest coast, have healthy, high density populations of *A. palmata* and *A. cervicornis*. The primary cause of this significant decline in population densities and distribution probably was the widespread WBD epizootic event of the early 80's. In following years, surviving colonies were hit by hurricanes, storms, beaching, more disease, and an increasing deterioration of the environment around coastal coral reefs due to anthropogenic activities has also affected these corals. Other, long-term natural factors, such as snail and fireworm predation, and damselfish territorial behavior, have caused increasing tissue mortality and the pre-emptive competition of corals by filamentous algae. In recent years, patchy necrosis and substrate monopolization by an aggressive, endolytic sponge, *Cliona aprica*, have become important factors in the loss of live tissue in *A. palmata*. Protective legislation by the DNR, the presence of healthy populations and sexual recruits in many localities, and the high growth rates of these species may provide a good combination for some recovery.

1. Historical perspective

Acroporid corals (*A. palmata* and *A. cervicornis*) were important components of shallow fore reef and lagoonal habitats in coral reefs of the tropical western Atlantic until the late 70's and early 80's. These species formed the famous *Acropora* zones, dense stands of high profile, spatially complex, monospecific thickets in shallow and intermediate depths in most Caribbean coral reefs (Vaughan, 1919; Goreau, 1959; Lewis, JB, 1960, 1965; Scatterdat, JW, 1974; Ross, PJ, 1964, 1971; Glynn, 1973; Colin, 1978). In the late 70's and early 80's, a white band disease (WBD) epizootic event produced extensive mass mortality of these species throughout their distribution range in the wider Caribbean. Consequences included significant changes in community structure, loss of habitat and loss biodiversity (Gladfelter, 1982). In many localities, acroporids have but disappeared as a consequence of this event and subsequent impacts of hurricanes, bleaching events, more disease, and a generalized deterioration of local environmental conditions.

In Puerto Rico, acroporid coral populations have declined significantly in the last two decades in almost all reef localities where they used to be abundant by the late 70's. Dense and well developed thickets of both *A. palmata* and *A. cervicornis* were present in many reefs in the north-east, east, south, west and north west coast of the main island, the shelf edge, and offshore islands such as Mona, Vieques and Culebra (Fig. 1) (Almy and Carrión-Torres, 1963; McKenzie and Benton, 1972; Rogers, 1977; Goenaga and Cintrón, 1979, Boulon, 1980). In an extensive survey of 35 localities around the island in 1978-79 by Goenaga and Cintrón (1979) (Fig. 1), 40 % of all coral reefs and coral communities surveyed had well developed, high profile thickets and/or several dense patches with high colony densities of *A. palmata*, 20 % had high density of colonies and few patches, 20 % had isolated colonies, and 12 % had no growing *A. palmata*. Live cover of *A. palmata* varied from 5 to 100% in 15 of the 35 localities. On the other hand, *A. cervicornis* was abundant, in some cases forming dense thickets (at intermediate and some deep sites), in 20 % of the reefs, isolated colonies were found in 28 % of the reefs, and it was absent in the rest. Some reefs were already showing signs of anthropogenic impacts such as high siltation and turbidity (Goenaga and Cintrón, 1979). Today, evidence of this "healthy period" can be seen in many of these sites, where standing dead skeletons of *A. palmata* and rubble piles of *A. cervicornis* can be seen. With the exception of few reefs in the southwest and offshore islands, the dense, high profile, monospecific thickets of both species have disappeared from Puerto Rico coral reefs.

The primary cause of this significant decline in population densities and distribution probably was widespread white band disease (WBD) epizootic event of the early 80's (Gladfelter, 1982), then the surviving colonies were hit by hurricanes, storms, bleaching, more disease, and an increasing deterioration of the environment around coastal coral reefs due to anthropogenic activities in the following years (Table 1). In the east coast for example, after WBD decimated acroporid populations, hurricane Hugo (1989), caused almost total destruction to the remaining *A. palmata* thickets (Goenaga and Boulon, 1992). Other population had been affected by earlier storms, like Edith in the early 60's, which hit the southwest and caused destruction of 10-50% of

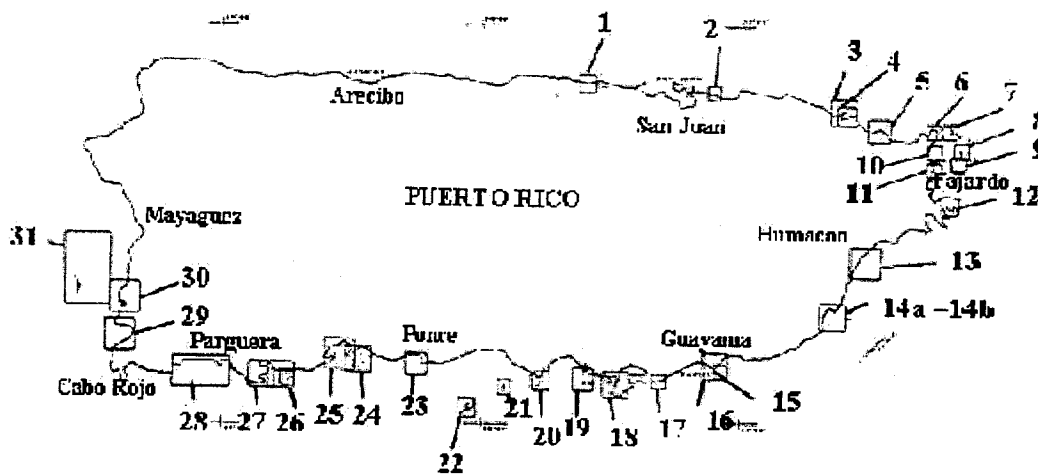


Figure 1. Map of Puerto Rico showing major coral reef areas and surveyed (lines) areas by Goenaga and Cintrón (1979). Letter (A to C) indicate surveyed areas in the offshore Islands by other authors.

the *A. palmata* thickets. Coral fragments were observed to reattach and recovery was rapid (Glynn et al., 1964) however. Many coral reefs (i.e., Islote Palominitos, Los Corchos Reef, Cayo Dákity, Playa Larga; Culebra) showed severe physical destruction of the *A. palmata* framework and *A. cervicornis* thickets as a result of several hurricanes [e Louis (1995), Marilyn (1995), and Georges (1998)] (Goenaga, 1990, Hernandez-Delgado, 2000).

In other instances, a timely combination of factors seem to have cause the demise a acroporid populations; Hurricane David (1979) had devastating effects to *A. palmata* thickets located on fore reefs habitats throughout the south and west coast, with a high proportion of colonies being dislodged from the reef substrate and deposited onto the reef flat, and a high amount of mortality occurred (Vicente, 1993). Then, WBD hit in the early 80's, and up to 30% of the colonies were reported to be affected in many reefs (Davis et al., 1986). White band disease has remained present in many populations but rates of incidence were apparently low. In the same area studied by Davis (1986), remaining populations in two of the outer reefs were reported to have WBD on 8.5% of the living colonies by 1993 (Williams et al., 1999).

Other, long-term natural factors, such as damselfish (Pomacentridae) territorial behavior has caused increasing tissue mortality and the pre-emptive competition of corals by filamentous algae (Hernández-Delgado, unp. data). In addition, coral bleaching was documented in *Acropora* spp. in 1987, 1989, 1990, and 1998 (Williams et al., 1987; Goenaga et al., 1989; Goenaga and Canals, 1990; Weil, 2000), but not associated mortality was reported. Localized anthropogenic impacts (i.e., historic coral collection for souvenirs, reef trampling, snorkeling, SCUBA diving, some fishing methods) have also caused some destruction of corals on the Fajardo region (Mckenzie and Benton, 1972; Torres, 1975; Hernández-Delgado, 1992). Ship groundings have caused significant mechanical destruction of *Acropora* assemblages in Los

Corchos, Culebrita Island, Islote Palominitos, off Fajardo (Hernandez-Delgado, 2000), Guanica and Mona island (Bruckner and Bruckner, 2001). Military activities has caused some damage also in Culebra and Vieques (Hernández-Delgado, pers. obs.)

Most of these impacts have never been quantified. Today however, quantitative information on the impact of the Fortuna Reefer ship grounding on a *A. palmata* population in Mona has been collected for over two years (Bruckner and Bruckner, 2001), an ongoing project is evaluating the impact of Hurricane George's in *A. palmata* populations of some reefs of La Parguera and Guánica (Ortiz, unp. data), and the impact of predation by the snail *Coralliophilla abbreviata* was assessed by Bruckner (2000). Ongoing anthropogenic degradation of coastal (urban development, sewage, pollution) and inland areas (deforestation) continue to affect the quality of the coastal reef environments (i.e., higher turbidity, high nutrient input, pesticides and herbicides, solid suspended material, high sedimentation rates, etc.), and may contribute even more, to the decline of acroporid populations.

2. Current status

Although there is a major lack of quantitative data regarding the current ecological status of acroporids in Puerto Rico, a wealth of qualitative observations and information on their distribution and relative abundances have been collected over the years for many coral reefs in the eastern, southwest and west coasts, and some of the offshore islands. This provides a good baseline for comparative purposes and a clear picture of the current status of acroporid populations. Recent surveys of over 100 reefs along the coast and islands, indicate that acroporid populations have continued to decline in some areas from persistent disease, storms, and sedimentation coupled with the poor coastal environmental conditions (low water quality, high turbidity, etc.) and algal overgrowth (Appendices 1 and 2).

Many environmentally-degraded fringing coral reefs along the shoreline of Puerto Rico (i.e., Punta Picúa, Punta Miquillo; Río Grande, Guanica, La Parguera, Mayaguez) show large stands of dead *A. palmata* in their growing position, which indicates that mortality was produced mainly by non-destructive factors such as disease outbreaks, bleaching, siltation, algae competition or a combination of any, or all of these (Table 1). Total colony mortality is not the common outcome however. In many cases, the capacity for recuperation of these two species (fast growth rate, tissue regeneration, asexual reproduction, high survivorship) seem to be playing an important role in maintaining some populations. A recent event of patchy necrosis in southwest reefs for example, produced moderate levels of partial tissue mortality in a high proportion of colonies in a relatively short period of time (November 13-18, 2002). On average, between 35 and 74 % of all colonies of *A. palmata* in six reef areas were affected by this problem (Fig. 2). Average tissue loss varied between 14 and 17% of the surface area of the colonies (Fig. 3) (Weil and Ruiz, unp. data). This event happened after a period of extreme calm weather and seas that lasted for 15 days approximately. In many occasions, tissue mortality was associated with high residence time (calm weather) of fish and other organisms feces on the surface of *A. palmata* colonies. Almost all colonies however, have shown rapid regeneration of the loss tissue.

Table 1. Historical and actual causes of partial and total mortality of acroporid corals in Puerto Rico

<u>Natural factors</u>	<u>Species</u>	<u>Anthropogenic Factors</u>	<u>Species</u>
Disease		Siltation	Ap, Ac
White band	Ap, Ac	Pollution	Ap, Ac
White plague	Ap, Ac	Ship and boat groundings	Ap, Ac
Black band	Ac	Euthrophication	Ap, Ac
Bleaching	Ap, Ac	Floating debris	Ap, Ac
Patchy necrosis	Ap	Divers	Ap, Ac
Predation		Anchors	Ap, Ac
Snails	Ap, Ac		
Fireworm	Ac		
Parrotfish	Ap		
Damselfish	Ap, Ac		
Storms	Ap, Ac		
Clionid sponges	Ap		
Algae competition	Ap, Ac		

2.a. Eastern coast

Eighty eight northern and eastern coral reefs and coral communities have been surveyed in the last decade and the information compared with previous reports from the same sites (Table 2). Data was geographically sub-divided into four main areas: northern inshore, eastern inshore, eastern offshore close (<6 km), and eastern offshore remote (>6 km). This classification was originally based on a Bray-Curtis ordination analysis for coral species presence/absence data sets for classifying coral reefs (Hernández-Delgado, 2000). *A. palmata* was an important component of coral reefs and coral communities in most of the sites (93%) of four major localities surveyed many years ago (Almy and Carrión-Torres, 1963; Pressick (1970), Mckenzie and Benton, 1972; Goenaga and Cintrón, 1979; Goenaga and Vicente, 1990), Goenaga and Boulon, 1992, Hernández-Delgado, 1992, and unp. data). Today, however, *A. palmata* has been observed only in 36.7 % of these sites, as one moves across an anthropogenic stress gradient of water transparency, sedimentation and concentration of solid suspended material (Hernández-Delgado, 2000).

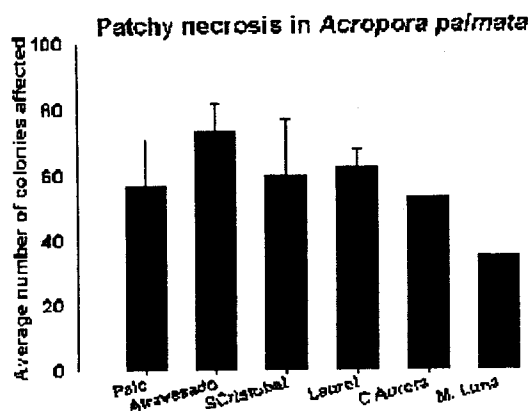


Figure 2. Average number of colonies of *A. palmata* affected by patchy necrosis in six coral reefs off La Parguera and Guánica

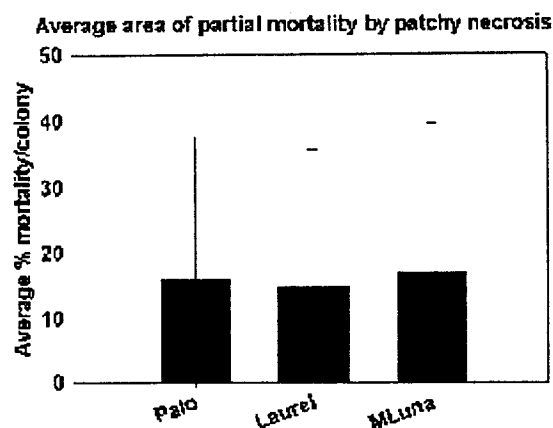


Figure 3. Average tissue loss in *A. palmata* by patchy necrosis in three coral reef areas with dense populations in La Parguera

The northern inshore localities showed the highest decline (68.4 %) and the offshore remote reefs (>6 km) the lowest *A. palmata* has disappeared from 62 % of the sites in northern and eastern Puerto Rico where it used to be found in high densities many years ago.

A. cervicornis, was documented from the northern and eastern reefs in past reports. It was present in 52.9 % of the sites surveyed many years ago, but today, it is only found in 24 % of these sites. It has but disappeared from 43% of the eastern close offshore reefs, and from all the northern and eastern inshore sites. It is present in 100 % of the eastern offshore remote reefs. The relative abundances of these populations of *A. cervicornis* have declined significantly. The hybrid *A. prolifera*, was rare in all of the four geographic localities. It disappeared from 100% of the northern reefs and from 60% of the eastern offshore close reefs. It disappeared also from 27% of the eastern offshore remote reefs. No colonies were ever documented in eastern inshore reefs. Recent surveys of reefs in Culebra and the northwest coasts of Vieques, showed presence of isolated colonies of *A. palmata* and *A. cervicornis* (Weil et al., 1998).

Low abundance of large mature colonies and low abundance or lack of juveniles and sexual recruits or reattached fragments is a clear indication that recovery is not going in the right direction in the majority of the localities. Moreover, many recently dead colonies, and colonies showing partial tissue mortality are common sights today in many of these localities. Despite the ability of acroporid corals to regenerate tissue lesions (Matos-Caraballo, 1988) and grow fast, it seems that the combination of natural and anthropogenic factors is preventing a fast potential recovery in eastern reefs.

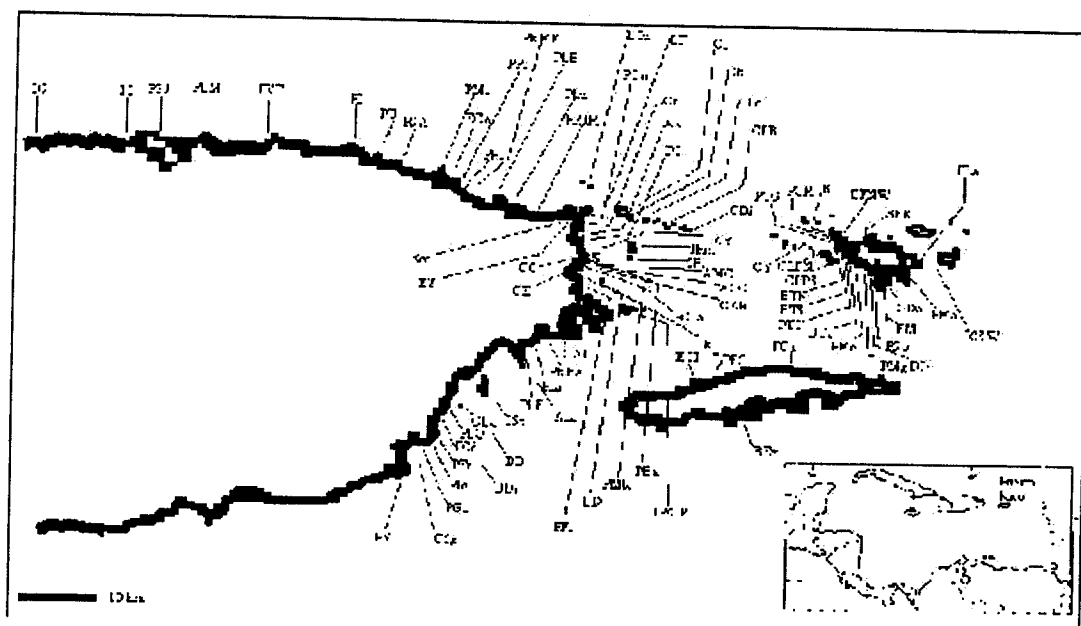


Figure 4. Map of the eastern section of Puerto Rico showing the location of 88 reef localities surveyed in the last 10 years. Many of these localities were surveyed in 1978-79 by Goenaga & Cintrón. List of localities can be found in Appendix 1. From Hernandez-Delgado (2000).

2.b. Southwest and western coasts

With few exceptions, nowadays *A. palmata* occur at low densities from 0.5-5 m depth in most of the south coast of Puerto Rico. Colonies continue to experience partial mortality in many localities. This species is now rare below 5 m, but it can still be found in few, deep patch reefs. High densities of medium to large colonies can still be found in at least two exposed reefs in La Parguera (Laurel and San Cristobal), and dense, high profile thickets along the exposed fore reef of Atravesado (Appendix 2) (Bruckner et al., 1997; Weil, pers. obser.). No *A. palmata* thickets were observed in extensive surveys from La Parguera to Ponce between 1995-1997.

Colonies were widely scattered (<1 colony every 5 m), or corals occurred in aggregates of less than 4 colonies) (Bruckner and Morelock, unp. data). Incidence of corallivores and disease was high (Bruckner, unp. data). Small elkhorn coral thickets still occur on the west coast of Puerto Rico near Rincón (Steps Reef) and the northwest coast near Isabela (Shacks Reef) in 1-2 m depth. These populations were largely unaffected by disease or predation between 1994-1997 (Bruckner, pers. obs.).

Table 2. Percent decline in the number of northeastern and eastern reef sites with *Acropora* spp. populations in the last 20 years.

Geographic province	Reefs Surveyed	Reefs with acroporids old survey	Reefs with acroporids today	Percent Change
<i>Acropora palmata</i>				
Northern inshore	19	19	6	68.4
Eastern inshore	18	15	7	53.3
Eastern offshore close	24	22	15	31.8
Eastern offshore remote	27	23	22	4.3
Total number of localities	85	79 (93 %)	50	36.7
<i>Acropora cervicornis</i>				
Northern inshore	19	2	0	100
Eastern inshore	18	3	0	100
Eastern offshore close	24	14	8	42.9
Eastern offshore remote	27	26	26	0
Total number of localities	85	45 (52.9 %)	34	24.4
<i>Acropora prolifera</i>				
Northern inshore	19	1	0	100
Eastern inshore	18	0	0	N.P.*
Eastern offshore close	24	5	2	60.1
Eastern offshore remote	27	11	8	27.3
Total number of localities	85	17 (20 %)	10	41.1

*N.P.= Not present in any survey.

A more recent problem, that probably started in the early to mid 90's, is the mortality of *A. palmata* colonies by the intrusive colonization and fast advance of a brown, endolytic, clionid sponge (*Cliona aprica*). In 1999, an average 16 % of all colonies of *A. palmata* from three reefs in La Parguera, were attacked by the sponge. Average coral tissue mortality rate was 9 cm/year, which is faster than the coral growth rate (Weil, 1999a,b) (Fig 5). The sponge is resilient and in almost all cases, once it invades the colony, it kills it within a short period of time

In the late 90's, high mortality in many reef localities was associated with Hurricane Georges (1998); over 90% of the coral was removed from Laurel, Pinnacles, Media Luna and Turrumote reefs (Bruckner, pers. obs, Ortiz, unp. data). In 1999, average disease incidence was low in general, and for *A. palmata*, it was 1.3 % in three reefs in La Parguera (Weil, 2002), an apparent decline from previous years. Average live cover of this species on most reefs near La Parguera Is now low (less than 1% in some reefs, Weil, unp. data, Bruckner, unp. data).



Figure 5. Large colony of *Acropora palmata* that has been killed by endolytic sponge *Cliona aprica* in the platform of Mario Reef, La Parguera, PR.

A. palmata has been virtually eliminated by active disease and other factors in some localities. In shallow areas of La Parguera, surviving fragments were abundant and exhibited substantial growth by February 1999 (Fig. 6) (Ortiz, unp. data). Most colonies damaged by the Hurricane were recovering (Bruckner, Earthwatch report, 1999; Ortiz, unp. data), however, the survival of the fragments is now being hampered by partial tissue mortality on the average of 46 % (± 10) of the total live tissue in one year (Ortiz, unp. data). Elkhorn coral thickets on fringing reefs near Rincón (Tres Palmas and Steps) were still in excellent condition in 1999, one year after George's (Earthwatch report, 1999) (Appendix 2)

A. palmata has been virtually eliminated from other reefs off the west coast (near Mayaguez) possibly from anthropogenic disturbances (Morelock and Bruckner, unp. data). One of the largest remaining healthy stands of *A. palmata* is located in Bajo Gallardo Reef; 3-5 m deep and approximately 13 km off the west coast of Puerto Rico. Coral disease outbreaks were observed during 1996 and 1997, however live coral cover remained high (30-90%), with corals in good shape with low incidence of recent mortality. Small thickets of *A. palmata* in fairly good shape exist to the north and south of the Fortuna Reefer restoration site in Mona island.

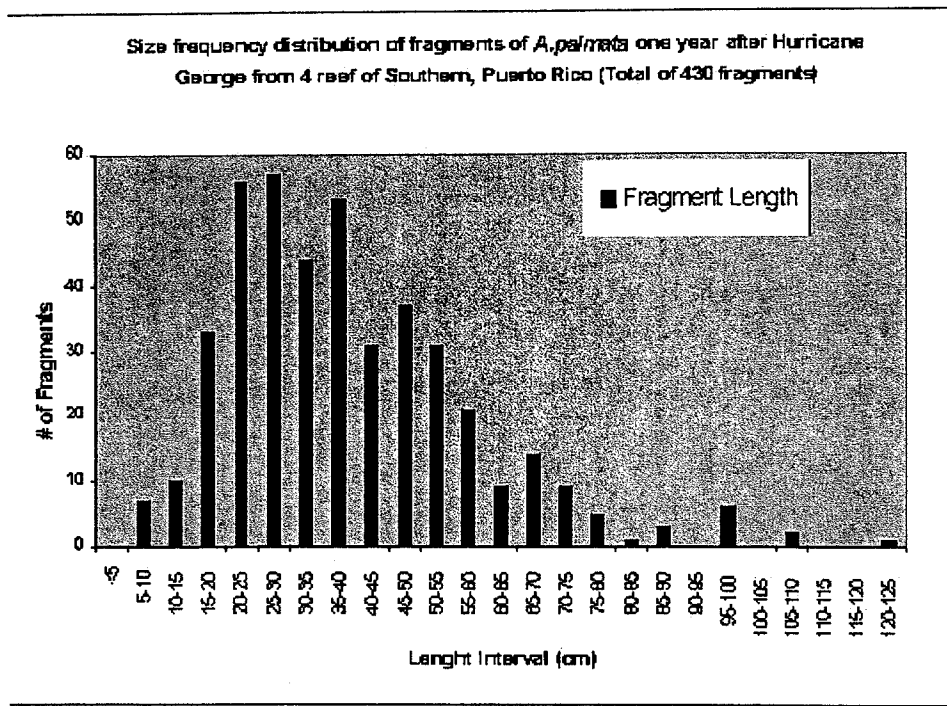


Figure 6. Size frequency distribution of *A. palmata* fragments one year after hurricane George's hit Puerto Rico.

Populations of *A. cervicornis* off the southwest coast of Puerto Rico are continuing to be impacted by WBD and other factors such as the occasional storm can be devastating. In 1996, white-band disease affected 0.5-10% of the colonies in four locations in La Parguera (Bruckner, unp. data; Bruckner and Bruckner, 1997); disease incidence varied seasonally, with a peak infection in August and September. In 1999, average disease incidence for *A. cervicornis* was 1.15 % in three reefs in La Parguera (Weil, 2002), an apparent decline from previous years. Nevertheless, small, isolated thickets and extensive populations in good shape can be found in several fringing reefs in La Parguera and Mona island. High growth rates appear to exceed mortality in many localities, and dense thickets have been reestablished in some localities (Turrumote, San Cristobal, Mona). The largest thicket (approximately 50 x 100 m) is in a back reef lagoonal area (1-3 m) in San Cristobal, La Parguera. Another extensive *A. cervicornis* field was observed during three years in Mujeres reef in Mona island, before Georges's hit in 1998. This was a deep thicket, approximately 70 x 50 m, in 12 - 15 m of water. Its status today is unknown. Offshore shelf edge populations (18-25 m) have been virtually eliminated as a result of WBD, predation and damselfish algal lawns (Bruckner unp. data). Isolated colonies occur in western Puerto Rico, but no extensive thickets are known to remain. There were many small-sized thickets (10 x 5 m or less) of *A. cervicornis* in the southwestern side of Culebrita Island, but most of these were destroyed by recent hurricanes and disease outbreaks. Several isolated patches of *A. cervicornis* growing on Los Corchos Reef, south of Culebrita Island are doing well (Hernández-Delgado, unp. data, pers. obs). A WBD outbreak in August, 2001 caused partial to total colony mortality in 51% of the surveyed *A. cervicornis* colonies (n=118) within the Luis Peña Channel Marine Fishery Reserve, at Culebra (Hernández-Delgado, unp. data). No current information is available for the east coast of Puerto Rico or other offshore islands.

Several populations of *A. palmata* and *A. cervicornis* on the southeast and west coast Mona island have been monitored in recent years. Two surveys in 1998 and two in 1999 indicate that in general, populations are in poor shape, with significant recent mortality, moderate-to-high incidence of disease, predation, algae and cyanobacteria overgrowth, and tissue loss by *Cliona* sponges moving in (Bruckner, Earthwatch data, 1999; Bruckner and Bruckner, 2001; Weil unp.data). Small thickets of *A. cervicornis* were identified on Pajaro Reef (12-15 m) in apparently good condition in 1996-1997; these experienced near total mortality in 1998 after hurricane George's, and few living colonies were observed in August, 1999 (Bruckner, unp. data).

A recent study of the impact of snail predation on populations of acroporids indicate that they are playing an important role in the decline of acroporids in some reefs (Bruckner, 2000). Surveys of 12 reefs around La Parguera and the west coast found that snails were on 18 % of all colonies of *A. palmata* and that the average snail density on those colonies was 3.7 snail/col. A larger proportion of colonies supported more snails in inshore reef habitats compared to exposed habitats. In some areas, up to 32 snails have been observed on a single colony. Larger snails were found on *A. palmata* (Fig. 7) and they caused conspicuous feeding lesions and in several occasions, consumed entire colonies (Bruckner, 2000).

The Department of Natural Resources has conducted monitoring surveys in several reefs around Puerto Rico in the last three years. In 16 reefs surveyed in 2001, most of the transects sampled did not contain colonies of *A. cervicornis* or *A. palmata*. A total of 3 colonies were observed in 80 transects. The colonies ranged in size from 10 to 85 centimeters measured as the distance intercepted by the chain transect. The mean percent cover of *A. cervicornis* for the Canoas, Botes, and Media Luna reef sites was 1.7%, 0.5%, and 0.2% respectively. The overall mean percent cover for the 80 transects of the study is 0.15%. Additionally one of the colonies at Desecheo (21 kilometers west of Puerto Rico and frequently flushed by oceanic waters) was observed with white band disease. It is worth noting that the location with the highest frequency and cover, Desecheo Island, exhibits minimal water quality degradation. This is an uninhabited island 21 kilometers from Puerto Rico that is frequently flushed by oceanic waters.

3. Management Approaches in Puerto Rico DNER Pertinent to Conservation

Existing and Proposed Regulations

Law 147-Law for the Protection, Conservation, and Management of Coral Reefs in Puerto Rico

In Puerto Rico there exist several laws and proposed regulations that may aid in the conservation of the corals from the genus *Acropora*. The most pertinent statute is the Law for the Protection, Conservation, and Management of Coral Reefs in Puerto Rico, Law 147. This law explicitly mandates the conservation and management of coral reefs in order to protect their functions and values. The Department of Natural and Environmental Resources (DNER), the agency in charge of implementing the law, will do so through a regulation that is currently being prepared. Law 147 provides for the creation of zoned areas in order to mitigate impacts from human activities.

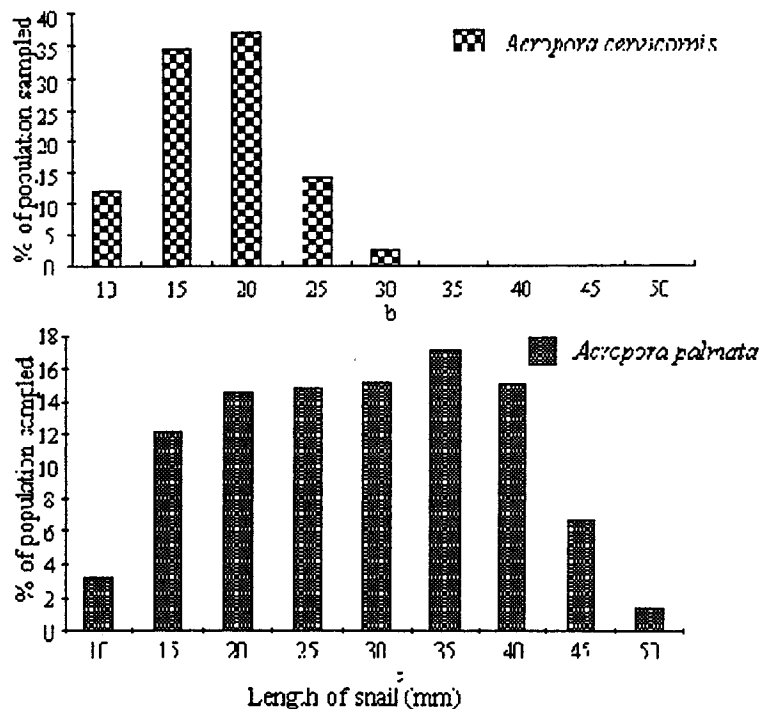


Figure 7. Shell length frequency distribution of *C. abbreviata* in acroporids from reefs off the southwest coast of Puerto Rico (from Bruckner, 2000).

These zones include (1) Reef Recuperation Areas and (2) Ecologically Sensitive Areas. Although the specifics are being worked out, these zones will facilitate the DNER in controlling human activity that can directly impact *Acropora* spp. such as anchoring. Law 147 also directs the DNER to identify and mitigate threats to coral reefs from degraded water quality due to pollution, a measure that can also be used to protect reefs with *Acropora* spp. In this regard the law requires Environmental Impact Statements (EIS) for projects or activities that can negatively affect coral reefs. An interagency committee will be convened to coordinate government activities that may affect coral reefs. In Puerto Rico there exist several laws and proposed regulations that may aid in the conservation of the corals from the genus *Acropora*. The most pertinent statute is the A Law for the Protection, Conservation, and Management of Coral Reefs in Puerto Rico, Law 147. This law explicitly mandates the conservation and management of coral reefs in order to protect their functions and values. The Department of Natural and Environmental Resources (DNER), the agency in charge of implementing the law, will do so through a regulation that is currently being prepared. Law 147 provides for the creation of zoned areas in order to mitigate impacts from human activities. These zones include (1) Reef Recuperation Areas and (2) Ecologically Sensitive Areas. Although the specifics are being worked out, these zones will facilitate the DNER in controlling human activity that can directly impact *Acropora* spp. such as anchoring. Law 147 also directs the DNER to identify and mitigate threats to coral reefs from degraded water quality due to pollution, a measure that can also be used to protect reefs with *Acropora* spp. In this regard the law requires Environmental Impact Statements (EIS) for projects or activities that can negatively affect coral reefs. An interagency committee will be convened to coordinate government activities that may affect coral reefs.

Marine Reserves Law

Law #137 from 2000 directs the DNER to designate priority areas as marine reserves. Marine reserves are defined as areas where all extractive activities are prohibited in order to help recover depleted fishery resources and protect biodiversity. The law states that that 3 percent of the insular platform must be designated within 3 years. This mechanism could be helpful in the conservation of *Acropora* spp. if it is determined that overfishing of coral reefs is affecting survivorship of these corals. It has been hypothesized that overfishing of reef fish and lobster may lead to an increased abundance of *Acropora* spp. predators. Currently there are 2 marine reserves in Puerto Rico, Reserva Natural Canal Luis Peña in Culebra and Desecheo Island.

Existing Conservation Strategies

Natural Reserves

There are currently 13 natural reserves in Puerto Rico that have coral reefs within their boundaries. The natural reserves are a logical setting to adopt the zoning measures mentioned above because of the available infrastructure and experience. Zoning strategies that regulate direct human impacts, such as no anchor zones, may be more easily applied due to the existing jurisdiction. This remains to be seen. It should be noted that natural reserves probably have minimal success in preventing impacts to coral reefs from degraded water quality because these impacts are not excluded by reserve boundaries. More information is needed on the location of *Acropora* spp. in the natural reserves in order to apply the conservation strategies, particularly those pertaining to direct impacts.

Mooring Buoys

Another existing strategy that may assist in the conservation of these species is the use of mooring buoys. The DNER has been utilizing this strategy since 1990 principally in Fajardo, Culebra, Guanica, and La Parguera. It is apparent that *Acropora* spp. are very vulnerable to anchor damage because of their branching growth form and their presence in shallow reef zones where anchoring is common. This strategy can be applied in cases where heavy anchoring is occurring on reefs with high abundance of these species. As mentioned above it is necessary to obtain more information on the location of reefs with existing *Acropora* spp. populations that may be important to their conservation.

Restoration Projects

Currently there is a restoration project being conducted with *Acropora* spp. in southwest and west Puerto Rico. This project involves a coral nursery that uses fragments to propagate colonies for restoring populations. This project will be presented in detail at the current workshop. Another restoration effort involving *A. Palmata* involves the grounding of the vessel Fortuna Reefer at Mona Island. Fragmented colonies of this species were fixed to the bottom in order to aid in their natural reattachment. This effort needs to be evaluated in order to determine the viability of this strategy.

Needs for Improving Conservation

Water Quality

In order to improve the current conservation efforts there are some gaps in knowledge that need to be addressed. One important question is understanding how water quality impacts are affecting the persistence of *Acropora* spp. in Puerto Rico? Previous research has highlighted the degraded condition of many near-shore reefs in Puerto Rico (Goenaga and Cintron 1979, Goenaga and Boulon 1992, Hernandez-Delgado and Sabatt 2000, Velazco et al. 1985). It is evident that there are multiple factors causing this degradation but there seems to be a general consensus that water quality impacts are a major force involved in this decline. Two major threats to water quality on coral reefs in Puerto Rico are high loads of suspended sediments and nutrient contamination, although direct evidence is only available implicating sediment impacts. Since it is probable that impacts from degraded water quality play a role in the health of these species, a logical step in conservation may be to determine thresholds in the important parameters in order to establish adequate standards.

Information on Location and Status

More information is needed on the location and condition of these species, particularly information on areas that may be important to conservation because of high abundance. Management efforts should compile all of the available information for Puerto Rico to determine where there are information gaps. Habitat maps are currently available from the NOAA biogeography program. These could be useful for mapping and quantifying the existing *Acropora* spp. A methodology should be developed to aid in this quantification and it should provide for comparing abundances among reefs such that spatial priorities can be established.

Case study- Proposed Natural Reserve in Rincon to Protect Reef with Abundant *Acropora palmata*

A situation that can be used to examine conservation strategies for *A. palmata* in Puerto Rico involves a fringing reef in Rincon with a high abundance of healthy colonies. Several years of monitoring has showed that the colonies at this site are some of the healthiest in the northwest (A. Bruckner, Unpub. Letter to DNER). The adjacent coastal zone exhibits low levels of development although the reef experiences increases in turbidity from storm runoff (A. Bruckner, Unpub. Letter to DNER). There are currently several large resort development projects proposed for the adjacent terrestrial areas. Possible threats from this type of development to the *A. palmata* include water quality degradation from increased run-off, and direct impacts from increased recreational activities. Several local NGO's have proposed the creation of a natural reserve encompassing the reef, adjacent marine habitats and available land areas, as mechanism to mitigate impacts. The strategy aims to use the natural reserve designation to prevent or minimize the development, although there is no evidence that this has been successful elsewhere. Any effort should strive to prevent the creation of a Paper Park by providing effective solutions. The best case scenario for this reef would be the avoidance of impacts by not doing the development projects. If this is not successful then the impacts should

be minimized and mitigation should include monitoring programs to insure the *A. palmata* is not affected. Impacts from recreational activities could be managed with the use of zoned areas as provided by the Coral Reef Conservation Law. The question arises as to the role of ESA designation for this case in Rincon.

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Appendix 1. Relative abundance of acroporid corals and presence of sexual recruits in coral reefs of the south west and offshore islands in Puerto Rico. (** = abundant; ** = few patches and isolated colonies, * = isolated colonies or present).							
Locality	Reef	Depth m	Latitude	Longitude	<i>A. palmata</i>	<i>A. cervivornis</i>	Sexual recruits
Guanica	Aurora	0.5 - 15	17° 56.652		**	*	*
	Coral	0.5 - 15			*	***	
Parguera	Corral	0.5 - 15			**	*	*
	Pinnacles W	1.5 - 20	17° 55.973	67° 00.726	*	*	*
	Pinnacles E	2 - 20	17° 55.973	67° 00.720	*	*	*
	Turumote	0.5 - 20	17° 56.061	67° 01.066	**	**	*
	Mata la Gata	0.5 - 12	17° 57.664	67° 02.253	**		*
	Caracoles	0.5 - 12	17° 57.65	67° 02.175			
	Enrique	0.5 - 18	17° 57.223	67° 03.119	*	*	*
	Media Luna	0.5 - 20	17° 56.092	67° 02.952	*	*	*
	Laurel	0.5 - 18	17° 56.581	67° 03.296	**	**	*
	Mario	0.5 - 18	17° 57.157	67° 03.380	*	*	*
	Conserva	0.5 - 14	17° 57.442	67° 03.397	*	*	
	Long Reef	4 - 20	17° 55.439	67° 00.962	*	*	*
	San Cristobal	0.5 - 18	17° 56.581	67° 04.673	**	**	*
	Atravesado	0.5 - 15	17° 56.521	67° 05.094	***	***	*
	El Palo	0.5 - 12	17° 56.006	67° 05.702	**	*	*
	Margarita	0.5 - 12			*	*	*
	Acuario	15 - 20			*	*	*
	Black Wall	17 - 30				*	
	Buoy site	17 - 30	17° 53.304	66° 59.074		*	*
	Shelf edge	17 - 30	17° 52.104	66° 61.104		*	
Cabo Rojo	El Ron	0.5-18			*	*	
	Buye	0.5-10	18° 08.068	67° 11.210	*		
Joyuda	El Negro	0.5-20	18° 09.162	67° 14.758	**	*	*
Mayaguez	Gallardo	1.5-18			***		
Rincon	Tres Palmas	1-12			**		
	Stepts				*		
Aguadilla	El Natural	5-20			*		
Desecheo Is.	South Gardens	1-22	18° 22.69	67° 29.044	*	**	*
	West	1.5-18	18° 22.740	67° 29.120	*		
Isabela	Shacks Reef				*		
Mona Island	Fortuna site	1-12			**		*
	Pajaro	4-15			*	*	*
	Mujeres	10-20	18° 04.503	67° 56.278	*	***	*
	Sardinera	0.5-10			*		
Culebra		0.5-18			*	*	*
Vieques West		0.5-18			*	*	*



Appendix 1a. Distribution of *Acropora* spp. in northern inshore Puerto Rican coral reefs (based on presence/absence data).

Location	Informed			Present		
	<i>A. pal</i>	<i>A. cer</i>	<i>A. pro</i>	<i>A. pal</i>	<i>A. cer</i>	<i>A. pro</i>
Playa de Vega Baja	*			*		
Cerro Gordo, Vega Alta	*					
Isla de Cabras, Cataño						
Punta San Jorge, San Juan	*					
Punta Las Marías, Carolina	*			*		
Punta Vacía Talega, Loíza	*					
Punta Iglesias, Loíza	*					
Punta Uvero, Río Grande	*					
Punta San Agustín, Río Grande	*					
Punta Miquillo, Río Grande	*					
Ensenada Comezón, Río Grande	*					
Punta Picúa, Río Grande	*					
Punta Percha, Río Grande	*					
Patch reef off Río Grande	*					
Punta La Bandera, Luquillo	*			*		
Playa de Luquillo	*			*		
La Selva, Luquillo	*					
Playa El Convento, Fajardo	*	*		*		
Ensenada Yegua, Fajardo	*	*	*	*		
<i>n=19</i>	<i>19</i>	<i>2</i>	<i>1</i>	<i>6</i>	<i>0</i>	<i>0</i>

Appendix 1b. Distribution of *Acropora* spp. in eastern inshore Puerto Rican coral reefs (based on presence/absence data).

Location	Informed			Present		
	<i>A. pal</i>	<i>A. cer</i>	<i>A. pro</i>	<i>A. pal</i>	<i>A. cer</i>	<i>A. pro</i>
Playa Canalejo, Fajardo	*			*		
Playa Las Croabas, Fajardo	*					
Playa Sardinera, Fajardo	*					
Punta Gorda, Fajardo						
Punta Barrancas, Fajardo	*					
Punta Mata Redonda, Fajardo	*					
Bahía Demajagua, Fajardo	*					
Punta Figueras, Ceiba						
Cayo Algodones, Naguabo	*	*		*		
Patch reef off Bahía Algodones, Naguabo	*			*		
Punta Lima, Naguabo	*			*		
Playa Fanduca, Naguabo	*			*		
Playa Las Ochenta, Humacao						
Punta Candelerero, Humacao	*	*		*		
Punta Fraile, Humacao	*	*		*		
Punta Icacos, Humacao	*					
Punta Guayanés, Yabucoa	*					
Punta Yegua, Yabucoa	*					
<i>n=18</i>	15	3	0	7	0	0

Appendix 1c. Distribution of *Acropora* spp. in eastern offshore close (<6 km) Puerto Rican coral reefs (based on presence/absence data).

Location	Informed			Present		
	<i>A. pal</i>	<i>A. cer</i>	<i>A. pro</i>	<i>A. pal</i>	<i>A. cer</i>	<i>A. pro</i>
Cayo Obispo, Fajardo	*	*				
Cayo Zancudo, Fajardo	*					
Arrecife Mata Caballos, Fajardo	*					
Arrecife Roncador, Fajardo	*	*	*	*		*
Arrecife Corona Carrillo, Fajardo	*					
Cayo Ahogado, Fajardo	*	*				
Isla de Ramos, Fajardo	*	*		*		
Isla Piñero/Cabeza de Perro, Ceiba	*	*		*		
Arrecife Lima, Naguabo	*			*		
Cayo Santiago, Humacao	*			*		
Cayo Batata, Humacao	*					
Bajo Blake, Humacao						
Bajo Drift, Humacao						
Cayo Sargento, Yabucoa	*	*				
Cayo Largo, Fajardo	*	*		*	*	
Las Cucarachas, Fajardo	*			*		
Los Farallones, Fajardo	*			*		
Cayo Icacos, Fajardo	*	*	*	*	*	
Cayo Ratones, Fajardo	*	*		*	*	
Cayo Lobo, Fajardo	*	*		*	*	
Islote Palominitos, Fajardo	*	*	*	*	*	
Isla Palominos, Fajardo	*	*	*	*	*	
Cayo La Blanquilla, Fajardo	*	*		*	*	
Cayo Diablo, Fajardo	*	*	*	*	*	*
<i>n</i> =24	22	14	5	15	8	2

Appendix 1d. Distribution of *Acropora* spp. in eastern offshore remote (>6 km) Puerto Rican coral reefs (based on presence/absence data).

Location	Informed			Present		
	<i>A. pal</i>	<i>A. cer</i>	<i>A. pro</i>	<i>A. pal</i>	<i>A. cer</i>	<i>A. pro</i>
Cayo de Yerba, Culebra		*			*	
Cayo de Luis Peña (norte), Culebra		*	*		*	
Cayo de Luis Peña (sureste), Culebra *	*	*		*		
Playa Flamenco, Culebra	*	*		*	*	
Bahía Flamenco (este), Culebra	*	*	*	*	*	
Impact Beach, Culebra	*	*		*	*	
Playa Carlos Rosario, Culebra	*	*	*	*	*	*
Punta Tamarindo Grande, Culebra	*	*		*	*	
Bahía Tamarindo (norte), Culebra	*	*		*	*	*
Bahí Tamarindo (sur), Culebra	*	*	*	*	*	*
Punta Tamarindo Chico, Culebra	*	*	*	*	*	*
Bahía Tarja, Culebra	*	*	*	*	*	*
Punta Melones, Culebra		*	*		*	*
Playa Dátiles, Culebra *	*	*		*		
Punta de Maguey, Culebra	*	*		*	*	
Playa Cascajo, Culebra	*	*		*	*	
Punta Soldado, Culebra	*	*			*	
Ensenada Malena, Culebra	*	*		*	*	
Cayo Dákity, Culebra	*	*		*	*	
Playa Manzanillo, Culebra	*	*		*	*	
Playa Larga, Culebra	*	*		*	*	
Isla Culebrita, Culebra	*	*	*	*	*	*
Arrecife Los Corchos, Culebra	*	*	*	*	*	*
Punta Campanilla, Vieques		*			*	
Playa El Gallito, Vieques	*	*		*	*	
Ensenada Claque, Vieques	*			*		
Cayo La Esperanza, Vieques	*	*		*	*	
<i>n</i> =27	23	26	11	22	26	8

***Acropora palmata*: Historical Status, Extent of Decline,
and Projection for Recovery, on St. Croix Reefs**

William B. Gladfelter and Elizabeth H. Gladfelter

The distribution of *Acropora palmata*-dominated reefs on the St. Croix shelf during the mid-1970s is summarized. These reefs totaled nearly 10 sq. km. in area. Surface coverage (defined as % of projected planar surface area) exceeded 70% in some areas (e.g. the forereef of Buck Island). In this zone there were actually several m² of live coral tissue per m² of reef due to the layering of branches. By the mid-1980s white band disease (WBD) had devastated populations of *A. palmata* everywhere on St. Croix, and surface coverage had decreased to a maximum of a few percent, but was less than 0.1% in many areas. Following demise of the *A. palmata* population from WBD, a study was initiated in 1988 on a 200 sq. m quadrat on the eastern forereef of Buck Island to monitor individual coral colonies and to observe initial stages of recovery of the *A. palmata* population in the previously densely populated reef zone. This study plot was subsequently monitored in 1991, 1996 and 2002. In 1988, the population of *A. palmata* in this plot, although enormously reduced, had 5% surface coverage. It appeared to be healthy, recovering from destruction, and no WBD disease was observed. Hurricane Hugo in 1989 caused further reduction of the population to 0.8% in the study plot. Post-Hugo recruitment of *A. palmata* was first observed on the northeastern reefs of St. Croix in 1992, where numerous 10-15 cm high *A. palmata* colonies were observed on Prtzel Reef. Nine former *A. palmata*-dominated reef sites were surveyed in March 2002 to ascertain present coverage and recent recruitment of *A. palmata*, and where data exist, compared to prior coverage during the 1970s, 1980s or 1990s. Size-frequency distributions, densities and % (planar) surface cover were determined for four of these sites: % surface cover ranged from <0.1% for south shore forereefs to 1.4, 2.4 and 3.6% cover for three north shore reefs. The population structure, including the presence of recent recruits, as well as the healthy appearance of the colonies suggest young, healthy and actively growing populations of *A. palmata* on the north shore reefs that, barring devastation by storms, predators, or disease, appear to be on their way to recovery.



STATUS OF ACROPORID POPULATIONS IN COLOMBIA

Jaime Garzón-Ferreira and Juan Manuel Díaz
INVEMAR, Santa Marta, Colombia

According to a recently published base line study of coral reefs in Colombia (Díaz et al., 2000), the total extension of recent coral formations in Colombian maritime areas, both in the Caribbean and the western Pacific, is about 1,090 km², of which more than 99% are placed in the Caribbean. In the latter, only 1/3 of the coral reefs are found along the continental coast and shelf, most of them surrounding the offshore islands of the archipelagos of San Bernardo and Rosario. On the other hand, 2/3 of Colombian reefs are found in the oceanic archipelago of San Andrés and Providencia, in the southwestern part of the Caribbean, off the continental shelf of Nicaragua and Honduras. Here, coral formations comprise two barrier reefs surrounding the two major islands, five large atolls, and several coral banks. According to Geister's typical ecological zonation of Caribbean reefs based on wave exposure zones, which includes a zone dominated by *Acropora palmata* in the highly exposed areas and an *A. cervicornis* dominated zone in medium exposed areas, the base line study estimated the total extension of *A. palmata*-dominated reefs in about 28 km² (2.6% of the total coral reef extension) and that of *A. Cervicornis*-dominated reefs in only 0.8 km² (0.07%). However, the relative cover of living tissue of both species in their respective zones is very variable from a reef area to another, ranging from nearly 90% in a few scattered patches to less than 15% in the majority of reefs. Many of the *Acropora* dominated reefs, as they were described in the 70's from San Andrés and Providencia are currently reduced to cementeries of broken skeletons covered by algae. The decline of *A. cervicornis* in this area has been estimated in 99% in the course of the last three decades, and that of *A. palmata* in about 75%. Even worse is the situation in most reef areas along the continental coast. In some areas like the San Bernardo and Rosario Islands, the decline of both species has attained levels of nearly 100%. Only in a few areas, such as Isla Arena and in some bays nearby Santa Marta, scattered small patches or isolated thickets of *Acropora* exhibit living cover over 50% and show even signs of recovery after the widespread mortalities occurred in the course of the last decades. The occurrence of scattered living thickets of *A. prolifera* has been recorded in several places in the Colombian Caribbean, in both oceanic and shelf reefs. A single record of *A. valida* from Gorgona Island off the Colombian Pacific coast has not yet been corroborated but, according to Glynn & Ault (2000), although the record do may have been valid, this species appears to be now extinct in the eastern Pacific.

Two detailed studies about the status and health of *Acropora* reef habitats have been performed very recently in the Colombian Caribbean. One of them was carried out in May-December 2001 at several bays of the Tayrona Natural Park (TNP) (central part of the northern coast of Colombia: continental reefs) and included mapping of all *Acropora* formations as well as assessments of their current composition, cover, health, and growth rates (Moreno-Bonilla et al, 2002.). The other evaluated only *A. palmata* populations within different geomorphological units of the San Andrés island reef complex (SAI) (southwestern Caribbean: oceanic reefs), in January 2002 (Rueda and Acosta, 2002). Preliminary analysis of the results show that cover of reef surfaces at both *A. palmata* and *A. cervicornis* formations of the TNP are now strongly dominated by algae (means 80.6% and 79.4% respectively), while mean live coverage by these corals is very

low (7.2% and 2.4% respectively). In contrast, average cover of live *A. palmata* in SAI is about twice, with a highest mean value in the fore-reef terrace (19%) and the lowest in the lagoon terrace (5%). In the TNP the ratio of live:dead coral is about 1:14 in the case of *A. cervicornis* and 1:7 in the case of *A. palmata*, based on cover estimates. This relationship is about 1:2 for *A. palmata* in SAI, based on volume estimates. Live populations of *A. palmata* and *A. cervicornis* in the TNP show a high incidence of partial mortality (29.7% and 58.8% respectively), *Stegastes planifrons* territories (55.8% and 58.1%) and *Coralliophila abbreviata* (22.3% and 51.2%). White pox disease is also frequent (18.1%) there in *A. palmata*, while algae overgrowth (72.5%) and fragmentation (54.4%) are common conditions in *A. cervicornis* as well. Partial mortality in SAI is found affecting about 2.7% of the *A. palmata* tissues, associated in part with bleaching, white pox disease and white patches. Linear growth estimates in healthy colonies of the TNP resulted in mean rates of 7.52 cm/year for *A. palmata* and 9.62 cm/year for *A. cervicornis*.

All three Caribbean *Acropora* species have been listed recently in the “red book” of threatened marine invertebrates of Colombia by a technical commission coordinated by the Ministry of the Environment (Mejía et al., 2002). *Acropora cervicornis* was considered as a critically endangered species in Colombia, while *A. palmata* was included as endangered, and *A. prolifera* as vulnerable, according to the IUCN categories.

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White-band disease and the changing face of Caribbean coral reefs

Richard B. Aronson¹ & William F. Precht²

¹Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, AL 36528, U.S.A.; and
Department of Marine Sciences, University of South Alabama, Mobile, AL 36688, U.S.A.

²PBS&J, 2001 Northwest 107th Avenue, Miami, FL 33172, U.S.A.

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Abstract

In recent decades, the cover of fleshy macroalgae has increased and coral cover has decreased on most Caribbean reefs. Coral mortality precipitated this transition, and the accumulation of macroalgal biomass has been enhanced by decreased herbivory and increased nutrient input. Populations of *Acropora palmata* (elkhorn coral) and *A. cervicornis* (staghorn coral), two of the most important framework-building species, have died throughout the Caribbean, substantially reducing coral cover and providing substratum for algal growth. Hurricanes have devastated local populations of *Acropora* spp. over the past 20–25 years, but white-band disease, a putative bacterial syndrome specific to the genus *Acropora*, has been a more significant source of mortality over large areas of the Caribbean region.

Paleontological data suggest that the regional *Acropora* kill is without precedent in the late Holocene. In Belize, *A. cervicornis* was the primary ecological and geological constituent of reefs in the central shelf lagoon until the mid-1980s. After constructing reef framework for thousands of years, *A. cervicornis* was virtually eliminated from the area over a ten-year period. Evidence from other parts of the Caribbean supports the hypothesis of continuous Holocene accumulation and recent mass mortality of *Acropora* spp. Prospects are poor for the rapid recovery of *A. cervicornis*, because its reproductive strategy emphasizes asexual fragmentation at the expense of dispersive sexual reproduction. *A. palmata* also relies on fragmentation, but this species has a higher rate of sexual recruitment than *A. cervicornis*. If the *Acropora* spp. do not recover, macroalgae will continue to dominate Caribbean reefs, accompanied by increased abundances of brooding corals, particularly *Agaricia* spp. and *Porites* spp. The outbreak of white-band disease has been coincident with increased human activity, and the possibility of a causal connection should be further investigated.

Introduction

Until the late 1970s, the open surfaces of Caribbean reefs were dominated by corals, algal turfs, and coral-line algae. These reefs displayed a generalized zonation pattern of three common species of scleractinian corals, which were the primary builders of reef framework (Goreau, 1959; Goreau & Wells, 1967; Goreau & Goreau, 1973). 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) under all but the most energetic conditions. While *A. palmata* was confined to a narrow depth range, the more thinly branching staghorn coral, *A. cervicornis*, was dominant at intermediate depths (~5–25 m) on

wave-exposed fore reefs. *A. cervicornis* ranged into shallower habitats on more protected fore-reefs, and it was also found in back-reef and lagoonal habitats (Geister, 1977; Adey, 1978; Rützler & Macintyre, 1982; Hubbard, 1988). Massive corals of the *Montastraea annularis* species complex were common in fore-reef habitats from ~5 to >30 m, as well as in back-reef and lagoonal areas. Today, macroalgae are the dominant space-occupiers on many, if not most, Caribbean reefs, and the coral zonation pattern has essentially disappeared (Jackson, 1991; Hughes, 1994). A question of great significance to scientists, managers, and policymakers is whether the recent changes are something new or part of a long-term pattern of repeated community shifts.

Explanations for the transition to macroalgal dominance on Caribbean reefs revolve around reduced herbivory ('top-down' hypotheses), increased nutrient input ('bottom-up' hypotheses), or models that combine the two (e.g. Littler & Littler, 1985; Lewis, 1986; Hughes, 1994; Steneck, 1994; Lapointe, 1997). Attention to herbivory and nutrient loading, however, de-emphasizes the pivotal role of coral mortality in precipitating the transition (McCook, 1999; Aronson & Precht, 2001). Although fleshy macroalgae generally have higher growth rates and are capable of outcompeting corals, they must recruit to the reef in order to do so (Umar et al., 1998). The death of corals and other sessile benthos provides the space required for macroalgae to settle, and low herbivory and high nutrient levels promote the accumulation of macroalgal biomass.

The devastation caused by Hurricane Allen on the reef at Discovery Bay, Jamaica in 1980 (Woodley et al., 1981), for example, was an important precondition for the phenomenal level of macroalgal overgrowth that occurred over the following decade (Hughes et al., 1987; Liddell & Ohlhorst, 1993). The *Acropora* species, dominant and with a branching morphology, were particularly affected by Hurricane Allen. Direct mortality of *Acropora* from the storm and collateral mortality from corallivorous fish and invertebrates, combined with reduced herbivory from a long history of overfishing and the Caribbean-wide mass mortality of the echinoid *Diadema antillarum* in 1983–84, transformed the benthic community (Hughes et al., 1987; Knowlton et al., 1990; Knowlton, 1992). Coral cover on some Jamaican fore reefs is currently <5%, down from $\geq 50\%$ before 1980, and macroalgal cover is generally >60% at this point (Aronson et al., 1994; Hughes, 1994; Aronson & Precht, 2001; but see Edmunds & Bruno, 1996; Aronson & Precht, 2000).

Two case histories from Belize also highlight the importance of coral mortality. First, Hurricane Hattie struck the barrier reef and offshore atolls of Belize in 1961, destroying acroporids and other corals on many reefs. Hurricane Hattie occurred two decades before the *Diadema* mass mortality, at a time when Belizean reefs were subject to negligible fishing pressure and virtually no anthropogenic nutrient input. Nevertheless, Stoddart (1963, 1969, 1974) documented more than ten years of macroalgal dominance on some hurricane-damaged reefs. The sudden decline in topographic complexity caused by Hurricane Hattie could have inhibited the activity of herbivores and thereby increased macroalgal cover (see Kaufman, 1983; Szmant, 1997).

Second, coral cover declined during the 1980s in the spur-and-groove zone dominated by *A. cervicornis* (12–15 m depth) on the fore reef at Carrie Bow Cay, in the central section of the Belizean Barrier Reef. During the same period, macroalgal cover increased from <5% to >60% (Littler et al., 1987; Aronson et al., 1994). Carrie Bow Cay was lightly fished. *D. antillarum* were virtually absent below 6 m depth both before and after their mass mortality, and nutrient levels were extremely low (Lewis & Wainwright, 1985; Lapointe et al., 1987, 1997). Although Hurricane Greta damaged some corals at Carrie Bow Cay in 1978 (Highsmith et al., 1980; Rützler & Macintyre, 1982), white-band disease was responsible for most of the coral mortality, which occurred in the 1980s. There is no information available to suggest that coral mortality at Carrie Bow Cay led to the reduced activity of herbivorous fish.

Woodley (1992) suggested that reefs along the north coast of Jamaica historically may have had low coral cover much of the time, independent of the *Diadema* mass mortality and such human activities as the exploitation of herbivorous fishes. Woodley reasoned that an unusual lack of hurricane disturbance for several decades prior to Hurricane Allen explained the high coral cover that characterized Jamaican reefs before 1980. The alternative interpretation is that high coral cover is the usual condition of Caribbean reefs, and that the current situation in Jamaica and elsewhere reflects a novel combination of circumstances (Jackson, 1991, 1992; Hughes, 1994). Whichever view is correct, a primary reason for the dramatic loss of coral cover in the Caribbean has been the mortality of *Acropora* spp. Although populations of other coral species have experienced local mortality for a variety of reasons, the regional decline of *A. palmata* at shallow depths and *A. cervicornis* at intermediate depths has radically altered the composition of reef assemblages and opened large areas of space for colonization by macroalgae and other benthic organisms (Hughes, 1994; Steneck, 1994; Aronson & Precht, 1997).

In this paper we examine the mortality of *Acropora palmata* and *A. cervicornis* populations in the Caribbean. We argue that, although hurricane damage has been important on some reefs, white-band disease has probably been the most significant factor on a regional scale in reducing populations of these primary framework builders. We then consider paleontological evidence suggesting that the recent, regional mass mortality of *Acropora* spp. is a novel event, unique in the late Holocene. These results lead to the conclusion that Caribbean reefs are currently experi-

encing conditions different from those that prevailed during the past several millennia. Finally, we review the life history characteristics of *Acropora* spp. and other coral species and use that information to predict what Caribbean reefs will look like in the coming decades.

Hurricanes and white-band disease

Our collective understanding of coral mortality in the Caribbean has been heavily influenced by intensive research at Discovery Bay and elsewhere along the north coast of Jamaica. Mortality of *Acropora cervicornis* and *A. palmata* from Hurricane Allen and collateral effects were followed by further damage during Hurricane Gilbert in 1988 (Woodley, 1989; Hughes, 1994). Studies in Jamaica and elsewhere have led to the opinion that hurricanes are a primary cause of present and past coral mortality, diversity, and distribution on Caribbean reefs (Connell, 1978; Hubbard, 1989; Rogers, 1993a; Blanchon, 1997; and many others).

Hurricanes have been important at some localities, but they do not explain recent patterns of coral mortality in much of the Caribbean region. Catastrophic hurricane damage is patchy on many spatial scales. Some areas, such as Trinidad, Costa Rica, and Panama, receive virtually no hurricanes while others, including the north coast of Jamaica, are exposed to hurricanes with predictable frequency on a time scale of decades to centuries (Neumann et al., 1987; Woodley, 1992; Tremblay et al., 1997). On a regional basis, corals suffer greater damage from chronic disturbances and stresses, such as disease outbreaks (Bythell et al., 1993; Rogers, 1993b). At Carrie Bow Cay, for example, white-band disease (WBD), rather than hurricane damage, has been the principal cause of *A. cervicornis* mortality in the spur-and-groove zone since the 1980s. WBD has also nearly eliminated *A. cervicornis* from the (physically protected) shelf lagoon of the Belizean Barrier Reef (Aronson & Precht, 1997).

WBD is a presumed bacterial infection that is specific to *Acropora* spp., although the pathogen(s) remain unidentified (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

are poorly understood, and recent work suggests that there are several varieties of the disease (Peters, 1997; Santavy & Peters, 1997; Richardson, 1998).

Other sources of *Acropora* mortality include bleaching (Cortés, 1994), predation by corallivores (Knowlton et al., 1990), nutrient loading and sedimentation (Weiss & Goddard, 1977; Rogers, 1990; Bell & Tomascik, 1994; Cortés, 1994), and, in Florida and the Bahamas, cold water stress (Davis, 1982; Porter et al., 1982; Jaap & Sargent, 1994). Although quantitative data are generally lacking, it is apparent that WBD epizootics have been an important cause of the recent mortality of *A. cervicornis* and *A. palmata* over wide areas of the Caribbean (Bythell & Sheppard, 1993; Fig. 1). Even at Discovery Bay, WBD was noted on *A. cervicornis* prior to Hurricane Allen, and the disease may have killed surviving branch fragments after the storm (Knowlton et al., 1990; Woodley et al., 1997).

At a number of localities, including Florida, the Bahamas, and Belize, *A. cervicornis* has been more severely affected by WBD than *A. palmata*. This may be true elsewhere as well, although the information available is mostly anecdotal. An interspecific difference in susceptibility may explain the persistence of *A. palmata* on some reefs where *A. cervicornis* has been extirpated. Nevertheless, populations of *A. palmata* in Anguilla, St. Croix, and other areas have experienced heavy to nearly complete mortality from WBD.

There is no association of WBD outbreaks with proximity to human influences; reefs both near and far from human population centers have been affected. Of course, it could be argued that the Caribbean is so small that the entire region lies in close proximity to sources of anthropogenic stress (Connell, 1997). There may be a link between coral disease and outbreaks of corallivorous snails (Antonius & Riegl, 1997; Bruckner et al., 1997), but a firm connection has not been established at this point.

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 (Aronson & Precht, 1997). *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, and St. Croix, for example. Dead stands of *A. palmata* are then leveled by storms (Bythell et al., 1989; Hubbard et al., 1991).

In summary, the recent shift to macroalgal dominance is a regional phenomenon, and the widespread mortality of incumbent coral populations was clearly a prerequisite. White-band disease has been the most

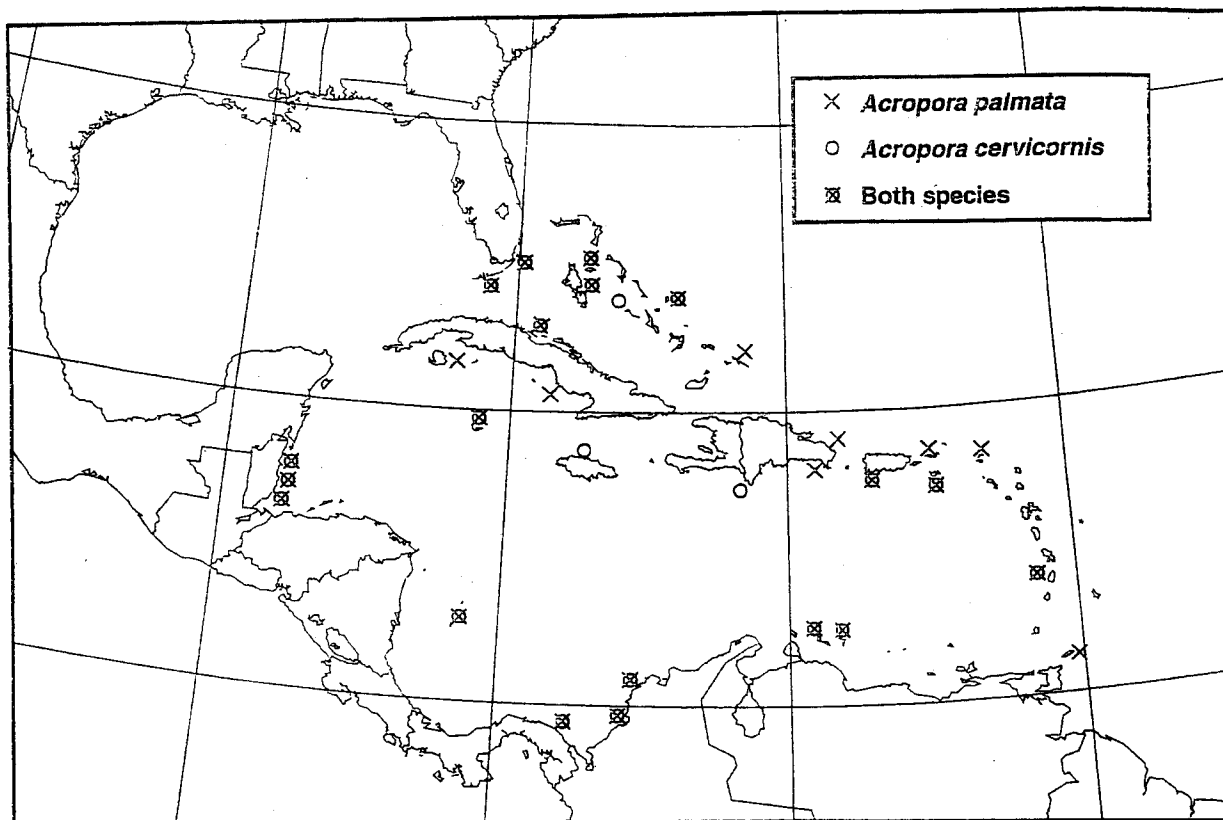


Figure 1. Reports of white-band disease as a cause of significant *Acropora* mortality on Caribbean reefs over the past few decades. Data from Wilkinson (2000) and Aronson & Precht (2001).

important regional-scale cause of *Acropora* mass mortality over the past decades. Since *Acropora* spp. were among the dominant space-occupiers on many reefs, their decimation substantially reduced coral cover in the Caribbean. We now turn to the fossil record of Caribbean reefs to place the recent WBD epizootic in a historical context.

The fossil record of *Acropora* mass mortalities

Local abundances of *Acropora palmata* and *A. cervicornis* can be highly variable on a time scale of decades to centuries (Shinn et al., 1989; Jaap, 1998). Both species experienced significant local mortality from hurricanes and other severe storms in the Pleistocene and Holocene and have recently experienced similar damage (Ball et al., 1967; Lighty, 1977; Macintyre et al., 1981; Curran & White, 1984; Hubbard, 1989; Blanchon et al., 1997). Other probable causes of local mortality in the past include increased terrigenous input associated with the early phases of European colonization (Lewis, 1984) and cold water stress at subtropical latitudes (Davis, 1982).

Jackson (1992) synthesized information on the composition of Pleistocene reef terraces in Barbados and elsewhere in the Caribbean. From the pioneering work of Mesolella (1967) and others, Jackson showed that the composition and zonation of Pleistocene reefs were essentially similar to what had been found on living Caribbean reefs prior to the 1980s. In particular, he noted the ubiquity of large accumulations of *A. palmata* and *A. cervicornis* in Pleistocene reef-crest and fore-reef zones. Jackson (1992) concluded that acroporids dominated more or less continuously during the high sea-level stands represented by the terraces, although small-scale fluctuations may have occurred.

Increases in relative sea level during the Pleistocene deglaciations and during the rapid sea-level rise early in the Holocene (10 000 to ~5500 yr b.p.) affected *Acropora* populations on a regional scale. Some *Acropora* populations were drowned outright, while others were poisoned as sediment- and nutrient-laden waters flowed from flooded lagoons and adjacent coastal plains onto fore-reef habitats (Adey, 1978; Shinn et al., 1981; Lighty et al., 1982; Neumann & Macintyre, 1985; Macintyre, 1988; Fairbanks, 1989;

Blanchon & Shaw, 1995). Nevertheless, in many cases *Acropora* populations caught up to and kept pace with rising sea level early in the Holocene. This phenomenon seems to have been especially well recorded in the fossil record in certain protected, lagoonal settings, where water quality was evidently not inimical to rapid growth of *A. cervicornis* (Macintyre et al., 1977; Taylor et al., 1985; Macintyre, 1988; Aronson et al., 1998).

The question we pose is whether there was a regional *Acropora* kill at any time in the late Holocene (the past 3000–4000 yr) that was comparable to the one observed during the past decades. Sea level rose only ~1 m in the last 3000 yr (Lighty et al., 1982; Fairbanks, 1989; Precht, 1993; Macintyre et al., 1995), which is slow relative to *Acropora* accumulation rates (e.g. Macintyre et al., 1977; Westphall, 1986; Aronson & Precht, 1997); therefore, if any regional mass mortalities occurred in the last 3000 yr, they cannot be attributed to Caribbean-wide drowning or poisoning by inimical waters. By coring lagoonal reefs in Belize, we tested the hypothesis that the recent, disease-induced mortality of *A. cervicornis* has no precedent in the late Holocene.

The central shelf lagoon of the Belizean barrier reef system is characterized by numerous atoll-like, diamond-shaped reefs known as rhomboid shoals. The narrow, steep-sided 'ribbon reefs' that form the perimeters of these shoals reach sea level and surround sediment-filled basins (Macintyre & Aronson, 1997; Macintyre et al., 2000). Thick, uncemented accumulations of Holocene coral skeletons and associated sediments underlie the living reef communities of the rhomboid shoals. Radiocarbon age determinations indicate that the Holocene deposits, which are up to 20 m thick, have accreted over the past 8000–9000 yr (Westphall & Ginsburg, 1984; Westphall, 1986).

The lack of submarine cementation on these lagoonal reefs is typical of protected, low-energy sites (Purser & Schroeder, 1986; Macintyre & Marshall, 1988). Debris fans at the bases of the outer reef flanks (21–30 m water depth) may indicate occasional storm disturbance. Hurricane Greta in 1978, the last major storm in Belize prior to this study, leveled some stands of *A. cervicornis* on lagoonal reefs. Hurricane Greta, however, apparently had no long-term effect on the living communities or the Holocene sediments of the rhomboid shoals (Westphall, 1986). (Hurricane Mitch in 1998 likewise had no impact on the ecology or geology of the rhomboid shoals.)

A. cervicornis dominated the living reef communities of the rhomboid shoals in the 2–15 m depth range until 1986 (Shinn et al., 1979; Westphall, 1986; Figs 2,

3). The lettuce coral *Agaricia tenuifolia* and other corals in the family Agariciidae were major components of the community below 15 m and minor constituents above 12 m depth (Westphall, 1986). The shallowest depths (≤ 1 m) were dominated by the finger coral *Porites divaricata* and the hydrocoral *Millepora alcicornis* (Aronson et al., 1998; Macintyre et al., 2000). During the late 1980s, white-band disease virtually exterminated the *A. cervicornis* populations on the rhomboid shoals and along the outer barrier reef (Aronson & Precht, 1997).

A. cervicornis colonies that were killed by WBD collapsed due to the weakening of their skeletons by bioerosion. On the rhomboid shoals, algae that colonized the coral skeletons were consumed by the echinoid *Echinometra viridis*, which was considerably more abundant in the lagoon than in fore reef habitats (Aronson et al., 1994; Aronson & Precht, 1997). *A. tenuifolia* and the other agariciids recruited to the *Echinometra*-grazed *A. cervicornis* rubble, as predicted by Sammarco's (1982) experiments at Discovery Bay. The cover of *Agaricia* spp., primarily *A. tenuifolia*, then increased dramatically (Figs 2, 3). Colonies of *A. tenuifolia* growing in this environment have an overall trapezoidal shape and a high center of gravity, and as they grew tall and toppled over, the deposition of *Agaricia* rubble increased. Herbivory by *E. viridis* prevented the *Agaricia* rubble from becoming covered by algal growth, and the low algal cover (<10%) permitted *A. tenuifolia* to continue recruiting at a high rate (Edmunds et al., 1998). This *Acropora*-to-*Agaricia* transition occurred throughout the central and southern lagoon in Belize. In Belizean fore-reef environments, where *E. viridis*, *Diadema antillarum*, and other herbivorous echinoids were less abundant and less active, fleshy macroalgae came to dominate areas formerly occupied by large stands of *A. cervicornis* (Aronson et al., 1994; Macintyre & Aronson, 1997).

Fleshy macroalgae do not preserve in fossil reefs, but corals, of course, preserve extremely well. The shift in dominance from *Acropora cervicornis* to *Agaricia tenuifolia* in the Belizean shelf lagoon can be used as a preservable proxy for the mortality of *A. cervicornis* and its replacement by macroalgae elsewhere in the Caribbean. Push-cores extracted from 5–9 m water depth in 1994–97 enabled us to reconstruct the history of the rhomboid shoals during the late Holocene (see Aronson & Precht (1997) for coring methodology). The cores contained a topmost layer of *A. tenuifolia* rubble overlying a thick accumulation of *A. cervicornis* (Fig. 4). There was minimal taphonomic alteration of the *A. tenuifolia* layer.

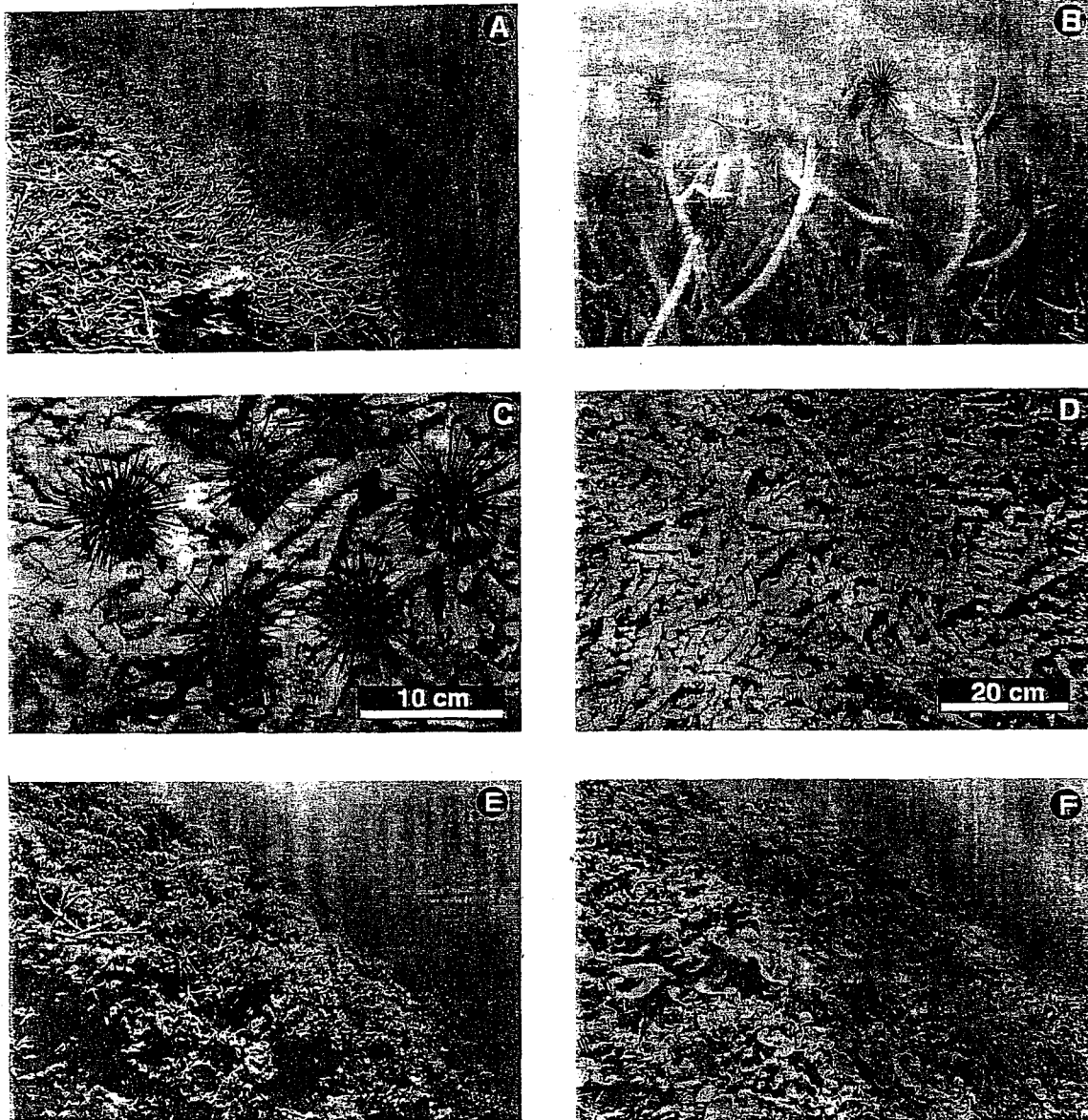


Figure 2. Photographs along the flanks of the rhomboid shoals in Belize. (A) Wide-angle, panoramic view of *Acropora cervicornis* dominant in April 1986, 7 m depth. Note toppled colony of *Agaricia tenuifolia* in the foreground; this colony is 1 m in longest dimension. (B) Dead *Acropora*, still in growth position, being grazed by the sea urchin *Echinometra viridis*. (C) Closeup of *Echinometra* grazing *Acropora* rubble. (D) Heavily eroded *Acropora* rubble in August 1990, 7 m depth. (E) Wide-angle view of *Agaricia* dominant in June 1994, 5 m depth. Note small *Acropora* colonies on the left. (F) Wide-angle view of plating *Agaricia* spp. dominant in June 1994, 13 m depth.

A. cervicornis rubble in a thin layer just beneath the *A. tenuifolia* was encrusted, bored, and highly abraded, which indicates exposure at the sediment-water interface (Greenstein & Moffat, 1996). This interval was produced by the recent (post-1986) WBD epizootic. Abrasion was caused by the grazing activity of *E. viridis*, and boring was due primarily to clionid sponges. Many pieces of *A. cervicornis* had fragments of *A. tenuifolia* colonies encrusting to them, corresponding to our observation that *A. tenuifolia* recruited

to the *A. cervicornis* rubble after 1986. The existence of a discrete layer of taphonomically altered *A. cervicornis* means that past *Acropora* mortality events should be detectable whether or not they led to dominance by *Agaricia* or other corals. Neither the layer of taphonomically altered *A. cervicornis* rubble nor the layer of imbricated *A. tenuifolia* plates was observed at the tops of cores extracted from the rhomboid shoals before 1986 by other investigators (Shinn et al., 1979; Westphall, 1986).

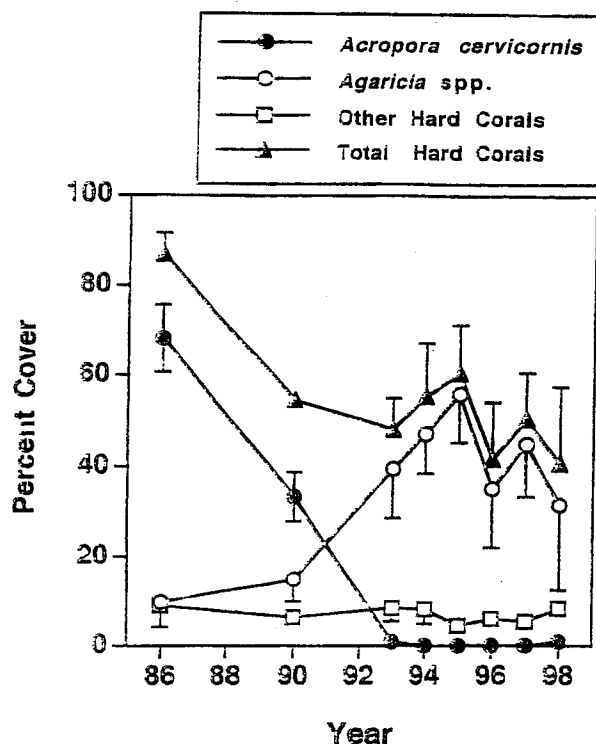


Figure 3. Changes in percent cover in the living community at Channel Cay, in the central shelf lagoon of Belize, during the period 1986–1998. Percent cover values are based on point counts every 10 cm along transects that ran perpendicular to the reef slope from 3–15 m depth at two stations. One station was on the windward side and one station was on the leeward side of the cay, and depths were pooled within stations (Aronson & Precht, 1997). Points represent means and error bars represent standard deviations.

The subsurface Holocene prior to 1986 consisted of an open framework of interlocking *A. cervicornis* skeletons. These buried *A. cervicornis* colonies were generally found in growth position, surrounded by muddy, carbonate sediment. Much of the *A. cervicornis* was relatively well-preserved and taphonomically unaltered, indicating rapid burial under further accumulations of *A. cervicornis* (Fig. 4). *A. tenuifolia* was a minor component throughout. There was virtually no evidence of bioturbation, and *E. viridis* spines were common throughout the cores.

Radiocarbon analysis of coral material from the bottoms of our cores yielded a maximum uncorrected ^{14}C date of 3130 ± 100 yr (Aronson & Precht, 1997; Aronson et al., 1998). The cores showed no evidence that an episode of *A. cervicornis* mortality or a transition to *A. tenuifolia* occurred throughout the central lagoon in the 3000 years before 1986. Two cores extracted in 1997 showed evidence of *A. cervicornis* mortality and *A. tenuifolia* growth, but these events were localized in time (probably decades at

the most) and space (tens of meters at most). We can draw two conclusions from these results. First, it was possible to detect pre-1986 *A. cervicornis* mortality events and *A. tenuifolia* layers in the cores. Second, although *A. cervicornis* mortality and *Acropora*-to-*Agaricia* transitions occurred locally in the past, it was only after 1986 that *A. cervicornis* died and *A. tenuifolia* replaced it throughout the central lagoon. If a widespread event had occurred before 1986, we would have detected it in most or all of the cores.

The recent *Acropora*-to-*Agaricia* transition was not caused by shallowing upward of the reefs. Shallowing upward appeared in cores extracted near sea level as a transition from *A. cervicornis* to *Porites divaricata* and *Millepora alcicornis*, occurring at a water paleodepth of ~ 1 m (Fig. 4). The shift to *A. tenuifolia*, in contrast, occurred over a broad depth range, down to 15 m, on the rhomboid shoals. It also occurred on incipiently drowned reefs of the southern shelf lagoon in Belize, which have not kept pace with sea-level rise in the Holocene (Aronson et al., 1998). Furthermore, it is worth bearing in mind that, before the demise of *A. cervicornis*, agariciids were more characteristic of deep water than they were of shallow water.

Judging from the distribution of sea urchin spines in the cores, *E. viridis* probably controlled algal abundance on a long-term basis. Both the widespread mortality of *A. cervicornis* and the subsequent, opportunistic rise to dominance of *A. tenuifolia*, however, were unprecedented in the late Holocene. Data from other areas of the Caribbean also show patterns of continuous Pleistocene-Holocene accumulation of *Acropora* spp. and their recent, steep decline.

Stemann & Johnson (1995; see also Taylor et al., 1985) examined a subaerially exposed Holocene reef in the Enriquillo Valley, Dominican Republic. The shallow outer slope of this lagoonal reef, which spanned the interval from 9000 to 5000 yr b.p., was composed almost entirely of well-preserved *A. cervicornis*. The absence of layers of poorly preserved *A. cervicornis* suggests that the species dominated continuously.

Hubbard et al. (1994), working with cores extracted from reefs in St. Croix, noted compositional similarities between *A. palmata*-dominated, shallow fore-reef facies over the past 7000 yr and the living, shallow fore-reef community in 1976, before the *A. palmata* populations on those reefs were devastated by WBD. Hubbard et al. (1994) concluded that their data may indicate that WBD outbreaks are something new on Caribbean reefs. Greenstein et al. (1998; and references therein) noted the recent, WBD-mediated replacement of *A. cervicornis* by *P. porites* on a patch

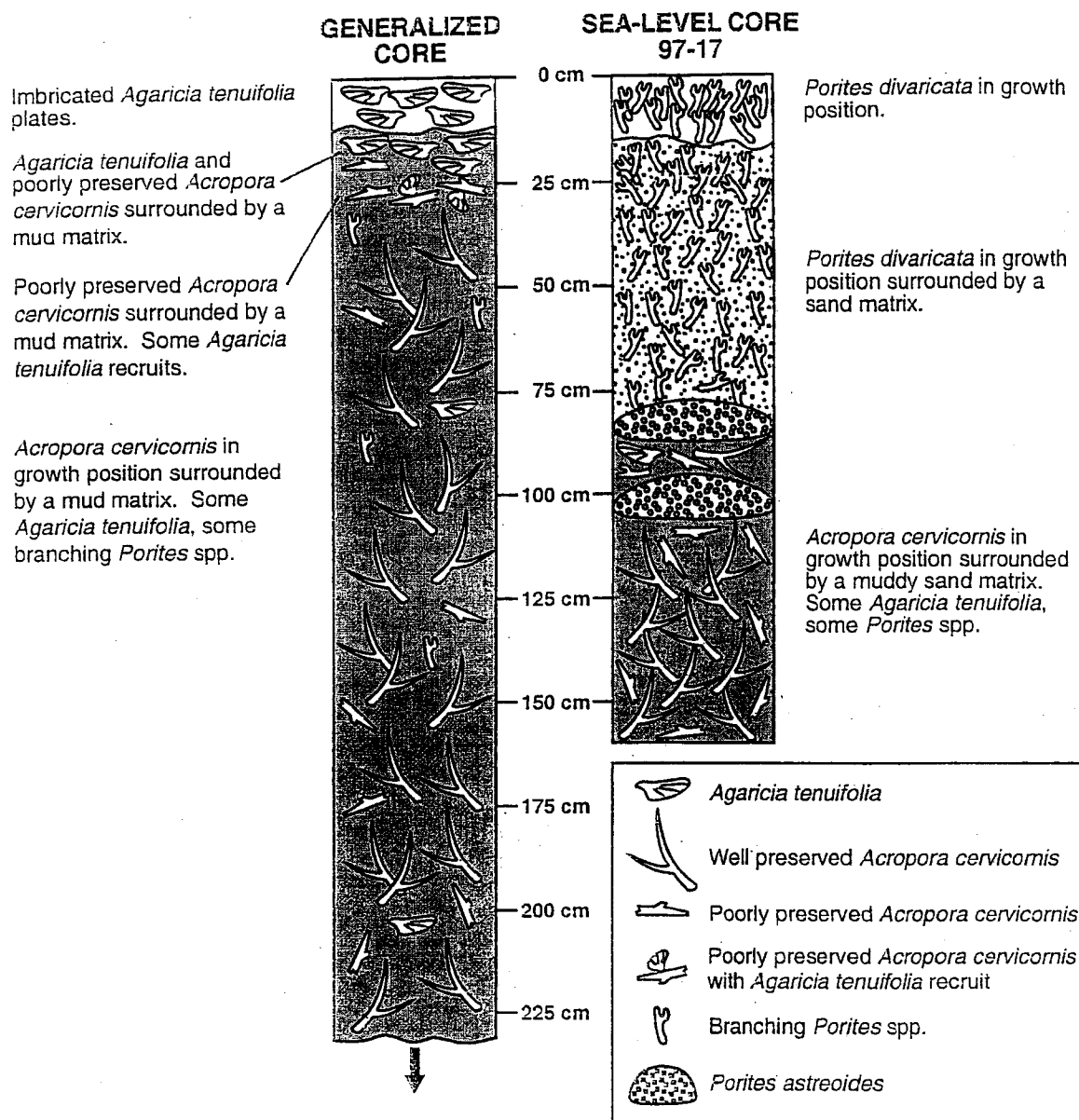


Figure 4. Schematic drawings of push-cores. Left: Composite diagram based on 12 cores recovered from 5–9 m water depth in 1995 and 1997. The upper layers, which were dominated by taphonomically altered *Acropora* rubble and imbricated plates of *Agaricia*, were deposited in the late 1980s and early 1990s. Right: Core 97-17 from 0.5 m water depth at Channel Cay, showing a typical shallowing-upward sequence. *Porites divaricata* dominated the community beginning ~500 b.p. Sediments are indicated by shading: gray fill represents mud, stippling represents sand, and together they represent muddy sand. Wavy, horizontal lines demarcate the upper limit of sediment; skeletal material above that interface was not packed in mud or sand. Modified from Aronson et al. (1998).

reef at San Salvador Island, Bahamas. The lack of evidence for such a species replacement in nearby Pleistocene deposits was taken as evidence that the recent transition to *Porites* was a rare or unique event.

These studies support the hypothesis that this is the first time in the past several millennia (and possibly longer) that *Acropora* spp. have died off throughout

the Caribbean region. The implication is that WBD is an emergent disease of *Acropora*. The time course and extent to which *Acropora* spp. recover will depend on their life history strategies, the life history strategies of the species that have replaced them, and the frequency and severity of future disturbances.

Recovery of *Acropora* populations in the Caribbean

In the Indo-Pacific, *Acropora* spp. rapidly recolonize hard substrata in the wake of crown-of-thorns starfish (*Acanthaster planci*) outbreaks, coral bleaching episodes, and other disturbances. Post-disturbance periods of algal dominance are generally shorter than in the Caribbean (Sammarco, 1985; Done, 1992; Kojis & Quinn, 1994). 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 reproductive strategies are probably also a factor.

The dominance of *A. cervicornis* in the Caribbean prior to 1980 was due to its rapid growth, coupled with its asexual reproductive strategy of wave-induced fragmentation (Shinn, 1966; Tunnicliffe, 1981; Highsmith, 1982). This dependence on asexual propagation comes at the expense of larval production (Hughes, 1985; Knowlton et al., 1990). The resulting low levels of sexual recruitment have slowed recovery at most Caribbean localities. Although rapid growth and fragmentation are also strategies employed by *A. palmata*, this species shows higher rates of sexual recruitment to disturbed areas than *A. cervicornis* (Stoddart, 1974; Highsmith, 1982; Rosesmyth, 1984; Jordán-Dahlgren, 1992).

Like *Montastraea* spp., *A. palmata* and *A. cervicornis* are broadcast spawners, releasing their eggs into the water column for fertilization and development. Because they are now rare, *Acropora* spp. may be experiencing an Allee effect: colonies may be too far apart for high fertilization success (Knowlton, 1992). The same may be true for the *Montastraea annularis* species complex, although adult mortality has not been as precipitous and large stands still occur throughout the region (Shinn et al., 1989; Precht, 1993; Edmunds & Bruno, 1996; McClanahan & Muthiga, 1998; Bak & Meesters, 1999). At this point brooding coral species, which retain their eggs after internal fertilization and release their offspring as planula larvae, are recruiting more successfully than broadcast spawners (Smith, 1992). All Caribbean representatives of the families Agariciidae and Poritidae are brooders, and *Agaricia agaricites*, *A. tenuifolia*, *Porites astreoides*, and *P. porites* are among the first coral species to appear on disturbed reef surfaces, including *Acropora* rubble fields (Bak & Engel, 1979; Rylaarsdam, 1983; Rogers et al., 1984; Hughes, 1989; Smith, 1992). *Acropora* spp. and the *M. annularis* complex, the primary

framework builders of Caribbean reefs, are presently recruiting only at very low levels.

Broadcast spawning, which produces planktotrophic planulae, generally entails a developmental time of one to several weeks in the water column. In contrast, brooded planulae, which are lecithotrophic, can settle as early as a few minutes to as long as 100 d after their release (Fadlallah, 1983; Harrison & Wallace, 1990; Richmond & Hunter, 1990; Edinger & Risk, 1995). The flexibility of larval lifespan enables brooded planulae to settle either near or far from the mother colony, which may explain their current success in the Caribbean (Szmant-Froelich et al., 1985; Richmond, 1987).

Brooders may also have an advantage over broadcasters in fertilization success. Many species of Caribbean corals, including *Acropora* spp., *Agaricia agaricites*, and *P. astreoides*, are hermaphroditic (Szmant, 1986; Harrison & Wallace, 1990; Richmond & Hunter, 1990), but the propensity for self-fertilization may differ between brooders and broadcasters (Carlson, 1999). *P. astreoides*, *A. agaricites*, and *Favia fragum* (another brooder) exhibit high rates of self-fertilization (Brazeau et al., 1998; D. F. Gleason, pers. comm.), but rates of selfing in other brooding species remain unstudied. Rates of self-fertilization are unknown for Caribbean *Acropora* spp., but other broadcasting, hermaphroditic species, including members of the *Montastraea annularis* species complex, do not appear to self-fertilize extensively (Knowlton et al., 1997; Szmant et al., 1997; Hagman et al., 1998).

Conclusion

The ultimate causes of the dominance and subsequent demise of acroporids in the Caribbean are historical in nature. Features such as high growth rates and an emphasis on fragmentation, acquired before the Pleistocene, probably helped these species persist through the Pleistocene sea-level fluctuations to become framework builders on modern reefs (Jackson, 1994; Johnson et al., 1995). *Acropora* spp. have been decimated over the past two decades as the fragmentation strategy has become less advantageous or even detrimental in the face of new kinds of disturbance and stress (Jackson & Budd, 1996). For example, low genetic variability resulting from asexual reproduction may have increased the susceptibility of *Acropora* populations to white-band disease (Bak, 1983).

Since the disease-induced mass mortality of *Diadema antillarum* in 1983–84 (Lessios et al., 1984), ecologists and microbiologists have been identifying

new diseases on coral reefs at an alarming rate. A rapidly-expanding roster of pathologies threatens such important sessile organisms as corals, sponges, gorgonians, and coralline algae (Peters, 1993, 1997; Antonius, 1995; Littler & Littler, 1995; Richardson, 1998; Richardson et al., 1998). At least one recently discovered disease, a fungal infection of Caribbean sea fans, is caused by a pathogen of probable terrestrial origin (Smith et al., 1996; Geiser et al., 1998). This fungal epizootic could be the result of altered patterns of land use (Santavy & Peters, 1997). High population densities of *D. antillarum*, possibly due to overfishing in the Caribbean (Hay, 1984), could have facilitated the spread of the pathogen that caused their mass mortality (Lessios, 1988). Other diseases appear to increase in virulence when their hosts are stressed by high temperatures and various forms of pollution (Rützler et al., 1983; Edmunds, 1991; Kushmaro et al., 1996). A crucial question, then, is whether *Homo sapiens* is a vector for one or more diseases on coral reefs.

The long-term implications of the regional demise of *Acropora* and other disease-induced mortality events are not known. Recent changes on Caribbean coral reefs could persist for decades, and it is unclear how global climate change will interact with diseases and other stresses (Brown, 1997; Harvell et al., 1999; Kleypas et al., 1999). If one or both of the *Acropora* species do not recover, continued high abundance of fleshy macroalgae and increasing roles for *Porites* spp. and *Agaricia* spp. are likely. Finally, if the recent mass mortality of *Acropora* really is a unique event in the late Holocene, then a connection between the novel outbreak of white-band disease and the ever-increasing impact of human activity should be further investigated.

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THE EXPANDING SCALE OF SPECIES TURNOVER EVENTS ON CORAL REEFS IN BELIZE

RICHARD B. ARONSON,^{1,2,5} IAN G. MACINTYRE,³ WILLIAM F. PRECHT,⁴ THADDEUS J. T. MURDOCH,^{1,2} AND
CHERYL M. WAPNICK¹

¹Dauphin Island Sea Lab, 101 Bienville Boulevard, Dauphin Island, Alabama 36528 USA

²Department of Marine Sciences, University of South Alabama, Mobile, Alabama 36688 USA

³Department of Paleobiology, Smithsonian Institution, Washington, D.C. 20560 USA

⁴PBS&J, 2001 Northwest 107th Avenue, Miami, Florida 33172 USA

Abstract. Beginning in the late 1980s, white-band disease eliminated the staghorn coral *Acropora cervicornis* from reefs in the central shelf lagoon of Belize. The lettuce coral *Agaricia tenuifolia* replaced *Acropora cervicornis* in the early 1990s, but anomalously high water temperatures in 1998 caused severe bleaching and catastrophic mortality of *Agaricia tenuifolia*. The short-lived transition in dominance from *Acropora cervicornis* to *Agaricia tenuifolia* left an unambiguous signature in the fossil record of these uncemented lagoonal reefs. Analysis of 38 cores, extracted from 22 sampling stations in a 375-km² area of the central lagoon, showed that *Acropora cervicornis* dominated continuously for at least 3000 years prior to the recent events. *Agaricia tenuifolia* occasionally grew in small patches, but no coral-to-coral replacement sequence occurred over the entire area until the late 1980s. Within a decade, the scale of species turnover increased from tens of square meters or less to hundreds of square kilometers or more. This unprecedented increase in the scale of turnover events is rooted in the accelerating pace of ecological change on coral reefs at the regional level.

Key words: *Acropora*; *Agaricia*; Belize; Caribbean; coral bleaching; coral disease; coral reef; Holocene; paleoecology; patch dynamics; species turnover; white-band disease.

INTRODUCTION

Coral reefs of the Caribbean region (the western Atlantic, including Florida and the Bahamas) have changed markedly since the late 1970s (Ginsburg 1994, Hughes 1994, McClanahan and Muthiga 1998). The essential features of this change are that (1) coral mortality from natural and, possibly, human causes has reduced coral cover and opened space on most reefs, (2) herbivory has been reduced by the 1983–1984 mass mortality of the sea urchin *Diadema antillarum* and, in at least some places, by overfishing of parrotfish (Scaridae) and surgeonfish (Acanthuridae), and (3) the increase in available space relative to the potential for herbivory has resulted in greatly increased cover and biomass of fleshy and filamentous macroalgae, especially forms that are unpalatable to herbivorous fishes (Knowlton 1992, Hughes 1994, Szmant 1997, Miller et al. 1999, Aronson and Precht 2000, 2001a, Williams and Polunin 2001). The increase in macroalgae has in turn limited coral recruitment and the recovery of coral populations, and has obscured zonation patterns that were formerly typical of Caribbean reefs (Jackson 1991, Edmunds and Carpenter 2001). If these recent decadal-scale changes are unique on a centennial to millennial scale, then the popular suspicion that hu-

mans are important agents of reef degradation could be well founded. Conversely, if changes of this sort occurred in the past, then human interference could be merely a minor factor contributing to the present situation.

Until the late 1970s, three framework-building coral species displayed a zonation pattern that was common throughout the region (Goreau 1959, Goreau and Goreau 1973, Graus and Macintyre 1989). Thickly branching elkhorn coral, *Acropora palmata*, dominated substratum cover from the reef crest down to 5 m depth on the fore reef under all but the most energetic wave conditions. The more thinly branching staghorn coral, *Acropora cervicornis*, dominated intermediate depths (5–25 m) on wave-exposed fore reefs. *Acropora cervicornis* ranged into shallower habitats on protected fore reefs and also occurred in back-reef and lagoonal habitats (Geister 1977, Rützler and Macintyre 1982, Hubbard 1988). The third primary framework builder of Caribbean reefs, the *Montastraea annularis* species complex, consists of at least three sibling species (Knowlton et al. 1992). Massive colonies of *Montastraea* spp. were (and remain) common in a variety of reef habitats, exhibiting interspecific zonation as well as intraspecific changes in morphology along depth gradients (Goreau 1959, Graus and Macintyre 1982, Knowlton et al. 1992).

The overall zonation pattern has largely disappeared because the *Acropora* spp. have been killed and re-

placed by macroalgal species on most Caribbean reefs (Jackson 1991, Hughes 1994). A major cause of this regional-scale turnover has been white-band disease, a bacterial disease (or group of diseases) that affects only the genus *Acropora* (Rogers 1985, Santavy and Peters 1997, Richardson 1998, Bythell et al. 2000, Aronson and Precht 2001a, b). Hurricanes have also killed populations of *Acropora* spp., but mortality from hurricanes passing through particular areas has been localized to reefs in and near the storm tracks (Woodley et al. 1981, Woodley 1992). Furthermore, a number of areas within the Caribbean are rarely affected by cyclonic activity (Neumann et al. 1987, Treml et al. 1997). Other sources of local mortality of *Acropora* include cold water stress in Florida and the Bahamas (Porter et al. 1982, Roberts et al. 1982, Burns 1985, Jaap and Sargent 1994), coral bleaching associated with high temperatures (Cortés 1994), sediment and nutrient input (Weiss and Goddard 1977, Lewis 1984), and predation by corallivorous fish and invertebrates (Antonius 1977, Knowlton et al. 1990, Bruckner et al. 1997).

Pleistocene reefs around the Caribbean display fossilized patterns of coral zonation similar to those observed on modern reefs prior to the late 1970s (Meso-solella 1967, Boss and Liddell 1987, Jackson 1992, Greenstein et al. 1998, Pandolfi and Jackson 2001). Despite large fluctuations in sea level during the Pleistocene, the composition of Caribbean coral assemblages remained stable and predictable within habitats on a time scale of tens of thousands to hundreds of thousands of years. When viewed at finer spatial and temporal scales, however, the within-habitat composition of Pleistocene coral assemblages displays high variability (Jackson et al. 1996, Pandolfi 1996, Pandolfi and Jackson 1997). The transition to the present macroalgal-dominated state of Caribbean reefs, observed on a scale of decades, could be an aspect or a consequence of this short-term variability (Woodley 1992). On the other hand, the coral-to-algal transition could represent a rare or even unprecedented departure from the previous community composition, brought about by a unique conjunction of circumstances (Jackson 1991, 1994, Knowlton 1992, Hughes 1994).

Implicit in the latter alternative is a hypothesis about the scale of species turnover. If the current state of Caribbean reefs is unique, then the spatial scale of turnover events must have increased greatly, from localized areas of coral mortality and species replacement before the late 1970s to recent changes in biotic composition that transcend reefs and even reef systems. The most direct way to test this hypothesis is to examine the fossil record of reefs during the late Holocene (the last 3000 yr) on an intermediate temporal scale of hundreds to thousands of years.

Cores from the reef at Buck Island, St. Croix, (7000 yr BP to the 1970s) displayed an uninterrupted accumulation of well-preserved *Acropora palmata*, suggesting continuous reef growth and supporting the hy-

pothesis that the current situation is unusual (Hubbard et al. 1994). Likewise, cores extracted from Channel Cay, a lagoonal reef in central Belize, showed that *Acropora cervicornis* dominated that reef for at least the last several millennia, until it was killed by white-band disease after 1986 (Aronson and Precht 1997). The lettuce coral *Agaricia tenuifolia* then increased opportunistically and became the dominant space occupant. Although they are suggestive, these two studies were limited to small areas and did not explicitly test hypotheses about the changing scale of species turnover.

In this paper we expand Aronson and Precht's (1997) study in the Belizean shelf lagoon. We report the results of an intensive coring program carried out over a 375-km² area at two hierarchical levels (and two corresponding spatial scales): within sampling stations (meters to tens of meters) and among stations (hundreds of meters to kilometers). Although transitions from *Acropora cervicornis* to *Agaricia tenuifolia* occurred previously during the late Holocene, they were confined to small patches on reefs over distances of meters to tens of meters. Only recently did a transition to dominance by *Agaricia tenuifolia* take place over the entire area. Our findings reveal an orders-of-magnitude increase in the spatial extent of species turnover, which was unprecedented on a time scale of centuries to millennia.

STUDY AREA

Geological setting

The central sector of the Belizean shelf lagoon is characterized by diamond-shaped reefs known as rhomboid shoals (Fig. 1). These reefs reach sea level and surround sediment-filled basins that can be as deep as 30 m (Macintyre and Aronson 1997, Macintyre et al. 2000). The Holocene deposits on the rhomboid shoals, which are up to 20 m thick, accumulated over the past 8000–9000 yr (Westphall and Ginsburg 1984, Precht 1993), and they lie directly atop bathymetric highs composed of Pleistocene reef limestones (e.g., Halley et al. 1977). The cause of the atoll-like configuration has been debated but structural control appears to be of primary importance, with the original reef growth occurring around the edges of fault blocks (Purdy 1974a, b, Lara 1993, Precht 1997, Esker et al. 1998; but see Ferro et al. 1999). Subsequent accretion followed and exaggerated the antecedent topography, resulting in reef slopes that can be quite steep (Westphall 1986, Macintyre et al. 2000).

The energy of waves impinging on the central lagoon is attenuated by the continuous barrier reef to the east (seaward) and by Glovers Reef, an atoll-like carbonate platform east of the barrier reef (Burke 1982). Because the rhomboid shoals are situated in a low-energy environment, there is little or no submarine cementation of the reefs (see Purser and Schroeder 1986, Macintyre

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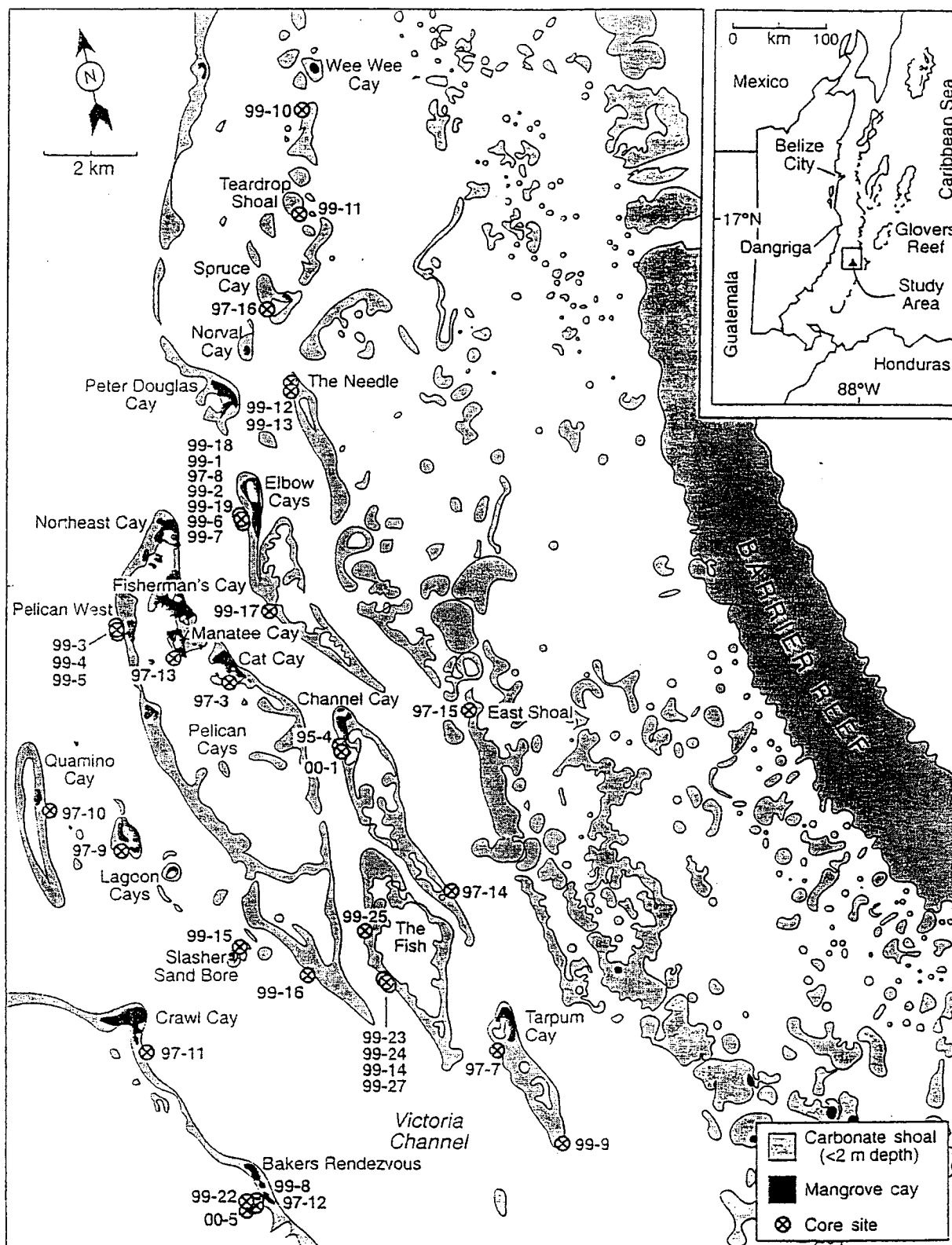


FIG. 1. Map of the central shelf lagoon of the Belizean Barrier Reef, showing the rhomboid shoals and coring stations. Each station is a length of reef, meters to several tens of meters long, within which one or more cores were extracted. The map is based on a Landsat 5 TM image (18 September 1987) supplied by G. Madejski, NASA Goddard Space Institute, Greenbelt, Maryland, USA.

and Marshall 1988). Living and dead coral colonies are stabilized on the reef slopes by the interlocking of their skeletons. Debris fans at the bases of the rhomboid shoals (22–30 m water depth) suggest occasional storm disturbance; however, Hurricanes Greta (September 1978), Mitch (October 1998), Keith (October 2000), and Iris (October 2001; a Category 4 storm and nearly a direct hit) did not appreciably affect the layering of Holocene sediments as reported in this paper (Westphall 1986, Aronson et al. 2000; R. Aronson and W. Precht, unpublished data).

The Holocene deposits at Channel Cay, the best-studied of the rhomboid shoals, are composed primarily of an open framework of interlocking branches of *Acropora cervicornis* (Shinn et al. 1979, Westphall 1986, Aronson and Precht 1997, Aronson et al. 1998). Coring operations and observations of submarine exposures in the present study revealed the same Holocene architecture on the other rhomboid shoals. The steep slopes of 45° or more observed in some areas along the outer flanks of the shoals were created by the rapid growth of *Acropora cervicornis* as the reefs caught up with sea level (Westphall 1986, Macintyre et al. 2000).

Recent ecological changes

Before the late 1980s, the outer flanks of the rhomboid shoals were covered by living populations of *Acropora cervicornis* (>70% cover in some places; Fig. 2A) from 2–15 m depth (Shinn et al. 1979, Westphall 1986, Aronson and Precht 1997). *Agaricia tenuifolia* and other coral species in the family Agariciidae were subdominant components in that depth range, and they dominated the benthos below 15 m. The most common corals in the shallowest depths (≤ 1 m) were the finger coral *Porites divaricata* and the hydrozoan fire coral *Millepora alcicornis* (Aronson et al. 1998, Macintyre et al. 2000). During the 1980s, white-band disease (WBD; Fig. 2B) virtually exterminated the *Acropora cervicornis* populations on the rhomboid shoals.

Acropora cervicornis colonies killed by WBD collapsed rapidly due to the weakening effects of bioe-

rosion. Fleshy and filamentous macroalgae that colonized the coral skeletons were consumed by the echinoid *Echinometra viridis* (Fig. 2C). *Agaricia tenuifolia* and the other agariciids readily recruited to and grew on the *Echinometra*-grazed *Acropora cervicornis* rubble (cf. Sammarco's [1982] experiments in Jamaica, in which grazing by *E. viridis* promoted the recruitment of agariciids). The cover of *Agaricia tenuifolia* then increased dramatically (Fig. 2D), reaching levels as high as 85% (Aronson et al. 2000). Colonies of *Agaricia tenuifolia* growing in this lagoonal setting formed assemblies of vertical blades with an overall inverted-pyramid shape. As they grew tall (>0.5–1 m height), their high center of gravity eventually caused them to topple over, leaving small scree slopes of *Agaricia* rubble. Although large amounts of coral rubble were available for settlement, herbivory by *E. viridis* kept the rubble free of algal growth (<10% cover), permitting *Agaricia tenuifolia* to continue recruiting at a high rate (Edmunds et al. 1998). The cover of 18° or more other coral species remained low ($\leq 9\%$) from 1986 to 2000 (Aronson and Precht 1997, Aronson et al. 2000). This *Acropora*-to-*Agaricia* transition occurred throughout the central and southern shelf lagoon over an area of at least 500 km².

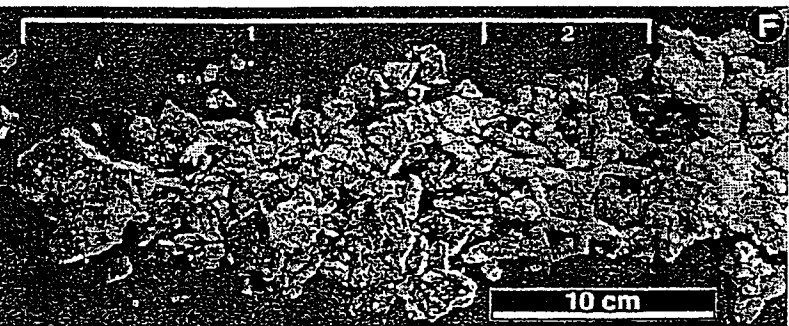
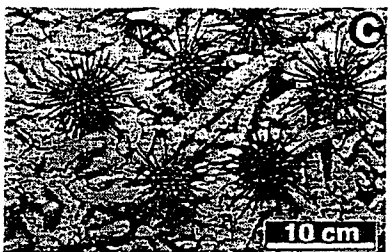
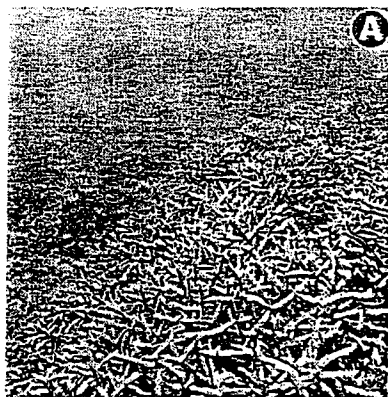
The upward growth of interlocking *Acropora cervicornis* colonies produced the slopes that characterized the flanks of the rhomboid shoals, as described in the previous section. In contrast, *Agaricia tenuifolia* was uncommon on steep slopes. We determined that the maximum angle of repose for *Agaricia tenuifolia* was ~45°, based on (1) the cover of live *Agaricia tenuifolia* in 1996, and (2) measurements of the accretion of *Agaricia tenuifolia* (thickness of accumulation of *Agaricia tenuifolia* rubble) over the period 1986–1996 on slopes of varying steepness. Slopes of 35–45° had reduced quantities of living *Agaricia tenuifolia* and *Agaricia tenuifolia* rubble. Slopes >45° were generally barren of *Agaricia tenuifolia* and were characterized by dead interlocking branches of *Acropora cervicornis* protruding from the reef flanks. Living and dead col-

FIG. 2. Photographs from the rhomboid shoals in Belize. (A) Stand of *Acropora cervicornis*, the species that dominated at 2–15 m water depth until the late 1980s. (B) Closeup of a branch of *Acropora cervicornis* infected with white-band disease. The diseased, white segments along the branch in the foreground, left and center, are characterized by dead skeleton and sloughing tissue. The darker segments, enclosed in ellipses, contain polyps that are beginning to show signs of the disease. (C) *Echinometra viridis* grazing on rubble of *Acropora cervicornis* killed by white-band disease. Note the complete removal of surface sculpture from the branch fragments. (D) *Agaricia tenuifolia* dominant at Cat Cay in June 1994, 5 m depth. Note *Acropora cervicornis* colonies on the left. The *Agaricia tenuifolia* was killed by high water temperatures in 1998. (E) Divers positioning a 5-m core tube. Tubes were driven into the reef framework with the aid of adjustable core slips, visible in the foreground below the diver's arms. (F) Top portion of a core from Channel Cay, showing (1) uppermost layer of *Agaricia tenuifolia* plates, and (2) layer of degraded branch fragments of *Acropora cervicornis* just below uppermost layer. Coral rubble at the extreme right of the photograph (lower in the core) is packed in muddy sediment. The layers in the pictured core were especially obvious, but they were discrete and easily identifiable in the other cores as well. (G) Eroded branch fragments of *Acropora cervicornis* from just below the uppermost *Agaricia tenuifolia* layer in core 97-12, encrusted with *Agaricia* recruits. (H) Segment of a core from the Pelican Cays, spanning (left to right) 40–65 cm below the top. The dominant constituents are lightly altered branch fragments of *Acropora cervicornis*. The sand- and mud-sized sediments have been washed away.

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onies of *Agaricia tenuifolia* were too top-heavy and accumulations of imbricated *Agaricia tenuifolia* plates were too unstable to persist on these steep slopes.

Agaricia tenuifolia dominated benthic cover on the rhomboid shoals in the 3- to 15-m depth range from the early 1990s until 1998. Abnormally high water temperatures in the summer and fall of 1998 caused almost all coral colonies in the central lagoon to expel their zooxanthellae and bleach. By January 1999, the *Agaricia tenuifolia* had died catastrophically, dropping to near-zero cover (Aronson et al. 2000). A few small colonies survived in deeper water (>15 m), but there were no signs of recovery as late as February 2000.

METHODS

Coring operations

In order to reconstruct the ecological history of the rhomboid shoals during the late Holocene, 38 push cores were extracted by hand from the study area (Fig. 1). In this diver-operated, open-barrel, coring technique, a 4- to 5-m segment of 7.6 cm (3 inch) diameter aluminum tubing was forced into the reef (Fig. 2E). While one diver held the top of the core tube to maintain its vertical orientation, two others worked the tube into the reef using adjustable core slips with handles. Once the tube had been driven in ~1 m, the first diver sleeved a sliding hammer weight over the top of the tube and tapped the tube to aid penetration. Teeth on the bottom of the core tube also enhanced penetration, by cutting through branching and massive coral skeletons (Dardeau et al. 2000).

The tube was generally driven 3–4 m into the sediment, leaving 0.5–1 m extending above the sediment–water interface. At that point, penetration was calculated by measuring the final length of the exposed portion of the tube and subtracting that from the total length of the tube. Recovery was estimated in situ by feeding a weighted fiberglass surveyor's tape into the core tube until it reached the top of the recovered sediment; the estimated recovery was calculated as the difference between the length of the tube and the length of the empty (water-filled) portion of the tube. After these measurements were made, the exposed (top) end was capped and then sealed with electrical tape. The core was pulled from the reef by hand and the bottom was capped and taped. It was carried to the water surface, loaded onto a boat, and taken to the Smithsonian Institution's field station at Carrie Bow Cay. For some cores, penetration was measured and recovery estimated in situ at intervals during the coring operation to ascertain whether material was entering the core tube continuously or instead binding and preventing further recovery.

The cores were extracted from water depths of 4.2–9.0 m, with the exception of four cores taken from depths 9.6–11.5 m (Table 1). Considering the depths of penetration of the cores and the position of sea level

over the past 3000 yr, the cores sampled the reefs at paleodepths <15 m. The 15-m limit is the depth below which agariciids predominated before the recent *Acropora* kill, according to ecological observations (Aronson and Precht 1997); coring paleodepths below 15 m would not have been relevant to testing hypotheses about transitions from *Acropora cervicornis* to *Agaricia tenuifolia*, because *Acropora cervicornis* may never have dominated at those depths.

Contemporary slopes and paleoslopes >45° should be biased against the preservation of *Agaricia tenuifolia* layers but not against the preservation of *Acropora cervicornis*. Westphall (1986) showed from patterns of vertical accretion and horizontal progradation at Channel Cay that paleoslope angles are necessarily lower than the overlying modern slope angles, and Macintyre et al. (2000) obtained similar results for the Pelican Cays (Fig. 1). To eliminate any bias introduced by slope angle, we extracted cores only from areas in which the contemporary slope angles, and therefore the paleoslope angles, were less than the critical angle of 45°. For each core, the contemporary slope angle was measured underwater with a hand-held inclinometer, and almost all were <35° (Table 1).

Laboratory analysis

Each core was extruded in the laboratory. Samples of the interstitial sediment were collected for analysis, and the remaining sand-sized and smaller fractions were washed away. The core was logged in 5-cm intervals. The relative abundances of coral species were assessed visually and recorded for each interval, along with their taphonomic states and spatial orientations. Most of the coral material was *Acropora cervicornis* and *Agaricia tenuifolia*. The calcareous remains of other invertebrates and algae were also noted. A detailed column diagram was made of the core, and a coral sample was collected from the base of each core for radiocarbon dating.

The taphonomic state of *Acropora cervicornis* was categorized as either lightly altered or degraded. Lightly altered branch fragments retained most or all of their surface sculpture and were not heavily encrusted or bored (taphonomic categories 1 and 2 established for *Acropora cervicornis* by Greenstein and Moffat [1996]). Degraded branch fragments were eroded to the point that they retained little or none of their original surface sculpture, and they were encrusted and/or bored (categories 3–5 of Greenstein and Moffat [1996]). The same criteria were applied to plates of *Agaricia tenuifolia*.

A coral species in a particular taphonomic state was considered dominant if it constituted >50% of the skeletal fragments in the interval, but in practice the dominants often constituted 70% or more of the material. Subdominant categories were those that constituted 10–50%, and rare categories constituted <10%. Quantitative analysis of the cores, beyond placing the con-

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TABLE 1. Data on cores from the rhomboid shoals, presented in chronological order of extraction.

Core	Location	Slope angle (°)	Water depth (m)	Penetration (cm)	Recovery (cm)	¹⁴ C age (yr ± SE)
95-4	Channel Cay North	21	6.1	428	267	3130 ± 100
97-3	Cat Cay	18	7.8	339	145	500 ± 70
97-7	Tarpum Cay North	32	9.0	315	100	880 ± 60
97-8	Elbow Cays	10	5.1	347	200	1500 ± 40
97-9	Lagoon Cays	25	5.4	347	150	730 ± 70
97-10	Quamino Cay	26	5.4	337	140	1280 ± 70
97-11	Crawl Cay	4	8.7	332	200	2670 ± 70
97-12	Bakers Rendezvous	12	4.5	344	145	470 ± 60
97-13	Manatee Cay	10	5.7	226	90	520 ± 60
97-14	Channel Cay South	11	6.0	317	145	970 ± 70
97-15	East Shoal	30	4.2	179	45	640 ± 60
97-16	Spruce Cay	19	5.4	341	75	2220 ± 60
99-1	Elbow Cays	22	6.0	405	210	310 ± 60
99-2	Elbow Cays	30	11.5	400	110	510 ± 60
99-3	Pelican West	16	6.0	384	110	1210 ± 60
99-4	Pelican West	16	6.0	370	65	940 ± 60
99-5	Pelican West	34	9.6	407	30	1140 ± 70
99-6	Elbow Cays	29	9.0	391	85	330 ± 40
99-7	Elbow Cays	29	9.0	414	115	440 ± 70
99-8	Bakers Rendezvous	10	6.6	405	150	170 ± 60
99-9	Tarpum Cay South	36	6.6	165	75	1470 ± 60
99-10	Wee Wee Cay	30	4.8	400	110	1340 ± 60
99-11	Teardrop Shoal	10	7.5	292	72	1290 ± 60
99-12	The Needle	28	7.2	270	85	1250 ± 70
99-13	The Needle	32	7.2	400	150	2060 ± 70
99-14	The Fish	20	10.0	375	170	470 ± 70
99-15	Slasher Sand Bore	38	6.6	403	204	610 ± 60
99-16	Pelican South	20	6.3	338	90	630 ± 60
99-17	Elbow Cays	24	6.6	266	100	280 ± 60
99-18	Elbow Cays	18	7.2	380	115	490 ± 60
99-19	Elbow Cays	17	7.5	400	115	350 ± 60
99-22	Bakers Rendezvous	31	6.3	400	100	270 ± 60
99-23	The Fish	28	10.8	290	100	620 ± 60
99-24	The Fish	18	7.2	410	210	730 ± 60
99-25	The Fish	15	5.1	375	215	1040 ± 50
99-27	The Fish	26	8.7	341	120	3480 ± 70
00-1	Channel Cay North	28	9.0	394	105	1670 ± 70
00-5	Bakers Rendezvous	8	6.0	375	20	250 ± 60

Notes: The year in which each core was extracted is indicated by the number 95, 97, 99, or 00. Ages are reported as uncorrected radiocarbon years before 1950 ± 1 SE for coral samples taken from the bottoms of the cores. All dates are based on standard radiometric dating except the date for core 97-8, which was obtained from a small coral sample using absorption mass spectroscopy (AMS). Core 95-4 is from Aronson et al. (1998).

stituents in these ranked categories, was not necessary. In another study, the ranked-category approach was compared to two analyses of a more quantitative nature. Fifteen push cores were extracted from similar, un cemented, lagoonal reefs in the Bahía Almirante, near Bocas del Toro, northwestern Panamá. These cores were assessed visually as described above, but in addition the constituents of each 5-cm interval were quantified by both weight and volume. Core logs based on weights and volumes were essentially identical to core logs based on visual assessments, validating the non-parametric ranking approach employed in the present study.

The dominant constituents of most of the core intervals were lightly altered (or unaltered) branch fragments of *Acropora cervicornis*. Some cores contained

subsurface layers of plates of *Agaricia tenuifolia*, indicating species turnover on a local or possibly larger scale. Other cores contained subsurface layers of heavily eroded *Acropora cervicornis* rubble encrusted with juvenile colonies of *Agaricia* spp. and other coral species; these layers of degraded material indicated mortality of *Acropora cervicornis* and exposure of the dead skeletons at the sediment-water interface, but incomplete species replacement. Both types of layers were discrete and plainly obvious from visual examination of the cores and from the core logs. A sample was collected from the base of each of these layers for radiocarbon dating.

Radiometric age determinations were performed using standard techniques by Beta Analytic, Inc. (Miami, Florida, USA). Dates are reported as uncorrected ra-

diocarbon years before 1950, using a Libby half-life of 5568 yr and a modern standard based on 95% of the activity of the National Bureau of Standards' oxalic acid. Uncorrected dates are used so that they may be compared with published sea-level curves; most sea-level curves for Belize and elsewhere in the Caribbean are based on uncorrected dates (Lighty et al. 1982, Macintyre et al. 1995). Correcting for the DeVries effect, the reservoir effect, and natural isotopic fractionation yielded calibrated dates that were generally within a few decades of the uncorrected dates. The uncorrected dates, therefore, provide reasonable approximations of the corresponding ages in calendar years before present. Whether the radiocarbon dates are corrected or not has no bearing on the tests of hypotheses.

Sampling design

The coring program was carried out at two spatial scales. There were 22 coring stations spread over the central lagoon, with the locations chosen to maximize the area sampled. We extracted multiple cores from six of these stations. The intensively sampled stations included Elbow Cays, The Fish, and Bakers Rendezvous, because a core from each of these stations contained a layer suggesting complete or incomplete *Acropora*-to-*Agaricia* turnover at an age of 270–380 radiocarbon years. The two-tiered sampling design made it possible to determine whether such layers in particular cores represented events that had occurred over shorter distances within stations (meters to tens of meters) or over longer distances among stations (hundreds of meters to kilometers).

In a number of cases more than one station was sampled on a single rhomboid shoal. Given the known dispersal abilities of coral larvae (Harrison and Wallace 1990, Edinger and Risk 1995, Richmond 1997) and the regional nature of WBD outbreaks, there was no reason to expect that stations on the same shoal would be more similar to each other than to stations on other shoals, which in many cases were closer. For the purpose of this analysis, the stations were treated as replicates at the scale of the study area.

Taphonomic and methodological considerations

Hubbard et al. (1994) reported low preservation potential of *Agaricia* spp. in fore-reef environments, possibly due to taphonomic alteration prior to burial. In contrast, Aronson and Precht (1997) observed that *Agaricia tenuifolia* had a high preservation potential in the subsurface sediments of the rhomboid shoals. Furthermore, push cores extracted from the Bahía Almirante in Panamá contained large quantities of *Agaricia tenuifolia* in various preservational states, as well as branching *Porites* spp. and *Acropora cervicornis*. There did not appear to be a taphonomic bias against *Agaricia tenuifolia* in that case either.

The coring procedure used in this study has distinct advantages over other techniques, such as piston cor-

ing, percussion coring, and vibracoring. Although other methods allow greater penetrations and can yield greater recoveries, they require complex logistics, including more divers, more hardware, and surface support. The open-barrel push-coring method is simple, quick, portable, and relatively inexpensive, enabling us to obtain records of sufficiently long time intervals with sample sizes sufficiently large for statistical analysis (Dardeau et al. 2000).

RESULTS

Species dominance and turnover

Thirty-eight cores were recovered from 22 sampling stations in the central sector of the shelf lagoon of the Belizean Barrier Reef (Fig. 1). The cores penetrated several meters into the uncemented reef framework. Radiocarbon analysis yielded a maximum uncorrected ^{14}C date of >3000 yr (Table 1).

All 38 cores contained an uppermost layer of imbricated, lightly altered *Agaricia tenuifolia* plates overlying a thick accumulation of *Acropora cervicornis* branches (Figs. 2E, 3). This *Agaricia tenuifolia* layer was ~0.25 m thick in most of the cores. From the lower half of the uppermost *Agaricia tenuifolia* layer down to the bottom of each core, the coral skeletons were surrounded by a matrix of sandy carbonate mud; only the upper half of the uppermost *Agaricia tenuifolia* layer was free of matrix (see also Aronson and Precht 1997). There was no evidence of bioturbation or other large-scale reworking of the sandy-mud matrix.

In all the cores, the length of the recovered material was shorter than the depth of penetration into the reef (Table 1). The actual recoveries, measured as the lengths of the extruded material, differed little from the in situ estimates of recovery, indicating little or no loss from the bottoms of the core tubes during removal from the reef. The measurements of penetration and the in situ estimates of recovery made at intervals during some of the coring operations indicated that material entered the core tubes continuously as they were forced into the reef. This means that the differences between penetration and recovery were due to compaction; sediment did not bind in the tubes and prevent further recovery. There was no indication that the low recoveries were due to voids in the reef framework; there were no sudden periods of rapid penetration, nor were there any suggestions of empty spaces from the measurements of recovery during the procedure.

A thin layer of eroded and encrusted *Acropora cervicornis* rubble lay just beneath the uppermost *Agaricia tenuifolia* layer, with the branch fragments in a horizontal orientation (Fig. 2F, G). This layer of degraded *Acropora cervicornis* rubble recorded the mass mortality of the populations from WBD. Post-mortem exposure of the skeletal branches at the sediment–water interface allowed extensive abrasion by grazing echinoids prior to burial, to the extent that almost none of

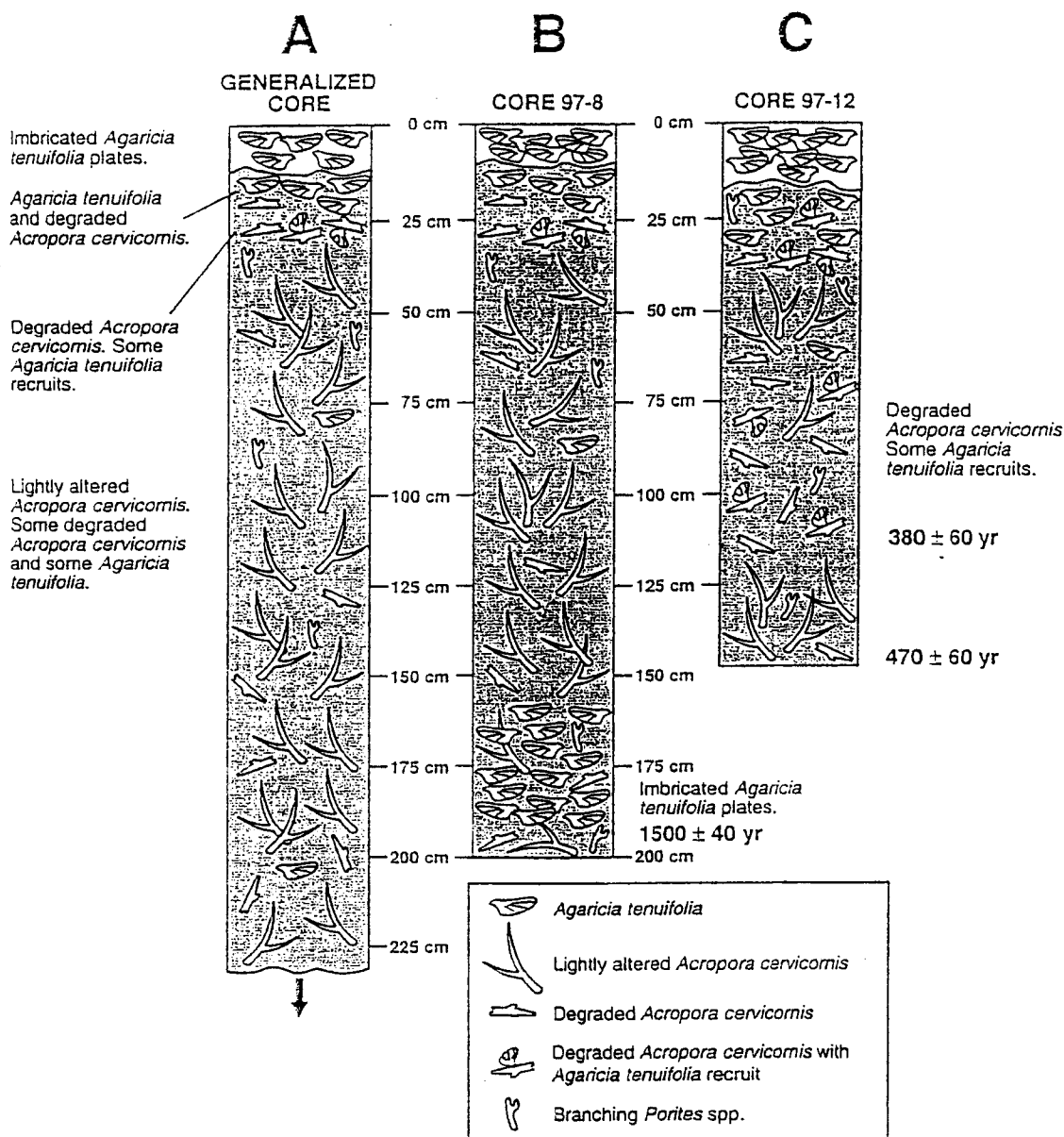


FIG. 3. Representative cores. Gray fill represents sandy mud, and wavy horizontal lines demarcate the upper limit of sandy-mud sediment. (A) Composite diagram based on the majority of core logs. The uppermost layers of imbricated *Agaricia tenuifolia* plates and eroded, encrusted *Acropora cervicornis* rubble were deposited in the 1980s–1990s. (B) Log of core 97-8 from Elbow Cay, showing a 1500-yr-old layer of plates of *Agaricia tenuifolia*. (C) Log of core 97-12 from Bakers Rendezvous, showing a 380-yr-old layer rich in *Acropora cervicornis* rubble that was heavily eroded and encrusted with small colonies of *Agaricia tenuifolia*.

the original surface sculpture remained (see Greenstein and Moffat 1996). Encrustation of the eroded *Acropora cervicornis* rubble resulted from the recruitment and growth of *Agaricia tenuifolia*, other agariciids, other coral species, and occasionally crustose coralline algae (Fig. 2G; Aronson and Precht 1997).

Below the layer of degraded *Acropora cervicornis*, the subsurface Holocene was dominated by unaltered to lightly altered branches of *Acropora cervicornis*. These branches were generally unencrusted and un-

bored, and they retained much of their original sculpture (Figs. 2H, 3A). Many of these fresh-looking branches were oriented at positive angles from the horizontal, suggesting that for >3000 yr *Acropora cervicornis* colonies grew rapidly on top of the dead skeletons of their conspecific predecessors. Rapid growth and rapid burial were also reflected as accumulations of lightly altered coral branches oriented in growth or near-growth position in trenches dug into the reef flanks (Aronson and Precht 1997) and in natural exposures of

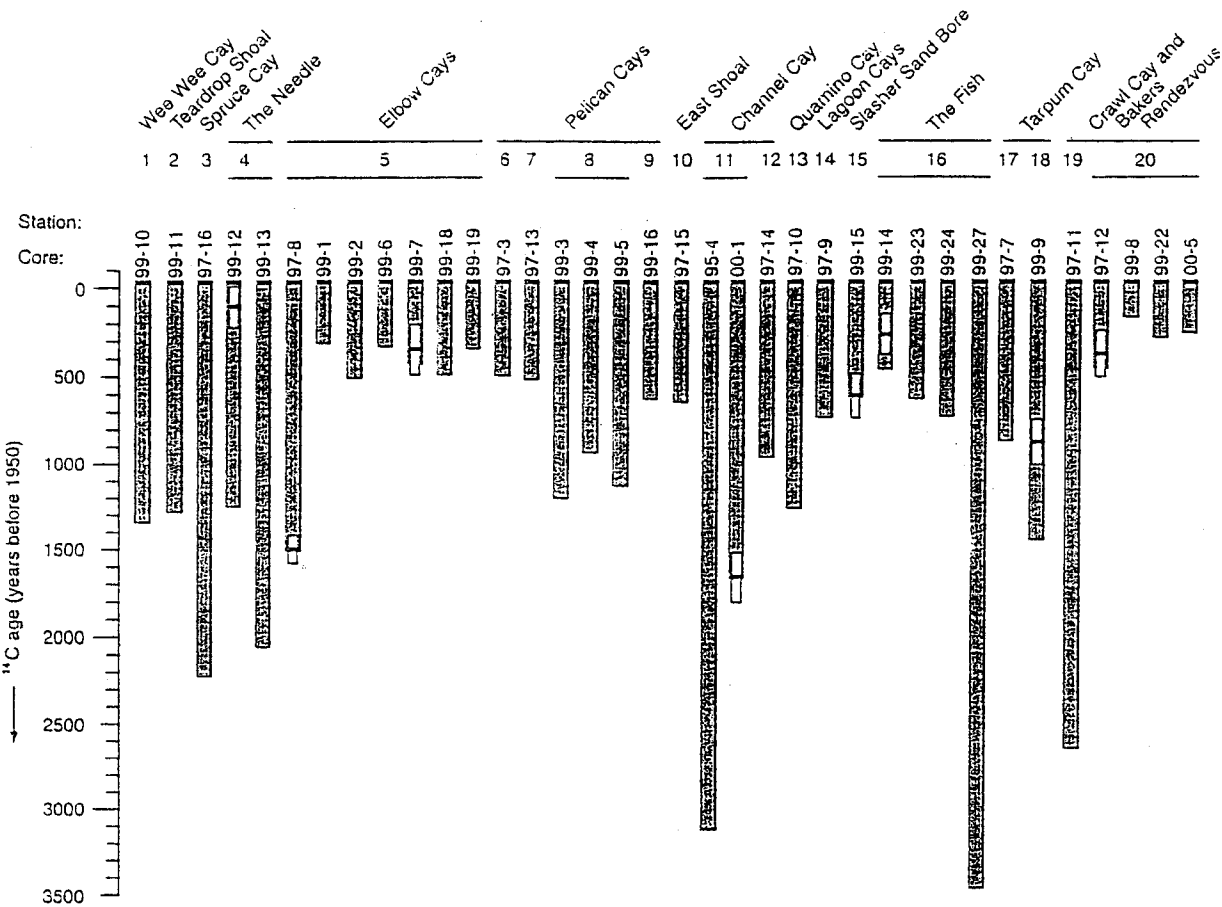


FIG. 4. Radiocarbon ages of the cores. The cores are grouped by shoal, and the shoals are arranged roughly from north to south. The coring stations are shown in Fig. 1. Gray fill represents ecological dominance by *Acropora cervicornis*, and horizontal black bars mark departures from the *Acropora*-dominated state. The black bars at the tops denote the recent mortality of *Acropora cervicornis* and the transition to *Agaricia tenuifolia*, visible in all cores. Other black bars mark the complete and incomplete transitions to *Agaricia tenuifolia* reported in Table 2. The vertical white bars represent the 95% confidence intervals of the radiocarbon dates of these anomalous layers, calculated as ± 1.96 SE. For clarity of presentation, confidence intervals are omitted from the dates of the bottoms of the cores, except where the bottom of an anomalous layer is also the bottom of a core.

Acropora cervicornis branches observed on steep slopes.

The highly ordered layering pattern of well-preserved, fragile corals in all but two of the 38 cores indicated that the corals were buried and preserved in place with minimal transport. In other words, the core samples were composed primarily of autochthonous material, which reflected the constituents of the living communities at various times (Greenstein and Pandolfi 1997). Two cores, 99-17 from Elbow Cays and 99-25 from The Fish, contained more homogeneous, less structured accumulations of degraded *Acropora cervicornis* mixed with small amounts of *Agaricia tenuifolia* rubble. The mixed nature of these death assemblages suggested allochthonous sources. The presence in core 99-25 of large quantities of *Porites divaricata*, a coral from much shallower water (see Study area), also suggested allochthonous input. These two cores are interpreted as coming from leeward drapes of

storm-transported material (cf. Logan 1969) or from downslope transport of slumped material, and they are not considered further. This leaves 36 cores from 20 sampling stations that can be used to reconstruct the late Holocene history of reefs of the central lagoon.

The massive corals *Colpophyllia natans*, *Porites astreoides*, *Montastraea* spp., and several other species of scleractinians, appeared occasionally in the cores as they did in the living community. The cores showed no obvious evidence of area-wide replacement by and subsequent disappearance of *Agaricia tenuifolia* in the three millennia before the late 1980s. Nevertheless, five cores displayed distinct subsurface layers of lightly altered *Agaricia tenuifolia* plates (Fig. 3B). Three cores contained distinct layers of eroded *Acropora cervicornis* branch fragments, with some of the fragments encrusted by recruits of *Agaricia tenuifolia* and other coral species (Fig. 3C).

The geographic distribution of these "anomalous"

TABLE 2. Records of anomalous layers in the cores.

Core	Location	Type of layer	¹⁴ C age
97-8	Elbow Cays	<i>Agaricia tenuifolia</i> plates	1,500 ± 40
97-12	Bakers Rendezvous	eroded <i>Acropora cervicornis</i> , recruits	380 ± 60
99-7	Elbow Cays	<i>Agaricia tenuifolia</i> plates	340 ± 70
99-9	Tarpum Cay	eroded <i>Acropora cervicornis</i> , recruits	890 ± 60
99-12	The Needle	eroded <i>Acropora cervicornis</i> , recruits	110 ± 60
99-14	The Fish	<i>Agaricia tenuifolia</i> plates	270 ± 60
99-15	Slasher Sand Bore	<i>Agaricia tenuifolia</i> plates	610 ± 60
00-1	Channel Cay	<i>Agaricia tenuifolia</i> plates	1,670 ± 70

Notes: Layers of *Agaricia tenuifolia* plates indicate *Acropora*-to-*Agaricia* transitions. Layers of eroded branches of *Acropora cervicornis* encrusted with *Agaricia tenuifolia* recruits indicate incomplete transitions. Dates are for coral samples from the bases of the layers.

layers suggests spatial isolation of the turnover and incomplete turnover events they represent, since none of the layers occurred more than once at a single sampling station or on a single shoal (Fig. 4). Furthermore, five of the layers were temporally unique (Table 2). These five layers can be interpreted tentatively as recording occurrences over distances smaller than the distances between stations. An *Agaricia tenuifolia* layer could, in fact, represent the temporary establishment and growth of a single colony. In a similar vein, a layer of eroded *Acropora cervicornis* branches encrusted with *Agaricia* recruits could represent the death of a small patch on which *Agaricia tenuifolia* was not fully able to establish itself before growth of *Acropora cervicornis* from the periphery closed the patch.

The remaining three cores with anomalous layers are more difficult to reconcile with the idea that episodes of species turnover occurred only on small spatial scales. Core 97-12 from Bakers Rendezvous, core 99-7 from Elbow Cays, and core 99-14 from The Fish contained layers that suggest approximately contemporaneous interruptions in the growth of *Acropora cervicornis* dating to 270–380 radiocarbon years. In all three cases, the 95% confidence interval about the date of the layer, calculated as 1.96 SE, overlapped the dates of the anomalous layers in the other two cores (Fig. 4).

There are two simple, mutually exclusive explanations for these data. The first is the alternative hypothesis that the three cores contain the record of an event that occurred throughout the central lagoon, but that signal was lost from all the other cores through degradation, slumping, downslope transport, or other taphonomic processes occurring at the scale of the coring station or at smaller scales. It should be noted that area-wide episodes of downslope transport would have been unlikely, considering the low angles of the paleoslopes sampled and the low wave energy that characterized the lagoonal environment. Cores 99-17 and 99-25 suggest transport in at least some places, however.

The second explanation is that the three dates are coincidental. In this null hypothesis, the fossil record is taken at face value: prior to the late 1980s, complete and interrupted replacements of *Acropora cervicornis*

by *Agaricia tenuifolia* occurred locally and independently. Binomial probability analysis can be used to test these hypotheses.

Probability analysis

Let us assume that cores 97-12, 99-7, and 99-14 contain evidence of a large-scale replacement event in the 200–400-yr range, which was not preserved in the other cores from those three stations, nor in the cores from any other stations. Let us further assume that the failures of preservation were due to taphonomic processes occurring at the scale of the coring station or at smaller scales. Working from these assumptions, we can first estimate the probability that such an event layer appearing in one core at a station will be lost from sediments sampled by other cores at the same station. We can then use the within-station failure estimate to calculate the probability that only three stations will show any evidence of the putative large-scale event.

Nine cores collected from the stations at Elbow Cays, The Fish, and Bakers Rendezvous had bottom dates that were ≥ 388 radiocarbon years ($270 \text{ yr} + 1.96 \text{ SE}$ in core 99-14; Fig. 4). Only one of the four cores extracted from Bakers Rendezvous—the one containing the anomalous layer—is relevant to this analysis, because the material in the other three cores was too young to span the time interval of that anomalous layer (Table 1, Fig. 4). The cores from Bakers Rendezvous, therefore, cannot be used to calculate the within-station failure rate because there is no within-station replication at the radiocarbon age of interest. Eight cores from Elbow Cays and The Fish can be used, and two of these contain evidence of the alleged large-scale event. The estimated probability of an individual core failing to preserve evidence of a species turnover event suspected to have occurred at the scale of the coring station or at a larger scale is thus $(8-2)/8$, or 0.75.

Since 30 cores from 20 stations dated to ≥ 388 radiocarbon years, the mean number of cores per station for this analysis is 30/20, or 1.50. The average probability of no cores from a given station recording a large-scale turnover event is $q = 0.75^{1.50} = 0.6495$. The probability of at least one core from that station re-

cording the event is $p = 1.0000 - 0.6495 = 0.3505$. (Calculating q separately for each station and then averaging does not substantially affect the outcome of this analysis.)

The probability of seeing the observed pattern of alleged failures of preservation over all the stations is the one-tailed, cumulative binomial probability of three or fewer successes out of 20 stations, where the probability of a success is $p = 0.3505$. This binomial probability is $P = 0.044$. We therefore reject the alternative hypothesis of preservational failure in favor of the null hypothesis. We interpret the existence of the three approximately contemporaneous layers as the coincidental result of local processes occurring within stations over distances of meters to tens of meters. This conclusion is supported by the fact that layers in the 270–380-yr range did not appear in cores extracted from stations closer to one or more of the three cores containing the layers than those three cores were to each other.

None of the remaining five anomalous layers (Table 2, Fig. 4) occurred in other cores from the same station or in cores from any other stations. Applying the same probability analysis to these singleton layers yields results that vary with sample size; the P value increases as the age of the layer increases, because the number of cores and stations sampled declines with increasing age. The probability that the 110-yr layer in core 97-12 represents a large-scale event is $P = 0.0005$, and for the 610-yr layer in core 99-15 the probability is $P = 0.025$. The probabilities associated with the three remaining singletons, from cores 99-9 (890 yr), 97-8 (1500 yr), and 00-1 (1670 yr), are $P = 0.10$, 0.45, and 0.54. Using Fisher's method of combining probabilities (a chi-square test; Sokal and Rohlf 1981), the alternative hypothesis can again be rejected ($\chi^2 = 30.01$, $df = 10$, $P < 0.001$). Like the three 270–380-yr layers, the five singleton layers represent localized events rather than the attenuated signals of larger scale episodes.

Another way to analyze this problem is to posit the alternative hypothesis that downslope transport due to processes at scales larger than the station but with variable effects at scales smaller than the study area (i.e., storms or tectonic events) removed substantial amounts of accumulating coral material, obscuring the fossil record of layers representing species turnover events. This explanation is unrealistic a priori, considering the protected location of the rhomboid shoals, the low angles of the paleoslopes sampled, and the orderly composition of the cores at all but two of the stations. If we estimate the loss due to downslope transport at an absurdly high 50% of reef accretion ($p = q = 0.5000$), the one-tailed, cumulative binomial probability of the putative large-scale layer remaining at three or fewer stations out of 20 is $P = 0.0013$. (Of course, we can arbitrarily raise the loss rate to 65% of reef accretion and obtain $P = 0.044$ as before.)

Perhaps a large-scale turnover event occurred, but it

was completely lost from the record. The probability of an event not being preserved as a layer at any of the 20 sampling stations is $0.50^{20} = 0.000001$ (one in a million). As discussed above, fewer stations were sampled at older ages. With only 10 stations available for consideration, the probability of an anomalous layer having been lost at all stations is $0.50^{10} = 0.001$ (one in a thousand). Thus, the second version of the alternative hypothesis can also be rejected at $P < 0.05$ in favor of the null hypothesis that the observed patterns resulted from localized events.

Finally, it is possible that system-wide hiatuses in reef growth occurred at times, due to population crashes of *Acropora cervicornis*. Such mass mortalities could not have been detected by our methods if the growth of *Acropora cervicornis* resumed rapidly enough that a layer of poorly preserved coral was not deposited. These cryptic hiatuses, if they occurred, are not equivalent to species turnover events and are not relevant to this analysis.

DISCUSSION

Disturbance and life history strategies

Reef communities living in the central Belizean lagoon are different now from the way they were during the rest of the late Holocene. *Acropora cervicornis* was the dominant coral for at least 3000 yr. High linear extension rates of *Acropora cervicornis*, combined with the propensity of this species to reproduce asexually by fragmentation (Shinn 1966, Gilmore and Hall 1976, Tunnicliffe 1981, Knowlton et al. 1990), ensured that the reefs were able to catch up to sea level, which was rising slowly during this period (Westphall 1986, Macintyre et al. 1995, 2000, Aronson et al. 1998).

The relatively unaltered *Acropora cervicornis* material in the cores suggested continuous burial in growth or near-growth position and rapid upward extension of the open framework of interlocking branches. During this period of rapid accumulation, *Acropora cervicornis* occasionally died over small areas and *Agaricia tenuifolia* recruited to the dead skeletons. In some cases the growth of *Acropora cervicornis* then resumed in the dead patches; in other cases *Agaricia tenuifolia* grew to dominate those small areas temporarily, before being overtopped by *Acropora cervicornis*.

White-band disease virtually eradicated *Acropora cervicornis* from the rhomboid shoals beginning in the late 1980s. Since *Acropora cervicornis* depends primarily on fragmentation to reproduce, its potential for recolonization was low once it had been removed (Knowlton 1992). High levels of herbivory allowed *Agaricia tenuifolia* to increase opportunistically and literally cover the entire study area for the first time in at least the last 3000 yr.

In less than a decade of dominance, *Agaricia tenuifolia* produced a layer of skeletal plates ~0.25 m

thick. By the time the cores were extracted, the lower half of this *Agaricia* layer was already part of the Holocene record, having been stabilized in sandy mud. Considering the rapid rate of burial, the high preservation potential of *Agaricia* in the central lagoon, and the fact that the paleoslopes sampled were less than the critical angle of repose for *Agaricia tenuifolia*, it is unlikely that an earlier, large-scale, *Acropora*-to-*Agaricia* replacement sequence would have gone unrecorded or undetected.

Agaricia tenuifolia possesses physiological and life history characteristics that favored its spread, by rapid growth and intensive local recruitment, once the incumbent populations of *Acropora cervicornis* had been removed by WBD. *Agaricia tenuifolia* tolerates the wide range of light and flow conditions experienced in the central lagoon (Helmuth et al. 1997a, b), and it grew rapidly there (Shyka and Sebens 2000). Caribbean agariciids reproduce by brooding internally fertilized planula larvae (Fadlallah 1983, Richmond and Hunter 1990, Richmond 1997), and *Agaricia tenuifolia* is no exception (Morse et al. 1988). Brooded lecithotrophic coral planulae have a flexible larval lifespan, enabling them to settle near their mother colonies (Fadlallah 1983, Harrison and Wallace 1990, Edinger and Risk 1995). The brooding coral species that have been studied, including *Porites astreoides* and *Agaricia agaricites*, are also hermaphroditic and self-fertilizing, enhancing reproduction at low colony densities in disturbed areas (Brazeau et al. 1998, Carlon 1999; D. F. Gleason, *personal communication*, for *Agaricia agaricites*). Brooding species, especially *P. astreoides* and *Agaricia agaricites*, are among the first corals to colonize disturbed reef surfaces in the Caribbean (Samarco 1985, Smith 1992, Edmunds 2000, and many others). If *Agaricia tenuifolia* is also hermaphroditic and self-fertilizing, that would help explain its ability to increase rapidly in the Belizean lagoon from initially low colony densities after the WBD outbreak had run its course.

Several months of high water temperatures in 1998, related in part to the El Niño–Southern Oscillation and in part to global warming (Hansen et al. 1999, Karl et al. 2000), bleached and killed almost all *Agaricia tenuifolia* colonies in the central lagoon, leaving only a few small colonies and colony fragments alive. Since *Agaricia tenuifolia* had not dominated previously in the last several millennia, its loss due to bleaching was another novel event in the late Holocene history of the rhomboid shoals (Aronson et al. 2000). Whether the death of *Agaricia tenuifolia* and any subsequent replacement sequence will be preserved in the fossil record is a question for the future.

Rising sea level

Populations of the two *Acropora* species were killed and replaced by different coral species (and other taxa) during the Pleistocene deglaciations and in the Holo-

cene, as reef accretion fell behind rapidly rising sea levels (reef drowning; replacement by deeper-dwelling species) and as inimical lagoonal and coastal waters flooded fore-reef habitats (reef poisoning; replacement by more stress-tolerant species; Lighty 1981, Neumann and Macintyre 1985, Macintyre 1988, Fairbanks 1989, Blanchon and Shaw 1995). In other cases, populations of *Acropora* were able to catch up to and keep up with rising sea level in the Holocene. Relative sea level has risen only ~1 m over the last 3000 yr in the Caribbean (Lighty et al. 1982, Fairbanks 1989; Macintyre et al. 1995 and I. G. Macintyre, *unpublished data*, for Belize), which is slow relative to accretion rates measured for lagoonal *Acropora cervicornis* (Macintyre et al. 1977, Westphall 1986 for the rhomboid shoals).

That rising sea level did not cause sudden, widespread species turnover between *Acropora cervicornis* and *Agaricia tenuifolia* on the rhomboid shoals of Belize over the past three millennia is clear from the data presented in this paper. Furthermore, the recent transition to dominance by *Agaricia tenuifolia* cannot be attributed to rising sea level, considering (1) the fact that the shoals were keeping pace with sea level rather than lagging behind prior to the transition, and (2) the direct observation that white-band disease was the cause of mortality of the incumbent *Acropora cervicornis* populations (see Aronson and Precht 1997, Aronson et al. 1998). Nor was the transition a shallowing-upward effect of reef accretion; this explanation is negated by the broad depth range (3–15 m) of the transition to *Agaricia tenuifolia*. Shallowing-upward sequences on the rhomboid shoals involve the replacement of *Acropora cervicornis* by *Porites divaricata* and *Millepora alcicornis*, not *Agaricia tenuifolia* (Westphall 1986, Aronson et al. 1998, Macintyre et al. 2000).

Regional implications

In less than a decade, the scale of species turnover events in the central shelf lagoon of Belize increased from tens of square meters or less to hundreds of square kilometers or more. At approximately the same time *Acropora cervicornis* succumbed to white-band disease on the rhomboid shoals, *Acropora* spp. were killed en masse by WBD in back- and fore-reef habitats in Belize and throughout the Caribbean region (Aronson and Precht 2001a, b). Unlike the situation on the rhomboid shoals, however, herbivory on most reefs did not keep pace with coral mortality, leading to dramatic increases in the cover and biomass of macroalgae. These changes raise the possibility that the spatial scale of turnover on Caribbean reefs in general has increased.

Prior to the late 1970s, variation in the cover and composition of coral assemblages was generally high at small spatial scales, among quadrats within reef habitats (Jackson 1991). Kaufman (1977), for example, described small-scale patchiness in stands of *Acropora cervicornis* in Jamaica. This small-scale variability was

brought about by the activities of damselfish (Pomacentridae), which killed *Acropora cervicornis* to cultivate algal lawns. Shinn et al. (1989) and Jaap and Sargent (1994) noted short-term volatility in populations of *Acropora cervicornis* within reefs along the Florida Reef Tract during the 20th century. We suggest that the recent regional decline of *Acropora cervicornis* (and other corals) has eliminated much of this small-scale variation by limiting the scope for turnover events at small spatial and temporal scales.

The loss of *Acropora cervicornis* (as well as *Acropora palmata*), its limited prospects for rapid recovery in a small ocean basin now beset by disturbances and stresses, and the success of brooding corals as replacements (Sammarco 1985, Smith 1992, Connell 1997) lead us to concur with predictions that brooders, particularly in the families Poritidae and Agariciidae, will become increasingly dominant components of coral assemblages on Caribbean reefs (Kojis and Quinn 1994; Aronson and Precht 2001b). Regardless of their life history strategies, however, corals will not occupy the majority of space if severe disturbances and stresses continue at their present levels.

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Unprecedented" *Acropora* Die-Offs: 6,300 & 3,000 ybp

Dennis Hubbard, Dept. of Geology-Oberlin College, 52 W. Lorain St. Oberlin OH 44074

In 1992, Jeremy Jackson observed that Pleistocene coral reefs exhibited general spatial stability. In contrast, monitoring and anecdotal observations have documented short-term variability and decline in reefs over recent decades. The result is an increased interest in the fossil record as a "pre-anthropogenic" frame of reference for conditions today. Proposals that recent disease outbreaks are "unprecedented" and largely anthropogenically induced are becoming increasingly common. This position requires three assumptions. First, changes in reef-community structure over periods of decades (i.e., monitoring records) can be identified in the fossil record. Second, spatial continuity of species and reef zones in the Pleistocene reflects uninterrupted temporal stability. Finally, examples of community disruption on the scale of the recent decimation of *Acropora* by White Band Disease do not exist in the Holocene record.

Cores through the shelf-edge reef communities off St. Croix, Puerto Rico and Florida reveal active *Acropora*-reef development starting around 10,000 ybp and ending suddenly between 7,000 and 6,300 ybp at all three sites. This is associated with a dramatic decrease in the number of *A. palmata* samples reported in the literature. Cores from a reef around Buck Island (U.S. Virgin Islands) reveal a species composition similar to that seen in monitoring records prior to the onset of WBD, implying that the "average" forereef community over the past 7,000 years was similar to what existed there before disease decimated *A. palmata* throughout the region. At 3,000 ybp, however, *Acroporids* disappeared at Buck Island, and community dominance shifted to massive corals. This corresponds to a second interval during which no *A. palmata* samples have been reported in the literature. While the overall pattern of reef development better matches the pre-WBD community at Buck Island, a more detailed look at the record implies a second Caribbean-wide interruption in the *A. palmata* record. Thus, spatial persistence is not necessarily equivalent to temporal continuity. Our cores have documented at least two regional gaps in the *A. palmata* record that appear analogous to the recent near-extirpation of the species by WBD. A re-examination of our new-found confidence in separating natural from anthropogenic change seems in order.



Population dynamics and life-history traits of *Acropora palmata*: costs and benefits of fragmentation

Several unique characteristics differentiate *Acropora palmata* from other coral species. Although *A. palmata* can be very susceptible to the physical disturbance caused by storms, it can also exhibit extraordinary regeneration and regrowth capabilities. The ability of *A. palmata* to form new colonies from storm-generated fragments, together with the reportedly low success of sexual recruitment in this species, suggest a strong connection between storm disturbance and survivorship and persistence of this species.

Here, I present the results from a simulation model developed to test the potential impacts of physical disturbance on elkhorn populations. This stage-based transition model identifies storm intensity and frequency as important factors influencing damage and recovery patterns of *Acropora palmata* populations. The simulations highlight an important trade-off between the primary and secondary negative impacts of storm damage and the need for this species to propagate asexually in light of its limited sexual recruitment success. After a severe storm, *A. palmata* populations can be numerically dominated by fragments and crusts. The shift in biomass from units with high survivorship (i.e., colonies) to units with higher mortality probabilities (i.e., fragments and crusts) can affect the recovery and long-term survivorship of disturbed populations.

Clearly, the difference between a storm being a destructive force or an external factor that promotes asexual propagation and population expansion is often a small one, and the balance between these two will ultimately influence the long-term survivorship of *A. palmata* populations already decimated by diseases and other stressors.

Diego Lirman, Ph.D.
Assistant Scientist
Center for Marine and Environmental Analyses
Rosenstiel School of Marine and Atmospheric Science
University of Miami
4600 Rickenbacker Cswy.
Miami, FL 33149

Tel: 305-361-4168
Fax: 305-361-4077
Email: dlirman@rsmas.miami.edu



Genetic Status of *Acropora palmata* populations in the Caribbean

Iliana B. Baums

Acropora palmata populations showed a significant Caribbean-wide decrease in the 1980s together with its congener *A. cervicornis* and are still in a depressed state. It has been suggested that White Band Disease, a disease specific to Acroporids (WBD, Antonius 1981, Gladfelter 1982, Peters 1993) is the primary cause of the recent mortality observed in wide areas of the Caribbean. It might have served as a strong selective agent, i.e. killing non-resistant genotypes and thereby reducing genetic variability. Additionally, Acroporids are particularly susceptible to hurricane breakage and have undergone major bleaching events in the last decade.

Clonal structure

A. palmata reproduces both sexually and asexually. Asexual reproduction can be the dominant mode of reproduction (Highsmith 1982). The high Acroporid cover of Caribbean reefs prior to the 1980s resulted from the combined effects of fragmentation and high growth rates.

Asexual reproduction leads to the multiplication of a particular genotype and results in an assemblage of genetically identical individuals that can function and survive on their own (Carvalho 1994), called a clone. Asexuality per se has no effect on allelic or genotypic frequencies in populations. It does not allow for genetic segregation and recombination, however, and so preserves the effects of selection, genetic drift, or founder effect on the genetic diversity. Bak (1983b) hypothesized that high asexual reproduction rates led to low genotypic diversity so that Acroporids were more susceptible to disease compared to non-branching species.

A. palmata reproduces sexually by releasing egg-sperm bundles in the water (broadcast spawning, Szmant 1986). Larvae settle out after about 1-2 weeks in the plankton. The pelagic life stage provides the opportunity for long-distance transport of larvae with the surface currents (Sheltema 1977, Crisp 1978).

The dominance of asexual reproduction combined with broadcast spawning has implications for the recovery potential of declining *A. palmata* populations. The effective population size, that is the number of breeding individuals, reaches its maximum if all genets contribute to the next generation. *A. palmata* is expected to have a small effective population size: both fertilization success of spawned gametes and the recruitment of larvae is highly stochastic and dependent upon local conditions. By chance, only a few individuals might contribute a large number of offspring to the next generation (sweepstake effect, Hedgecock 1994a, b). Once colonies become rare, the distance between them might limit fertilization success (Allee effect) even further. Populations with small effective population sizes are far more prone to extinction due to demographic stochasticity, reduction in gene diversity, or accumulation of deleterious mutations (see Grosberg and Cunningham 2000).

We need to understand the clonal structure of local *A. palmata* populations if we want to assess the status of this coral in the Caribbean. Several avenues have been pursued to detect clonal identity in Cnidaria. The first studies utilized self-recognition analyses (Neigel and Avise 1983) in *A. cervicornis*. This study found that *A. cervicornis* clones do not extend further than 20m. One clone may dominate areas of 10m² and these clones are generally spatially discrete with tight boundaries. The genetic basis of tissue compatibility has since been challenged by studies showing fusion of electrophoretically distinct ramets.

Analysis of protein (allozyme) and DNA markers show patterns from dominantly asexual to dominantly sexual reproduction in the Scleractinia. Even within the same species, contrasting reproductive behavior over large geographical scales is not exceptional (reviewed in Harrison and Wallace 1990). However, a lack of appropriate sampling design and the limited power of allozymes to resolve all genotypes limits the extend to which studies can be compared.

The consequences of asexual reproduction on genotypic diversity depend largely on the frequency of sexual recruitment and genet longevity. Empirical and theoretical studies have suggested that genotypic diversity at a local scale might decrease over time through elimination of genets by intraspecific competition or stochastic effects. In contrast, genotypic diversity might remain high if sexual recruits, however rare they might be, have a long life span after establishment occurred (McFadden 1997). In either case, interpopulation differences can be maintained (Hoffmann 1987).

Gene flow in the Caribbean

Opposing patterns of genetic population structure in the Caribbean have been predicted. High gene flow along major current paths (most recently Roberts 1997) may result in a gradient of genetic similarity, correlated within a current system, and would likely reduce subpopulation structure on small scales. Cowen et al. (2000) and others suggested that retention of larvae, aided by local current features, larval behavioral adaptations and high mortality rates should lead to highly subdivided populations. Studies of marine organisms demonstrate population patterns, from strongly structured to homogenous across the Caribbean basin. In the latter case, slight but significant microgeographic structure has been reported in the presence of high gene flow.

To date, there have been no studies on the population structure of Caribbean Scleractinia. However, geographic variation has been found in a number of Anthozoa in temperate and in tropical systems using allozyme and nuclear markers.

Burnett et al.(1995) predict that reef building corals show considerably more population structuring than has been described in strictly sexual species. The zoanthid *Zoanthus coppingeri* is only partly clonal but exhibits strong population structure between localities separated by only 50m, a consequence of random changes in gene frequencies as a result of low levels of gene flow. High clonal longevity and low sexual recruitment rates seem to maintain genetic differences over long periods.

If coral populations are largely self seeding and long-distance transport of larvae is a rare event, the Island Stepping Stone model predicts that genetic differentiation should increase with geographic distance. Indeed, geographic and genetic distance were correlated in some cases. This correlation is sometimes more pronounced in species with limited dispersal capacity in the Anthozoa (Hellberg 1996, Adjeroud and Tsuchiya 1999 but see McFadden 1997).

Underlying the above discussion is the assumption that species with long lived planktonic larvae should have a higher dispersal potential than species with philotrophic, short lived, benthic or no larval stages. It cannot be ruled out that the failure to consistently relate reproductive strategies, with the amount of gene flow in marine organisms, is due to the shortcomings of the markers and the statistical methods, rather than lack of pattern. Additionally, the fundamental differences between clonal and non-clonal species, both in terms of genetic structure and spawning strategies, further complicate predictions and call for different experimental approaches. It is essential to test the ability of the chosen marker system to reliably differentiate between clones (ramets, identical by descent) and closely related individuals (genets, identical by state) to reach confident conclusions about population structure. Furthermore, broadcast spawning corals like *A. palmata* only spawn annually and do so synchronously Caribbean wide. Thus, the potential for larval retention in local current features is likely to be different and, as of now unpredictable, across the Caribbean basin. Lastly, long generation times and low sexual recruitment will likely result in different time scales of larval exchange rates compared to sexual species.

Genetic structure of *A. palmata* is currently under investigation. Both clonal structure and reef connectivity will be estimated by combining highly variable, mendelian markers (microsatellites) with a nested sampling approach on a variety of spatial scales.

Summary

The presumed dominance of asexual reproduction in *A. palmata* leads to a number of predictions, namely small effective population size and low genotypic diversity within populations. Genet longevity and low sexual recruitment are expected to produce population substructure in the Caribbean. This substructure might not conform to geographic distance or cluster along major current patterns. Rather, it is expected to be influenced by the volatile nature of local currents and eddies. Failure to detect subpopulation structure does not exclude the possibility of extremely rare exchanges of sexual recruits between populations due to the presumed long generation times in *A. palmata*. In the latter case, conclusions about the population status and Caribbean reef connectivity will be limited. Nevertheless, information on the clonal structure of the populations will aid in the decision making process on marine reserves and management plans.



Fragmentation in the branching coral *Acropora palmata* (Lamarck): growth, survivorship, and reproduction of colonies and fragments

Diego Lirman*

Center for Marine and Environmental Analyses, Rosenstiel School of Marine and Atmospheric Science,
University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

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Abstract

Acropora palmata, a branching coral abundant on shallow reef environments throughout the Caribbean, is susceptible to physical disturbance caused by storms. Accordingly, the survivorship and propagation of this species are tied to its capability to recover after fragmentation. Fragments of *A. palmata* comprised 40% of ramets within populations that had experienced recent storms. While the survivorship of *A. palmata* fragments was not directly related to the size of fragments, removal of fragments from areas where they settled was influenced by size. Survivorship of fragments was also affected by type of substratum: the greatest mortality (58% loss within the first month) was observed on sand, whereas fragments placed on top of live colonies of *A. palmata* fused to the underlying tissue and did not experience any losses. Fragments created by Hurricane Andrew on a Florida reef in August 1992 began developing new growth (proto-branches) 7 months after the storm. The number of proto-branches on fragments was dependent on size, but growth was not affected by the size of fragments. Growth-rates of proto-branches increased exponentially with time (1.7 cm year⁻¹ for 1993–1994, 2.7 cm year⁻¹ for 1994–1995, 4.2 cm year⁻¹ for 1995–1996, and 6.5 cm year⁻¹ for 1996–1997), taking over 4 years for proto-branches to achieve rates comparable to those of adult colonies on the same reef (6.9 cm year⁻¹). In addition to the initial mortality and reduced growth-rates, fragmentation resulted in a loss of reproductive potential. Neither colonies that experienced severe fragmentation nor fragments contained gametes until 4 years after the initial damage. Although *A. palmata* may survive periodic fragmentation, the long-term effects of this process will depend ultimately on the balance between the benefits and costs of this process. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Asexual reproduction; Coral fragmentation; Fragment survivorship; Hurricanes

*Tel.: +1-305-361-4168; fax: +1-305-361-4077.

E-mail address: dlirman@rsmas.miami.edu (D. Lirman)

1. Introduction

Coral colonies are made up of modules (ramets) capable of surviving alone or in small groups. The sum of all ramets derived from a single zygote constitutes the coral's genet, and, unlike aclonal organisms, a coral's genotype can exist as independent units that may experience diverse environmental conditions (Coates and Jackson, 1985; Harper, 1985; Heyward and Collins, 1985). The population dynamics of several reef-building corals in the Caribbean are largely determined by the formation and death of ramets as the recruitment of new genets through the sexual recruitment of planula larvae is often limited. For example, sexual recruits of *Acropora palmata* and *Montastraea* spp. were absent, or present in very low numbers, in several settlement studies (e.g. Dustan, 1977; Bak and Engel, 1979; Hughes and Jackson, 1980, 1985; Rylaarsdam, 1983; Rosesmyth, 1984).

For *Acropora palmata*, a species with documented limited sexual recruitment, asexual reproduction by tissue fission or fragmentation can have a significant influence on its survivorship and propagation. The main goal of this study is to describe the incidence of fragmentation within populations of *A. palmata*, determine the survivorship and growth of fragments, and evaluate some of the costs and benefits of fragmentation for this reef-building species.

Several benefits of asexual reproduction have been described for clonal organisms. The organization of coral colonies into modules allows the biomass of a genotype to increase beyond the mechanical limits of individual colonies by the formation of fragments (Jackson, 1977; Hughes et al., 1992). Moreover, where growth-rates decline with increasing colony size (e.g. Maragos, 1974; Loya, 1976; Hughes and Jackson, 1985), fragmentation may help maintain high growth-rates. The larger size of fragments compared to planulae may result in higher survivorship after recruitment (Jackson, 1977) and the colonization of areas not suitable for larval development, such as soft-bottom habitats (Highsmith, 1982; Heyward and Collins, 1985). Also, unlike sexual reproduction, which is restricted seasonally for *Acropora palmata* (Szmant, 1986), fragmentation can take place year-round.

Despite these potential benefits of fragmentation, there are disadvantages associated with this process that have to be considered. The final outcome of fragmentation may be a total increase in biomass after a period of growth (Clark and Edwards, 1995), but tissue losses and the initial reduction in colony size can produce negative consequences as colony size in cnidarians has been directly associated with survivorship, growth, and reproduction (e.g. Connell, 1973; Loya, 1976; Highsmith, 1982; Jackson, 1985; Karlson, 1986, 1988; Hughes and Connell, 1987; Lasker, 1990; Babcock, 1991; Hughes et al., 1992).

Severe fragmentation, as commonly observed after storms, may limit future sexual reproduction by reducing the biomass of colonies and shifting the energy allocation of damaged colonies from reproduction to regeneration (Van Veghel and Bak, 1994; Van Veghel and Hoetjes, 1995; Hall and Hughes, 1996). Also, the size and weight of fragments may limit their dispersal range (Williams, 1975; Wulff, 1985; Jackson, 1986), slowing the recovery of damaged areas where the cover of adult colonies has been reduced significantly. In such cases, recovery will depend on the recruitment of sexual propagules produced in distant, undisturbed areas (Connell and Keough, 1985).

In this study, I examine fragmentation of the branching coral *Acropora palmata* to document some of the costs and benefits of this process. Specifically, I document: (1) abundance and percent cover of fragments within several *A. palmata* populations, (2) survivorship of fragments with respect to size and substrate type, and (3) effects of fragmentation on the growth and reproduction of colonies and fragments.

2. Methods

2.1. Study species

Acropora palmata forms tree-like colonies on shallow, high-energy reef environments throughout the Florida Reef Tract and Caribbean (e.g. Goreau, 1959; Geister, 1977; Gladfelter et al., 1978; Highsmith, 1982; Rogers et al., 1982; Wells, 1988). It is one of the most important reef-building corals in the region because of fast growth-rates (up to 10 cm year⁻¹, Gladfelter et al., 1978), high reef-accretion rates (7–15 kg CaCO₃ m⁻² year⁻¹, Gladfelter and Gladfelter, 1979), and rapid C-fixation rates (gross C fixation = 84–109 mg C cm⁻² day⁻¹, Bythell, 1988). Populations of *A. palmata* have undergone a recent regional decline attributed to their susceptibility to diseases such as White Band Disease and physical disturbance (e.g. Bak et al., 1981; Davis, 1982; Gladfelter, 1982; Bythell and Bythell, 1991; Tunnell, 1992; Bythell and Sheppard, 1993; Jaap and Sargent, 1993). Fragmentation and dislodgment of this species were reported after Hurricanes Hattie (Stoddart, 1963, 1965), Edith (Glynn et al., 1964), Gerta (Highsmith et al., 1980), Allen (Woodley et al., 1981), David and Frederic (Rogers et al., 1982), Hugo (Gladfelter, 1991), Gilbert (Kobluk and Lysenko, 1992; Jordan-Dahlgren and Rodriguez-Martinez, 1998), and Andrew (Lirman and Fong, 1996, 1997a), as well as after Tropical Storms Bret (Van Veghel and Hoetjes, 1995) and Gordon (Lirman and Fong, 1995, 1997a,b).

2.2. Study sites

Two reefs with dense populations of *A. palmata* were studied within Biscayne National Park in the northern Florida Reef Tract, Elkhorn Reef (25° 21.766' N, 80° 09.961' W, depth of *A. palmata* population = 1–3 m) and Ball Buoy Reef (25° 18.524' N, 80° 11.996' W, 2–5 m, Fig. 1). These reefs were damaged by two storms: Hurricane Andrew (24 August 1992, maximum sustained winds = 225 kph, Powell and Houston, 1993; Rappaport and Sheets, 1993) and Tropical Storm Gordon (14–17 November 1994, maximum sustained winds = 84 kph; NOAA, 1994; Rappaport and Avila, 1995; Lirman and Fong, 1997a).

Additional populations of *A. palmata* were surveyed along the Florida Reef Tract at Key Largo Dry Rocks (2–4 m), Little Grecian Reef (2–5 m), French Reef (2–7 m), Pickles Reef (2–5 m), and Dry Tortugas (2–4 m), and in the US Virgin Islands at Saba Island, St. Thomas (1–3 m), Hawksnest Bay, St. John (0.5–3 m), and Buck Island, St. Croix (2–8 m) (Fig. 1).

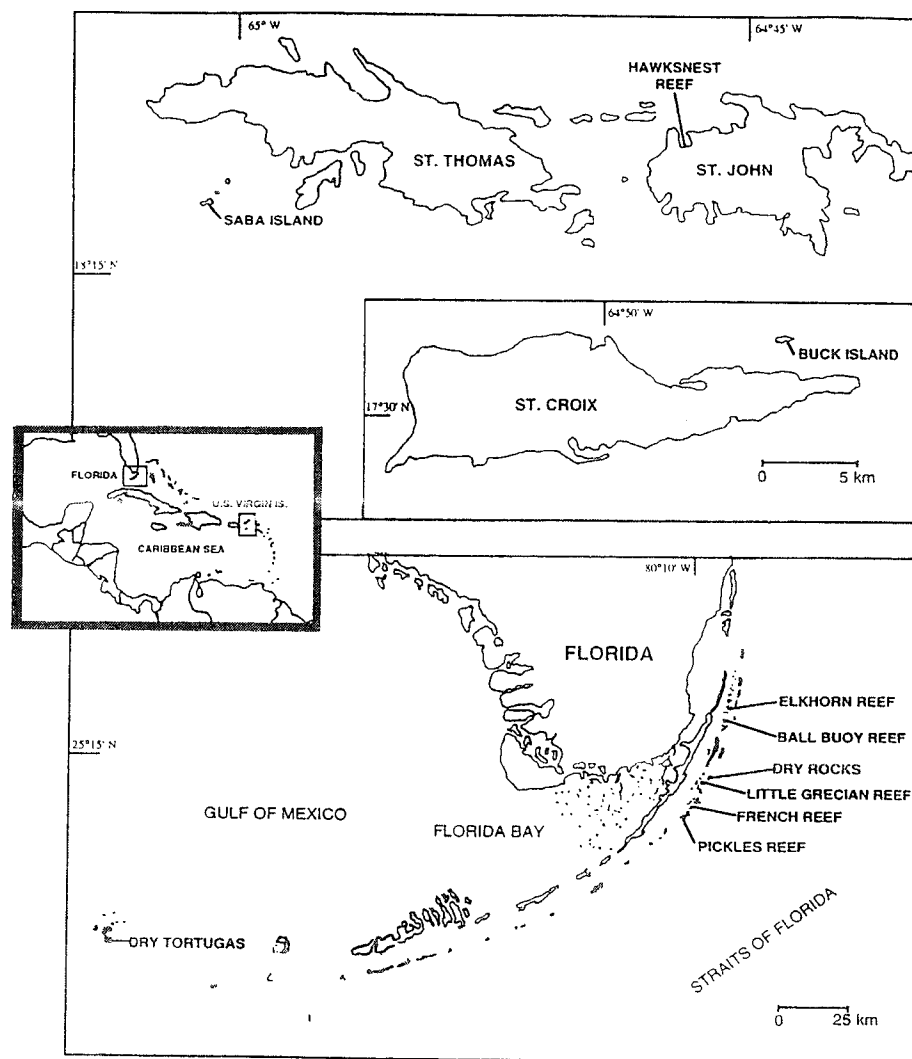


Fig. 1. Map of the study sites in Florida and the US Virgin Islands. The insert shows the general location of the study areas in the Caribbean region.

2.3. Abundance and percent cover of fragments

Coral populations are commonly described in terms of coral abundance and percent cover. Given the numerous reports of storm damage to *A. palmata*, it was hypothesized that populations that experienced recent storm damage may be dominated in both abundance and percent cover by fragments as opposed to standing colonies. The percentage of ramets within populations that was comprised of fragments was determined with belt transects (25×1 m) on ten reefs with abundant *A. palmata*

populations (seven in the Florida Keys and three in the USVI). On each reef, the location of *A. palmata* was established and a meter tape was positioned bisecting the population. The position of the belt transects ($n = 4$ per reef), which were run perpendicular to the main line, was determined from a set of random numbers previously drawn. All colonies and fragments within these transects were counted. Standing *A. palmata* were defined as those colonies that remained upright and had a single attachment to the bottom through the characteristic stalk. Fragments were defined as broken branches of *A. palmata* covered by live tissue lying on the substratum and lacking an obvious stalk.

Also, to determine the percent cover of colonies and fragments after storms, three 100-m long line-intercept transects (LITs, Loya, 1972, 1978) were surveyed on two reefs of the northern Florida Reef Tract. The LITs, placed parallel to each other on an E–W direction (the general direction of the storm paths), were separated by a distance of 15 m. Elkhorn Reef was surveyed in March, 1993, 7 months after Hurricane Andrew, and Ball Buoy Reef was surveyed before (August, 1994) and after (January, 1995) Tropical Storm Gordon (November, 1994). The cover of fragments and standing colonies was estimated at 1-m intervals by calculating the fraction of the length of the line these intercepted.

2.4. Survivorship of fragments and colonies

In a previous study, the survivorship of *A. palmata* fragments was monitored starting 7 months after Hurricane Andrew (Lirman and Fong, 1997b). Because these fragments were not marked until 7 months after fragmentation, no information was obtained on early survivorship (0–6 months). In the present study, the hypothesis that early survivorship will be affected by the size of fragments and type of substratum was evaluated using a transplant experiment.

Fifty fragments of *A. palmata* created by a ship grounding on Elkhorn Reef were collected within 24 h of fragmentation and assigned haphazardly to one of the following four types of substratum ($n = 12$ –13 fragments per group): (1) hard-bottom (consolidated carbonate framework), (2) rubble (loose, dead pieces of *A. palmata* and *A. cervicornis*), (3) sand, and (4) live coral. All transplant sites were located in the back-reef area of Elkhorn Reef at a depth of 2 m. Maximum distance between transplant sites was 50 m. Each fragment was labeled with a metal tag, photographed with a fixed-distance framer and transported to the transplant sites where they were placed individually on the bottom separated from each other by at least 50 cm. Fragments transplanted onto live coral were placed on top of *A. palmata* colonies. Photographs of each fragment were taken at monthly intervals starting in June, 1994; size was determined by digitizing the developed prints using NIH Image Analysis Software.

Mean percent tissue mortality for fragments was estimated as:

$$\frac{\sum_{i=1}^n \left(\frac{IA - FA}{IA} \right)}{n} * 100$$

where IA = initial live tissue area (cm^2), FA = final live tissue area (cm^2), n = number of fragments.

To test the hypothesis that fragmentation will affect the survivorship of fragmented colonies, fragmented and unfragmented colonies were surveyed on Elkhorn and Ball Buoy Reefs between 1993 and 1997 ($n=25$ fragmented and 25 unfragmented colonies per reef). Fragmented colonies had one to three branches recently removed as evidenced by the presence of skeletal lesions (Fong and Lirman, 1995).

2.5. Growth of fragments and colonies

Starting on May 1993, many of the fragments of *A. palmata* generated by Hurricane Andrew on Elkhorn Reef began developing new vertical growth features ('proto-branches') on their upper surfaces. A previous study documented a direct relationship between the size of fragments (mean size = 4752 cm^2) and the number of proto-branches formed, but no significant relationship between size and mean height of proto-branches after 5 months (Fong and Lirman, 1995).

Here, the size-range of fragments surveyed was expanded to include smaller units (mean size = 651 cm^2 , $n=30$ fragments), to re-test the hypothesis that size will determine the number of proto-branches growing on a fragment as well as their growth-rates. Also, the growth of proto-branches was followed over a longer period of 4 years (1993–1997) to document the development of the branching patterns leading to the tree-like morphology seen on adult colonies. All of the fragments studied were originated during Hurricane Andrew in August, 1992 and found in the back-reef area of Elkhorn Reef. Over 100 of these fragments were labelled with numbered metal tags after the hurricane and a subset of 30 was chosen at random for this study by their tag number. The growth of proto-branches was averaged within fragments.

The linear extension of branches on 30 colonies of *A. palmata* was measured over a 6-month period between May–November, 1996 at Elkhorn Reef. Three branches were marked per colony and an average extension-rate was obtained for each colony. Growth-rates of proto-branches were compared to the growth-rates of standing colonies.

2.6. Fragmentation and sexual reproduction

The reproductive state of colonies and fragments was determined 1 week prior to the predicted spawning dates in 1995–1997 to test the hypothesis that fragmentation will have negative effects on sexual reproduction as resources are directed away from this process and into repair and re-growth. Tissue samples were collected from: (1) small fragments (longest dimension = 20–50 cm), (2) medium fragments (51–80 cm), (3) large fragments (81–145 cm), (4) colonies damaged by storms (three or more branches missing), and (5) undamaged colonies (no signs of fragmentation). All of the samples were collected from units that had been identified after Hurricane Andrew on Elkhorn Reef and after Tropical Storm Gordon on Ball Buoy Reef, establishing their disturbance history. Tissue samples ($10\text{--}15 \text{ cm}^2$) were fixed with Zenker's solution within 30 min of collection, decalcified in 10% HCl within 24 h (Szmant, 1991), and inspected under a dissecting microscope for the presence or absence of gametes.

3. Results

3.1. Abundance and cover of fragments

Both the abundance and percent cover of fragments within *A. palmata* populations can be high, especially in reefs that experienced recent storms such as Elkhorn and Ball Buoy Reefs, where fragments comprised 40% of the total number of ramets (Fig. 2). Fragments occupied 14.8% (S.E.=2.1, $n=3$ transects) of the bottom on Elkhorn Reef after Hurricane Andrew, while standing colonies occupied 12.1% (± 2.4). On Ball Buoy Reef, the cover of fragments increased from 2.3 (± 0.8) to 10.0% (± 2.6) after Tropical Storm Gordon.

Nevertheless, surveys at other reefs showed that fragmentation may be prevalent even in the absence of hurricane damage as evidenced by the large proportion of fragments within *A. palmata* populations on Little Grecian Reef (35%) and the Dry Tortugas (43%), two areas with no significant storm activity reported in the recent past.

3.2. Survivorship of fragments

No significant relationships were found between size and the survivorship of fragments (regression, $P=0.52$). However, there was a significant difference between

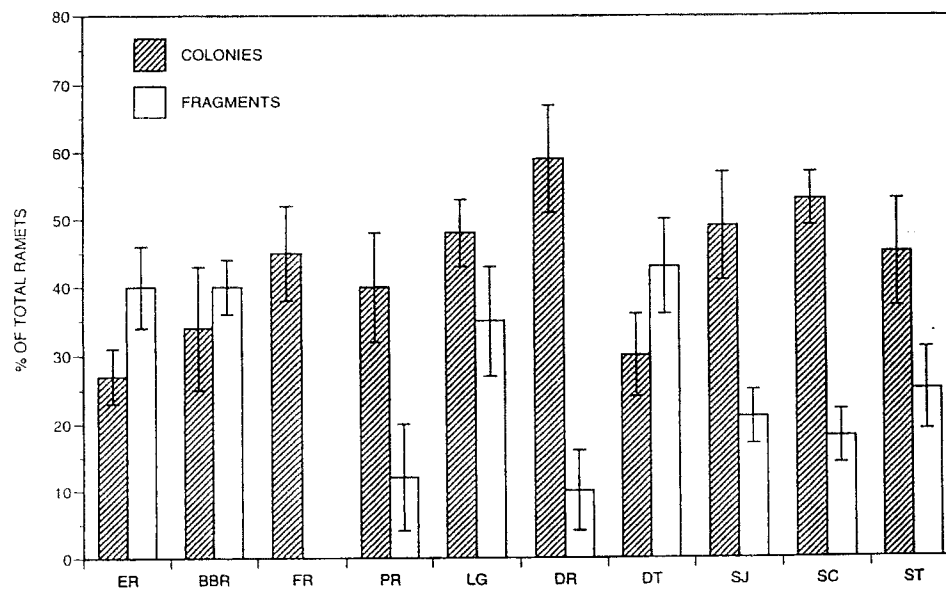


Fig. 2. Mean relative abundance ($\pm$ S.E.) of colonies and fragments of *Acropora palmata* on different reefs expressed as the percentage of total ramets (isolated units) in a population. A third category, crusts, is not represented here. Florida reefs: ER=Elkhorn Reef (sampling date=7/95), BBR=Ball Buoy Reef (6/95), FR=French Reef (8/96), PR=Pickles Reef (8/96), LG=Little Grecian Reef (7/97), DR=Key Largo Dry Rocks (7/97), DT=Dry Tortugas (3/96). US Virgin Islands: SJ=St. John (7/95), SC=St. Croix (7/95), ST=St. Thomas (7/95). n =four transects (25×1 m) per site.

the size of those fragments that remained within transplant sites and those that were carried away; fragments removed from the reef by waves and currents were significantly smaller (mean size = $77.6 (\pm 13.4) \text{ cm}^2$, $n=10$) than those fragments that remained ($289.3 (\pm 16.1) \text{ cm}^2$, $n=40$, Mann-Whitney U -test, $P<0.05$). Non-parametric tests were used to compare size of fragments in this case because even though variances were homogeneous (Bartlett's test, $P>0.1$), the size-distribution of those fragments that were removed from the reef was not normal (Shapiro-Wilk test, $P<0.05$) and no data transformations were successful in achieving normality (Sokal and Rohlf, 1981).

Partial mortality on fragments was high initially as 35.5% (± 6.5) of live tissue was lost within the first month. Although mortality continued, subsequent losses were not as high as those recorded during the first month (38.4 (± 6.4), 45.7 (± 6.9), and 47.1% (± 3.4) after 2, 3, and 4 months, respectively). Fragments placed on sand were covered by sediments and showed signs of bleaching within a week. Fragments placed on live *A. palmata* colonies fused to the underlying tissue without any apparent tissue rejection within 3 weeks.

Survivorship of transplanted fragments was significantly affected by type of substratum (Fig. 3). Fragments transplanted to rubble ($n=12$), hard ($n=13$), or sandy bottoms ($n=12$) experienced high mortality during the first month. In contrast, fragments placed on live adult *A. palmata* colonies ($n=13$) did not experience any tissue losses. Mortality during the first month was significantly greater in the sandy bottom than on rubble or hard-bottom areas (ANOVA, $P<0.05$, Tukey's *a posteriori* comparisons).

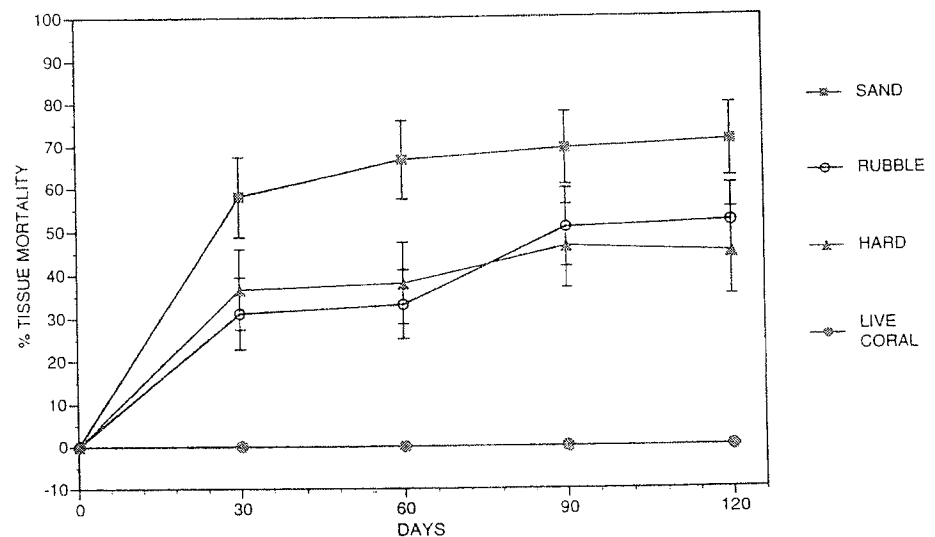


Fig. 3. Mean tissue mortality ($\pm$ S.E.) of *A. palmata* fragments transplanted to different types of substratum on the back reef of Elkhorn Reef, Florida. $n=12$ fragments for transplants onto rubble and sand, $n=13$ for transplants onto live and hard substrata.

Table 1

Height of proto-branches (PB) on fragments of *Acropora palmata* generated by Hurricane Andrew (24 August 1992) at Elkhorn Reef ($n=267$ PB on 35 fragments; a mean PB height was obtained for each fragment)

	7/93	6/94	5/95	9/96	4/97
Mean PB height (± 1 S.E.) (cm)	2.6 (0.1)	4.5 (0.2)	7.64 (0.3)	14.1 (0.5)	16.9 (0.6)
Maximum PB height (cm)	9	13	18	30	38
Mean # PB/m ² of live tissue (± 1 S.E.)	11.1 (1.9)	11.8 (2.1)	10.2 (2.4)	9.1 (1.1)	6.4 (0.8)

3.3. Growth of fragments

Most proto-branches were formed on the upper surfaces of fragments within the first year after fragmentation, with only a few additional proto-branches formed subsequently. The number of proto-branches was directly related to the surface area of fragments ($r^2=0.64$, $P<0.05$). Mean density of proto-branches on fragments decreased with time as some partial mortality occurred and some proto-branches fused to each other (Table 1).

Proto-branches reached a mean height of 2.6 (± 0.1) cm within 1 year. After this initial growth, growth-rate of proto-branches increased exponentially with time (Fig. 4). Growth-rates calculated from regression were 1.7 cm year⁻¹ for 1993–1994, 2.7 cm year⁻¹ for 1994–1995, 4.2 cm year⁻¹ for 1995–1996, and 6.5 cm year⁻¹ for 1996–

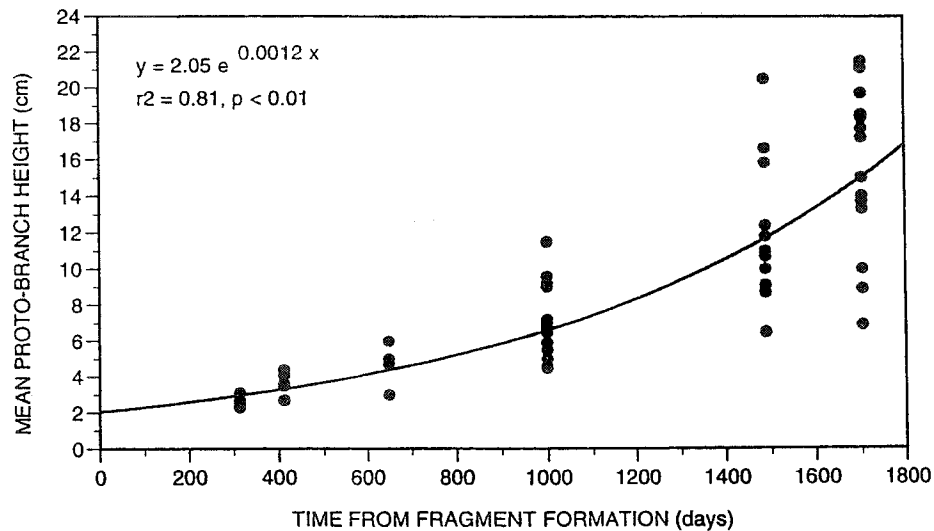


Fig. 4. Relationship between mean proto-branch height and time from fragment formation (24 August 1992). $n=267$ proto-branches in 35 fragments.

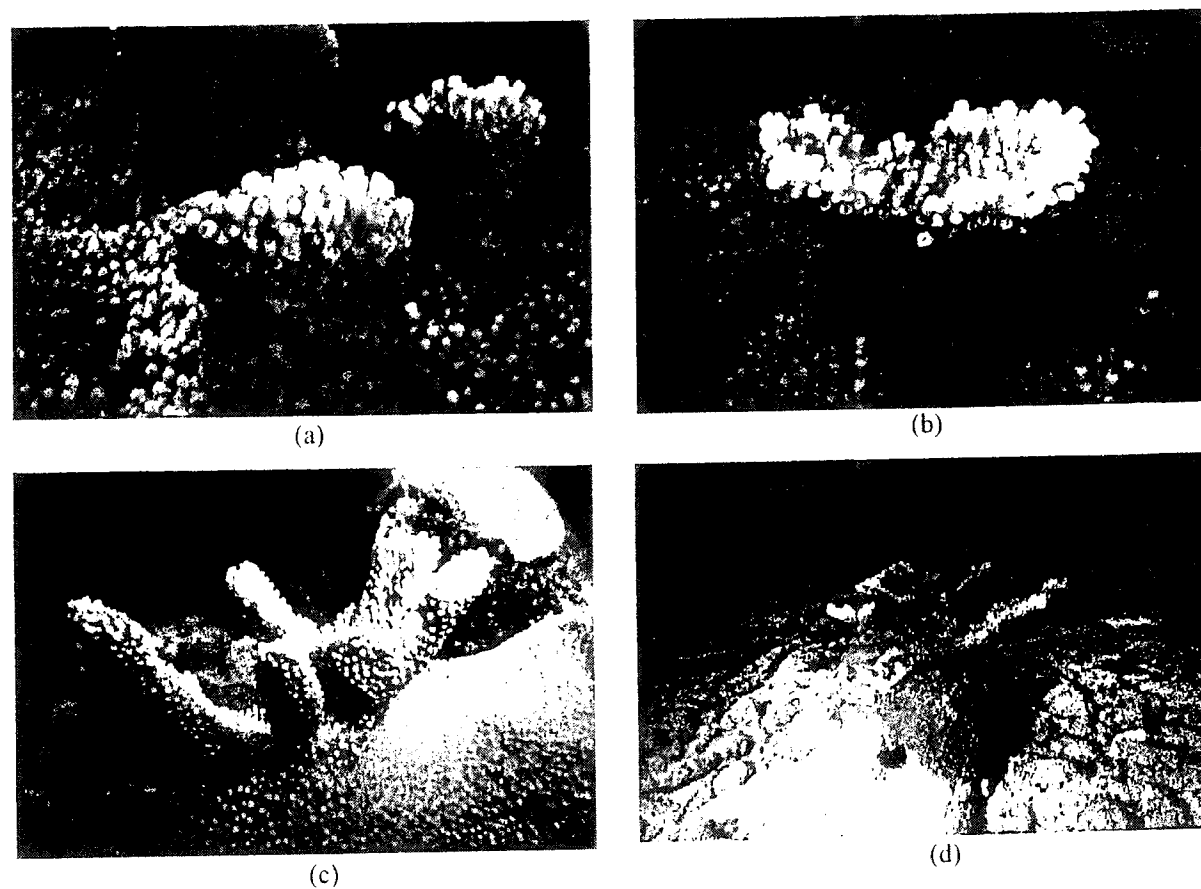


Fig. 5. Photographs of *A. palmata* proto-branches at different times of development on fragments created by Hurricane Andrew on Elkhorn Reef on August 1992. (a) December 1993, (b) July 1994, (c) July 1995, (d) August 1996. Depth = 1.5–2.0 m.

1997. A regression of size and mean proto-branch height showed no significant relationships in 1995, 1996, and 1997 ($r^2=0.07$ – 0.48 , $P=0.10$ – 0.33).

After formation, proto-branches grew upwards with a cylindrical shape until they reached a height of 4–5 cm (Fig. 5a), when a mushroom-type cap developed (Fig. 5b). The first branching pattern was observed as proto-branches reached 6–10 cm and began developing the typical tree-like morphology seen in adult colonies (Fig. 5c). Secondary branching patterns were observed in 1996 on the tallest proto-branches (Fig. 5d).

3.4. Survivorship and growth of colonies

Survivorship of adult colonies was high on both Elkhorn and Ball Buoy Reefs. Partial mortality attributed to competition with algae or feeding activities of corallivores was observed, but none of the adult colonies surveyed, fragmented or unfragmented, exhibited complete tissue mortality between 1992 and 1996 ($n=100$). The linear growth-rate of *A. palmata* colonies was $6.9 (\pm 0.3) \text{ cm year}^{-1}$ ($n=30$).

3.5. Fragmentation and sexual reproduction

Production of gametes in *A. palmata* was affected by size and previous disturbance history (Table 2). In August, 1995, 3 years after Hurricane Andrew, none of the *A.*

Table 2
Reproductive state of *Acropora palmata* colonies and fragments^a

Date	Type	Reef	Mean size (cm)	<i>n</i>	% With gametes
8/95	Fragment/small	ER	28.8 (4.8)	5	0
8/95	Fragment/medium	ER	63.4 (2.5)	5	0
8/95	Fragment/large	ER	131.0 (12.1)	5	0
8/95	Colony/damaged	ER	193.0 (27.4)	5	0
8/95	Colony/undamaged	ER	161.0 (49.0)	5	80
8/95	Fragment	BBR	48.6 (9.9)	6	0
8/95	Colony/damaged	BBR	91.0 (23.8)	11	18
8/96	Fragment/small	ER	35.8 (7.2)	6	0
8/96	Fragment/medium	ER	62.4 (5.6)	6	0
8/96	Fragment/large	ER	140.7 (11.1)	6	33
8/96	Colony/damaged	ER	167.0 (18.9)	6	50
8/96	Colony/undamaged	ER	185.0 (33.3)	6	67
8/96	Fragment	BBR	52.3 (12.6)	6	67
8/96	Colony/damaged	BBR	120.0 (13.5)	9	67
7/97	Fragment/small	ER	27.3 (3.8)	7	0
7/97	Fragment/medium	ER	55.8 (3.6)	7	43
7/97	Fragment/large	ER	127.2 (10.2)	7	72
7/97	Colony/damaged	ER	170.5 (16.5)	9	78
7/97	Colony/undamaged	ER	179.3 (22.5)	9	78
7/97	Fragment	BBR	44.7 (6.9)	6	67
7/97	Colony/damaged	BBR	156.3 (32.1)	8	62

^a Colonies on Elkhorn Reef (ER) were fragmented during Hurricane Andrew (August 1992). Colonies on Ball Buoy Reef (BBR) were fragmented during Tropical Storm Gordon (November 1994). Mean size (± 1 S.E.) was estimated as longest length of live tissue on fragments and maximum canopy diameter on colonies.

palmata fragments sampled at Elkhorn Reef had gametes, irrespective of size. A lack of gametes also occurred in adult colonies that had been damaged by the hurricane. The only samples that contained gametes in 1995 were taken from undamaged colonies. In August, 1996, neither small nor medium fragments had any gametes, but two of six large fragments sampled were reproductive. Colonies, both damaged and undamaged, had gametes at this time. In July, 1997, a high proportion of both damaged and undamaged colonies had gametes (seven of nine colonies sampled from each group). Also, three of seven medium fragments and five of seven large fragments had gametes. In contrast, none of the small fragments surveyed had gametes in 1997.

At Ball Buoy Reef, fragments did not have any gametes in August, 1995, 8 months after Tropical Storm Gordon. However, two of eleven damaged colonies had gametes at this time. In August, 1996, four of six fragments and six of nine damaged colonies had gametes. Finally, four of six fragments and five of eight damaged colonies had gametes in July, 1997.

4. Discussion

Fragmentation is prevalent within populations of *Acropora palmata*. Surveys conducted at different locations revealed that, especially within populations that experienced recent storms, fragments can comprise a large percentage of ramets as well as cover a large percentage of the bottom (Lirman and Fong, 1997a). This is consistent with a previous study by Highsmith (1982) where an average of 69% of all *A. palmata* colonies were derived from fragments on several reefs in Panama.

The effects of storms on coral populations can extend beyond the direct physical disturbance that causes significant tissue mortality (reviewed by Harmelin-Vivien, 1994 and Connell, 1997). A secondary effect documented for *A. palmata* is the shift in biomass from ramets with low mortality probabilities (i.e. colonies) to units with higher mortality probabilities (i.e. fragments). This secondary effect highlights the importance of fragment survivorship and regrowth in the recovery and persistence of damaged *A. palmata* populations.

Survivorship of fragments of *A. palmata* can be influenced by the type of substratum where fragments land. Highest survivorship was observed for those fragments placed on top of live *A. palmata* colonies. These fragments fused to the underlying tissue and showed no signs of mortality. In contrast, fragments placed on sand lost 58% of their tissue within the first month and 71% after 4 months. Similar effects of substratum or location within reefs on fragment survivorship were documented for other coral species (e.g. Yap and Gomez, 1984, 1985; Heyward and Collins, 1985; Wallace, 1985; Bruno, 1998).

The relationship between the size of fragments and survivorship is not consistent. Although there is a general indication that survivorship increases with size (Loya, 1976; Highsmith et al., 1980; Heyward and Collins, 1985; Liddle and Kay, 1987; Lasker, 1990), several exceptions have been reported. Results from the transplant experiment support findings from previous studies where no relationship between the size of fragments and survivorship was found (Kobayashi, 1984; Lewis, 1991; Lirman and

size. A lack of size may still affect the long-term survivorship of fragments indirectly through its effect on rates of removal. Here, fragments that remained within transplant sites were larger than those removed by waves or currents. Thus, if smaller fragments are removed more easily from reefs, size may still influence their long-term survivorship.

The transport of fragments away from reefs can provide a mechanism for the creation of additional primary space and reef expansion as suggested by Highsmith (1982). Patch reefs on the Florida Reef Tract are commonly surrounded by sand and seagrass beds that are not optimal habitats for coral recruitment and survivorship (Jaap, 1984). Although mortality of transplanted fragments was high on sand, those fragments placed on rubble substrate showed high survivorship. Thus, even if fragments experience high mortality on sand, the rubble produced by these fragments can increase the survivorship of fragments created by subsequent storms, expanding the potential settlement area around a reef, and resulting ultimately in reef expansion.

Fragments of *A. palmata* showed rapid regrowth through the formation of proto-branches less than a year after fragmentation. The number of proto-branches was directly related to the size of fragments, as can be predicted based on limited resource availability (Fong and Lirman, 1995). The growth of proto-branches was slow initially, but increased with time, showing an exponential behavior. As proto-branches first develop, growth would be supported by the tissue on the upper surface of the fragments as the translocation of resources from the central portions of colonies often support the growth of the distal portions of branches (Pearse and Muscatine, 1971; Taylor, 1977; Gladfelter et al., 1989). This may limit initial growth-rates as several proto-branches can be found even in small fragments. As proto-branches grow in size and complexity, they would no longer rely on resources produced by the fragment, and their growth-rates would be expected to increase as a function of their own surface area. On average, it took more than 4 years for proto-branches to achieve linear growth-rates comparable to those measured for *A. palmata* colonies on the same reef. Slower growth-rates of fragments and coral transplants compared to undamaged colonies were also observed by Kobayashi (1984) and Cox (1992).

The success of asexual propagation in *A. palmata* contrasts with the limited sexual recruitment reported for this species (Dustan, 1977; Bak and Engel, 1979; Rylaarsdam, 1983; Rosesmyth, 1984). In this study, it was shown that fragmentation can have long-term effects on gamete production in *A. palmata*. Three years after Hurricane Andrew, gametes were present only in large *A. palmata* colonies that had not experienced direct fragmentation during the storm. Neither those colonies that were damaged by the hurricane nor any of the hurricane-generated fragments had produced gametes at this time. These results are in contrast to those reported by Ward (1995) who found that fragmented colonies of *Pocillopora damicornis* had a higher reproductive output than non-damaged colonies.

The cessation in gamete production in fragments and recently fragmented colonies suggests a differential allocation of energy towards stabilization, lesion repair, and growth. Reproduction may only resume after a certain size and/or level of repair or growth has been achieved. A similar trade-off between reproduction and regeneration was observed for the coral *Montastraea annularis* (Van Veghel and Bak, 1994), and

differential allocation of resources to repair and growth at small colony sizes has been noted for other hard corals (Kojis and Quinn, 1985; Szmant, 1986; Hughes et al., 1992) and zoanthids (Karlson, 1988).

The combination of high frequency of fragmentation and the apparent lack of sexual reproductive success has been considered as evidence of the adaptive value of fragmentation for several coral species (Bak and Engel, 1979; Highsmith et al., 1980; Tunnicliffe, 1980, 1981; Bothwell, 1981; Highsmith, 1982). The emerging picture of fragmentation in *Acropora palmata* seems to fit well within the conceptual framework proposed in previous studies. *A. palmata* fragments often and, except in cases of widespread mortality (e.g. Woodley et al., 1981), populations can recover and propagate as fragments and damaged colonies regrow (Fong and Lirman, 1995). However, as remarked by Hughes et al. (1992), claims on the adaptive value of fragmentation should be made with caution since the potential costs of this process may be significant and have not been well-documented. Such indirect costs of fragmentation were observed in the present study, as both reduced growth and loss of reproductive potential were documented. This evidence suggests that the ultimate fate of coral populations damaged by storms can only be predicted after the potential indirect costs of fragmentation have been carefully considered.

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Report of the NMFS CITES Criteria Working Group

The following document describes the criteria the NMFS working group (chaired by Pamela Mace) recommended to identify and address species of concern that would qualify for listing in Appendix I or Appendix II of CITES. The text included here is not the complete document developed by the working group. Rather, it only includes a summary of existing CITES Criteria and the parameters the NMFS group thought were relevant to a listing, but not properly addressed in the existing criteria.

1. Specific questions to be addressed: At present, the CITES criteria used to assess whether a population qualifies for inclusion in the CITES Appendices relate to:

- A. Size of the population
- B. Area of distribution of the population
- C. Decline in the size of the population

The guidelines in Annex 5 of the CITES criteria (CITES Resolution 9.24) suggest that a "small" population would be one that is less than about 5,000 individuals and a small sub-population would be one with less than 500 individuals; a restricted area of distribution would be represented by one that was less than about 10,000 km² for the entire population and 500 km² for each sub-population; and a rate of "decline" that might be cause for concern would be anything in excess of 50% or more within the longer of 5 years or 2 generations, or 20% or more within the longer of 10 years or 3 generations for a small wild population. These figures are presented only as examples. (For more details and explanations, refer to CITES Resolution Conf. 9.24).

Some questions to initiate the WG discussions are:

- 1. Which is more important, the rate of decline or the extent of decline?
- 2. Is it necessary to have a time frame for the extent of decline?
- 3. If so, is generation time an appropriate metric for the time frame?
- 4. Is it better to use absolute numbers for population size and area of distribution, or to use percentages of some historical and/or potential level?
- 5. Are different absolute numbers or percentages needed for different taxonomic groups?
- 6. Would it be better to use life history characteristics rather than taxonomic groupings (or both) to define appropriate absolute numbers or percentages?
- 7. Is it at all valuable to have numeric guidelines?

2. Background: CITES Resolution Conf. 9.24

CITES Resolution Conf. 9.24, "Criteria for Amendment of Appendices I and II", was adopted at the Ninth Meeting of the Conference of the Parties in Fort Lauderdale, USA in November 1994. The Resolution consists of a preamble and six annexes. Annex 1 concerns biological criteria for Appendix I; Annex 2 concerns criteria for the inclusion of species in Appendix II, with Annex 2a indicating listing criteria specific to particular species of concern, and Annex 2b covering the situation of look-alike and taxonomically related species; Annex 3 covers special cases such as listing of a species in more than one Appendix (split listings); Annex 4 outlines the precautionary approach; Annex 5 contains definitions,

notes and guidelines; and Annex 6 provides a format for proposals to amend the Appendices. Annexes 2b, 3, 4 and 6 are not addressed in this report, and will not be mentioned further.

Annex 1 lays out the conceptual basis for considering species for listing in CITES Appendix 1. The conceptual basis includes four factors: (A) the wild population is small, (B) the wild population has a restricted area of distribution, (C) there has been a decline in the number of individuals in the wild, and (D) the species is likely to satisfy one of the previous three criteria within a period of five years. Each of criteria A, B and C also list additional relevant factors. Annex 2a is less specific, essentially stating that a species should be included in Appendix II if it is likely to meet at least one of the criteria in Annex 1 unless subject to strict regulation of international trade, or if harvest rates have exceeded sustainable levels over an extended period. There are no numeric thresholds or guidelines in Annexes 1 and 2a, but both are prefaced with a statement that they must be read in conjunction with the definitions, notes and guidelines listed in Annex 5.

Annex 5 defines and discusses the terms: area of distribution, decline criteria, an extended period, fragmentation, generation time, large fluctuations, population, possibly extinct, subpopulations, and threatened with extinction. Numeric guidelines are provided as indicators of a restricted area of distribution for a population (less than 10,000 km²), a restricted area of distribution for a subpopulation (less than 500 km²), a high rate of decline (a decrease of 50% or more in total within 5 years or two generations whichever is longer or, for a small wild population, a decline of 20% or more in total within ten years or three generations whichever is longer), a small population (less than 5,000 individuals), a small subpopulation (less than 500 individuals), large fluctuations (population size or area of distribution varies widely, rapidly and frequently, with a variation greater than one order of magnitude), and a short-term fluctuation (one of two years or less). However, it is emphasized that each of these numbers are provided only as guidelines and not thresholds, and that there will be many cases where such numerical guidelines do not apply.

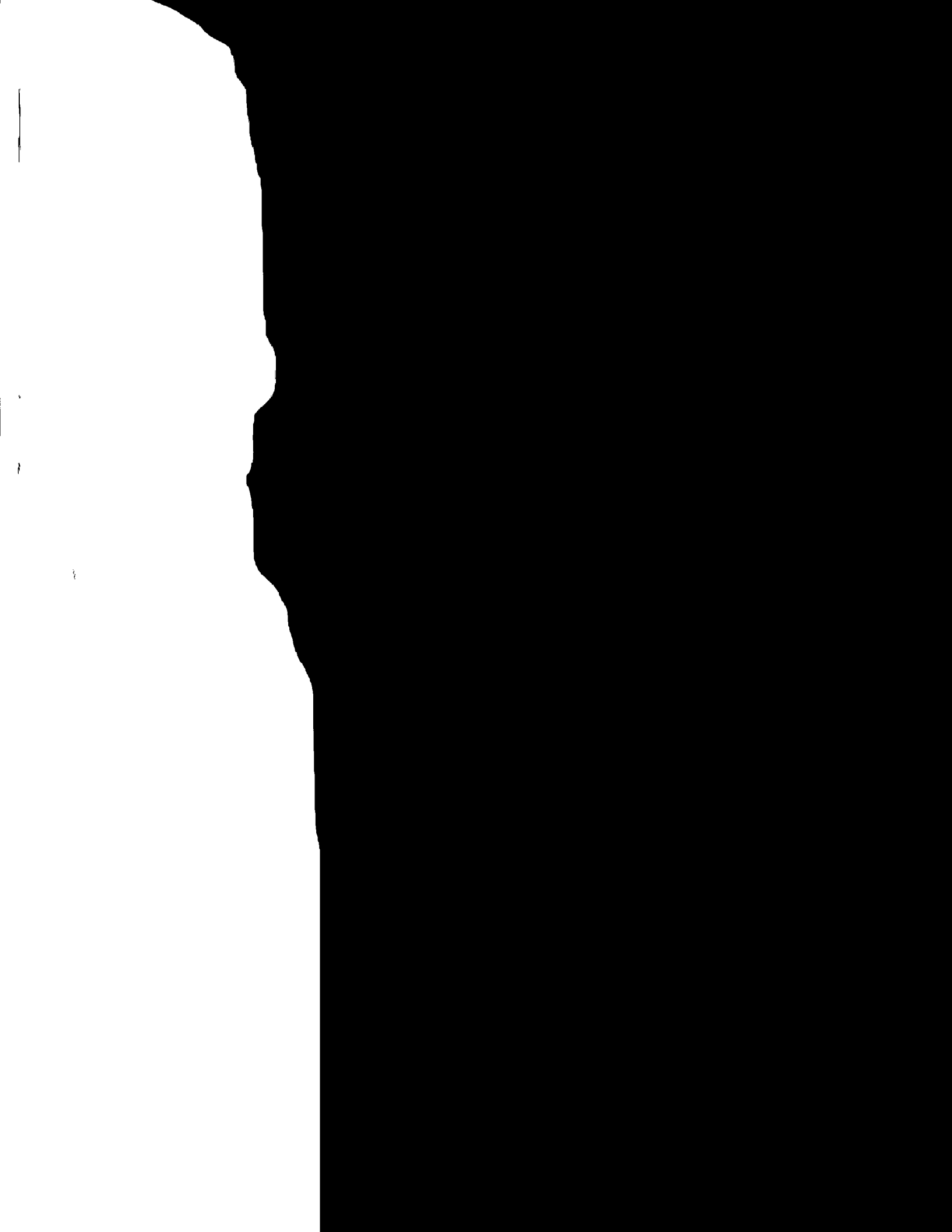
During initial meetings, the Working Group decided to focus primarily on Annex 5, rather than Annexes 1 and 2a because modifications to the latter will depend on which modifications to Annex 5 are adopted.

3. Issues and Recommendations

The Working Group discussed several broad issues of relevance to the CITES criteria and guidelines. These included the importance of the historical *extent* of decline versus the *rate* of decline; the utility of absolute numbers for defining small populations or small areas; the appropriateness of generation times as time frames for examining declines; and the overall utility of numeric thresholds or guidelines.

A. Decline

A decline is a reduction in some measure of, or proxy (surrogate) for, the abundance of a species; for example, numbers, biomass, or area of distribution. Decline can be considered in two fundamentally different ways: the overall long-term extent of decline or the recent average annual rate of decline. The Working Group asked the question, "which is more important, the rate of decline or the extent of decline?". It was concluded that the overall extent of decline will generally be more relevant to triggering concern about the long-term viability of a species than will the rate of decline; however, the recent rate of decline may also be important in certain situations such as in the case where a population has already experience a pronounced extent of decline and is continuing to decline. Also, it was agreed that a given



historical extent of decline and/or a given terminal rate of decline is more worrisome for a low productivity species than it is for a high productivity species.

Extent of decline

The historical *extent* of decline should be the ultimate criterion for considering a species for listing in the CITES Appendices. However, different baselines may be appropriate in different situations. Depending on the species under consideration, the baseline may relate to some point in history,¹ or to a *reasonable* or *potential* baseline given alterations to the environment that have affected current carrying capacity. Use of *reasonable* or *potential* baselines reflect, respectively, the reality that habitat changes have occurred in the past, and the possibility that such changes may be reversible. However, if the potential baseline is very small due to dramatic reductions in the carrying capacity of the habitat over time, it then becomes necessary to ask whether the current carrying capacity is adequate to ensure survival of the species. The Working Group did not have time to fully address the issue of shifting baselines, but does consider this issue to be important and relevant (to what extent should or can changes in the baseline due to "development" or other factors be accepted, and expectations adjusted accordingly?).

Within reasonable limits, it is not necessary to have a time frame for the extent of decline.² However, the threshold extent of decline should be a function of the productivity of the species.³ For a very high productivity species (e.g. one with high fecundity and a rapid turnover of generations), consideration for listing in CITES Appendices might not be triggered until the species has declined to relatively low levels, while for a very low productivity species (e.g. one with low fecundity and a long period between generations), consideration for listing in CITES Appendices might be triggered at much higher levels of relative population size. The decline need not necessarily be continuing.

Rate of decline

The *rate* of decline may also be important in several respects: for example, when a population has already experienced a large extent of decline; as a surrogate for the extent of decline; or as a general indicator of the urgency of the need for remedial action. In addition, an unplanned rapid rate of decline might be indicative of a rapid change in environment, or a disease attack, or competition with an invasive species. The rate of decline is only relevant if a decline is still occurring (i.e. the population has exhibited a declining trend over the last several years) or has the potential to resume. A given recent (5-10 year) rate of decline is more problematic for species with higher historical extents of decline and for species with lower productivity. Thus, the (recent) rate of decline generally needs to be combined with the (historical) extent of decline and species productivity³. A potentially-useful method for combining these three factors where species productivity is indexed only by generation time is depicted graphically in

¹Some experts argue that historical baselines are often impossible to estimate, yet when trying to determine whether a population is "small", the question becomes "small relative to what", and the mental gymnastics most experts would perform would involve comparing current population size or area of distribution to some estimate of, or informed guess about, historical size. Note that historical size can also be inferred.

²If the current population size is only a small fraction of its historical size, it should not matter whether this change took place over 3 generations or 30 generations. However, if the change took place over geological time, or over thousands of generations, the species may have evolved adaptations to enhance survival at smaller population sizes.

³Productivity is a complex function of fecundity, growth rates, age of maturity, generation time, and other relevant factors, commonly subsumed in a single parameter, r , the intrinsic rate of natural increase. Species with high productivity are said to be r -selected, whereas species with low productivity are said to be K -selected, where K is the symbol for environmental carrying capacity. Most species will fall between the extremes of the r - K spectrum. Also see Appendix I of this document.

Appendix II of this document. Use of this graph would imply that the threshold rate of decline for a species with a mean generation time of three years would be an average recent rate of decline of about 9.1% per annum if it had previously been reduced to about 50% of its baseline level, or about 1.8% per annum if reduced to 10% of its baseline level. The corresponding thresholds for a species with a mean generation time of 10 years would be about 4.3% per annum if the population had previously been reduced to 50% of its baseline level and about 0.9% per annum if reduced to 10% of its baseline level.

Recommendations: The historical extent of decline should be the ultimate criterion for triggering concern about the long-term viability of a species. The timeframe for estimating or inferring the decline should be as long as possible. Recent (5-10 year average) rates of decline should also be considered in combination with historical extents of decline.

B. Absolute Numbers, Biomass or Area

The Working Group considered and discussed at length the absolute numbers suggested as guidelines (not thresholds) in Annex 5; viz, 5,000 individuals for a population and 500 individuals for a subpopulation; and an area of distribution of 10,000 km² for a population or 500 km² for a subpopulation. The Working Group found it much easier to come up with examples for which the numbers would be either far too high, or far too low, or simply not meaningful (an example of the latter is an area of distribution for a highly migratory species) than it was to think of examples where the numbers might be reasonable. For example, the number of 5,000 individuals was believed to be far too low for most commercially exploited finfish and invertebrates, and too high for large whales. Comparisons of large whales and small invertebrates (e.g. shrimp) suggested that, in fact, biomass may be a better metric than numbers, because it integrates body size. However, even at a taxonomic group as low as species, it does not make sense to apply the same numbers across all populations within the species. Consider, for example, Atlantic cod (*Gadus morhua*). There are numerous separate stocks of Atlantic cod throughout the North Atlantic, with more than 25 stocks being of commercial importance. The range in maximum observed recent biomass levels is at least 2,000 to 1.6 million metric tons, and the degree of resilience of the stocks also appears to differ substantially between geographic areas. It was agreed that there were so many exceptions to the validity of these numbers that they were not useful, even as "a guideline, not a threshold". Meaningful numbers may be able to be developed on a taxon-by-taxon basis for numbers of individuals (or related metrics such as biomass or percent cover) but not necessarily for area of distribution.

Recommendation: The Working Group recommends that the relative (e.g. percentage) historical extent of decline and the recent rate of decline should be preferred over absolute numbers as triggers for considering species for listing in CITES criteria. If absolute numbers of individuals or areas of distribution are to be used at all, they should be developed on a taxon-by-taxon basis.

C. Generation Times⁴

There are two related ways in which generation times appear to have been interpreted and used in the CITES criteria and guidelines. First, generations times are explicitly used in the guidelines as the basis for time frames over which to consider rates of change in population sizes. Second, generation times are implicitly assumed to be inversely related to productivity and/or resilience (i.e. positively correlated with relative vulnerability). Long mean generation time is often considered to be correlated

⁴ There are several ways of measuring mean generation time. Here we assume the Annex 5 definition of generation time; viz. "Generation is measured as the average age of parents in the population; except in the case of species that breed only once a lifetime, this will always be longer than the age at maturity." However, we note that this measure can vary considerably depending on the extent of exploitation of a population. It is suggested that generation time be measured or inferred as the average age of parents that would exist in an unexploited population.

with relatively low productivity. However, the correlation is more likely to apply within taxonomic groups and may not hold when making comparisons across taxonomic groupings, due to the large diversity of combinations of life history characteristics.

The Working Group agreed that mean generation times are appropriate as ingredients of population rebuilding or recovery plans (in that long-lived species can generally be expected to rebuild at a slower rate than short-lived, high productivity species), but could not agree on their applicability as time frames for decline criteria. If all else is equal⁵, a given average annual rate of exploitation will result in more rapid depletion of a low productivity species than a high productivity species. The reason is that the high productivity species will generally replenish itself faster. For the same reason, a large⁶ decline from one year to the next would be more worrisome for a low productivity species than for a high productivity species. Thus, for any specific rate of decline, one should become concerned sooner and act more quickly, the lower the productivity of the population. Based on these examples, and contrary to common usage, the time frame for decline criteria should actually be inversely related to mean generation time, as it is in the examples given in Appendix II of this document.

An alternative viewpoint is that use of generation times as time horizons forces one to look further back in time for long-lived species, which may have exhibited a protracted, gradual decline, or may have been relatively stable for the past 10-20 years but experienced a substantial decline 2-3 generations ago. The basic premise is that it is not sufficient to look back (or forward) only 10-20 years for long-lived species. The flip side of this premise is that it must therefore be reasonable to look back (or forward) only 10 years or so for short-lived species. However, there are equally valid reasons for looking far back into history for highly-productive, short generation species, which often exhibit pronounced fluctuations over time (e.g. Pacific sardine and anchovy). In fact, it may be difficult to interpret the current situation outside of the context of the magnitude and frequency of historical fluctuations. Appendix III of this document describes two hypothetical examples that illustrate this point. In the first, a highly-productive, short generation species has recently declined substantially but the most recent peak in population size was unusually high compared to the rest of the 100-year recorded history of the stock, and the stock is currently well above historical average levels. In the second, there has been a relatively slow decline over the past two or three generations, but the most recent population peak was well below the historical average, and the stock is currently lower than the lowest stock size recorded over the previous 100 years.

Discussion of the utility of generation times also evoked discussion of the "minimum sufficient data" or the "minimum sufficient time horizon" for estimating or inferring a decline. It was quickly concluded that it would be dangerous to attempt to define "minimum sufficient" and that the best approach would be to equate "minimum sufficient data" with "all available data" and encourage analysts to always take a historical perspective, to the extent possible.

One way of simultaneously satisfying both sides of the debate about the utility of generation times is to express the rate of decline as an average annual rate and develop guidelines that embody the points of consensus that (a) a given average annual rate of decline should be more worrisome for a species that has already experienced a large extent of decline, (b) a given average annual rate of decline should be more worrisome for a low productivity species than for a high productivity species, and (c) recent rates of decline can be extrapolated forward in time to infer likely future reductions in population size, rather than waiting to see if they actually happen. It should also be noted that, although it may be reasonable to index

⁵ "If all else is equal" means, for example, that the starting population biomass and exploitation rates are identical in the two cases.

⁶ e.g. 20%.

productivity by some function of the inverse of generation time, it may be preferable to use other metrics which relate more directly to productivity, even though these may require more data to calculate; for example, the intrinsic rate of natural increase³

Recommendations: Although threshold rates of decline of the form "x% in y years or z generations, whichever is longer" are currently a key feature of both the CITES and IUCN guidelines, the Working Group believes that alternative constructs may be more valid and more widely applicable. In particular, for the historical extent of decline, the time frame to consider should extend as far back into history as possible regardless of the mean generation time of the species in question. For the recent rate of decline, a literal interpretation of the above construct could be taken to imply that one should wait for y years or z generations, or at least until the x% cumulative decline has accrued, before taking action. Adoption of the concept that a given average annual rate of decline is likely to be more problematic for a species with low productivity (which may be associated with long generation time), may trigger concern for a species sooner. It is suggested that the time period over which to consider recent average annual rates of decline should be purposely left vague; for example, by expressing it as an approximate range of 5-10 years. In this formulation, generation time is not used explicitly to set a time frame, but rather is used implicitly to set threshold average annual rates of decline that are related to species productivity (the latter is true only if it can be assumed that productivity is some inverse function of generation time). Use of generation times in this manner may be preferable because it is essential that lack of a long time series of data not preclude a species for consideration. The "minimum sufficient data" is whatever usable quantitative, qualitative, or inferential data are available.

D. The Utility of Numeric Guidelines

Despite the difficulty of developing numeric guidelines that are broadly applicable across a wide diversity of taxonomic groups and life history strategies, the Working Group felt there was merit in continuing the attempt to develop generic thresholds (based on percentage declines in relevant metrics, not absolute numbers of individuals or absolute areas) that would trigger concern about the long-term viability of a species. Based on experience in fisheries, the development of numeric reference points has been instrumental in reversing overexploitation in many fisheries, even though specification and estimation of such reference points often stretches the limits of available data and methodologies. The guidelines and thresholds suggested in the next section appear to work reasonably well for commercially exploited marine species, although further work is needed to determine their applicability to terrestrial taxa. It may well be that somewhat different numeric guidelines are needed for certain other taxonomic groups. Regardless of the specificity of any numeric guidelines developed, there is no escaping the need for informed and reasoned judgement as the ultimate criterion for considering a species for listing in the CITES Appendices.

Recommendation: Development of generic thresholds based on percentage declines in relevant metrics should continue, recognizing that it may be necessary to have different numbers for different taxonomic groups.

4. Proposal for Revised CITES Guidelines

Determination of CITES classifications must be based on the status of populations and their associated habitat. The pertinent conditions may vary across both taxa and habitat. The Working Group attempted to develop generic conceptual biological criteria, and possibly generic numeric guidelines, that

would trigger concern about the long-term viability of a species. It was concluded that quantitative, qualitative and inferential aspects of population status suitable for making CITES decisions that should apply to all taxa are (A) the historical extent of decline or a population or subpopulation, and (B) the recent rate of decline of that population or subpopulation. These are insufficient in themselves, however, and must be considered in the light of several (C) relevant modifying factors specific to individual situations. The historical extent of decline, the recent rate of decline, and the relevant modifying factors all need to be considered in conjunction with one another, not as a hierarchy. Of course, the Working Group recognized that the biological and other factors that "trigger concern about the long-term viability of a species" are only one of the considerations that will influence whether or not a species is or should be proposed for a CITES listing (other important considerations include the effects of international trade or trade demand).

A. Historical Extent of Decline

The extent of decline in populations should be considered relative to some appropriate baseline. However, different baselines may be appropriate in different situations. Depending on the species under consideration, the baseline may relate to some point in history¹, or to a *reasonable* or *potential* baseline given alterations to the environment that have affected current carrying capacity. Use of *reasonable* or *potential* baselines reflect, respectively, the reality that habitat changes have occurred in the past, and the possibility that such changes may be reversible. However, if the potential baseline is very small due to dramatic reductions in the carrying capacity of the habitat over time, it then becomes necessary to ask whether the current carrying capacity is adequate to ensure survival of the species. Within reasonable limits, it is not necessary to have a time frame for the extent of decline; i.e. the entire known or inferred history of the species should be considered.²

Populations can be measured in many different ways, and appropriate units of measurement vary across taxa. For example, for some taxa, it may not make sense to refer to numbers of individuals (e.g. clonal organisms). The Working Group identified the following metrics as potentially relevant for measuring or indexing the extent of decline.

- numbers (of individual organisms in a population or subpopulation)
- biomass (total weight of a population or subpopulation)
- area inhabited
- migratory range (for highly migratory species)
- coverage (for sessile organisms)
- relative spawning per recruit (see Appendix I)
- numbers or biomass of new recruits (recruitment)

It may be appropriate to use more than one of these metrics for a given taxonomic group, but it is certainly true that not all of these metrics are valid or useful for all taxonomic groups.

Larger historical declines in one or more of the above metrics would suggest greater risk of extinction, and hence would trigger greater concern for consideration for a CITES listing. It is also likely that a given extent of decline may be considered more worrisome for a low productivity species than it is for a high productivity species, due to the likelihood that a high productivity species is probably able to rebound faster (see Appendix I of this document for a discussion of the relationship between risk of extinction, resilience and productivity). Therefore, the threshold extent of decline should be a function of the productivity of the species. The decline need not necessarily be continuing.

For a very high productivity species (e.g. one with high fecundity and a rapid turnover of generations), consideration for listing in CITES Appendices might not be triggered until the species has declined to relatively low levels; for example, about 5% of the baseline. For a very low productivity species (e.g. one with low fecundity and a long period between generations), consideration for listing in CITES Appendices might be triggered at much higher levels of relative population size; for example, a decline to about 30% of the baseline level. If productivity is indexed by generation time alone, then for exploited marine species the extreme of 5% of the baseline might be roughly applicable for species with mean generation times of 3-5 years or less (e.g. some squids and small pelagic fishes), while the extreme of 30% of the baseline might be applicable for species with mean generation times of 30 years or more (e.g. some sharks and deepwater species). For species between these two extremes, the threshold percentage decline should be interpolated. Here and in Appendix II of this document, generation time is used as a proxy for productivity because compared to most demographic variables it is relatively easy to estimate or infer. However, there are other metrics that may be superior indices of productivity; for example, intrinsic rates of natural increase calculated from life tables or surplus production models.

Support from the peer-reviewed fisheries scientific literature for the applicability of the 5-30% range and the role of productivity is summarized in Appendix I of this document. Most of the studies included in this review were based on consideration of either population biomass or spawning biomass per recruit. However, the Working Group felt that the same or similar decline criteria could be applied for each of the metrics in the bulletized list above. Preliminary evaluations conducted by the Working Group suggested that the 5-30% range, with high productivity species being nearer the 5% end, low productivity species being nearer the upper end, and average productivity species being somewhere in the middle, worked reasonably well for exploited marine species. Other ranges may be more appropriate for other taxonomic groups. For example, in a taxonomic group in which all species can be considered low productivity or "K-selected", a narrower range excluding the lower end of the spectrum may be more appropriate

B. Recent Rate of Decline

The *rate* of decline may also be important in several respects: for example, when a population has already experienced a large extent of decline; as a surrogate for the extent of decline; or as a general indicator of the urgency of the need for remedial action. In addition, an unplanned rapid rate of decline might be indicative of a rapid change in environment, or a disease attack, or competition with an invasive species. The rate of decline is only relevant if a decline is still occurring (i.e. the population has exhibited a declining trend over the last several years) or has the potential to resume. A given recent (5-10 year) rate of decline should be considered more problematic for species with higher historical extents of decline and for species with lower productivity. Thus, the (recent) rate of decline generally needs to be combined with the (historical) extent of decline and species productivity.

One straightforward, simple and coherent way of defining threshold average annual rates of decline that take account of the historical extent of decline and species productivity is to calculate the cumulative annual rate that would drive a population down from its current level to the threshold extent of decline within 10 years. The following text table summarizes the calculations for cumulative 10-year rates of decline (and corresponding average annual rates of decline). Values of % baseline greater than 50% should rarely cause concern for marine species, except perhaps in the case of small or endemic populations (see Section C), unless recent average annual rates of decline have been extremely high.

Current population as % unexploited	Productivity		
	low	medium	high
100%	70% (11.3%)	80% (14.9%)	95% (25.9%)
90%	67% (10.4%)	78% (14.0%)	94% (25.1%)
80%	63% (9.3%)	75% (12.9%)	94% (24.2%)
70%	57% (8.1%)	71% (11.8%)	93% (23.2%)
60%	50% (6.7%)	67% (10.4%)	92% (22.0%)
50%	40% (5.0%)	60% (8.8%)	90% (20.6%)
40%	25% (2.8%)	50% (6.7%)	88% (18.8%)
30%	0%	33% (4.0%)	83% (16.4%)
20%	0%	0%	75% (12.9%)
15%	0%	0%	67% (10.4%)
10%	0%	0%	50% (6.7%)
5%	0%	0%	0%

Values of threshold average annual rates of decline are set to zero once the population is at or below the extent of decline threshold because once a population has fallen to such critical levels, a decline need not necessarily still be occurring. In the table, low productivity is equated with an extent of decline threshold of 30% of the baseline, medium productivity with a threshold of 20% of the baseline, and high productivity with a threshold of 5% of the baseline. For example, the cumulative 10-year rate annual rate of decline that would reduce a high productivity population from 50% of its baseline to the threshold extent of decline of 5% is 90%, and the corresponding average annual rate of decline is 20.6% per year. The corresponding annual rate for a low productivity population would be only 5.0% per year. Note that the annual rates must be cumulated over time⁷ and therefore they cannot simply be multiplied by a number of years to calculate the total decline over those years.

An alternative but related method for combining historical extent of decline, recent rate of decline and productivity (as indexed by an inverse function of generation time) is presented in Appendix II of this document.

⁷ The formula for cumulating annual rates over time is $F = (1-AR)^t$, where F is the fraction of the starting number remaining after t years, and AR is the annual rate of decline expressed as a proportion. This is equivalent to taking a starting number, multiplying it by the annual rate of decline, subtracting to determine the number remaining, then multiplying this number by the annual rate of decline, subtracting from the previous number, and continuing the process for the desired number of years. The number remaining after the desired number of years divided by the starting number is the fraction remaining (F). Subtracting F from 1 and multiplying the result by 100% gives the total percentage decline.

The significance of both the extent and rate of decline should be evaluated using whatever data are available over as long a time period as possible. While longer time series are better, there is no basis for establishing either maximum or minimum lengths of time series. Further, while quantitative levels of population condition are preferable, qualitative information can be used where necessary, and even bounds on the degree of change inferred from such data can be useful. This is particularly relevant for species for which good quantitative data do not exist for periods prior to exploitation. Use of all available data including qualitative data and inference facilitates determination of appropriate reference levels to use as a baseline, as well as determination of expected rates of change of the population (as illustrated in Appendix III of this document). In addition, examining as long a time series as possible may allow identification of causes of change; for example, changes in habitat availability or in other sources of mortality. In the case of changes not directly related to harvest, examination of such data may help identify changes in the habitat or the population that, while possibly irreversible, may have increased the risk of extinction.

C. Relevant Modifying Factors

The extent and rate of decline of populations must be considered in light of vulnerability factors that may be specific to one or a few taxonomic groups. Vulnerability can be defined as the susceptibility of a species to over-exploitation or, conversely, the inverse of the capacity of a species to recover from overexploitation (i.e., the inverse of resilience). Vulnerability must be taken into account when evaluating a species against the CITES criteria. In general, low productivity species are more vulnerable or susceptible to exploitation than are high productivity species. Low productivity species (often referred to as "K-selected" species) are those that have one or a combination of long generation times, slow growth rates, or low fecundity; high productivity species (often referred to as "r-selected" species) have the reverse characteristics.³ K-selected species generally have lower resilience to exploitation because they have less potential to rebound as quickly.

There are also several additional risk factors that cannot easily be incorporated into a generic risk evaluation because they are applicable only to particular taxonomic groups, certain life history strategies, or in specific instances. Such factors include population density (especially for sessile or semi-sessile species that rely on air, water, or other vectors to disperse and mix spawning products), migration, degree of endemism, habitat specificity, dietary specificity, and symbiotic relationships. These and other factors may increase (or decrease) the risks to the species, and may therefore necessitate appropriate modification to any thresholds suggested in these guidelines. For example, for a factor that increases vulnerability, the historical extent of decline and/or the recent rate of decline that would qualify a species for inclusion in the Appendices could be lower than it would in the absence of these factors. An alternative way of viewing vulnerability factors is that they increase the risk for a specific extent or rate of decline. For this reason, these additional risk factors are classified as modifiers of the decline criteria. The wide range of potential taxon-associated vulnerability factors supports the contention that there is no escaping the need to consider each species on a case-by-case basis.

A non-exhaustive list of vulnerability factors (that would increase concern) and mitigating factors (that would decrease concern) that may be relevant to particular taxonomic groups is presented below. Those marked with an arrowhead are defined or discussed further in Appendix IV of this document.

A. Vulnerability factors that would increase concern

- Low absolute numbers or biomass
- Selectivity of removals
- Age, size or stage structure of a population
- Social structure, including sex ratio
- Density
- Specialized niche requirements (e.g. diet and habitat)
- Species associations such as symbiosis
- Secondary ecosystem-based effects
- Uncertainty
 - Fragmentation
 - Reduced genetic diversity
 - Severe habitat loss
 - Degree of endemism
 - Existence of disease
 - Existence of invasive species
 - Existence of rapid environmental change
(e.g. climate regime shifts)

B. Mitigating factors that would decrease concern

- High absolute numbers or biomass
- Existence of natural refugia
- Adaptations to small population size
- Selectivity of removals



RECRUITMENT FAILURE, LIFE HISTORIES, AND LONG-TERM DECLINE OF CARIBBEAN CORALS

TERENCE P. HUGHES¹ AND JASON E. TANNER²

Department of Marine Biology, James Cook University, Townsville, QLD 4811, Australia

Abstract. Population decline, local extinction, and recovery are profoundly influenced by variation in demography and life-history traits. In open populations, changes in patterns of recruitment may also have a major influence on the size of local populations, particularly for short-lived organisms. We examine here the demographic processes underlying a slow decline of corals on Jamaican reefs, where coral cover has decreased by fourfold over a 16-yr period. We divided the study into three approximately equal intervals (1977–1982, 1982–1987, and 1987–1993) and constructed size-based transition matrices for each of three abundant species of corals (*Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata*) that differ substantially in life history: *Montastrea* is slower-growing, longer-lived, and has lower rates of recruitment than the other two species. Rates of survival, population growth (λ), and recruitment declined substantially over time for all species and the stable size structures became increasingly dominated by small colonies. Elasticity and life table response analysis showed that changes in the persistence of large colonies had the biggest impact on population growth in all species. Simulations indicated that the levels of larval recruitment required to maintain populations at 1977 levels increased sharply over time, even as the actual recruitment rate declined. Recruitment failure was much more important to *A. agaricites* and *L. cucullata* than to *M. annularis*, which could survive long periods with minimal larval input. Recovery of these populations will require an increase in both survival and recruitment. The likelihood of the latter will depend on the scale of larval dispersal, and on the impact of large-scale mortality of adults on stock-recruitment relationships. Differences in connectivity and life histories of corals will determine future patterns of recovery or further decline.

Key words: *Agaricia agaricites*; coral reefs; demography; *Leptoseris cucullata*; life histories; matrix models; *Montastrea annularis*; population dynamics; recruitment; sensitivity analysis.

INTRODUCTION

The open nature of marine systems poses a unique set of issues for understanding the dynamics of populations and communities. Even undisturbed populations of site-attached adults such as barnacles, corals, and demersal fishes will go extinct within a generation if their offspring are widely dispersed and recruitment from elsewhere fails. Conversely, localized extinctions caused by acute events (such as hurricanes, ice scour, or an oil spill) are often quickly reversed by recruitment of propagules from upstream sources (e.g., Jackson et al. 1989, Aberg 1992, Connell et al. 1997). The degree of connectivity between local populations varies among marine species, depending on patterns of larval dispersal and recruitment. In some species the larval phase is truncated and local populations are largely self seeded. More typically, larvae are widely dispersed among local populations which collectively comprise a metapopulation (e.g., Gaines and Lafferty 1995, Roughgarden et al. 1985, Caley et al. 1996). Recruitment

failure has a greater impact on short-lived species that are composed of one or a few cohorts. In contrast, longer-lived taxa are buffered against fluctuations in recruitment (the storage effect, sensu Warner and Chesson 1985).

Clearly, the effects on marine species of elevated rates of mortality (e.g., due to natural disturbances or overexploitation) also depend on their life histories and patterns of recruitment (e.g., Munro 1983, Hughes 1984, 1990, Aberg 1992, Gaines and Lafferty 1995, Jackson 1997). The best evidence comes from the applied fisheries literature (see review by Jennings and Kaiser 1998): The abundance of short-lived species with early maturation times and high fecundities typically fluctuates greatly, especially in response to variation in recruitment. Such species can generally be harvested at relatively high intensities and are quick to recover from population crashes, so long as pulses of recruitment continue to maintain the stock size (e.g., Adams 1980). In contrast, slow-growing, long-lived species can only be fished at low intensities and take much longer to recover from over-exploitation, even though the storage effect tends to make them less sensitive to fluctuations in recruitment (e.g., Brander 1981, Jennings and Kaiser 1998). Depending on their life histories, different species vary in their response to the

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¹ E-mail: terry.hughes@jcu.edu.au

² Present Address: SARDI Aquatic Sciences, P.O. Box 120, Henley Beach, SA 5022, Australia.

enhancement of mortality caused by fishing. Consequently, multispecies fisheries often cause a predictable change in taxonomic composition (favoring short-lived species) even where there is relatively little targeting of individual species (e.g., Munro 1983, Russ and Alcala 1998). In turn, natural selection due to sustained harvesting of fishes can also result in evolutionary responses in life histories, such as a reduction in the size at maturation and an increase in fecundity early in life (e.g., Reznick 1993).

In this paper, we examine a sustained, long-term population decline in three species of reef-building corals that vary substantially in life histories and rates of recruitment. Our overall goal is to reveal the demographic processes (e.g., recruitment, growth, mortality) which alter population sizes in open marine systems. We first document long-term changes in abundance of corals over a 16-yr period. Secondly, we describe temporal trends in the demography and recruitment of three targeted species to understand why their abundance has declined. Thirdly, we use matrix modeling to examine further the components of population decline (increasing rates of mortality and shrinkage of colonies, combined with decreasing rates of growth and recruitment), and to quantify their relative importance. We begin this last section by quantifying differences among species and changes over time in terms of size-specific transition probabilities. Then we explore the properties of the transition matrices analytically to compare rates of population growth and stable-size distributions, and to examine the relative importance of different transitions (using elasticities and a life table response analysis). Finally, we use the matrices in simulation studies to examine the effects of declining recruitment. The advantage of this modeling approach is that it integrates numerous impacts on different transitions at different stages of the life cycle, providing a population-level response to environmental change (see, e.g., Harvell et al. 1990, Levin and Huggert 1990, Caswell 1996).

NATURAL HISTORY

We studied three abundant Caribbean corals that differ substantially in life history: *Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata*. Different morphs of *M. annularis* probably represent separate species (Knowlton et al. 1992, 1997, Weil and Knowlton 1994, Lopez et al. 1999; but see also Dustan 1975, Fitt et al. 1993, Van Veghel and Bak 1993, Szmant et al. 1997). In deep water, where this study was conducted, *M. annularis* occurs only as thick plates (of uncertain taxonomic status; Weil and Knowlton [1994] state that "the identity of deep water (>30 m) specimens requires further study"), while *A. agaricites* and *L. cucullata* form more delicate, foliaceous colonies. The more robust *Montastrea* is slower growing, a better competitor, and longer lived compared to the other two species (e.g., Lang 1973, Bak and Engel 1979, Bak and Luckhurst 1980, Hughes and Jackson 1985), and is the

main frame builder of many Caribbean coral reefs (e.g., Land and Goreau 1970). *Agaricia* and *L. cucullata* are both brooders, releasing well-developed planulae, while *M. annularis* is a broadcast spawner (Van Moorsel 1983, Szmant 1986, Van Veghel 1994, Knowlton et al. 1997). Rates of recruitment by *M. annularis* are typically much lower than the other two species (e.g., Bak and Engel 1979, Rylaarsdam 1983, Rogers et al. 1984, Hughes and Jackson 1985), although the possibility of rare "mast" years cannot be discounted. Like most clonal organisms, these corals exhibit variable rates of growth, frequently shrinking in size and undergoing asexual fission. A size-based matrix model can readily accommodate these demographic features (e.g., Hughes 1984, Gotelli 1991, Lasker 1991).

Our study was conducted in Jamaica, where the abundance of corals has declined markedly during the last two decades. Megafauna (e.g., turtles, dugongs, and crocodiles) were drastically reduced centuries ago (Jackson 1997), and reef fishes were already severely depleted on the most populated parts of the coastline when the first quantitative fisheries surveys were conducted in the 1960s (Munro 1983). Nonetheless, an extensive literature from the 1950s to late 1970s describes an abundant and diverse coral assemblage (e.g., Goreau 1959, Woodley et al. 1981), which has declined only relatively recently. Two major hurricanes, Allen in 1980 and Gilbert in 1988, caused extensive damage to corals, especially in shallow water (<20 m; see, e.g., Woodley et al. 1981). Corallivorous predators survived the hurricanes better than their prey, hindering the recovery of corals (Knowlton et al. 1981, 1990). In 1983, the most abundant invertebrate macroherbivore, the echinoid *Diadema antillarum*, suffered mass mortalities from disease, which in combination with long-term overfishing of herbivorous fishes, prompted unprecedented and highly persistent blooms of benthic macroalgae (e.g., Hughes et al. 1987, Liddell and Ohlhorst 1992; review by Lessios 1988). Episodes of coral bleaching and localized pollution are also likely to have caused damage (review by Goreau 1992). Hughes (1994) documented a gradual shift in Jamaican benthic community structure since the 1970s, from a coral- to an algal-dominated system. For example, between 1977 and 1993 coral cover at 10 m depth declined from a mean of 52% to only 3% at nine sites located along >250 km of coastline (Hughes 1994). Conversely, cover by fleshy macroalgae at these sites increased from a mean of 4% to 92% (see also Knowlton et al. 1990, Liddell and Ohlhorst 1992, Steneck 1993, Hughes and Connell 2000). Similar long-term and large-scale changes have occurred to a lesser extent on coral reefs in other parts of the Caribbean region (e.g., in Florida [Dustan 1977, Porter and Meier 1992]; the Virgin Islands [Carpenter 1990, Steneck 1993]; the Dutch Antilles [de Ruyter van Steveninck and Bak 1986, Bak and Nieuwland 1995]; the Lesser Antilles [Rogers 1985]; and Panama [Schulman and Robertson 1996]).

In the present study, we recorded long-term demographic changes (in recruitment, mortality, and transition rates between different size classes) for three abundant coral species from 1977 to 1993. The study originally spanned a range of sites and depths (see Hughes and Jackson 1985, Hughes et al. 1987). By 1985 (the midpoint of the study period), corals at all but the deepest site had declined by 73–92%, reflecting the large-scale decline in abundances in shallow water along the north Jamaican coast. Consequently, we focus here on the long-term dynamics of corals in deep water (35 m), where hurricane effects were relatively minor (e.g., Woodley et al. 1981, Hughes 1996) and where algal blooms have been less pronounced compared to shallower sites (Hughes et al. 1987, Liddell and Ohlhorst 1992). Deeper reefs potentially provide a spatial refuge for coral species with wide depth distributions (e.g., *L. cucullata*, Goreau and Wells 1967), and could serve as a source of larvae for seeding recovery in shallower water, where coral cover has fallen much more sharply.

METHODS

The abundance of all corals and the population dynamics (rates of recruitment, asexual fission, growth, and mortality) of the three targeted species were quantified by following the fate of large numbers of colonies for 16 yr, from 1977 to 1993. The colonies were located within twelve 1-m² quadrats that were positioned haphazardly at 35 m depth on Pinnacle 1 Reef, near the Discovery Bay Marine Laboratory on the north coast of Jamaica. Each 0.25 m² ($n = 48$) was photographed 14 times (approximately annually), and every colony was traced, numbered, and digitized to obtain its area at each census (see Hughes and Jackson 1985 for further details). Three categories of colonies were distinguished throughout the study: those that were initially present in 1977, new daughter colonies formed by fission of these older colonies, and new larval recruits. Fission occurred when patches of tissue on larger colonies became separated by partial mortality (although the skeleton always remained intact). Recruits were visible once they reached ~1 cm in diameter. The total number of records (the number of colonies summed over each census) for each species was: *Montastrea annularis*, 1217; *Agaricia agaricites*, 1596; and *Leptoseris cucullata*, 860.

Modeling

To examine further the long-term changes in population dynamics of the corals, we constructed and analyzed size-classified matrix population models for each species. The conventional form of a matrix model is

$$\mathbf{x}(t + 1) = \mathbf{A} \cdot \mathbf{x}(t)$$

where $\mathbf{A}$ is a matrix describing the probabilities of transition between different age or size classes and $\mathbf{x}(t)$ is a vector describing the number of individuals in each

class at time t . The population growth rate is given by the dominant eigenvalue (λ) of the matrix. The speed of convergence to a stable size distribution is given by the ratio of the largest to the next largest eigenvalue: the damping ratio (ρ). To obtain the stable age- or stage-distribution the first right eigenvector ($\mathbf{w}$) is calculated, and the relative contribution of each stage to population growth (the reproductive value when the matrix has fecundities) is represented by the first left eigenvector ($\mathbf{v}$). The proportional effect on population growth of changes in the transition probabilities is known as the elasticity, and is calculated as

$$\frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{a_{ij}}{\lambda} \frac{v_i w_j}{\langle \mathbf{w}, \mathbf{v} \rangle}$$

(DeKroon et al. 1986, Caswell 1989). To model an open system, we omitted fecundities from the matrix, and instead added externally derived recruits to the local population (Sainsbury 1982, Hughes 1984, 1990, Warner and Hughes 1988, Pascual and Caswell 1991). In this case, λ is < 1 (unless asexual reproduction occurs and exceeds mortality), describing the decline of a single cohort or the depletion of a population of mixed ages (Hughes 1984, Aberg 1992).

We arbitrarily divided the study period into three roughly equal intervals of five, five, and six years duration respectively (1977–1982, 1982–1987, and 1987–1993), and constructed separate transition matrices for each species in each period. Three time intervals were chosen to reduce the complexity of comparing all 13 census intervals for each species (39 matrices). An alternative approach would have been to construct matrices that encompassed specific events, such as the 1980 and 1988 hurricanes and the algal bloom from 1983–1993. However, these events often overlapped in time, and using matrices with very different census intervals would preclude comparisons of many of the analytical results.

We used three size classes (small, medium, large), which varied among species due to their markedly different size structures: *Agaricia agaricites* and *Leptoseris cucullata* were divided into size classes of 0–10 cm², 10–50 cm², and >50 cm², while *Montastrea annularis* had larger size classes of 0–50 cm², 50–200 cm², and >200 cm². Transition probabilities were calculated as the proportion of colonies changing size class during each of the three census periods. To test for differences in the transition matrices for the three intervals, we performed a log-linear analysis for each species with the factors initial size (state), fate (final size or death), and time. We used the hierarchical model: frequency = (state $\times$ fate) + (state $\times$ time), i.e., a model which includes all terms except for interactions involving both fate and time, to determine if fate was significantly affected by time. The effect of species was not incorporated into the analysis because it was appropriate to use different size classes for each, and

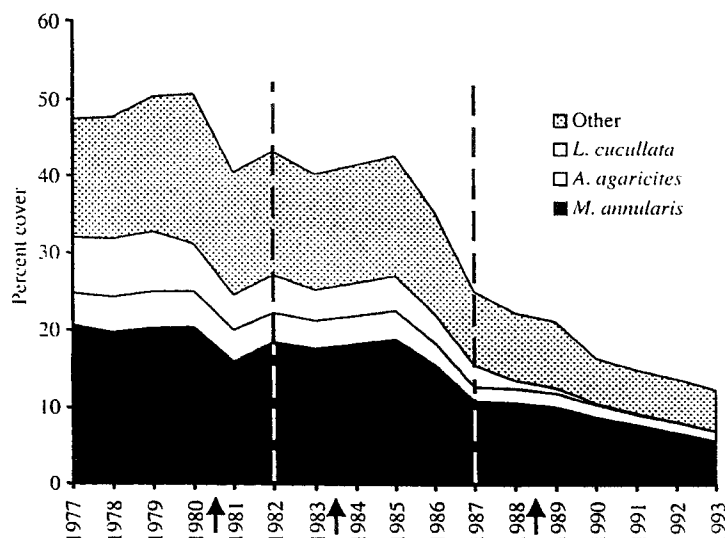


FIG. 1. Percent cover of *Montastrea annularis*, *Agaricia agaricites*, *Leptoseris cucullata*, and all other corals in twelve 1-m² plots from 1977 to 1993. The three arrows indicate hurricane Allen (in 1980), the die-off of the echinoid *Diadema antillarum* (in 1983), and hurricane Gilbert (in 1988).

interactions involving species would in part reflect the choice of size classes.

To investigate the population-level consequences of changes in demographic rates, we examined each transition matrix analytically to obtain population growth rates (λ), damping ratios (ρ), eigenvectors (w , v) and elasticity matrices (Caswell 1989). To facilitate comparisons of population growth rates and damping ratios, we constructed asymmetrical 95% confidence limits for λ and ρ by bootstrapping. To conduct the bootstrap analyses, individual colonies were randomly selected from the original data, with replacement, until the same number of colonies had been selected as the original sample size. After resampling, a transition matrix was constructed and analyzed, with the entire procedure being repeated for each of 3000 bootstrap iterations. The resulting series of values for each statistic (population growth and damping ratio) was analyzed using the Bias Corrected and Accelerated technique (BC_a), to obtain the confidence intervals (Efron and Tibshirani 1993).

The population-level effects of changes in demography over time were examined using a life table response analysis (*sensu* Caswell 1996). For each species, we calculate the contribution of each matrix element to the change in λ using the initial matrix as a baseline for comparing subsequent matrices (1977–1982 vs. 1982–1987 and 1987–1993). The contributions depend on the magnitude of the change in each matrix element over time, and on the sensitivity of λ to that element. Accordingly, we first calculated a matrix of sensitivities, S , using a matrix that was the mean of the initial and one of the subsequent transition matrices. Then, a matrix of contributions was calculated by multiplying each element of S by the observed change in each element over the same period (Caswell 1996). This analysis concentrates on the effects on population growth rate of the changes in transition rates,

as opposed to elasticities which show only the potential effects of transitions (regardless of whether or not they changed).

To examine the role of recruitment and to compare the transient population dynamics for each species and time interval, simulations were conducted according to the equation

$$x(t+1) = A \cdot x(t) + r$$

where fecundity is omitted from the transition matrix (A), and instead a recruitment vector (r) is added at each iteration. We began each simulation using the observed population composition for each species in 1977 as the starting vector $x(0)$. (This is an arbitrary choice since the population will eventually attain the same stable size distribution regardless of the initial vector.) Using each matrix, we performed two separate simulations: the first examined the depletion of an established population without any recruitment (i.e., $r = 0$), the second included recruitment at the rate observed in the field for that interval. We also calculated the amount of recruitment that would be required to maintain population sizes at the levels observed in 1977. All simulations were carried out for 100 yr (16 or 20 iterations depending on the census interval), by which time equilibrium growth rates had been reached.

RESULTS

Population decline

The percent cover of corals on Pinnacle 1 Reef declined from $47.5\% \pm 4.1\%$ (mean ± 1 SE) in 1977 to $12.6\% \pm 2.7\%$ in 1993 (Fig. 1). Cover was steady from 1977–1980, but dropped slightly in 1980–1981, when Hurricane Allen struck Jamaica (Woodley et al. 1981). From 1981 until 1985 coral cover remained just above 40%, but over the next eight years it slowly decreased by a further two-thirds. During this 8-yr period (1985–

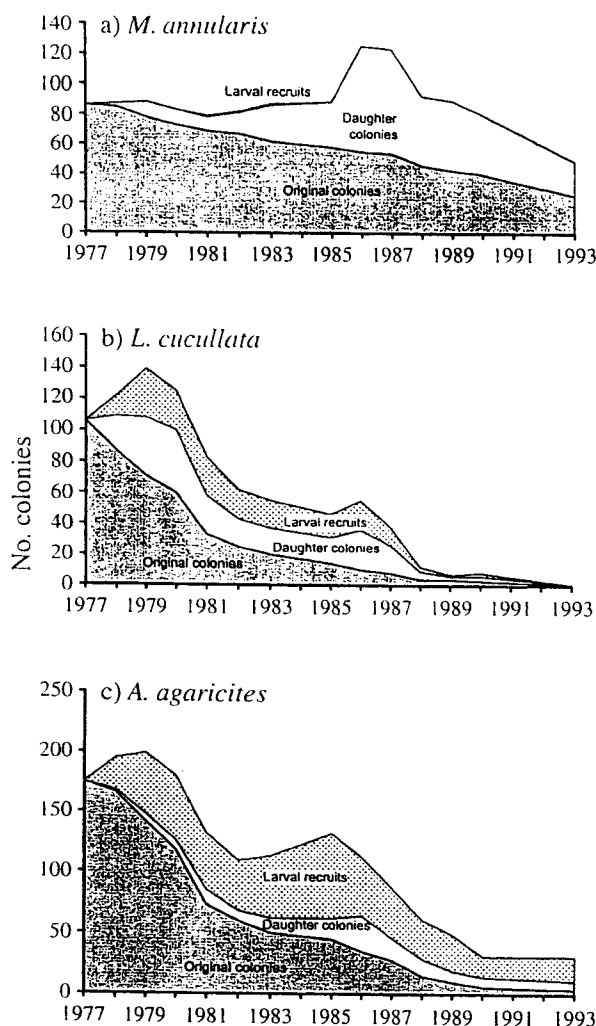


FIG. 2. Number of colonies of *Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata* over time. Colonies at each census are divided into three types: those originally present in 1977, daughter colonies formed by fission, and new larval recruits.

1993), cover by fleshy macroalgae on Pinnacle 1 increased from $26\% \pm 6\%$ to $76\% \pm 4\%$, and bare space declined to almost zero (Hughes 1996). The number of coral species within the 12 m^2 declined, from 17 in 1977 to 11 in 1993. At the outset of the study, *Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata* accounted for 67.5% of the total scleractinian cover, occupying 32.1% of the substrate. By 1993, the cover of the three species had declined by almost four-fifths, to 7.1% (Fig. 1), or 56% of the total cover by corals.

The number of colonies also exhibited a long-term decline (Fig. 2). In 1977, *Montastrea annularis* was represented by 86 colonies, *Agaricia agaricites* by 175, and *Leptoseris cucullata* by 106. By 1993, only 40 colonies of *M. annularis*, 17 of *A. agaricites*, and a single colony of *L. cucullata* were present. The first substantial decline in numbers occurred in 1980–1981,

when Hurricane Allen occurred. The number of colonies of the more robust *M. annularis* did not change, but the relatively delicate *A. agaricites* and *L. cucullata* declined in number by 27% and 34%, respectively. Over the next 12 years these latter two species continued to decline, dropping to 18% and 1% of their 1977 abundance by 1993. The number of colonies of *M. annularis* varied little up to 1985, but then increased by 40–42% during 1986 and 1987 (due to fission), before declining steadily up to 1993, to 57% of the original number in 1977 (Fig. 2). Note that the increase in the number of colonies of *M. annularis* in 1986–1987 occurred despite a decline in cover (Figs. 1 and 2).

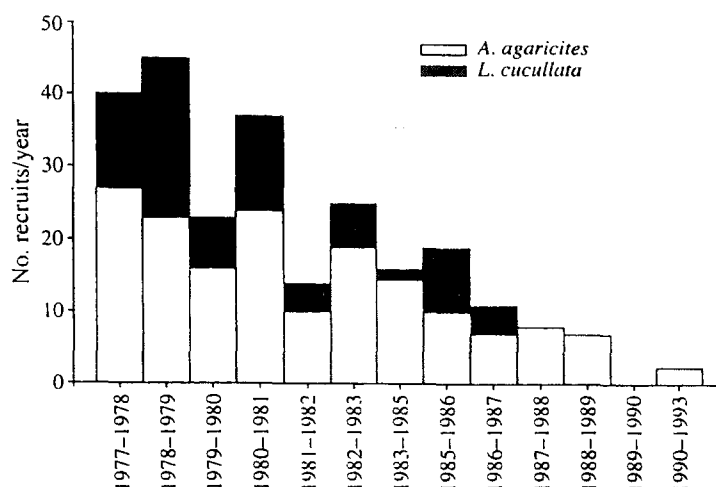
The three species differed greatly in their rates of mortality and turnover (Fig. 2). Survival of colonies that were already established in 1977 was markedly higher in *Montastrea annularis*; 30% remained alive after 16 yr compared to only 2% of *Agaricia agaricites* and 1% of *Leptoseris cucullata*. As these older colonies declined in number, new colonies were added by asexual fission and larval recruitment. The rate of fission was high for *M. annularis*, intermediate for *L. cucullata*, and low for *A. agaricites* (Fig. 2). Conversely, larval recruitment was by far the lowest for *M. annularis*, and was greatest for *A. agaricites* (Figs. 2 and 3). Until 1985, the majority of colonies of *M. annularis* were the original ones present in 1977. However, a marked increase in the rate of fission of *M. annularis* occurred in 1986–1987, so that from this date onwards, new daughter colonies and older individuals were almost equally abundant. Turnover was higher in the other two species. New colonies outnumbered the original ones from 1983 in *A. agaricites* and from 1981 in *L. cucullata*. For *A. agaricites*, most of the new colonies were larval recruits, while recruits and daughter colonies of *L. cucullata* were approximately equally abundant throughout the study (Fig. 2).

The rate of larval recruitment declined over time (Fig. 3). A total of 294 recruits were recorded at the 14 censuses; 160 in 1977–1982, 101 in 1982–1987, and only 33 in 1987–1993 (Fig. 3). Moreover, only about one-third of these recruits remained alive at the end of each census interval: (55, 35, and 8, respectively). Sixty-nine percent of the recruits were *Agaricia agaricites* and 30% were *Leptoseris cucullata*, while only a single recruit was recorded in 16 years for *Montastrea annularis*, in 1981.

Transition matrices

The population matrices are characterized by high rates of transition between most size classes, reflecting a plastic life cycle which includes variable growth rates, stasis (i.e., staying the same size), fission and colony shrinkage (i.e., transitions from large or medium to small size classes). Transitions were strongly size dependent for all species and times (Table 1). Small colonies invariably had the highest rate of mor-

FIG. 3. Rates of recruitment of *Agaricia agaricites* and *Leptoseris cucullata* from 1977 to 1993, into twelve 1-m² plots. *Montastrea annularis* had only one recruit, in 1981.



tality (q_x), and were usually the most likely to increase in size. Larger colonies survived better, but were more likely to shrink or contribute to smaller size classes by fission. Three of the matrices (*Montastrea annularis* in 1977-1982 and 1982-1987, and *Leptoseris cucullata* in 1977-1981) have one or more columns whose transition rates sum to more than one (Table 1), because (from that size class) new colonies generated by fission exceeded losses due to mortality.

The life history differences among species are most clearly observed in the initial matrix (1977-1982), before serious population decline occurred. *Montastrea annularis* had the lowest rate of mortality: only 19%

of the original colonies died in this first 5-yr period, compared to 60% of *Agaricia agaricites* and 77% of *Leptoseris cucullata*. The largest *M. annularis* in particular were virtually immune to mortality in the first (and second) time interval, with only a single colony dying in the first 10 years. In contrast, 27% and 52% of the largest colonies of *A. agaricites* and *L. cucullata*, respectively, died in the first interval (1977-1982, Table 1). These comparisons need to be made cautiously, given the different size categories we used for describing *M. annularis* vs. the other two species. However, even the smallest category of *M. annularis* (colonies <50 cm²) survived better than the largest *L. cucullata*

TABLE 1. Transition matrices, sample sizes, and size-specific mortality rates (q_x) for 1977-1982, 1982-1987, and 1987-1993.

Species and size class	1977-1982 Size class			1982-1987 Size class			1987-1993 Size class		
	I	II	III	I	II	III	I	II	III
<i>Montastrea annularis</i>									
Size class I	0.429	0.227	0.057	0.421	0.583	1	0.049	0.375	0.276
Size class II	0.107	0.5	0.257	0.053	0.583	0.474	0.066	0.188	0.276
Size class III	0	0.091	1.029	0	0.042	0.737	0	0.063	0.241
q_x	0.429	0.136	0.029	0.526	0.125	0	0.885	0.531	0.379
n	28	22	35	19	24	38	61	32	29
<i>Agaricia agaricites</i>									
Size class I	0.034	0.05	0	0	0.102	0.088	0	0.038	0
Size class II	0.125	0.183	0.346	0.217	0.306	0.441	0.111	0.135	0.286
Size class III	0.091	0.233	0.5	0.043	0.102	0.235	0	0.077	0.214
q_x	0.727	0.550	0.269	0.739	0.592	0.412	0.889	0.788	0.571
n	88	60	26	23	49	34	18	52	14
<i>Leptoseris cucullata</i>									
Size class I	0.022	0.053	0.095	0.071	0.05	0.115	0	0	0
Size class II	0.087	0.026	0.381	0.143	0.05	0.308	0	0	0.077
Size class III	0.043	0.158	0.714	0	0.15	0.385	0	0	0
q_x	0.87	0.789	0.524	0.929	0.8	0.654	1	1	0.923
n	46	38	21	14	20	26	7	12	13

Notes: Size classes are 0-50 cm², 50-200 cm², and >200 cm² for *Montastrea annularis*; and 0-10 cm², 10-50 cm², and >50 cm² for *Agaricia agaricites* and *Leptoseris cucullata*. The sample size, n , is the number of colonies at the beginning of each interval. Transitions from a given size class are in columns. Matrix elements and q_x are proportions.

TABLE 2. Population growth rates (eigenvalues, λ) and damping ratios (ρ) for *Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata*, based on transition matrices for 1977–1982, 1982–1987, and 1987–1993 (see Table 1).

Species	Census interval	λ	95% CI	ρ	95% CI
<i>Montastrea annularis</i>	1977–1982	1.074	(0.895, 1.258)	1.84	(1.41, 2.68)
	1982–1987	0.847	(0.660, 1.104)	1.49	(1.04, 2.87)
	1987–1993	0.388	(0.261, 0.529)	2.7	(1.16, 10.16)
<i>Agaricia agaricites</i>	1977–1982	0.673	(0.523, 0.864)	9.77	(5.04, 76.83)
	1982–1987	0.531	(0.400, 0.695)	7.18	(3.41, 87.22)
	1987–1993	0.330	(0.188, 0.519)	5.44	(2.58, ∞)
<i>Leptoseris cucullata</i>	1977–1982	0.801	(0.410, 1.722)	10.83	(2.26, 41.19)
	1982–1987	0.503	(0.252, 1.080)	7.47	(2.16, ∞)

(>50 cm²; 43% vs. 52% mortality, respectively, see Table 1). As noted above, recruitment rates and population structures also varied substantially between the three species.

A colony's fate was affected by time (i.e., transition probabilities varied significantly among the census intervals) for all three species (log-linear analyses; *Montastrea annularis*, $\chi^2_{18} = 116$, $P \ll 0.001$; *Agaricia agaricites*, $\chi^2_{18} = 31.6$, $P = 0.025$; *Leptoseris cucullata*, $\chi^2_{18} = 29.5$, $P = 0.042$), consequently, the matrices for each period were distinctive. In general, rates of mortality and shrinkage increased over time (especially in the third period), while rates of colony growth and stasis declined (Table 1). For *M. annularis*, overall mortality rates were 19%, 16%, and 67% respectively for the three periods. Size-specific mortality rates increased consistently over time across all size-classes, especially for the largest colonies (size class III), where 3%, 0%, and 38% died in the three intervals. Similarly, overall rates of mortality of *A. agaricites* were 60%, 57%, and 77% for the three periods, with the biggest increase occurring in large colonies (27%, 41%, and 57% mortality, respectively). Overall mortality rates for *L. cucullata* were 77% for both 1977–1982 and 1982–1987, rising to almost 100% in the final period (of 32 colonies alive in 1987, only one survived to 1993), which obviously precluded construction of a useful matrix for that period. Note that overall rates of mortality in the first and second intervals were essentially the same for all three species, even though size-specific rates consistently increased (Table 1). This disparity occurred because there were proportionally fewer small colonies (with high mortality rates) in 1982–1987 than in the previous interval (see Table 1 for sample sizes), which boosted overall survival despite worsening rates of attrition in each size-class.

Another important change occurred in rates of stasis or retention of colonies (the probability of staying the same size), particularly in the largest size class (Table 1). This "transition" (the bottom-right element of the matrices) steadily declined over time in all species, due to the increased rate of mortality and shrinkage of the largest colonies. In *Montastrea annularis*, this transition fell over time from 1.03 to 0.74, and finally to only 0.24. Similarly, retention rates for the largest

Agaricia agaricites dropped from 0.50 to 0.23 and then 0.21, while those for *Leptoseris cucullata* declined from 0.71 in 1977–1982 to 0.38 in 1982–1987. In the third interval, 12 out of the remaining 13 large colonies of *L. cucullata* died and the sole survivor shrank, giving a retention rate of zero.

Analysis of matrix properties

The dominant eigenvalues (λ) for all three species declined sharply over time (Table 2), indicating that the rate of depletion of each population was accelerating. In the initial period, survival of *Montastrea annularis* was substantially higher than the other species, as would be expected from previous studies of their life histories (e.g., Bak and Luckhurst 1980, Hughes and Jackson 1985). Indeed, λ for *M. annularis* in 1977–1982 was 1.07 (equivalent to an annual population growth rate of 1.4% per year), indicating that populations in that period were capable of growing slowly by asexual fission even with little or no larval recruitment. In 1982–1987, λ for this species dropped to 0.85 (although the 95% confidence limits still include values slightly greater than one; Table 1). At this rate of depletion, the population would decline by 50% every 20 yr, assuming no further larval recruitment. By 1987–1993, *Montastrea* was declining very rapidly, at a similar rate to the other species, with a population growth rate of only 0.39 (i.e., a decline of more than 95% every 20 yr). Ninety-five percent confidence intervals indicated that survival of *M. annularis* was significantly less in the final interval than either of the first two, while survival of *Agaricia agaricites* was also significantly lower in the final interval; *Montastrea* survived significantly better than *A. agaricites* only in the first interval. The decline in survival of *Leptoseris cucullata* is less clear cut because of the larger confidence limits, but the downward trend over time is the same (Table 2). Lambda for this species in 1987–1993 was almost zero since only a single colony survived the final period (Fig. 2).

The damping ratio, ρ , measures the rate of convergence of a cohort to a stable size structure (regardless of whether a population is increasing or decreasing). The ratio showed a declining trend over time for *Agaricia agaricites* and *Leptoseris cucullata* (Table 2). This

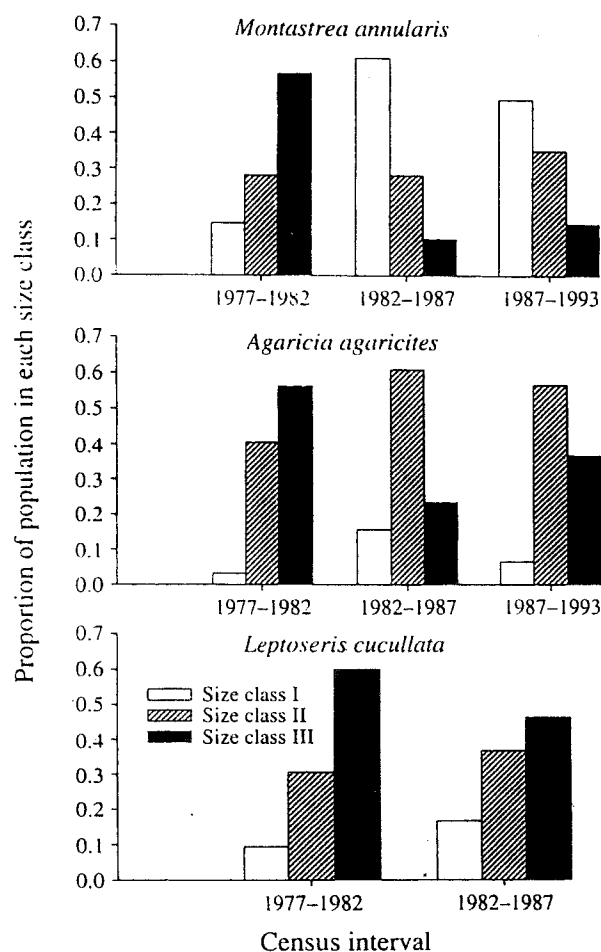


FIG. 4. The stable population structures of *Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata* based on transition matrices for 1977-1982, 1982-1987, and 1987-1993 (see Table 1).

is the expected result due to increasing rates of mortality and shrinkage (Table 1), which would make it more difficult for small colonies to attain a large size. The damping ratio for *M. annularis* is substantially lower than for the other species, and shows little change over time, indicating consistently slower rates of growth and mortality than *A. agaricites* and *L. cucullata*, and a much slower convergence to a stable size structure. The asymmetric confidence limits around ρ are very large in most cases (except for *M. annularis* in the first two intervals), and their upper value in particular increases over time (Table 2). This points to the importance of large colonies: bootstrap iterations which by chance included a smaller proportion of large colonies resulted in substantially higher damping ratios, i.e., faster times to attain an equilibrium population structure.

The stable size distribution calculated for each of the matrices became increasingly dominated by small colonies over time (Fig. 4), indicating that a cohort of recruits exposed to conditions early on in the study would eventually achieve a larger mean size than recruits which settled later on. For the initial matrices (1977-1981), the stable composition of each species was dominated by large- and medium-sized colonies, with only 5-15% occurring in the smallest size class, depending on species. For the later matrices (1982-1987 and 1987-1993), the predominance of larger colonies at equilibrium declined, especially in *Montastrea annularis*, where the proportion of colonies in the largest size class dwindled by fourfold, from 57% for the initial matrix to 12% and 15%, respectively.

Elasticities, a measure of the relative contribution of each individual transition to λ varied substantially over time (Table 3). The retention rate of large colonies was almost always the single-most important transition, especially for the first period and for *Montastrea annularis*. Later on, stasis and growth of medium-sized colonies also contributed significantly to λ (i.e., these elements

TABLE 3. Elasticity matrices for *Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata*; showing the proportional sensitivity of λ to changes in each element of the transition matrices (see Table 1).

Species	Size class, 1977-1982			Size class, 1982-1987			Size class, 1987-1993		
	I	II	III	I	II	III	I	II	III
<i>Montastrea annularis</i>									
Size class I	0.002	0.003	0.001	0.041	0.025	0.016	0.016	0.082	0.026
Size class II	0.004	0.036	0.037	0.042	0.200	0.063	0.110	0.210	0.130
Size class III	0	0.038	0.880	0	0.079	0.530	0	0.160	0.260
<i>Agaricia agaricites</i>									
Size class I	0	0.009	0	0	0.059	0.020	0	0.015	0
Size class II	0.004	0.071	0.190	0.059	0.330	0.180	0.015	0.150	0.210
Size class III	0.006	0.180	0.540	0.020	0.180	0.160	0	0.210	0.390
<i>Leptoseris cucullata</i>									
Size class I	0	0.002	0.008	0.004	0.007	0.020			
Size class II	0.003	0.003	0.089	0.027	0.021	0.160			
Size class III	0.007	0.090	0.800	0	0.180	0.580			

Note: Elements >0.1 are indicated in bold.

TABLE 4. Contribution of each transition to the observed declines in population growth rates.

Species and size class	Size class, interval 1-2			Size class, interval 1-3		
	I	II	III	I	II	III
<i>Montastrea annularis</i>						
Size class I	-0.0003	0.0093	0.0200	-0.0131	0.0050	0.0078
Size class II	-0.0149	0.0146	0.0311	0.0078	-0.0580	0.0036
Size class III	0	-0.0473	-0.2287	0	-0.0213	-0.6140
<i>Agaricia agaricites</i>						
Size class I	-0.0013	0.0103	0.0140	-0.0004	0.0015	-0.0065
Size class II	0.0069	0.0476	0.0295	-0.0004	-0.0148	-0.0196
Size class III	-0.0066	-0.0940	-0.1518	0.0053	-0.1004	-0.1956
<i>Leptoseris cucullata</i>						
Size class I	0.0008	-0.0001	0.0015			
Size class II	0.0028	0.0032	-0.0162			
Size class III	-0.0084	-0.0041	-0.2801			

Notes: Positive values indicate that the changes in transitions (between the first and second interval, or between the first and third interval) had a positive effect on population growth. Negative values result from changes in transitions that lead to population decline. Contributions >0.1 are indicated in bold. Matrix elements are proportions.

of the matrix played a proportionately greater role in slowing down the rate of attrition). Transitions to and from the smallest size class had little effect on λ for all species throughout the study. Similarly, a life table response analysis indicates that the reduction in λ over time is overwhelmingly due to the loss of large colonies

(Table 4). Positive values in Table 4 indicate changes in transitions that enhanced population growth, while negative values depict changes that contributed to population decline. The sum of entries in each matrix corresponds approximately to the differences in λ s between the initial (1977-1982) and subsequent matrices, which of course are negative (see Table 2). Consequently, most of the changes in transitions recorded during the course of the study had a negative effect on λ .

Simulation studies: recruitment failure

Here we explore the transient behavior of the populations in a series of simulation studies, to examine the role of declining rates of recruitment. We first examine the dynamics of the three species without larval recruitment to project changes in the number of established colonies in populations behaving according to the transitions recorded in each of the three intervals (Table 1). For convenience, we use the population structures of 1977 as a starting point. Our objective is to project the long-term behavior of the populations assuming they continued to act according to the "rules" we measured in each of the three intervals. Since the matrices changed over time, the long-term projections reveal further the consequences of the altered demography of the three species.

The rate of depletion of each species (Fig. 5) was slowest for the initial matrix, intermediate for the middle period, and fastest for the final matrix (as expected from their dominant eigenvalues, Table 2), reflecting the accelerating rate of decline during the 16-yr study. The differences between the three matrices are most dramatic for *Montastrea annularis*, where populations behaving according to the initial matrix grew slowly (at a rate of 7% every 5 yr) due to fission, then slowly declined according to the 1982-1987 matrix (decreasing by 13% every 5 yr), and finally under the third matrix declined rapidly by more than 50% every 5 yr

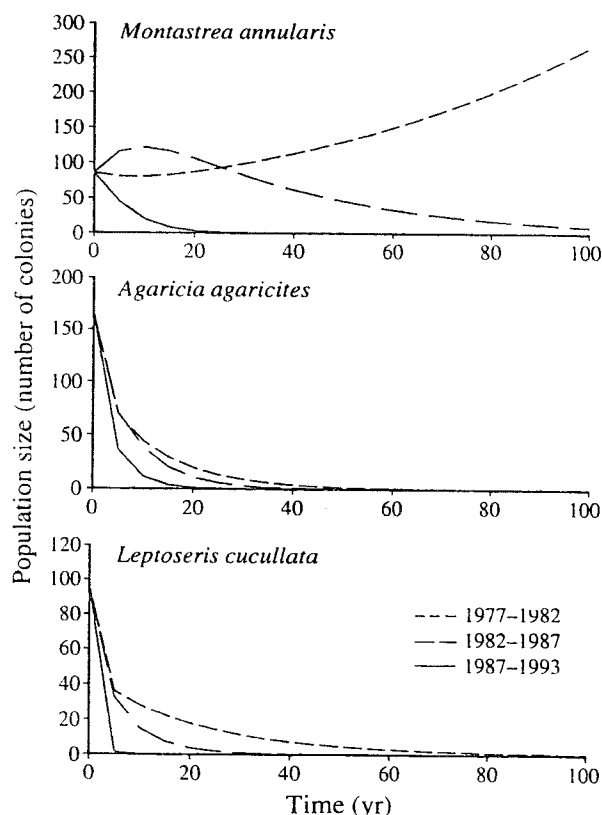


FIG. 5. Population size over time for *Montastrea annularis*, *Agaricia agaricites*, and *Leptoseris cucullata*, based on transition matrices for 1977-1982, 1982-1987, and 1987-1993 (see Table 1), with no recruitment.

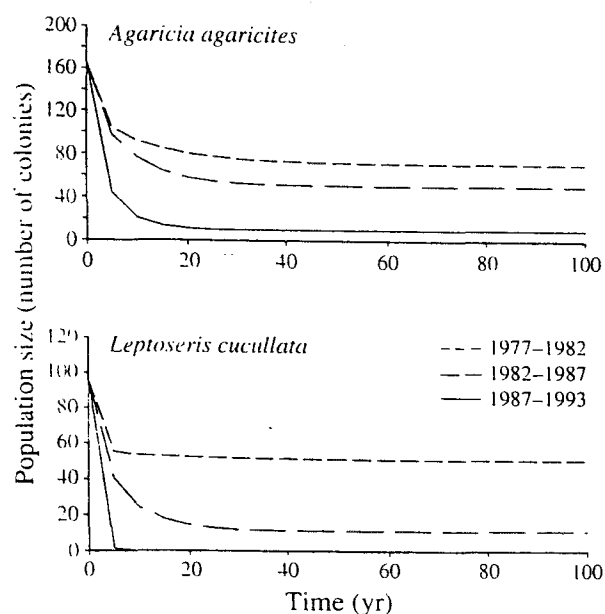


FIG. 6. Population size over time for *Agaricia agaricites* and *Leptoseris cucullata*, based on transition matrices for 1977–1982, 1982–1987, and 1987–1993 (see Table 1), with the observed level of recruitment for each interval. (Recruitment of *Montastrea annularis* was so low that it has no noticeable effect on population size.)

(Fig. 5). Note that these longer-term projections were not initially obvious for two of the matrices: for the 1977–1982 projection, the population first declined, but 20 yr later regained and then began to exceed 1977 levels. Similarly, the 1982–1987 projection grew initially, before declining slowly below initial levels 26 yr later. The rate of depletion of *Agaricia agaricites* and *Leptoseris cucullata* was much more rapid: if conditions recorded during the final 1987–1993 period are projected over time, their populations decline to zero without further recruitment within 10–20 yr (Fig. 5).

The addition of recruitment at each iteration of the simulation will obviously prevent the complete depletion of a population. However, as noted earlier, the observed rate of recruitment declined over time (Fig. 3). Accordingly, we added the observed amount of re-

cruitment during each interval (1977–1982, 1982–1987, and 1987–1993) to each iteration of the matrix projections, to examine the effects of recruitment on long-term changes in population size (Fig. 6). *Montastrea annularis* had only a single recruit in 16 yr, so the addition of recruits to its population was clearly not sufficient to halt the observed declines. For *Agaricia agaricites*, the net rate of recruitment (the number arriving during, and still alive at the end of each of the three time intervals) was 35, 27, and 8, while net recruitment for *Leptoseris cucullata* was 19, 8, and 0 (for the 1977–1982, 1982–1987, and 1987–1993 periods, respectively, Table 5). When these recruits were added to the simulations, the same declining trend occurs over time, indicating the extent to which declining recruitment gains were outstripped by accelerating losses from mortality. For example, for the 1987–1993 matrix, the number of *A. agaricites* equilibrated at only 7% of 1977 levels (and most of the population consisted of the latest cohort of recruits).

We also calculated the amount of recruitment that would be required to maintain population sizes at 1977 levels, for each matrix. As expected, the increasing rates of mortality over time required more and more recruitment to compensate for losses (Table 5). For the 1977–1982 matrices, the number of recruits required every 5 yr to maintain each population was the equivalent of 67% of the original number of colonies (i.e., those present in 1977) for *Agaricia agaricites*, and 47% for *Leptoseris cucullata*, with no recruitment being needed to maintain the population size of *Montastrea annularis*. In contrast, for the 1987–1993 matrices, the proportion of recruits (relative to the number of colonies in 1977) needed to maintain the populations of the three species was 86, 99, and 91%, respectively. However, the observed level of recruitment during this final period was less than one-sixth of that in 1977–1982, and well over an order of magnitude lower than the amount required to maintain rapidly declining populations (Table 5).

DISCUSSION

Life histories and mechanisms of population decline

Our study documents how life history variation among the three species of corals underlies their dif-

TABLE 5. Observed recruitment for each census interval, and the amount that would be required to maintain population sizes at 1977 levels.

Species	Time interval	Observed recruitment	Recruitment needed to maintain population size
<i>Montastrea annularis</i>	1977–1983	1	0
	1983–1987	0	35
	1987–1993	0	73
<i>Agaricia agaricites</i>	1977–1983	35	91
	1983–1987	27	101
	1987–1993	8	144
<i>Leptoseris cucullata</i>	1977–1983	19	49
	1983–1987	8	73
	1987–1993	0	96

ferential susceptibility to elevated rates of mortality and declining recruitment. *Montastrea annularis* was affected most by changes in survivorship, whereas recruitment failure also contributed substantially to the decline of *Agaricia agaricites* and *Leptoseris cucullata*. *Montastrea* had a much higher λ value than the other two species (Table 2) because colonies survived longer and underwent fission more often (Table 1; see also Bak and Engel 1979, Bak and Luckhurst 1980, Hughes and Jackson 1985). Conversely, the damping ratio, ρ , was lower for *M. annularis*, because its colonies are slow growing and take far longer than the other two species to attain a large size (e.g., Hughes and Jackson 1985). Population growth declined sharply over time for all species, indicating that the rate of depletion of each population was accelerating. Similarly, the damping ratios decreased over time for *Agaricia agaricites* and *Leptoseris cucullata* (Table 2), because slower growth rates and higher rates of shrinkage impeded the progression of small colonies into larger size classes, a further indication of populations under stress.

By the end of the study, there were fewer large colonies of all species because many of them had died or had undergone fission, and they had not been replaced by growth of smaller colonies. It is clear that asexual fission of large colonies was not adaptive, especially later on in this study (see also Highsmith 1982, Lasker 1991, McFadden 1991, Smith and Hughes 1999). Fission in these coral species occurs only when colonies are injured (e.g., by partial overgrowth by macroalgae), so that surviving patches of tissue on the same skeleton become separated. Therefore, there is a substantial loss of live cover associated with fission. In addition, small colonies have a much higher rate of mortality than intact, larger ones (Table 1). The large increase in the number of *M. annularis* in 1986–1987 (Fig. 2a) was a symptom of population decline, not growth: coral cover decreased as large colonies were being dismembered into small remnants, many of which were subsequently overgrown and killed by algae.

The accelerating rate of depletion of larger, older colonies is a clear sign of serious population decline, which will take decades or longer to reverse. In particular, a retention rate of only 0.24 for the largest colonies of *Montastrea annularis* in 1987–1993 has major consequences for the persistence of this population, given the length of time necessary to establish these old colonies. At 35 m depth, colonies of this species extend in diameter by a mean of less than 1 cm per year (Hughes and Jackson 1985), i.e., a colony with a diameter of 1 m is at least a century old. Yet in the last 6 yr of this study, nearly 40% of the largest colonies of this species died, while almost all of the survivors were injured, with two-thirds of them shrinking into smaller, more vulnerable size classes (Table 1). These losses are clearly not sustainable, even if rates of recruitment were to increase dramatically. By 1987–1993, the rate of mortality of *M. annularis* was so high

that the population would virtually need to be replaced by new recruits every 6 yr in order to maintain population size at 1977 levels (Table 5). Even then, these colonies would be so small that cover would only be a tiny fraction of that in 1977. Ironically, although *Montastrea* survived the best, its slow rate of recruitment and growth will ensure that it recovers much more slowly than the other species, even if conditions do improve.

Recovery in open systems

Rates of larval recruitment declined sharply over time (Fig. 3), providing only a very small fraction of the number of new colonies needed to maintain population sizes (Fig. 6). Clearly, more recruits and an improvement in survival will be required to ensure recovery. The causes of the decline in recruitment are uncertain. Pre-emption of space by macroalgae is liable to have inhibited settlement, while smothering or overgrowth by algae is likely to have killed new recruits (e.g., Bak and Engel 1979, de Ruyster van Steveninck and Bak 1986, Hughes et al. 1987). Given the large scale of the decline in coral stocks around Jamaica (e.g., Liddell and Ohlhorst 1992, Hughes 1994), it is also possible that the size of the larval pool has decreased. The distinction between these mechanisms of recruitment failure is important. For example, if the decline in recruitment is caused primarily by smothering, a reversal of the algal blooms (e.g., through increased rates of herbivory) would be followed quickly by a pulse of new coral recruits. Conversely, if the breeding stock has declined significantly, there would be a period of much slower colonization by coral recruits, even if free space became widely available. We cannot assume that there is an inexhaustible supply of larval recruits if diminished stock sizes or lower fecundities have altered large-scale stock–recruitment relationships (Lipcius and Van Engel 1990, Peterson and Summerson 1992, Hughes et al. 2000).

The scale of planktonic dispersal of coral propagules in the Caribbean is poorly known, so it is uncertain where the larvae necessary for recovery would come from, if they are not generated locally. Roberts (1997) recently predicted levels of connectivity among Caribbean islands based on large-scale current patterns, assuming that larvae are passively dispersed for 30–60 d. However, coral larvae are capable of settling much sooner; under laboratory conditions peak settlement typically occurs within 2–3 d of release for brooders and 5–10 d for spawners (although a small proportion of a cohort may settle much later, particularly if they are deprived of a suitable substratum; see review by Harrison and Wallace 1990, Wilson and Harrison 1998). Moreover, large-scale variation in recruitment by corals may depend on the size of the upstream breeding stock as well as the distance between sources and sinks. For example, Hughes et al. (2000) showed that regional-scale variation in the fecundity of adult corals

along the Great Barrier Reef explained 72% of the variation in subsequent recruitment by spawning corals. Furthermore, recruitment rates by spawning and brooding corals on the Great Barrier Reef are poorly correlated at all spatial scales, i.e., patterns of water flow do not ensure that locations consistently receive large or small numbers of recruits of all species (Hughes et al. 1999). For brooding corals like *Agaricia agaricites* and *Leptoseris cucullata*, recruitment rates on Jamaican reefs may remain depressed until local breeding stocks recover. Colonization by corals that are capable of long-distance dispersal (e.g., from Cuba) may be less affected, with potentially far-reaching consequences for community structure. Unfortunately, long-lived and slow-growing corals like *M. annularis* will take a century or more to recover to pre-1980 levels even if recruitment resumes quickly.

Long-term population trajectories

Our study demonstrates an accelerating decline of the three coral populations we investigated. In the initial period, the population of *M. annularis* had a stable size distribution, and a very low rate of mortality coupled with a modest rate of asexual fission. Consequently, the population was self sustaining, capable of growing slowly even with negligible levels of larval recruitment (Fig. 5). Hurricane Allen in 1980/1981 caused a slight decline in cover of *M. annularis* (Fig. 1), but it did not affect numbers because most of the tissue loss was through injuries to large colonies. Even including this hurricane, the long-term projection of vital rates during 1977 to 1982 reveals a population that is remarkably resilient. The cover and number of *Agaricia agaricites* and *Leptoseris cucullata* also increased initially, but then dropped in 1980/1981, due to Hurricane Allen, the worst storm for 30 yr (Woodley et al. 1981). Even with Hurricane Allen, population growth rates for 1977–1982 were relatively high: 0.67 for *A. agaricites* and 0.80 for *L. cucullata* (see Table 2 for confidence limits. On an annual basis, λ was 0.92 and 0.96, respectively). At this rate of depletion, for example, 20% of the original colonies of *L. cucullata* would remain alive after 32 yr (in 2009). This relatively slow rate of attrition would normally be balanced by high rates of larval recruitment (as it was in the 3 yr preceding Hurricane Allen, Hughes and Jackson 1985). However, the subsequent changes in demographic rates resulted in this level of depletion (20%) being reached much sooner, after only 6 yr (in 1983; Fig. 2c).

Coral reefs in many parts of the world are being increasingly affected by humans (e.g., reviews by Rogers 1985, Ginsburg 1993, Jackson 1997, Hughes and Connell 2000), and there is an obvious need to understand the degree of change and (more importantly) the underlying mechanisms causing change. The most commonly used attribute for describing the status of a reef is the abundance of corals, usually in terms of total cover: cover going down is "bad", going up is "good".

We caution, however, that coral abundance can easily increase for considerable periods, even in a population which is ultimately destined to decline (and vice-versa). For example, the simulations we conducted use the same matrices iteratively (i.e., rates of mortality and growth are constant), yet they show two examples of reversals in the long-term trajectories of the coral populations (Fig. 6). For the 1977–1982 matrix describing *Montastrea annularis*, the number of colonies first decreased slightly (even though λ was greater than 1), but then increased to exceed the initial levels after 20 yr. Conversely, the 1982–1987 matrix for *M. annularis* describes a population which first grew by over 40% (even though λ was only 0.85), before dropping below starting levels after 26 yr. These reversals arose because the initial population structures differed from the stable distributions of the respective matrices. For example, if a population contained a lower proportion of small, vulnerable colonies than the stable distribution, it could initially grow but then decline even where there is no change in demography. A nonequilibrium size- or age-structure is commonplace in fluctuating environments, and is most likely to occur in species with open populations that receive varying amounts of larval recruitment (such as *Agaricia agaricites* and *Leptoseris cucullata*). Detecting and understanding long-term patterns on coral reefs and elsewhere will be a major challenge, and will require a much longer time frame to investigate than that of most ecological studies.

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POPULATION DYNAMICS BASED ON INDIVIDUAL SIZE
RATHER THAN AGE: A GENERAL MODEL
WITH A REEF CORAL EXAMPLE

TERENCE P. HUGHES

Department of Earth and Planetary Sciences, Johns Hopkins University,
Baltimore, Maryland 21218

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Changes in the number of individuals in a population, and in their relative ability to replace themselves, form the quantitative basis for many ecological and evolutionary studies. The familiar demographic life-table traces these changes using two fundamental parameters, the age-related schedules of birth and mortality. Predictions of population dynamics based on age work best for cohorts of animals or plants which develop synchronously through consecutive life stages such as seed or larva, juvenile, and adult. For many organisms the growth rates of members of a single cohort can vary enormously from one individual to the next because of genetic or environmental differences, chance, or a combination of all three (Schaffer and Leigh 1976; Horn 1979; Hubbell and Werner 1979). Such developmental variance can result in a very poor correlation between age and the probabilities of mortality and natality. Often the fate of an individual can be predicted more accurately from its size (Connell 1973; Werner 1975; Harper 1977; Hughes and Jackson 1980; Highsmith 1982). Large individuals are typically more fecund, while small individuals usually have higher rates of mortality, regardless of age (Lefkovitch 1965; Hartshorn 1975; Jackson 1977; Werner and Caswell 1977; Enright and Ogden 1979; Highsmith et al. 1980). I present here a general model of population dynamics using size-related parameters appropriate to organisms with highly variable development. The model is based on a modified Leslie matrix and is designed to incorporate such diverse demographic processes as fragmentation, regression (shrinkage), and partial mortality, as well as the more familiar processes of growth, sexual reproduction, and death.

Clonal Organisms

A population model based on size rather than age is particularly useful in describing the dynamics of clonal invertebrates and plants. The body of a clonal organism is made up of repeated building blocks or modules, e.g., the polyps of a

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coral or hydroid, the zooids of a bryozoan, or the shoots of a clonal plant. After larval or seed settlement and metamorphosis, most of the growth of a colony is achieved by increasing the number of genetically identical modules (Harper 1977; Jackson 1977, 1979). Individual colony growth is potentially indeterminate in many species, but may be inhibited to varying degrees by physical stress, local availability of resources, or by mortality of modules. Therefore, there is often enormous variation in size between colonies within an age cohort (Harper 1977; Solbrig et al. 1980; Vaughan 1911). In addition, many colonies regress periodically from large adult size to small resting stages, especially in seasonal habitats, e.g., sponge gemmules, bryozoan hibernacula, or plant bulbs. Frequently, it is impossible to distinguish morphologically between a rejuvenating individual and a newly settled one (Mertz and Boyce 1956; Hughes and Jackson 1980).

In some species, single modules or larger clumps of modules may break off and lead a separate existence. Thus, clones of individuals or separated "daughter" colonies of identical genotype may be common (Rosen and Taylor 1969; Sarukhan and Harper 1973; Francis 1976; Janzen 1977; Highsmith 1982). Counts of distinct physiological individuals may therefore far exceed the genetic population size. After fragmentation, individual clone members may reproduce or die more or less independently. Even where modules remain firmly connected, some may be killed while others remain healthy. Because colonial organisms by definition have replicated feeding structures, gonads, etc., they can frequently survive extensive partial mortality (i.e., shrinkage) on a scale far beyond the regenerative capacity of most solitary animals or plants.

Many of these characteristics have been described in population studies of reef corals. Vaughan (1911) followed a newly settled cohort of the coral *Porites astreoides* for 12 mo, and found that a few of the survivors grew very quickly, while most showed only a small increase in size. Although the corals were all of the same age, there was a sixfold difference in maximum colony diameter within a single year (a tiny fraction of the potential life span). Connell (1973) and Loya (1976) showed further that smaller colonies usually have faster growth rates, but are more likely to be killed than larger corals. Hughes and Jackson (1980) measured rates of shrinkage, fragmentation, and colony fusion, and showed that these processes combine to decouple size-age correlations.

Conventional age-related population analysis is totally unsuited to the demographic characteristics of colonies. Small or medium-sized individuals are frequently older than large ones, especially if they are crowded, and may become even smaller if they regress or are injured. Furthermore, it is usually impossible or impractical to calculate ages without actually following a colony throughout its entire life, perhaps for many decades. Not surprisingly, data collection on the population biology of colonial organisms has been hampered by the lack of an appropriate theoretical framework. Here I present a simple size-related demographic model for animals and plants for which age-related models are unsuitable. Using a reef coral example, I show the effects of shrinkage, fragmentation, and differential growth on the population dynamics of clonal organisms. In addition, I use the model to make testable predictions on the effects of rare storms and the role of clonal population dynamics in community development.

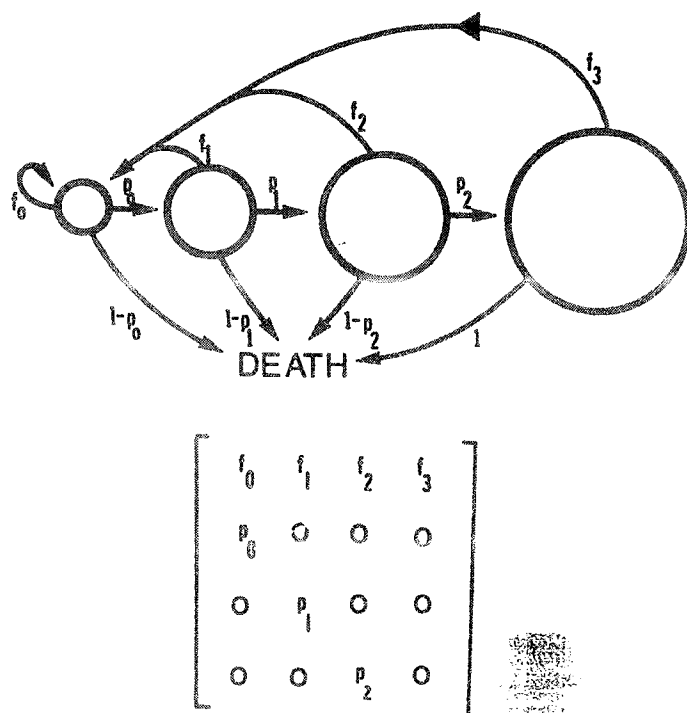


FIG. 1.—A graphic representation of the Leslie matrix model. Larger circles depict increasing age. During each time interval individuals may either die or survive, progressing into the next age class. Each age group (the columns of the matrix) may contribute sexual recruits to the youngest age class (the top row of the matrix). $0 \leq p \leq 1$, $0 \leq f$.

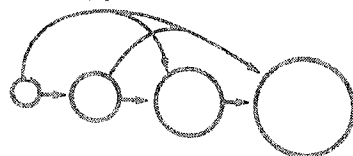
The Model

Leslie's (1945) deterministic model predicts the age structure of a population, given the age structure at some past time and the age-specific rates of fecundity and survival. The model is shown graphically in figure 1. The form of the model is:

$$\bar{x}_{t+1} = \bar{A} \cdot \bar{x}_t$$

where $\bar{x}_t$ is a column vector describing the population age structure at time t , and $\bar{A}$ is a matrix which determines the dynamics of the population. $\bar{A}$ has two types of elements: the elements f_i ($f \geq 0$) along the top row of the matrix represent the average number of sexual recruits born between time t and $t + 1$, to each individual of age i to $i + 1$ at time t . The elements p_i ($0 \leq p \leq 1$) along the subdiagonal of the matrix represent the probability that an individual, aged i to $i + 1$ at time t , will be alive at time $t + 1$, in the next oldest age class. It follows that $1 - p_i$ is the age-specific mortality rate. All other elements of the matrix are zero, reflecting the biological absurdity of, say, a 2-yr-old individual becoming a 1-yr-old again, or becoming a 4-yr-old without first being a 3-yr-old. An important property of this model is that whatever the population structure initially, the

GROWTH



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(A)

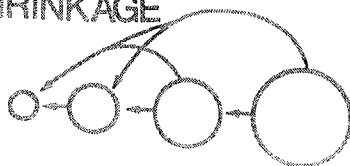
LOOP



$$\begin{bmatrix} L & f+s & f+s & f+s \\ f & L & s & s \\ f & g & L & s \\ f & g & g & L \end{bmatrix}$$

(B)

SHRINKAGE



$$\begin{bmatrix} f+L & f+s & f+s & f+s \\ f & L & s & s \\ f & g & L & s \\ f & g & g & L \end{bmatrix}$$

(C)

GENERAL MODEL

$$\begin{bmatrix} f+L & f+s & f+s & f+s \\ g & L & s & s \\ g & g & L & s \\ g & g & g & L \end{bmatrix}$$

(D)

FIG. 2.—A graphic representation of a size-dependent matrix model of population dynamics. Larger circles depict increasing individual size. During each time interval surviving individuals may (A) grow, (B) stay the same size, or (C) contribute to smaller size classes by shrinking or fragmentation. Sexual recruits are contributed by each size class to the smallest size class as in fig. 1. Transitional probabilities are as follows: (growth) $0 \leq g \leq 1$, (loop) $0 \leq L \leq 1$, (shrinkage) $0 \leq s \leq 1$, (asexual reproduction) $0 \leq s$, (sexual reproduction) $0 \leq f$.

population will grow (or shrink) ultimately at a constant rate, λ , and a stable age distribution will be maintained. Exponential growth of the population is indicated by λ greater than one, stability by λ equal to one, and a decline to extinction by values between one and zero.

This model can be adapted for populations whose structure is described by size rather than age classes (see review in Usher 1972; Werner and Caswell 1977). In a size-stage matrix, probabilities below the diagonal represent net growth into a larger size class (fig. 2A). The diagonal describes the likelihood of an individual

remaining in the same size class, either through a slowing down in growth rate, or a balance between growth and shrinkage (fig. 2B). Finally, probabilities above the diagonal represent contributions to a smaller size class, i.e., through shrinkage, fragmentation or sexual reproduction (figs. 2C, 2D). Thus, the elements of the original Leslie matrix which are usually zero, may here take on nonzero values. In the modified model, the size-specific mortality rate is one minus the sum of probabilities in each column of the matrix, provided individuals do not fragment or fuse.

The most general form of the size-staged matrix is given in figure 2D. All previously published population matrices are special cases of this general model (e.g., Enright and Ogden 1979; Hartshorn 1975; Lefkovitch 1965; Meagher 1982; Sarukhan and Gadgil 1974; Werner and Caswell 1977). I describe below the construction of a matrix for a population of the reef coral *Agaricia agaricites*. This massive or foliaceous stony coral is abundant over a wide depth range throughout the Caribbean. Individuals commonly live for 50 yr or more, but they cannot be accurately aged without disturbing or killing the colony (Hughes and Jackson 1980). I use the matrix firstly to predict changes in the number and sizes of colonies within a single cohort, over time scales that are impractical to measure directly. Secondly, sexual recruitment is added to the model to examine the dynamics of populations of mixed ages. Finally, I examine some of the assumptions of the model and their biological meaning.

A CASE STUDY

The fate of 246 *Agaricia agaricites* colonies was followed from analysis of several hundred in situ photographs taken of 12 1-m quadrats placed on a vertical wall between -10 m and -20 m at Rio Bueno, Jamaica. Colonies were assigned to one of four size classes based on their area in the first year of each set of observations. The size classes were 0-10 cm², 10-50 cm², 50-200 cm², and >200 cm². These particular categories were chosen to encompass the range of colony area observed in the population, while maintaining at least 25 corals in each size class. Dividing up the population into more than four size classes would have increased the resolution of the projected size structure (see below), but at the expense of increased sampling error around measured matrix probabilities. The transitional probabilities calculated from the field population (table 1) depend in part on the size-frequency distribution within each size class. I have attempted to minimize this source of error by defining size classes as narrowly as possible in the range most sensitive to size-related changes, i.e., size classes I and II.

At the beginning of the study, *Agaricia agaricites* occupied 15.2% of the space within the quadrats, and the measured population structure was dominated by small corals (see size class sample sizes in fig. 3). Total living cover, mainly by corals, sponges, and algae, was 61.7%. From one annual census (taken in August) to the next, surviving *Agaricia* colonies shrank, stayed in the same size class, or grew larger (fig. 3). In the first year (1977/1978), whole colony mortality was highest among small corals, and absent in the largest individuals. The largest colonies suffered extensive partial mortality, however, and shrank more often

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TABLE I

MATRICES OF TRANSITIONAL PROBABILITIES FOR FOUR SIZE CLASSES OF *A. agaricites* IN A CALM AND STORMY YEAR

CALM (1977/78)					STORMY (1978/79)				
	I	II	III	IV		I	II	III	IV
I	.6020	.1167	.0217	.0741	I	.5135	.0794	.0727	.0714
II	.1681	.6167	.1087	.0370	II	.2072	.6349	.2364	.2500
III	.0000	.2000	.8043	.1481	III	.0000	.1746	.6545	.0714
IV	.0000	.0171	.0217	.9259	IV	.0000	.0000	.0000	.7500
Σ	.7701	.9504	.9564	1.1851	Σ	.7207	.8889	.9636	1.1428
d_x	.2301	.0667	.0652	.0000	d_x	.2793	.1587	.2182	.1786
$\lambda = .9824$					$\lambda = .8869$				

NOTE.—Sample sizes as in fig. 3. The sum of transitional probabilities in each column exceeds one when the number of colonies alive increases from one time interval to the next, i.e., if gains from asexual reproduction exceed losses from mortality. d_x is the size-specific probability of mortality. Sexual reproduction is not included in either matrix. Lambda is the equilibrium growth constant. (Lambda less than one describes population decline.)

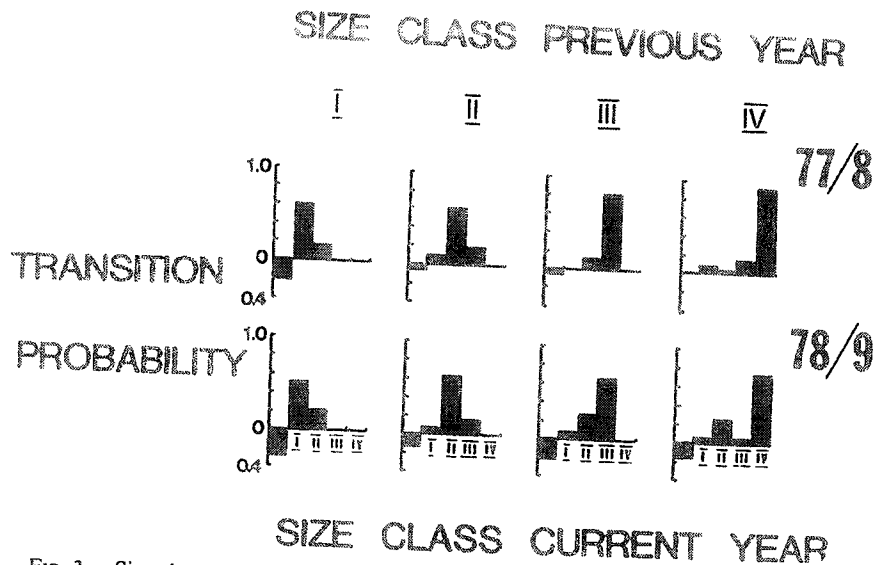


FIG. 3.—Size class transition probabilities of *A. agaricites* colonies in 1977/1978 and 1978/1979. Bars below zero represent colonies that died. Colony size was grouped as follows: I, 0–10 cm²; II, 10–50 cm²; III, 50–200 cm²; IV, >200 cm². Sample sizes are 113, 60, 46, and 27 colonies in 1977, and 111, 63, 50, and 28 colonies in 1978.

compared to small ones (Hughes and Jackson 1980). The zero whole-colony mortality rate for size class IV does not mean that colonies greater than 200 cm² are never killed; rather, it implies that mortality is preceded by shrinkage into a smaller size class. Most colonies remained in the same size class from one year to the next, reflecting the slow net growth rate of this species (<2 cm lateral extension rate per annum, Hughes and Jackson, unpubl. data). Colony fragmentation was initiated among large colonies when partial mortality severed tissue connections between polyps. Because one colony can produce several by fission, the sum of transitional probabilities in a column of the population projection matrix may overestimate survivorship, and mortality rates cannot be calculated directly from the matrix (see table 1 for the mortality rates and the matrix form of fig. 3).

The following year, in March 1979, a severe storm with waves up to 4 m high, caused extensive damage to many coral populations on the North coast of Jamaica (Tunncliffe 1980). In *Agaricia agaricites*, whole and partial mortality increased, especially in larger size classes, while there was a concomitant decrease in net rates of growth (fig. 3, table 1). In the year of the storm, there was a total absence of growth into the largest size class. Clearly, the 1978/1979 "storm" matrix cannot be too regular a demographic occurrence, or the observed population structure on Jamaican reefs would not be realized. Tunncliffe (1980) estimated that a storm of this severity only occurs about every 20 yr. The most recent severe hurricane before this storm was in 1917, and the next one was Hurricane Allen, 17 mo later in August 1980 (Woodley et al. 1981).

The deterministic Leslie matrix model defined earlier assumes transitional probabilities are constant from one time interval to the next. Frequently, however, changes in demographic parameters can result from a variety of factors, such as crowding or thinning, seasonal changes, or disasters. Sarukhan and Gadgil (1974) incorporated temporal changes in their models of buttercup populations by alternating different matrices for different seasons. A similar technique can be used here to simulate the effects of storms.

The differences between the calm and storm matrices become clearer when they are used to predict demographic behavior over a considerable time. Consider the dynamics of a single cohort, starting from an initial settlement of, say, 1,000 individuals, i.e., at t_1 , $\bar{x}$ equals [1000, 0, 0, 0]'. The population structure changes through time as surviving colonies grow into larger size classes. Using the calm matrix only (zero storm frequency) to project the dynamics of the cohort, peak numbers of colonies in the II, III, and IV size classes occur at 3, 9, and 21 years, respectively, after the initial settlement (fig. 4A). In contrast, for the storm matrix only (100% storm frequency), size classes II and III contain a maximum number of colonies after only 3 and 6 yr, while size class IV always remains empty (fig. 4B). The decreasing rate of elimination of smaller size classes from the cohort through time is caused by the formation of new, small corals from shrinking and fragmenting larger colonies. After a time, the rate of decline is constant for all size classes, reflecting an equilibrium size-frequency distribution analogous to the stable age distribution of the Leslie matrix model. The storm matrix dictates a

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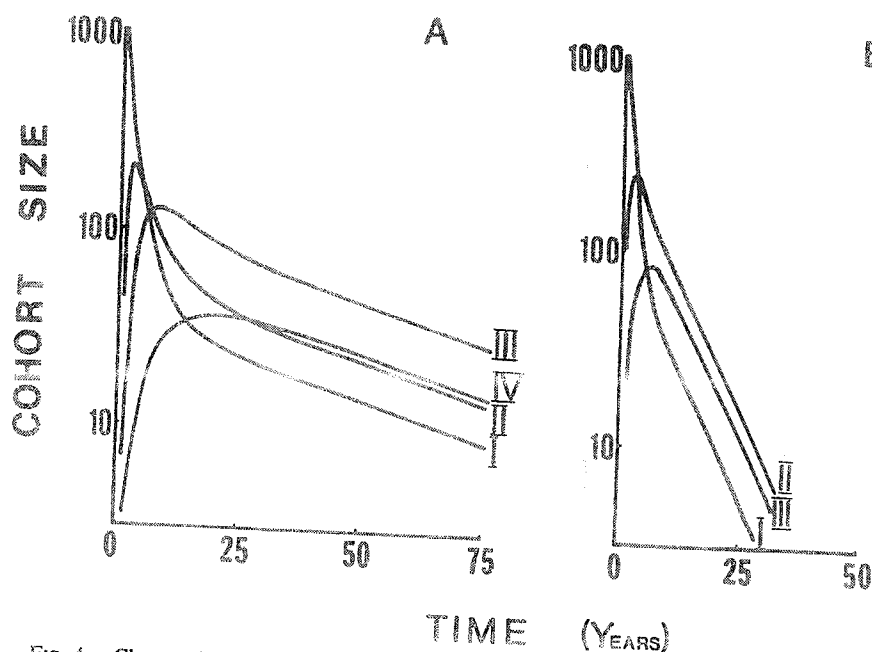


FIG. 4.—Changes in the number and sizes of coral colonies in a single cohort as a function of cohort age. Cohort behavior is projected by the rules of the calm (A) or storm (B) matrix (see table 1), from an initial settlement of one thousand colonies. Coral size classes as in fig. 3. Note that as size class I declines because of mortality and growth of colonies into larger size classes, each consecutive size group peaks and then declines to eventual extinction.

faster rate of turnover, so equilibrium size-frequency is reached much sooner, after 12 yr versus 35 for the calm matrix.

This analysis shows how differential growth causes huge variations in colony size within a single cohort (fig. 4A, 4B). Even if the size-frequency distribution within each size class is such as to minimize population variance, the ratio of variance to mean colony size of 20-yr-old colonies is over 45 for the calm population, and over five for the storm population. The exact value of this ratio is unimportant; the calculation is included to indicate how colony size can become extremely variable in a relatively short period of time because of individual differences in rates of growth and shrinkage. In addition, the coral population biomass (and presumably reproductive output) will be dominated in time by larger colonies. Colony longevity will also differ greatly between corals of equal age, because some remain small while others grow larger, and hence less likely to be killed.

In reality, of course, storms usually occur after some period of relative calm. An occasional storm would therefore have considerable impact on larger colonies which develop during more normal years. The effect of storm frequency other than 0% and 100% is modeled here by alternating the calm and storm matrices.

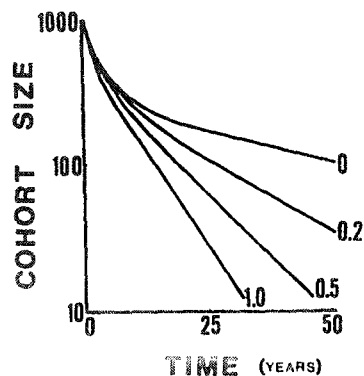


FIG. 5.—Cohort size through time as a function of storm frequency. The effect of storms was simulated by alternating the storm and calm matrices (table 1) in repeated multiplications of the population structure vector, e.g., a storm frequency of 0.2 is modeled by changing the matrix from the calm to the storm rules every fifth iteration of the simulation.

Starting again with an initial settlement of 1,000 individuals, the cohort declines to extinction at varying rates, proportionate to storm frequency (fig. 5). The rate of decline is not a linear function of number of storms, however, e.g., a doubling of storm frequency from every tenth to every fifth year would have less effect on extinction rate (λ) compared to a doubling from a 20- to a 10-yr cycle. Thus, the model predicts that the effect of a storm on the survival of a cohort is proportionately greater when it is a rare event. This prediction is independent of any conjectured acclimation by individual corals to frequent storms, and results from differences in population structure (see below).

As well as numbers of colonies, the coral population structure can be estimated as a function of storm frequency. As storms become more common, there is a steady decline at equilibrium in the relative numbers of large colonies (size classes III and IV) in the cohort, with a corresponding rise in the proportion of small individuals (size classes I and II; fig. 6). Note, however, that in absolute terms the numbers in all size classes decline as storms become more common.

Strictly speaking, only the 0% and 100% storm populations ever reach an equilibrium size structure. At intermediate storm levels, the population is perpetually recovering from the latest upset in size class distribution. This is shown by the range bars in figure 6. These indicate the variation caused by storms in population structure between t_{40} and t_{50} , well after fluctuations due to development of a size class structure from the original settlement have been eliminated.

The model predicts that population structure will change considerably along a disturbance gradient, e.g., between reefs close to, versus away from, storm tracks. The well-known phenomenon of deep-water gigantism in many species of corals (Goreau 1966; Glynn 1973) in part may result from decreased mortality and injury rates along depth gradients during severe storms (Woodley et al. 1981). Large *Agaricia* are more common in deeper water despite slower growth rates (T. P. Hughes and J. B. C. Jackson, in prep.).

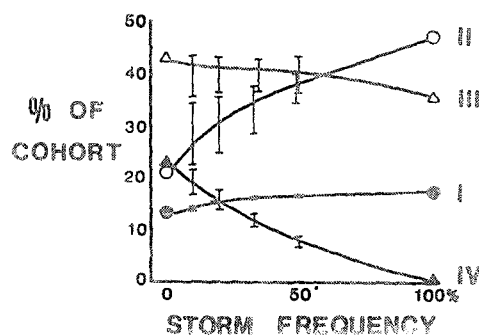


FIG. 6.—Cohort size structure between 40 and 50 yr after settlement as a function of storm frequency. The bars indicate the range in values as the cohort slowly tends to equilibrium between storms. Colony size classes as in fig. 3.

Sexual Reproduction

The analysis above shows the development of a size structure within a cohort because of differential rates of colony growth and shrinkage. In this section, I use the model to demonstrate how the rate of larval settlement will also influence population growth and structure. The probability of an individual producing sexual offspring is unknown for this and all other coral species (Connell 1973). Even if colony fecundities were known, they probably would be of very little use in predicting local population growth, because larvae are dispersed. Because of dispersal, there is a very poor correlation between a species' local population density and the rate of observed settlement (Rylaarsdam 1983). Annual larval settlement, from 1977 to 1981, into the smallest size class of the study population varied from 18 to 25 colonies per 12 m². The matrix model can be used to project population growth from annual larval input of, say, 20 colonies by adding that number to the first element of the population vector $\bar{x}$, each year. This approach makes no assumptions about size- or age-specific fecundities, but is probably a reasonable imitation of a planktonic input from a larval pool. It is of course true that the rate of recruitment in real life varied from year to year. However, a simulation run with fluctuating numbers of recruits around a mean of 20 larvae per year gave essentially the same results as those described below. The initial population structure and size will not affect equilibrium values, so for convenience I assume a local population of zero at t_1 . Using the calm matrix, the number of corals increased rapidly at first, then extremely slowly to an asymptotic level after about 250 yr (fig. 7, C_{20}).

Population growth declines to zero when the constant number of annual recruits balances the proportion of colonies dying. As the population increases in size, the number of larvae added per individual colony decreases. Therefore a constant input of recruits effectively becomes a fecundity term which is inversely related to population size. This in no way implies that mean individual reproductive output is density dependent. The number of sexual offspring produced by the coral population, whether increasing or not, is assumed to have no role in local larval

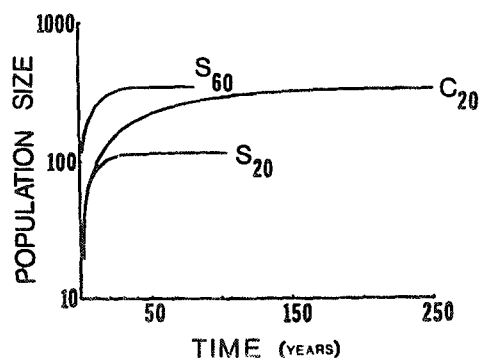


FIG. 7.—Population growth predicted respectively by the storm and calm matrices at various levels of larval recruitment. C_{20} represents a population behaving by the rules of the calm matrix, with an annual larval input of 20 colonies. S_{20} and S_{60} represent storm populations with annual inputs of 20 and 60 recruits, respectively.

input. More complex simulations could incorporate the likely decline in the rate of successful recruitment as the established population grows, e.g., by making the number of larvae added at time t_i some negative function of the area already covered at time t_{i-1} . There are no density-dependent mortality or growth terms in the simulation presented in figure 7, i.e., transitional probabilities are constant regardless of population size or structure. Yet population growth declines to zero just as it would if mortality increased as a function of population density. The length of time needed to reach equilibrium indicates how long it would take a totally obliterated population to recover if it relied solely on new sexual recruitment, probably far longer than the interval between catastrophes.

In comparison, for the same larval input of 20 colonies per yr, a population growing by the rules of the storm matrix will reach equilibrium size five times faster, after about 50 yr, but the maximum number of colonies is only one-third that of the calm population. To attain an equal number of corals at equilibrium, the storm matrix would need about 40 additional recruits every year (fig. 7).

The population structure at equilibrium for both the calm and storm matrices differs from that shown for a single cohort changing through time (fig. 4), because larval input increases the relative numbers of small corals. For the calm matrix, the relative numbers in size classes I and II increased by 17% and 31%. For the same larval input of 20 colonies, the distortion of the storm matrix population was even larger: the relative numbers of size class I increased by more than 150%, while II and III decreased by about 25% and 50%, respectively. Surprisingly, this population structure does not continue to change at higher recruitment rates. Even with 60 colonies added each year, the equilibrium size structure is exactly the same. Thus, the influence of sexual recruitment on size-frequency distribution decreases above a certain level, and may be predicted using the matrix model.

Finally, population development can be expressed in terms of area covered by using population structure and a rough estimate of mean colony size in each size

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class. With the same level of larval input of 20 colonies per year, the calm population grows to a maximum of 31% cover, while the storm population reaches only 3%. Three times the sexual input increases the storm population area to only about one-third the calm population (10% cover), even though the number of colonies is almost equal.

Biologically, this is a remarkable result. The model predicts that the measured demographic characteristics of this coral species will restrict population development, even where there is ample space remaining for settlement and growth.

DISCUSSION

The model clearly predicts that for organisms with developmental plasticity, individuals of the same age may be of very different size (fig. 4). Because of size-related variations in mortality and fecundity, individuals of the same age will have widely different capabilities of obtaining representation in subsequent generations. A corollary of variable size within a cohort is that individuals of similar size may vary greatly in age. This has been shown for colonies of *A. agaricites* by examining growth patterns in the coral skeleton (Hughes and Jackson 1980). In a similar study Mertz and Boyce (1956) showed that nearly three quarters of oak "seedlings" developing after a forest cutting were in fact sprouts attached to root systems varying in age up to 40 yr old. The age of stems inferred from size, number of terminal bud scars, and number of annual growth rings could not be used to establish the time of seed germination.

Ideally, the accuracy of predictions made by a size-staged model should be compared with a similar age-staged matrix, using long-term field observations. This has only been done once, in a 5-yr study of a nonclonal biennial plant *Dipsacus sylvestris* (Werner 1975; Werner and Caswell 1977). It was elegantly shown that various plant fates could be predicted more accurately from size than age. The size-staged matrix describing the dynamics of *Dipsacus* was relatively simple (Werner and Caswell 1977); there were no elements describing shrinkage or fragmentation, so that the decoupling of size and age resulted entirely from differential growth rates between individual plants. Presumably, the more complex development of *A. agaricites* or oak trees, and their much greater longevity, would make predictions based on age even less appropriate for them.

Historical Effects

Can size alone adequately predict the fate of an individual? The answer is often no, for a variety of reasons. One of the assumptions of the model is that there is no discrimination between individuals in a size class in the demographic options open to them. Thus, for example, all small individuals are supposed to behave identically regardless of whether they are newly settled recruits, asexually formed fragments, or a small remnant of a previously large individual that has shrunk. These distinctive demographic types will probably have rather different schedules of survivorship and fecundity. Daughter colonies of *Agaricia agaricites* usually share a common skeletal framework built before overlying tissue connections

TABLE 2
A TEST FOR HISTORICAL EFFECTS

		A. FATE OF COLONY IN 1978/1979			
		Injured	Escaped	Killed	Total
Fate in 1977/1978	Injured	50 (60.2)	15 (18.1)	18 (21.7)	83 (100)
	Escaped	37 (29.6)	61 (48.8)	27 (21.6)	125 (100)
		Chi sq. = 24.1, $P < .0001$			
		B. FATE OF COLONY IN 1979/1980			
		Injured	Escaped	Killed	Total
Fate in 1978/1979	Injured	47 (54.0)	31 (35.6)	9 (10.3)	87 (100)
	Escaped	22 (28.9)	45 (59.2)	9 (11.8)	76 (100)
		Chi sq. = 10.9, $P = .004$			
		C. FATE OF COLONY IN 1979/1980			
		Injured	Escaped	Killed	Total
Fate in 1977/1978	Injured	37 (56.9)	26 (40.0)	2 (3.1)	65 (100)
	Escaped	35 (35.7)	48 (49.0)	15 (15.3)	98 (100)
		Chi sq. = 10.3, $P = .006$			

NOTE.—A, Number (and percent) of colonies which were killed, injured, or escaped injury-free in 1978/1979 as a function of whether they were injured or not in 1977/1978. B, Number (and percent) of colonies killed, injured, or escaped injury-free in 1979/1980 as a function of past events in 1978/1979. C, Number (and percent) of colonies killed, injured, or escaped injury-free in 1979/1980 as a function of events 2 yr previously, in 1977/1978.

were severed. Because of their somewhat elevated position on top of old skeleton, small daughter colonies may avoid some sources of mortality prevalent in juvenile colonies of the same size, e.g., shading, or smothering by sedimentation. On the other hand, a small shrunken colony is often the result of partial overgrowth. If, for example, a long-lived sponge grows over and kills part of a coral, the chances are it will eventually smother the rest of the colony. These differences in fate as a function of past events may be termed historical effects. Note that historical effects are not necessarily caused by variations in age, since they also occur between individuals born at the same time. For example, Slobodkin (1954) showed that the level of food available early in the life of a cohort of *Daphnia* can produce differences in later growth rate and population structure.

A test for historical effects is shown in table 2A. All colonies surviving from 1977 to 1978 were classified as to whether they were injured or not (escaped injury-free) during that year. The injury and escape rates were then recorded for the next year, 1978/1979, as a function of this past history. The resulting contin-

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gency table shows clearly that injured corals were almost twice as likely to be injured again (chi square = 24.1, $P < .0001$, table 2A). This pattern occurs regardless of whether injury rates to the population as a whole increased or decreased. Consequently, historical effects were also highly significant the year after the storm, from 1978/1979 to 1979/1980 (chi square = 10.9, $P = .004$, table 2B). Furthermore, the fate of colonies in 1979/1980 depended on their past experiences 2 yr earlier, in 1977/1978 (chi square = 10.3, $P = .006$, table 2C). The observed decrease in the significance level of the chi-square values from 1-2-yr historical effects (table 2A, 2C) is to be expected, as injured corals recover and the demographic differences between them and uninjured colonies diminish.

Historical effects such as these probably vary considerably from year to year in both their intensity and persistence. In terms of the matrix, table 2 indicates that transitional probabilities for injured colonies into smaller size classes will tend to be higher, while growth and loop probabilities will tend to be lower relative to mean values. This trend may be somewhat offset by the common observation that rates of regeneration of damaged tissue are faster than new growth (Liming and Johnston 1944; Marshall and Sagar 1965; Loya 1976).

The model also assumes that there are no historical effects on fecundity. Again this is highly unlikely. Consider a hypothetical clonal organism which grows for a time before sexual reproduction can begin. After this prereproductive period, sexual modules develop, but are confined to the middle of the colony surrounded by nonreproductive tissue (e.g., Braverman 1963; Francis 1976). Such a reproductive colony, if it shrinks to a small size again, might still be reproductive, depending on what parts of it died, and on its physiological response to partial mortality and regression. Jackson and Palumbi (1979), Karlson (1981), and Wahle (1983) have suggested that energy depletion during regeneration results in reduced future reproductive output for a variety of clonal species.

The matrix model can take into account historical effects like these by calculating transitional probabilities for different demographic types within each stage. Human demographers often do this for simultaneous population analysis of males and females (Usher 1972). While no one has had to deal with more than two sexes, there is no mathematical limitation on the number of within-stage categories, e.g., individuals injured recently, injured a long time ago, or never injured. Unfortunately, these data do not exist yet for any nonhuman population, and their importance remains untested. Conceivably, the implied inability to distinguish between presently comparable individuals (i.e., same size or age) which will differ in the future because of unknown past experiences, could have important consequences for the outcome and variability of some experimental manipulations. Perhaps many of the differences within as well as between manipulated and control individuals are caused long before the experiment begins.

In addition to historical effects, there may be genetic or environmentally induced variation between colonies. The storm in 1979 killed 22% of the population. It is interesting to note that Hurricane Allen, which struck Jamaica in 1980, had very little effect on these corals (Hughes, table 1, in Woodley et al. 1981), probably because vulnerable colonies had already been dislodged or killed.

Community Structure

If a particular species is unable to increase its local population density, space may be available for others to coexist with it, even if they are competitively inferior. Thus, diversity is maintained by any mechanism which limits in space and time the dominance of better competitors (see review by Connell [1979]). Current models of community development and succession have focused almost exclusively on species interactions, especially competition and predation, to explain the coexistence of species between disturbances. While such interactions obviously exist and are important, the matrix model predicts that intrinsic demographic factors, e.g., the availability of recruits, could also strongly influence community structure and dynamics (fig. 7). This prediction is not new (e.g., Connell and Slatyer 1977, p. 1123; Sale 1978), but it has been somewhat neglected.

More direct inclusion in the *Agaricia* matrices of inputs resulting from sexual reproduction would require a detailed study of the relationship between coral size and fecundity, as well as information on dispersal and habitat selection. Our present knowledge of these factors, for any coral species, is disappointingly low (Connell 1973; Bak and Engel 1979; Rinkevich and Loya 1979; Rylaarsdam 1983). The model predicts that the larval input observed at Rio Bueno would be more than enough to maintain the population size and percent cover at 1977 levels, provided deviations from the demographic behavior projected by the calm matrix are small and/or infrequent.

Life Histories

The effect of changes in matrix probabilities on the population growth constant provides a powerful tool in life history analysis. For example, the effects of increased fecundity, faster growth rate, or enhanced survivorship of individuals can be examined by their effects on λ . Caswell (1978) has shown that the sensitivity of λ to perturbations in life history parameters can be calculated from the stage-specific reproductive values and the equilibrium population structure. However, the evolutionary interpretation of a size- rather than age-related reproductive value is unclear when more complex life cycles are considered. Asexually formed colonies are particularly bothersome. To be useful in evolutionary arguments, reproductive value must refer to the ability of a genotype to contribute its genes to future generations, regardless of how many bits and pieces make up its fragmented phenotype (Harper 1977; Janzen 1977). This distinction between physiologically and genetically distinctive individuals was recognized by Cook (1979) when he proposed that natural selection will favor asexual reproduction versus continued connected growth if the probability of genotype death is reduced by the formation of two or more physically separate individuals. This argument, however, neglects the fundamental role of sexual reproduction in defining fitness; i.e., if the combined reproductive output of clone mates is low, genotype fitness may be reduced even though survivorship is higher. The trade-offs involved could be examined using the matrix model presented here.

SUMMARY

Models of population dynamics based on age-related parameters do not provide accurate predictions if within-age-class variance in those parameters is high. Often the demographic fate of an individual or population may be predicted more accurately using size rather than age classifications. I describe here a general model of size-related population dynamics, based on a modified Leslie matrix. The model is designed to include demographic processes, such as fragmentation and shrinkage, which are excluded from conventional age-related demographic analysis. The parameters of the model were measured during a calm and a stormy year in a field study of a colonial, sessile coral. These data were used in computer simulations to predict the fate of a cohort over long periods of time. Measured differences in individual rates of growth and shrinkage resulted in huge long-term variations in calculated colony size, fecundity, and mortality rates, between corals of equal age. Therefore, individuals of the same age will have widely differing probabilities of obtaining representation in subsequent generations.

Population growth was simulated by adding a constant number of juvenile corals every year to the smallest size class. Although the model has no density-dependent parameters, population growth stops. The population size attained depends on the number of settling juveniles. Local populations of sessile organisms may be regulated by larval input, as well as by recurring disturbances or density-dependent interactions.

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NOTE

M. W. Miller

Corallivorous snail removal: evaluation of impact on *Acropora palmata*

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Abstract With the continuing decline of *Acropora palmata* throughout the Caribbean region, impacts of the gastropod corallivore, *Coralliophila abbreviata*, are becoming more noticeable. A snail removal experiment was performed in remnant *A. palmata* populations in the Florida Keys National Marine Sanctuary to quantify the area of coral tissue consumed by ambient snail aggregations and to assess the possible effectiveness of snail removal in conserving live coral tissue. Corals where ambient snail aggregations were removed maintained significantly more live tissue area during the 2-month experiment than those where feeding snail aggregations were left in place. The corals with feeding snails left in place lost more than 3 cm² tissue day⁻¹ on average. Thus, removal of *C. abbreviata* may be an effective measure for conserving depressed *A. palmata* populations, though secondary effects of such a manipulation remain to be carefully evaluated.

Key words *Acropora palmata* · *Coralliophila abbreviata* · Corallivore · Predator removal

Introduction

The recognition of significant predation by invertebrate corallivores has been largely restricted to Pacific echinoderms such as *Acanthaster planci* and *Eucidaris thouarsii* (e.g. Glynn et al. 1979; Moran 1986). Corallivorous gastropods such as *Drupella* spp. in the Indo-Pacific and *Coralliophila abbreviata* in the Caribbean have also at times been acknowledged for their significant impact on coral prey (Brawley and

Adey 1982; Knowlton et al. 1990; Turner 1994). Knowlton et al. (1990) suggested that the impact of *C. abbreviata* may be enhanced when coral prey species abundance was diminished by other factors (e.g. by hurricane damage).

Acropora palmata and *A. cervicornis*, common prey species of *Coralliophila abbreviata*, have undergone widespread decline throughout the Caribbean region (reviewed in Aronson and Precht 2000), leading the US federal agency responsible for marine and estuarine endangered species (NOAA Fisheries) to designate them as candidates under the Endangered Species Act (Diaz-Soltero 1999). In the Florida Keys, USA, multiple factors, including winter cold kills, summer bleaching, hurricanes, and various disease syndromes have contributed to this decline over the past 2 decades (Dustan and Halas 1987; Porter and Meier 1992) and over the past 2 years (personal observation). Recent survey work (1998–1999) in the Florida Keys has shown *C. abbreviata* to be present in all eight remnant *A. palmata* patches that were sampled (Baums et al., in preparation) and visually obvious coral loss to snail predation was observed in at least half of these sites.

Efforts to control invertebrate predators (specifically *Acanthaster planci* and *Drupella cornus*) in order to protect coral populations have been made at a range of scales, but have been judged inefficient or unsuccessful (Yamaguchi 1986; Johnson et al. 1990; Osborne and Williams 1992). These studies judged success on their effectiveness of suppressing predator abundance. No effort was made to evaluate success based on improved coral survival and/or growth.

The small-scale experiment described here was designed to evaluate the impact of ambient snail predators on remnant *Acropora palmata* populations (and, hence, the potential effectiveness of targeted predator removal in conserving *A. palmata*). The persistence of coral tissue was quantified in the presence, absence, and after experimental removal of the corallivorous snail, *Coralliophila abbreviata*.

M. W. Miller
NOAA Fisheries, Southeast Science Center,
1 Virginia Beach Dr, Miami, FL 33149 USA
E-mail: margaret.w.miller@noaa.gov
Tel.: +1-305-3614561; Fax: +1-305-3614562

Methods

The experiment was conducted at two sites in the Florida Keys National Marine Sanctuary, French Reef and Pickles Reef. These sites (5–9 m depth) contain remnant, individual *Acropora palmata* colonies, rather than the characteristic thicket configuration. The irregular, arborescent morphology of *A. palmata* makes quantification of tissue area difficult. Thus, individual snail-infested colonies were selected which had obvious snail feeding scars on exposed surfaces of the colony, to allow access by a Nikonos close-up framer for quantitative photo-monitoring of each treatment. Selected colonies appeared to be otherwise healthy.

An individual branch or basal tissue margin was the experimental unit, as *Coralliophila abbreviata* feed in aggregations along tissue margins advancing from the base of a colony outward to the branch tips. One branch with feeding snails was designated as the predation treatment and snails were left in place; one branch with feeding snails was designated as the removal treatment and the snails were removed from the area; one healthy branch with no snails present was designated as the control. In most cases, all three treatments were designated on a single colony. However, given the small number of colonies in these remnant populations (e.g. only 17 total colonies in the Pickles population) and the small size of many partially dead colonies, this was not always possible and the three treatments for one replicate were spread among adjacent colonies. A cable tie was placed around each experimental unit to provide a benchmark from which to measure tissue margin advance or retreat (i.e., tissue gain or tissue loss).

Ten replicates of each treatment were established between 23–25 June 1999, seven at French reef (involving a total of eleven colonies) and three at Pickles reef (four colonies). The experiment was monitored a total of six times during the 2-month experiment at intervals of 4 to 11 days. At each visit a census of snails present in each replicate was taken, and the snails were repositioned (i.e., snails moving into removal treatments were removed and, if all snails had left a predation treatment replicate, two to four snails were placed there from a nearby colony). Photographs of each replicate were also taken at each visit, with snails left in place. In most cases, the monitoring photographs were taken with a Nikonos close-up framer with 28-mm lens (total area ~300 cm²) but in cases where coral loss was large (extending beyond the 300-cm² framer area), the close-up lens was removed to view a larger area. In these cases, a scaled PVC frame was included in each photograph to aid in calibrating the image for quantifying surface area.

At the end of the experiment, the first and last photograph (59-day duration) from each experimental unit was scanned with a Minolta Dimage Scan Speed F-2800 slide scanner and the images were analyzed (cm² of dead tissue) using SigmaScan Pro 4.0 software (Jandel Scientific Software, San Rafael, CA) to quantify change in live coral surface area. In a few cases, an earlier end photograph was chosen from the time series if (1) the entire colony or region of the colony died within the experimental period (two cases) or (2) there was a mismatch in the angle or placement of the last photo in the time series that precluded accurate area determination (six cases). Thus, data for each replicate was standardized to cm² of tissue lost per day.

Because treatments were most often situated on the same (or adjacent) colonies, the response variable (cm² tissue lost per day) was analyzed using a randomized block design. Treatment and experimental block were the factors in a two-way ANOVA after verifying normality and homogeneity of variances assumptions. Dunn's a priori comparisons were used to compare the predation and removal treatments with the controls.

Results and discussion

For six censuses conducted during the experiment, the experimental removal treatments reduced snail incidence by 81% on average (Table 1).

Table 1 Snail incidence observed at each of six censuses throughout the experiment, given as mean number of snails per replicate (1 SD). Treatment effectiveness is described as the percent reduction in snail incidence in the removal treatment. No snails were found on any of the controls throughout the experiment

Date	Predation treatment	Removal treatment	Reduction (%)
6 July	3.8 (2.3)	0.63 (0.92)	83
10 July	2.5 (1.8)	0 (0)	100
19 July	2.4 (1.4)	0.25 (0.46)	89
23 July	2.6 (2.0)	0.30 (0.67)	88
3 Aug	2.2 (2.1)	0.80 (1.4)	63
23 Aug	1.8 (1.9)	0.70 (1.3)	61
Mean			81

The blocked ANOVA showed a significant treatment effect ($p = 0.003$, Fig. 1) but no significant block effect ($p = 0.191$). *Acropora palmata* colonies lost significantly less tissue when snails were removed than when snails were left in place. The removal treatment did not differ significantly from the healthy controls that had not been subject to snail feeding (Dunn's test, $p > 0.05$, Fig. 1). *Acropora palmata* branches on which snails were left in place suffered a mean loss of live tissue of 3.37 cm²/day (range 0.08 to 10.9 cm²/day). Both replicates that displayed complete mortality (out of a total 33 used in the experiment) were in the predation treatment.

These results indicate that *Coralliophila abbreviata* can have a substantial impact in removing coral tissue, and that targeted predator removal can have beneficial impacts in conserving live tissue of *Acropora palmata* colonies. Other sources of mortality may have also been operating in this experiment, such that 3.37 cm²/day may be an overestimate of snail-induced coral mortality. However, the fact that incomplete (81% effective) snail

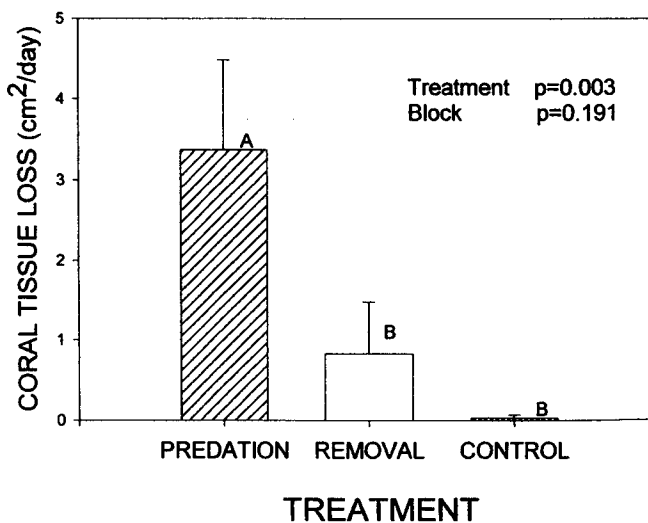


Fig. 1 Tissue loss rates from *Acropora palmata* (mean + 1 SE) under three levels of experimental removal of corallivorous snails. P -values are from a blocked ANOVA, $n = 10$. Treatments with the same letter do not differ significantly from each other ($p > 0.05$, Dunn's a priori comparisons)

removal had a large influence on tissue survival strongly suggests that snail predation was the dominant source of the mortality observed in this experiment.

The importance of quantifying surface area of coral loss in this experiment dictated the use of sub-colony experimental units (i.e., individual branches). The resulting coexistence of different treatments on a single colony probably reduced the effectiveness of the removal treatments, as *C. abbreviata* is fairly mobile on *Acropora* hosts (Hayes 1989). If snail removal was undertaken on a larger scale, whole colony removal would likely be more efficient in excluding snails than was observed in this experiment.

Small-scale (and incomplete) corallivorous snail removal in remnant *Acropora palmata* populations in the northern Florida Keys did preserve 75% (mean) more live *A. palmata* tissue than treatments where snails were left alone. Thus, targeted predator removal might be an effective conservation measure. However, effectiveness is far from the only consideration in evaluating the advisability of a management intervention. Other ramifications of such a manipulation in a complex coral reef community (e.g., the role of snails as prey for other reef residents) remain to be carefully evaluated.

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J.C. Bythell · P. Pan · J. Lee

Three-dimensional morphometric measurements of reef corals using underwater photogrammetry techniques

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Abstract We describe a novel technical approach to accurately measure surface area and other morphological characteristics of corals and similar irregular objects from underwater photography. A standard Nikonos camera system was used with a slide-scanner to produce multiple overlapping images of the object. PhotoModeler software was used to process the images and build a 3-D model of the object, which was subsequently analyzed using 3-D computer-aided design (CAD) packages. The accuracy of the technique was tested on irregularly shaped polystyrene models of known dimensions and on preserved coral skeletons. The technique was applied to the quantitative assessment of partial mortality in corals, but many applications are possible, including surface area measurements to standardize ecophysiological studies in the field and morphometric analyses. It represents the only noninvasive technique we are aware of for determining surface areas of large corals in the field. The most serious limitation of the technique is the time-consuming nature of the process, which increases with the complexity of the object and precludes many routine applications.

Keywords Coral surface area · Morphology · Photogrammetry · 3-D modeling

J.C. Bythell (✉)
Department of Marine Sciences and Coastal Management,
University of Newcastle, Newcastle upon Tyne,
NE1 7RU, UK
E-mail: j.c.bythell@ncl.ac.uk
Tel.: +44-191-2226659
Fax: +44-191-2227891

P. Pan
Department of Maritime Studies and International Transport,
University College of Wales at Cardiff,
Cardiff, CF1 3YP, UK

J. Lee
"Virtually Unlimited", 5 Mount Pleasant Close,
Kingskerswell, Devon, TQ12 5JH, UK

Introduction

Surface area is a fundamental determinant of the biological and physical processes affecting an organism. In scleractinian corals, as with many other organisms, surface area measurements are routinely used to allow indirect estimates of biomass and other measures related to photobiology (Myers et al. 1999; Lesser et al. 2000), nutrient dynamics (Hoegh-Guldberg and Williamson 1999), symbiont population regulation (Jones and Yellowlees 1997; Lesser 1997; Fagoonee et al. 1999), reproduction (McGuire 1998), and other ecologically important processes (e.g. Sharp et al. 1997; Hill 1998). However, this "routine" use belies the fact that obtaining accurate and repeatable measures of the 3-D surface area of highly irregular objects, such as corals, is problematic.

Perhaps the most widely practised method for measuring the surface area of corals, developed by Marsh (1970) for use with calcareous algae, involves wrapping the object tightly with aluminum foil, trimming the excess, and determining surface area using a surface area-to-mass calibration. A variation of the technique is to use a thin sheet of latex rubber for the covering (Meyers and Schultz 1985). Other similar techniques involve quantifying the amount of wax added after dipping the coral skeleton in molten wax (Stimson and Kinzie 1991) or analyzing the amount of dye adhering to previously plastic-coated skeletons (Hoegh-Guldberg 1988). All these methods are destructive, since they can only be applied once the coral is removed from the water, and they are only readily used on small corals or coral fragments that can be easily removed. The use of coral fragments in ecophysiological studies may introduce errors due to the stress of tissue damage during collection, the smaller collective resources available to the colony, and reversion of the colony to a nonreproductive juvenile stage (Szmant 1986, 1991). The routine measurement of only small or juvenile corals a few centimeters in diameter is also extremely restrictive in a group

of organisms that may reach several meters across (Soong et al. 1999) and in which both size and age are important characteristics of ecological function (Soong 1993; Meesters and Bak 1995; Bak and Meesters 1998). There is therefore a clear need for a non-invasive method to measure 3-D surface area of corals and other organisms in situ, unrestricted by size limitations.

Morphometric measurements of corals in situ have previously been limited almost exclusively to easily obtained linear measurements such as diameter and height of the colony. Estimating surface areas or volumes has only been possible for simple branching, plating, or blade-like morphologies (Hughes and Jackson 1985; Ben-Zion et al. 1991; Tanner 1995). Even then, obtaining accurate measurements of the surface has only been achieved using complex and bulky equipment underwater (Ben Zion et al. 1991), and is not feasible for the majority of applications. True 3-D measurements of surface geometry can, however, be obtained from underwater imagery, using the principles of photogrammetry (Wolf 1985). Photogrammetry has been previously applied to coral reef studies to correct planar (2-D) measurements of surface-area cover for perspective errors due to reef topography (Done 1981), but not to produce 3-D surface measurements.

Here we describe the use of commercially available photogrammetry software (PhotoModeler, EOS Systems Inc.) to obtain measurements of the surface geometry of corals from multiple angle photographs taken using a standard Nikonos underwater camera and digital slide scanner. Morphometric measurements such as diameter, height, 3-D surface area, and volume were obtained using standard 3-D CAD (computer aided design) software. The accuracy of the process was assessed using models of known dimensions with varying levels of complexity. For real coral skeletons with unknown geometry, surface area measurements were compared to the standard technique of foil wrapping developed by Marsh (1970).

Materials and methods

Image acquisition

In order to be widely applicable, we purposely developed the methods described here using standard underwater photography and scanning equipment. The accuracy of the process depends to some extent on the optical quality of the image produced (i.e. camera/scanner combination), but there is no fundamental reason why other camera/scanner combinations could not be used successfully, and the techniques should be particularly amenable to digital photography.

Underwater photography was carried out using a Nikonos V camera with 28-mm UW Nikkor lens and TTL light-metering using twin Nikonos SB103 strobes. The 28-mm lens was chosen over the wider-angle Nikkor 20- and 15-mm lenses due to lower edge distortion and lower cost. Kodak Ektachrome 100 ASA, 35-mm slide film was used and slides were scanned using a Nikon Coolscan II slide scanner. A resolution of 1,200 dpi (approximately 2-MB images) gave optimal quality for picking out control points with the highest precision. Lower quality images generated on a flat-bed

scanner were also useable, but not ideal, and the extra time involved in setting up and selecting individual photographs was prohibitive.

Image processing and analysis

Image and model processing were carried out on a Pentium 200 MHz personal computer with 64 MB RAM, running PhotoModeler version 2.1 or 3.1 software (www.photomodeler.com). Version 3.1 of the software provides some considerable time-saving features. Models were exported from PhotoModeler in AutoCAD Dynamic Interchange Format (*.dxf) and were analyzed for geometric information using AutoCAD or DesignCAD 3D software. Wire-frame and photographically rendered 3-D models were also successfully exported to Virtual Reality (VRML 2) format, which is useful for viewing 3-D images of models in relation to the original photographic images.

Generating 3-D models

In practice, several photographs are taken of the object from various angles, digital scans of the images are displayed on screen, and the operator marks control points in each image. The operator references the control points to indicate which points are identical in different images (Fig. 1). In order to process the model correctly, it is necessary that each marked point is located on three or more images and that the angle between camera stations is close to 90°. To do this, we have found that at least 8, and often 10 or more, overlapping images are needed, completely encircling the specimen to be measured. The number of photographs required increases with the complexity of the object. We have used up to 20 photographs to adequately model some coral specimens. There is no requirement to measure the position of the camera or to use fixed camera positions, although it helps the operator to interpret the images if the approximate positions are recorded.

The camera/scanner combination is calibrated using a similar set of photographs, taken off a standard test-pattern card, which is analyzed using a subroutine of the PhotoModeler program. Since this is focal length-dependent, it is simplest to maintain the same focusing distance throughout, in order to avoid having to use a range of different camera calibration solutions on the same project. The surface areas of complex, irregular objects such as corals were determined by producing a composite of triangular planes to fit the entire surface of the object and summing their individual areas (Fig. 1). The model is scaled using an object of known dimensions in at least three of the images. It is not necessary that the scale is visible in every photograph.

Assessing model accuracy

There are various stages at which errors can be introduced. The most fundamental is in the scaling and processing carried out within PhotoModeler, but this error is dependent on the optical properties of the image-acquisition system (i.e. the camera-scanner combination). We have tested the accuracy of models produced at this stage with the equipment and procedures outlined above using underwater photographs of simple cube framers of known dimensions constructed from metal bar (Fig. 1). Three known faces of a cube framer (total surface area = 0.771 m²) were used to assess measurement errors due solely to the scaling and processing procedure.

Using the simple cube-framer model involves no operator error due to the choice of appropriate control points (the eight corner points are used), minimal error due to the precision of point location on related images, and no error due to misidentification of control points. Additional errors will be incurred with the modeling procedure, due to the inherent inaccuracy of estimating curved surfaces from intersecting flat planes and the problem of obtaining good photographic coverage in crevices, particularly on more complex structures. The errors introduced due to the complexity of

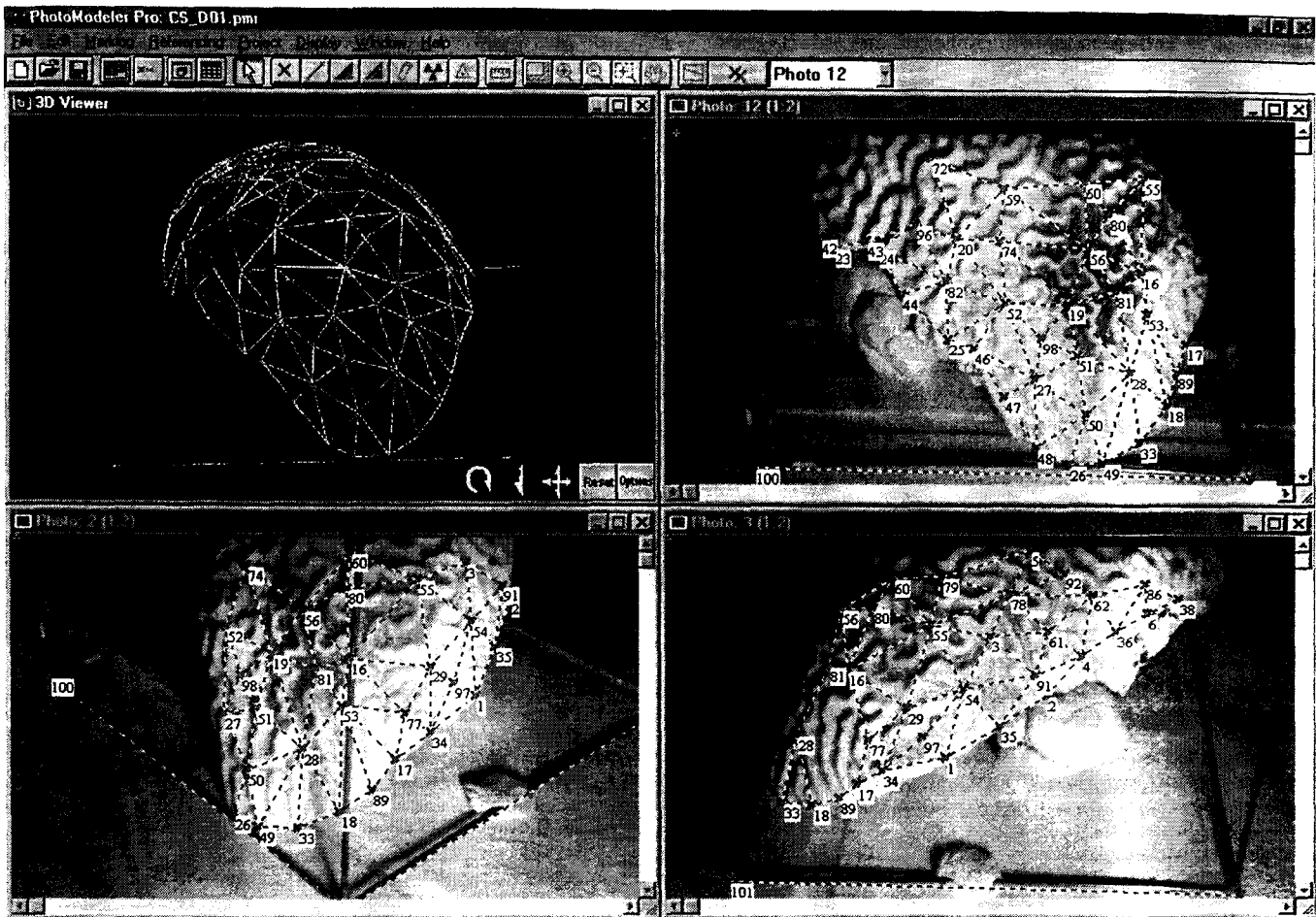
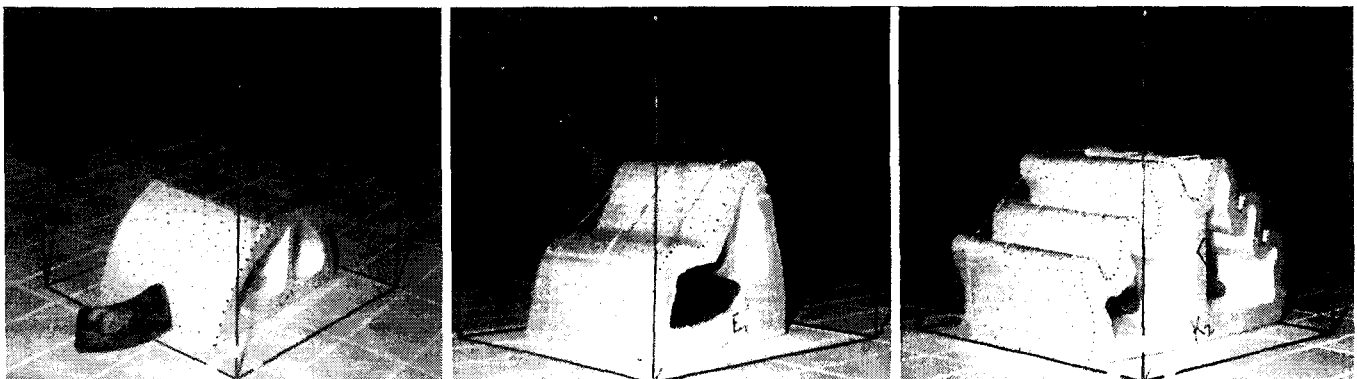


Fig. 1 Marking and referencing control points in PhotoModeler 3.0. Control points are tagged with a unique identifier and identical points on the object are cross-referenced in different photographs. For example, adjacent points 33, 28, and 18 appear in all three photographs. The processed, scaled model is shown *top left*, with orientation similar to that of photograph *top right*. In this example, a cuboid framer has been used to provide a scale, but this is not necessary so long as two points of known distance apart are present in some part of the scene being modeled. Framer cube dimensions are 15 cm on a side

The errors associated with estimating curved surfaces from intersecting triangular planes were investigated by “decomposing” models by removing randomly chosen points from completed models. Since this procedure depends to some extent on the adequacy of the original model, one coral skeleton was repeatedly remodeled using an increasing control point density with control points chosen independently at each stage. Results were compared with those obtained with the standard foil-wrapping technique of Marsh (1970). The relationship between the foil-wrapping technique and the 3-D modeling process was further investigated on a

the object were, therefore, first investigated using polystyrene models of three levels of complexity (Fig. 2). The models were constructed from 30-cm polystyrene block, thus giving a fixed dimension that allows their surface area to be simply and accurately measured using a flexible tape measure.

Fig. 2 Examples of polystyrene models used to assess additional errors introduced when modeling irregularly shaped objects. Five models were used of each of three levels of topographic complexity, from simple hemispherical (*left*) to the most complex (*right*). Framer cube dimensions are 50 cm on a side



variety of dried coral skeletons and fragments, with surface area determined by both techniques.

Results

When faces of a simple cube-framer were modeled using the techniques described, there were no significant differences between the actual and modeled surface area (one-sample t-test, $t=1.44$, $p=0.18$). The mean percent error was -0.21% , with a standard deviation of 0.47% ($n=10$) for the area chosen of 0.771 m^2 . The optical qualities of camera and scanner equipment used in the study are therefore sufficient to produce a highly accurate 3-D model of objects underwater using the PhotoModeler system.

When modeling polystyrene objects of known dimensions with varying topographic complexity, the results indicated that the process may have slightly underestimated the true surface area; however, the difference was not significant overall (paired samples t-test, $t=2.05$, $p=0.059$), with a mean percent error of only -0.85% and standard deviation of 1.18% ($n=15$). Although the variance increased slightly at the highest complexity (Table 1), there was no significant effect of

Table 1 Mean deviation (%) and standard deviation of surface areas of polystyrene models assessed by photographic modelling compared with direct measurement

	Simple	Moderate	Complex	All models
Mean deviation model:measured	-0.8%	-0.8%	-0.9%	-0.85%
Standard deviation	0.85%	0.72%	1.91%	1.18%
<i>n</i>	5	5	5	15

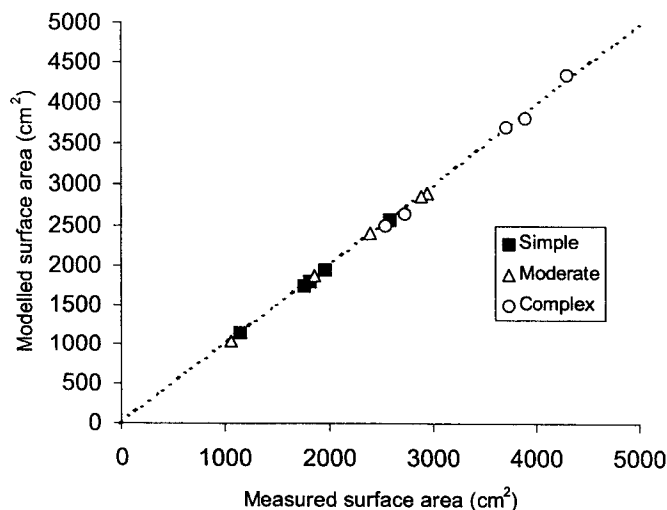


Fig. 3 Relationship between modeled and measured surface area of the 15 polystyrene objects of three levels of topographic complexity (simple, moderate, and complex; Fig. 2). Dashed line indicates 1:1 relationship. There was no significant effect of complexity on modeled surface area (ANCOVA, $F=0.43$, $p=0.662$)

model complexity on the very tight relationship between modeled and measured surface area (Fig. 3, ANCOVA, $F=0.43$, $p=0.662$). The additional errors associated with modeling these irregular objects over those found using the simple cube framer are apparent, but the difference is less than 1% of the surface area of the object.

There was a consistent asymptotic relationship between the surface area defined by the model and the density of control points used (Fig. 4), which can be explained by the relationship between the flat planes used for surface measurements and the curved surface of the coral. As the density of points is increased, the closer the adjacent planes fit to the true curved surface. Repeatedly remodeling the same coral skeleton with an increasing control point density suggests that a density of 0.25 to 0.4 cm^{-2} was sufficient to produce an adequate model (Fig. 5).

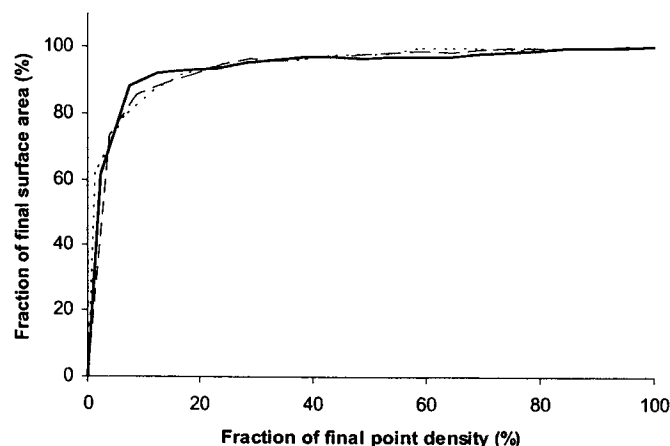


Fig. 4 Results of sequentially reducing control point density of coral models on surface area determined. Results for three different corals with similar, broadly hemispherical morphology are shown

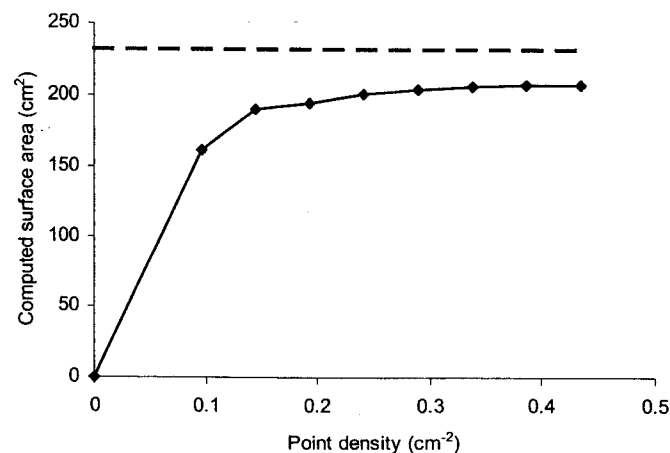


Fig. 5 Surface area of a head of *Diploria strigosa* repeatedly remodeled using an increasing point density. The asymptotic surface area obtained (207 cm^2) was 11% lower than that obtained by foil-wrapping technique ($232 \pm 20.5 \text{ cm}^2$; mean $\pm 95\%$ confidence interval), shown by dashed line

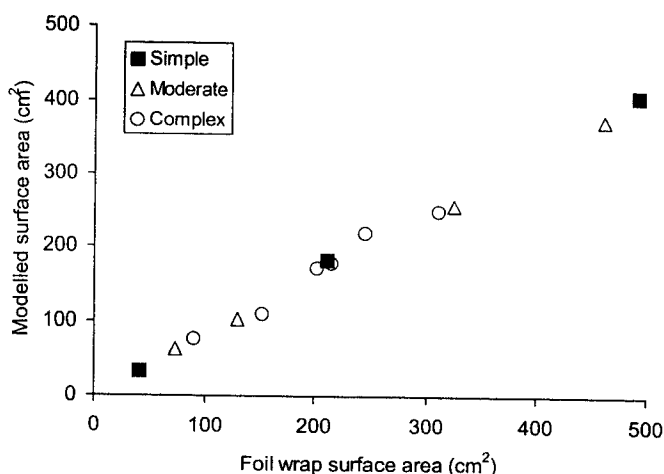


Fig. 6 Relationship between surface area determined by the foil-wrapping technique and by 3-D modeling technique for a variety of coral skeletons (Table 2). There was no significant difference in the relationship for different complexities of coral morphology (ANCOVA, $F=0.06$, $p=0.94$), but the modeled surface area was consistently lower than that of the foil-wrapping technique (linear regression, $y = 0.78 + 0.82x$, $r^2 = 0.99$)

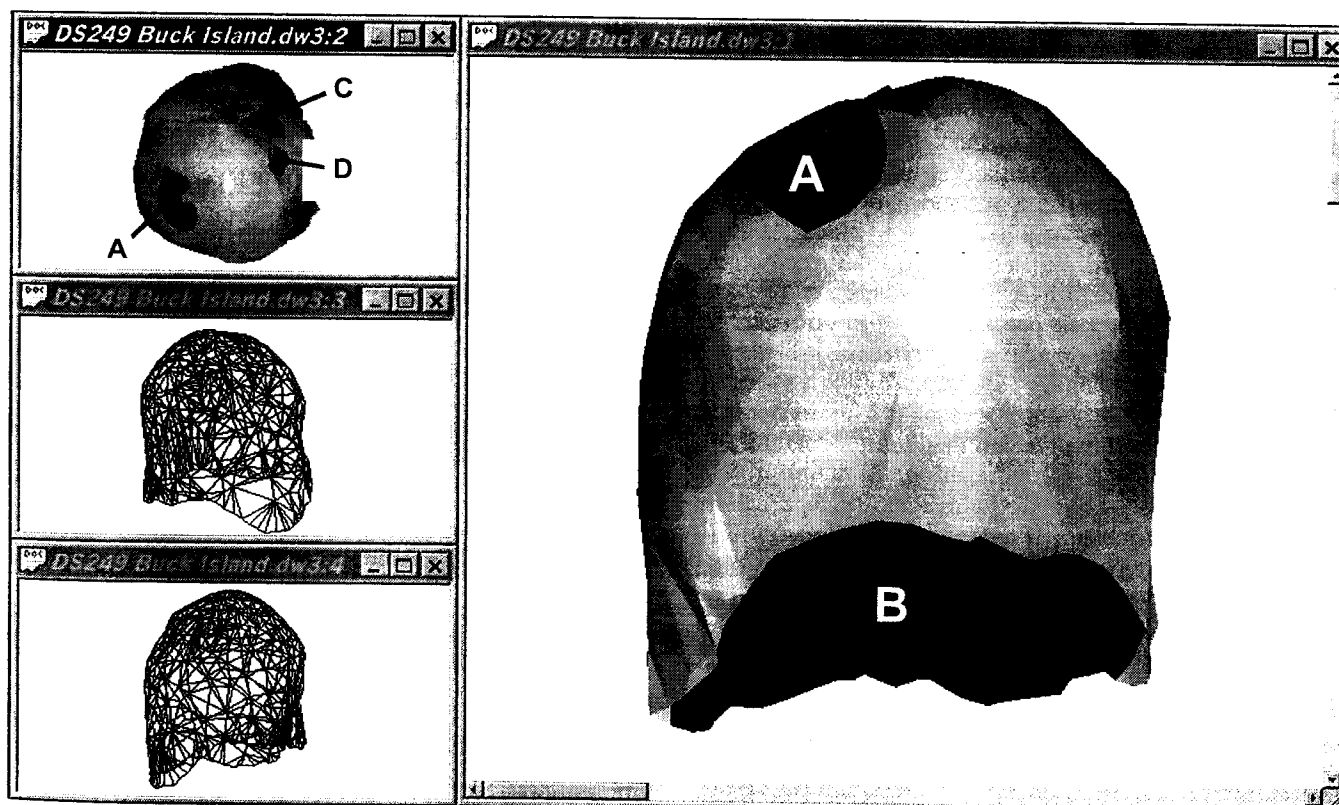
Using the foil-wrapping technique of Marsh (1970), we have found a precision (standard deviation) of between 0.4 and 3.3% (mean = 1.7%) of the surface area for three replicate determinations of corals ranging between 42 and 455 cm² ($n=13$). Thus, the accuracy and precision of the photographic modeling technique used on the polystyrene models appear to be comparable to or better than the precision obtained using the standard foil-wrapping technique on corals. However,

Table 2 Times recorded to produce the 3-D model of coral colony DS-249 (Fig. 6). Times do not include calibration (3 h 25 min), which must be completed once for each camera lens setting and scanner combination. Processing times will vary with computer specification but is an unattended operation

Operation	Time taken
Photography	45 min
Film scanning	1 h 30 min
Control point marking and cross-referencing	4 h
Process	10 min
Importing images	10 min
Extras (disc copying, etc.)	30 min
Total	7 h 5 min

direct comparison of the foil-wrapping technique and the photographic modeling technique using dried coral skeletons showed that there is an approximately 11% difference between the two techniques (Fig. 5). Consistent differences were found between the two techniques using corals with different morphologies, although there was no apparent effect of morphological

Fig. 7 Computer-aided design (CAD) model of coral colony DS-249 at Buck Island Reef National Monument, part of a long-term monitoring program in the US Virgin Islands. Patches of dead tissue (A-D) have been dark shaded. Three-dimensional measurements taken from the CAD model allow extent of such lesions (surface area of partial mortality) to be quantified: A 350 cm², B 1,125 cm², C 191 cm², D 73 cm². Total colony surface area = 16,954 cm², maximum colony diameter = 58 cm, and maximum colony height = 90 cm



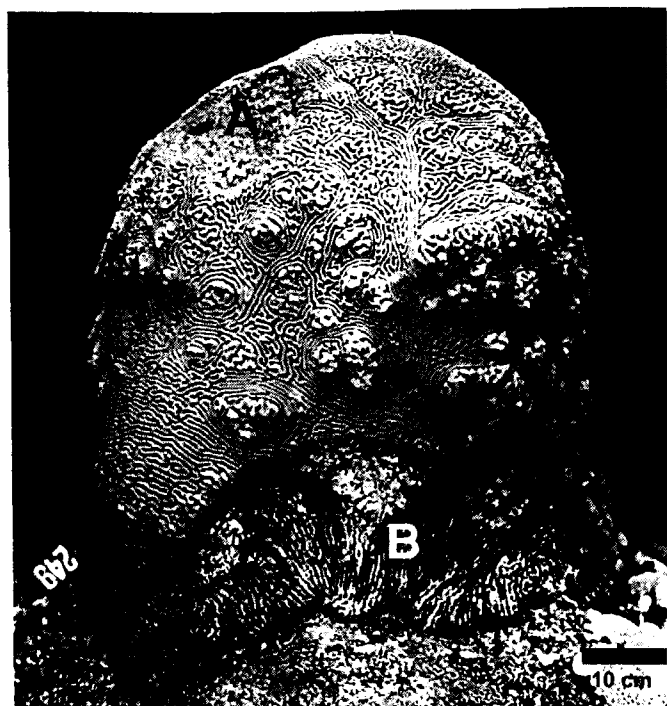


Fig. 8 One of the photographic images of coral DS-249 used to generate the CAD model in Fig. 7. Two of the patches of dead tissues highlighted in the model (main panel, Fig. 7) are clearly visible. Patch A (350 cm^2) was caused by an episode of black-band disease, whereas patch B ($1,125 \text{ cm}^2$) was created by damselfish predation/grazing

complexity in the relationship between techniques (Fig. 6, Table 2).

To demonstrate an application of the photographic modeling techniques described here, we used PhotoModeler to produce a 3-D model of coral DS-249, which has been part of a long-term monitoring program carried out by the US National Park Service in the US Virgin Islands since 1988 (Bythell et al. 1993). The colony is 58 cm maximum width by 90 cm maximum height and was photographed using a 28-mm Nikonos lens from a distance of approximately 1 m. Over the course of the past 9 years, DS-249 has been subject to four separate episodes of black-band disease and one episode of an unknown disease, exacerbated by tissue grazing by

damselfish (Figs. 7 and 8). This study has allowed us to take quantitative measurements of the relative severity of each of the disease episodes, which in total have caused $1,739 \text{ cm}^2$ or 10.3% (percent of the colony surface area) mortality to the colony.

Discussion

The methods developed here allow in situ nondestructive measurements of the 3-D geometry of corals and other irregular structures to be taken underwater. We have concentrated here on the measurement of 3-D surface area since a potential application is the standardization of ecophysiological studies of corals and related organisms to surface area (and hence to related variables such as tissue biomass, protein content, and symbiont population density). For the first time, accurate quantitative studies of the physiological responses of coral colonies of any size are feasible in situ. The technique is also applicable to other important morphometric measurements such as branch spacing, density, fork length, and fork angles of branching species (Bruno and Edmunds 1998) and the quantification of microenvironments within coral heads related to irradiance and water flow (Lesser et al. 1994; Helmuth et al. 1997; Rowan et al. 1997).

Given the high accuracy achieved with the photographic modeling technique using polystyrene models, the 11% difference between this technique and the established technique of Marsh (1970) when a real coral head was repeatedly remodeled was surprising. However, assuming that the coral head was truly hemispherical, the difference in surface areas translates to a radial difference of only about 2.5 mm. Using a variety of coral skeletons, the foil-wrapping technique consistently produced a 20% larger surface area estimate than the 3-D modeling technique (Fig. 6). It is possible that the foil-wrapping technique overestimates the true coral surface area (defined in this study as the smoothed surface lying perpendicular to the coral skeleton growth axis, intersecting the most distal skeletal structures) because the foil cannot form a perfect fit to the object. Hoegh-Guldberg (1988) similarly found that foil-based measurements were 19% larger than the dye-based method

Table 3 Total processing times for a variety of coral skeletons with different complexities of morphology. Processing time does not include photography or film scanning (9–12 photographs were used per colony), adding another 45–60 min to each project

	Simple	Moderate	Complex
			
Examples used			
	<i>Diploria strigosa</i> , <i>Diploria labyrinthiformis</i>	<i>Porites astreoides</i> , <i>Platygyra daedalea</i>	<i>Acropora palmata</i> , <i>Agaricia agaricites</i>
<i>n</i>	3	4	6
Mean size (range) (cm^2)	209 (34–408)	200 (64–375)	169 (77–250)
Mean point density used (range) (cm^{-2})	0.52 (0.22–0.99)	0.64 (0.37–1.08)	0.56 (0.44–0.70)
Mean modelling time (range) (h)	3.1 (2.75–3.5)	3.5 (1.45–6.0)	3.2 (2.0–4.0)

for estimating surface area and suggested that at least some of the error was due to overlap errors when foil wrapping. We are currently investigating this relationship further to establish the difference between the true accuracy of the two techniques using real coral skeletons. This problem is not trivial, however, since the surface area, as defined, is imaginary. The actual surface area depends on the scale of measurement. The solution will probably be to create the defined surface artificially (by stretching a plastic covering over the coral skeleton, for example) and using a laser scanner to determine the surface area. In any case, it is clear that the repeatability of the photographic modeling technique is at least comparable to that of foil wrapping. The definition of the 3-D surface used here was chosen to represent the gross morphological variation of the coral colony and for application to physiological studies where related variables, such as zooxanthellae densities, tissue biomass, etc., could be determined from tissue subsamples.

A significant advantage of the photogrammetry method is that no framer or other device is necessary in order to fix the position of the camera. Nor are stereo pairs required or any other direct measurement of relative camera positions. The method is therefore completely noninvasive, requiring only one known measurement between two fixed points to provide a scale (most easily achieved by laying a ruler or similar scale adjacent to the object being photographed). All images can be produced with a single camera, minimizing costs.

The only significant limitations of the technique are the time-consuming nature of the modeling process (Tables 2 and 3) and the increasing difficulty of modeling coral species with more complex morphologies. The most complex corals cannot be adequately modeled with this technique, since it is impossible to obtain complete photographic coverage of all surfaces. The time requirements (ca. 3–4 h for a small coral colony) will preclude many routine uses. However, the technique represents the only noninvasive way to obtain accurate geometric measurements of larger corals and other irregular objects underwater. For applications requiring only linear measurements of the 3-D structure, such as branch spacing and density, the processing time will be much shorter than those quoted, since only a relatively small number of points need to be referenced.

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The importance of evaluation, experimentation, and ecological process in advancing reef restoration success

Margaret W. Miller¹

Abstract The practice of coral reef restoration in the past has been largely confined to replacement of habitat with artificial structures and the transplant of coral colonies or fragments, either borrowed from nearby populations or rescued from the disturbance. Despite lip-service paid to monitoring in most restoration plans, the rigorous evaluation of these efforts has been, often, lacking completely and the declaration of success is often based on the most rudimentary criteria (stability of artificial structures or survival of x% of coral transplants). In very few cases, restoration projects have been designed to test the effectiveness of different restoration approaches (e.g. structure designs) in enhancing the biological performance (e.g., recruitment, growth, disease susceptibility) of key organisms and, in even fewer cases, in enhancing community function. However, these studies demonstrate the power of an adaptive management approach to restoration; that is, rigorously evaluating the ecological performance of alternative restoration approaches in order to do better in the future. Specific evaluative examples from other shallow coastal systems suggest that ecological success can be enhanced by simple and inexpensive restoration approaches. If coral reef restoration is to advance beyond its current build it and they will come paradigm, an experimental approach and the evaluation and implementation of ecological restoration measures built upon our understanding of reef community process and function must be pursued.

Keywords Restoration, Monitoring, Evaluation, Experimentation

Introduction

Coral reef restoration in the United States of America is largely confined to acute impacts such as ship groundings. Restoration approaches in this

context primarily consist of engineering activities, specifically, the constructional repair of damaged reef framework and the transplantation of adult coral colonies, either from undamaged reefs or rescued from the incident itself. Enhancing recovery of ecological function is one of the design criteria for structural restoration projects, but factors such as cost and aesthetics are also considered. In the past five years, the US National Oceanic and Atmospheric Administration has undertaken several reef restoration projects in the Florida Keys National Marine Sanctuary.

The engineering success of these structural restoration projects has been quite high. That is, restoration structures are mostly stable through hurricanes, and transplanted corals usually stay attached, survive and grow. However, the net benefit of coral transplantation is unclear when transplants are taken from already-depleted donor populations (as is the case in the Florida Keys) and the success of rescued colony transplants may be compromised by the stress endured in the original disturbance. The evaluation of ecological success and of cost/benefit ratio for these projects is rarely undertaken.

Monitoring versus Evaluation

Essentially all large scale reef restoration projects at least pay lip-service to including monitoring of project outcome as an explicit component of the restoration plan. However, such monitoring plans are usually inadequate to accomplish the rigorous evaluation of ecological restoration success because of poor design or poor (or even complete lack of) execution. For example, monitoring plans may not take into account all of the proper controls (i.e. undamaged controls AND damaged but unrestored controls) required to evaluate cost/benefit. Often specified monitoring protocols (e.g. photos or video footage) are not carefully executed to yield quantitative data. In the worst cases, monitoring

¹ NOAA-Fisheries, Southeast Fisheries Science Center, 75 Virginia Beach Dr. Miami FL 33149 USA, 305-361-4561, 305-361-4562 (FAX), margaret.w.miller@noaa.gov

plans are not executed at all, sometimes due to budget short-falls and/or logistical constraints. In the best cases, quantitative monitoring data is obtained, but it is rarely published or presented in a manner that facilitates the enhancement of future restoration practice.

Monitor	- Watch, observe, or check for a specific purpose - Keep track, regulate, control
Evaluate	- Express numerically or in monetary units - Examination and judgement concerning the worth, quality, significance, degree, amount, or condition

Table 1 Definitions of alternative assessment approaches to restoration projects (Grove 1961)

I would suggest, however, that even the best-designed, best-executed and best-disseminated monitoring plan is inadequate to make the greatest progress in the field of coral reef restoration. Table 1 recounts relevant aspects of dictionary definitions for *Amonitoring* and *Aevaluation*. If we are to make the greatest progress in advancing any aspect of reef restoration success, we must undertake to obtain quantitative, numerical bases on which to make rigorous judgements of worth and significance. That is, monitoring (i.e., watching, observing, and checking) is not enough; we must undertake rigorous evaluation of restoration actions. In a similar vein, Precht et al (2001) call for an approach where management restoration decisions are considered as hypotheses of ecosystem response and "scientific monitoring" is designed as an experiment to test these predictions. Such programmatic and methodological emphasis on evaluation of artificial reef projects has also recently been advocated by Seaman (2000).

Miller and Barimo (2001) used a comparative approach to evaluate ecological success (as defined by *in situ* recruitment of scleractinian corals) of two different reef restoration structures in the Florida Keys National Marine Sanctuary. Density and species richness of juvenile coral recruits were substantially higher on limerock boulder or cobble surfaces than on the flat concrete structure. An experimental component of this study (using standard settlement plates at both sites with isolated design characteristics) is underway to determine what aspects of structure/surface design are responsible for these differences in coral recruitment. Such an

experimental approach to evaluation may be required to determine why certain outcomes are observed and is detailed below.

Rigorous quantitative evaluation can also provide benefits in the more mundane aspects of ecosystem restoration such as the processes of litigation and assignment of damages to parties causing resource injury. Evaluating natural ecosystem recovery rates is an important pre-requisite to determine the benefit of active restoration. Such quantification and modelling of natural recovery applied to the scaling of restoration projects, known as Habitat Equivalency Analysis, has been advanced in natural resource litigation relating to seagrass ecosystems and has so far been upheld in court (Fonseca et al. 2000). This sort of recovery evaluation and modeling approach may be more difficult to apply in more biocomplex coral reef ecosystems, but warrants undertaking, especially in a global context where coral reefs= presumed resilience may be severely compromised by multiple anthropogenic stresses of long duration (Nyström et al. 2000, Jackson et al. 2001). Ironically, the legal strictures on settlement funds are interpreted to forbid recovery monitoring as a superfluous *Aresearch* activity despite the potential benefits to future litigation (both trustees and responsible parties) of providing a credible way to scale compensatory restoration projects (and therefore their cost) to equal the scale of the natural resource injury over time.

Experimentation as a tool in reef restoration

As students of science, we learn to contrast the purpose and the mechanics of observational versus experimental studies (for example, see Hairston 1989). Most restoration monitoring studies are observational in nature. They can reveal patterns of abundance or distribution. They cannot discern the cause or causes underlying such patterns. Therefore, if the pattern revealed in a restoration monitoring study is not the pattern expected (e.g., perhaps some target organism fails to recruit), there is no basis for determining why (was there some flaw in the project design, or was there simply a natural dip in recruitment levels in the whole geographical area). Similarly, and perhaps more importantly, a descriptive monitoring study will never be able to tell us how to conduct restoration better.

Along with evaluation and discernment of why projects may fail, experimentation is the only method

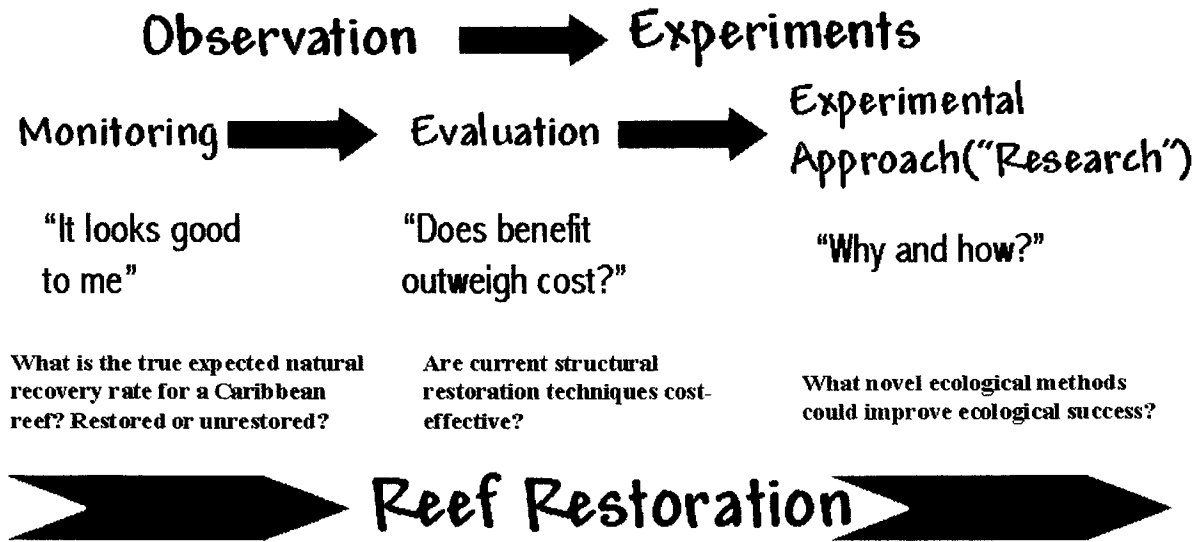


Fig. 1 Schematic depiction of the continua in types of science, types of restoration studies, related general and specific questions and/or outcomes from each as discussed in this paper

effectiveness of the restoration of reef ecological function. The outcomes of such an approach are not always technically complex and more expensive, though sometimes they are. It is imperative for the field of coral reef restoration to move along the continuum from observation/monitoring toward evaluation and experimentation if it is to advance beyond simpleminded engineering success criteria to accomplishing true restoration of ecological function (Fig 1). Below are some positive examples from other coastal ecosystems of using an experimental approach, guided by a basic understanding of ecological process and function in the given ecosystem, and the benefits to functional restoration success which resulted.

San Onofre Kelp Restoration

As mitigation for the destruction of an extensive kelp bed by thermal pollution from a nuclear power station, Southern California Edison was legally mandated in the mid 1980's to restore over 60 ha of kelp forest. This mandate was followed by a spate of observational ecological studies of existing natural and artificial reefs in southern California that aimed to discern what ecological factors and artificial reef designs would foster kelp recruitment, growth, and persistence. These observational studies clearly

example, in contrast to coral reef ecosystems, greater reef height and topographic complexity were determined to be detrimental to the overall restoration goals of establishing persistent kelp beds as the enhanced fish habitat fostered destructive grazing levels (Patton et al. 1994). Observations suggested that kelp often recruited but failed to persist and were replaced by sessile invertebrates. Experimental studies on several artificial reefs suggested that moderate sized reef elements would provide substrate disturbance (e.g., via overturn of boulders) at an interval (once every 7-8 years) that would help alleviate this competitive replacement (Patton et al. 1995).

In other cases, the benefit of certain factors or manipulations in the restoration context were equivocal. Kelp transplantation provided benefits at some artificial reefs, but not at others (e.g. Carter et al. 1994). Also, observations suggested that the spacing of artificial reef boulders and the areal extent of interstitial sand surface might be important, but it was not clear what spacing would be optimal. Hence, the restoration project was planned in a two-phase approach. The initial phase consists of, essentially, a large scale 3-way factorial experiment to test for the relative benefits of three levels of boulder spacing, two types of boulder material (concrete vs. quarried

rock), and active transplantation of juvenile kelp . The so-called Aexperimental reef@ was constructed in 1999, is 9 ha in size, will undergo a five-year evaluation period, and has a total estimated cost of US\$4-6 million, only half of which is the cost of construction with the remainder going to monitoring and evaluation activities (http://www.sce.com/songs_env/reef.html). The results from this experimental reef will be incorporated into the second phase, a full-scale mitigation reef which will be 61 ha in size.

Whereas this planning and pre-evaluation process has been long, cumbersome, and expensive, it has prevented a very large expenditure of mitigation effort and dollars on a restoration project that would have been unsuccessful (i.e. kelp would have been overgrazed on a short term or out-competed by sessile invertebrates on the medium term).

Oyster Reef Restoration

Oyster populations, landings, and oyster reef habitats in the estuaries of the eastern United States have been in dramatic decline due to destructive harvesting techniques, water quality degradation, disease, and feedback interactions exacerbating these factors (Lenihan and Peterson 1998, Lenihan et al. 1999). The Ajust do it@ approach had been undertaken by the state of North Carolina, USA in their restoration program which used dead oyster shell to form mounds about 1m tall (Lenihan 1999). These restored oyster reefs had minimal success (discerned with minimal evaluation effort via from normal harvest attempt by fishers) as most oysters that settled on the reefs died before they reached harvestable size (Frankenberg 1995 cited in Lenihan 1999). Thus a series of experimental evaluation studies were undertaken to understand why the restored reefs failed to provide the intended benefits and what alterations in restoration design and execution could enhance oyster success (Lenihan 1999, Lenihan et al. 1999).

The primary question was what habitat characteristics foster oyster performance and how? Basic ecology suggests many processes that may be important including physio-chemical tolerance, available trophic resources, recruitment, and predation and/or disease. Lenihan (1999) quantified all these aspects of oyster performance and hydrodynamic and hydrographic conditions on restored oyster reefs of different heights, depths, and on different positions of

these reefs. The results were extremely clear. All aspects of oyster performance were enhanced at positions higher up in the water column (i.e. crests of tall reefs or short reefs in shallow water) as seasonal anoxia or hypoxia were the major source of mortality of recruited oysters. Also, high water flow at the crests of reefs, especially tall reefs, enhanced oyster growth, condition, survival, and decreased parasitic infections (Lenihan 1999, Lenihan et al. 1999).

Hence, in this case, experimental evaluation yields extremely simple, cheap, and effective advise for enhancing oyster reef restoration success: Build TALL reefs!

Seagrass Restoration

Seagrass meadows are extremely susceptible to anthropogenic physical disturbance in shallow coastal areas favored by recreational boaters. The removal of sediments in such incidents often delays or prevents natural recovery over a decadal time scale and often results in expansion of the unvegetated scar by storms or other natural disturbance (Precht and Gelber, in press). Transplanting seagrasses has been a long-used technique for accelerating recovery of boat scars and numerous techniques have been used across a range of environments with little rigorous evaluation of the relative cost:benefit of the different methods. Fonseca et al. (1994) provide an experimental evaluation of a standard restoration technique (seagrass planting) undertaken in different locations and under a range of protocols (planting methods, enhancements such as fertilizer addition or cages to protect the transplants from destructive bioturbation). They found some geographical variation in the best techniques, but overall, peat-pots were the cheapest planting method. Such experimental evaluations for seagrass restoration techniques have made possible the development of a guidance handbook for restoration managers in the southeastern USA (Fonseca et al. 1998).

Ecological studies of natural seagrass succession suggest that nutrient accumulation in the sediments can be limiting to seagrass development, (Williams 1990) and the severe sediment excavation of boat groundings suggests that nutrient biogeochemical cycling may be severely disturbed over a long time frame. Nutrient addition was one of the factors that the experimental seagrass transplant evaluation by Fonseca et al. (1994) found to be equivocal, partly due to inconsistent nutrient release in the experiment. A subsequent study by focused on experimental

evaluation of two novel nutrient enhancement techniques: mechanical injection of a nutrient solution from a boat directly into the sediments using a large roller apparatus, and the placement of pvc stakes that serve as bird roosting stakes within the scars (Kenworthy et al. 2000). They found a clear enhancement of seagrass cover (50% within 1.5 yrs) in the bird stake treatments at very low cost (both in terms of materials and effort) and no discernable enhancement from the intensive boat/injection treatments (Kenworthy et al. 2000). This restored seagrass cover was in fact an earlier successional species known to (*Halodule wrightii*) than the one originally present in the scars (*Thalassia testudinum*) that is known to be outcompeted by *H. wrightii* in high nutrient conditions (Fourqurean et al 1995). However, the nutrient-enhanced colonization of seagrass cover, even if strictly "out-of-kind", decreases the likelihood of scar expansion and will allow the resumption of natural biogeochemical cycling in the sediments. Kenworthy et al. (2000) recommend removal of the bird stakes in one-two years which should result in resumption of *T. testudinum* dominance (Zieman 1982, Williams 1990), a strategy for restoration termed "compressed succession". Once again, a very simple and inexpensive technique utilizing natural ecological processes and interactors can be extremely effective in coastal restoration.

Conclusion

Based on these examples, it is clear that an experimental approach can uncover simple and cost-effective techniques for enhancing restoration function. Because such an approach has not really been pursued in coral reef systems, it may be difficult to predict what novel, cost-effective ecological restoration techniques (i.e. the bird stakes) for coral reef systems might be. I suspect they may involve broad categories such as manipulation or enhancement of herbivory, enhancing juvenile coral recruitment and growth (e.g. larval seeding, enhancing growth/production in coral nurseries), and possibly the use of sponge transplants for purposes of small rubble stabilization. These cost-effective techniques for coral reefs may not be as simple or cheap as some of the examples given above, but it is quite plausible that some low-tech ecological enhancements may be extremely effective and feasible for application even in less-developed countries.

We must move from an observational monitoring

mode along the continuum toward rigorous evaluation and experimentation with enhancements of ecological processes (Fig. 1) if we are truly to restore coral reef ecosystems. This endeavor gains all the more prominence in the global context of reef decline that has been demonstrated at the 9th ICRS, and in a context of suspicion that coral reef systems may have lost much of their ability to recover on their own (Nyström et al. 2000).

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Coral Culture as a Conservation Tool for *Acropora* spp.

Erich Mueller, Ph.D., Director
Center for Tropical Research
Mote Marine Laboratory
Summerland Key, FL

During the past 20 years, aquarists have developed techniques to successfully maintain, and propagate, scleractinian corals in closed systems. Much of this was accomplished by hobbyists with the goal of creating "mini-reefs" for display. But the requirements for scleractinians were based on knowledge of coral biology, particularly their need for oligotrophic water and high irradiances. Scientists have also developed closed coral systems to better understand coral biology and their effects on community metabolism. The acroporids are particularly amenable to culture because of their high growth rates and ease of asexual propagation. Coral model systems, such as the "microcolony," are the equivalent of lab rats and offer the potential to much more fully understand the complex physiological processes of corals and their symbiotic dinoflagellates. Closed-system culture offers opportunities to study diseases that affect acroporids (bleaching, white-band disease and patchy necrosis/white pox) in much more detail than possible in the field. Finally, such systems also offer a refuge of last resort for a genus that has seen dramatic population declines in much of the Greater Caribbean.



Coral Farm: the first step to restore reefs

Antonio L. Ortiz-Prosper, Coordinator
Puerto Rico Coral Farmers
Caborrojeños Pro Salud y Ambiente, Inc.

Puerto Rico Coral Farmers is a marine scientific group within Caborrojeños Pro Salud y Ambiente, Inc. (CPSA), a non-profit organization registered in the Puerto Rico State Department since 1991. The mission of our organization is to raise awareness on issues regarding the conservation and protection of our environment. CPSA has the support of several local and federal agencies, including the US Department of Commerce, Rural Economic Development, Environmental and Natural Resources Department, among others. At present, we are currently working with the National Fish & Wildlife Foundation to develop effective and low cost methodology to restore coral reefs.

Our goal is to implement methods for manipulating and enhancing depleted coral population through coral farming in the Southwest area of Puerto Rico, specifically in Cabo Rojo, Lajas, and Guánica. We have designed specific procedures to collect, transport and culture of several coral species that will be continually tested on this study. Coral Farming is a proposed plan to overcome part of the problem of reef deterioration in Puerto Rico and the Caribbean. Through the culture of a wide diversity of corals, we will be able to supply corals to deteriorated coral reefs, damaged by natural (storms, and disease) and human induced disturbances (ship grounding, pollution, military activities, among others.)

Our Partners

- Fish & Wildlife Foundation: Main partner that will provide the funding for the proposed project. Is the main sponsor of our current Reef Restoration Methodology Project (ending August 2001), where we developed the coral reef farming methodology, which will be implemented in a larger scale in the proposed project.
- Department of Natural Resources and Environment (DNRE), Guánica State Forest: Will provide storage facilities for the equipment and materials, and TO prepare the coral culture device needed for the coral nurseries.
- Other partners: Local organizations such as the Ferré Rangel Foundation, and the Ford Motor Company Foundation have manifested their interest to collaborate in the proposed project, by providing additional funding to cover the costs of a vehicle to be used in the project (to transport heavy equipment, coral culture device, and trailer), and for an educational component, respectively.

Statement of the problem

In an effort to overcome the problem of coral reef deterioration, the active restoration of damaged coral reefs is now at the scope of most conservation efforts. Coral reef restoration is a relative new field of research that will become increasingly important for management purpose. Restoration techniques have the potential to accelerate the re-growth of a reef after disturbance and created new reef where none previously existed. The basic approach is to introduce new colonies of fast growing species into the reef. The establishment, growth, development and maturing of these colonies may increase larvae production and recruitment locally or the increase the number of colonies by the establishment of broken off fragments from transplanted colonies.

Despite the fact that some corals are known to survive after transplantation (Highsmith, 1982), some techniques have been proven not to be feasible options because of the following:

- **Negative effects on collection sites:** The majority of the work done in coral reef restoration projects involve the collection of the coral colonies from one site, transported and transplanted to a second site. Harriot and Fisk (1988) have documented the negative impacts of transplantation on the collection site, such as the reduction of coral population from healthy reefs, among others.
- **Highs cost, and low percent of survival of coral transplanted:** Cost/effectiveness is not measured in most of coral reef restoration project. For example, after the M/V Fortuna Reefer Vessel Grounding at the Mona Island (Puerto Rico) the National Oceanic and Atmospheric Administration's Damage Assessment and Restoration Program initiate an emergency coral reef restoration. After an expedited \$1.25 million settlement funds to restore the reef less than 65 % of *Acropora palmata* fragments survived. Comparable results (68% after one year) were obtained without human intervention when hurricane Georges (September 22, 1998) passed through Puerto Rico, fragmenting many colonies of *A. palmata* in several reefs of La Parguera, southern Puerto Rico (Ortiz and Ruiz, 2000).

Farming corals (or coral nursery) is the best logical step in coral harvesting that will allow us to produce corals to be used on restoration projects. Our experience in coral farming has proved that coral nursery or coral culture is a useful tool in coral reef management. The coral nursery is based on the idea of the metapopulation concept. A metapopulation is a series of small, separate, populations united by some mechanism that allows genetic flow. In this scenario, even if the individual populations go extinct, other population survives and supply dispersing individuals who re-colonizes "extinct" patches (Harrison, 1991). By this concept, the coral culture of different species within the nursery sites may act as a source of corals to replenish extinct populations at different reefs. The proposed coral farm not only will increase the local genetic variability by the addition of new coral strains to the reef, it also will preserve coral strains (on coral nurseries) for future dispersion, including candidate species considered for the Endangered Species Act. For example, we have already successfully farmed *Acropora cervicornis* and *Acropora prolifera*, two of such threatened species.

Expected Results and Benefits

We will establish a total of 6 coral reef nurseries in three southwest towns: Cabo Rojo, Lajas and Guanica (2 nurseries in each town). Each of these nurseries will have at least 50 coral culture devices, for a total amount of 300. Initially, we will collect and culture in these device at least 8,400 coral fragments of different species. By the end of the second year, we expect to have harvested at least 30,000 fragments to be cultured in additional 1,440 new culture devices.

Outcomes

1. Implement effective methodologies for coral propagation and transplantation through human activities.
2. Increase of genetic diversity of local coral population by providing new individuals genetically different.
3. To have farmed large and diverse amounts of corals, including threatened species of the *Acropora* genus, available to be used in future local reef restoration efforts.
4. Direct involvement of coral reef resource managers; island fishing communities and other non-government partners in coral reef restoration projects.
5. Integration of coral transplantation techniques in the management strategies for improving the fishery resources in Puerto Rico.

6. Increase public knowledge about the importance of coral reefs as essential habitats for marine life, and the joint efforts to preserve and restore damaged coral reefs.
7. Coral farms will also produce direct and indirect benefits to local areas by expanding habitats for marine invertebrates, ornamental and commercial fishes, and underwater attractions for snorkels or scuba diving.

Our ultimate goal is to transfer our findings and experience in restoration and coral farming methodology to other Caribbean nations, as a sustainable method to increase coral population.

Research Evaluation

We propose the extensive use of experimental and proven methods of coral culture. All coral transplantation or cultured methods will be continually tested to determine the optimum approach. Each methodology will be tested and evaluated using appropriate experimental design. For example, experimental coral culture device will be set up in a complete randomized design. Triplicate coral culture device contained branches or fragments of one strain of each coral species will be randomly allocated within each coral nursery area. The number of coral fragments and its size within the experimental coral culture device will be recorded at the initiation of the project. Coral nursery sites will be visited periodically over the year period and the response variables to be measured are mortality rate of transplant, incremental growth, and colony conditions. All techniques (coral collection, transportation, transplantation, etc.) will be modified depending on previous results.

2001 Progress Report

Introduction

Farming corals (or coral nursery) is the logical step in coral harvesting that will allow us to produce coral to be used in restoration projects. But scientific knowledge is needed to improve large-scale coral farming. Thus, the goal of this project was to develop effective methodologies for coral propagation through human activities. In our way to fulfill this goal we developed specific procedures to collect, transport and transplant several coral species of the Caribbean.

The project began in August, with the arrival of the initial funding. The first two months were used to buy some of the equipment, materials, insurance, and to settle the agreements needed to begin the project. Coral collection and transplantation began in October. We transplanted about 360 fragments of *Acropora cervicornis*, 180 fragments of *Acropora prolifera*, 120 fragments of *Madrasia mirabilis* and 20 fragments of *Porites porites*, to the Aurora Reef located in the South of Puerto Rico. In El Negro Reef, located in the West of Puerto Rico, we transplanted 180 fragments of *Acropora cervicornis*, 120 fragments *Acropora prolifera*.

In the near future, we plan to increase the number of farming sites around the island, increasing the numbers of species to be cultured.

Goal Accomplished

Direct involvement of coral reef resource managers and island fishing communities in coral reef restoration projects.

Miguel Canals, management officer of the Guánica State Forest, and Carlos Pacheco, biologist and principal investigator of the Sport Fishery Restoration project at Guánica State Forest, are actively involved in our coral farm project. They helped us with their expertise and time. They also provided the facilities where we prepared our structures to culture corals. Because our coral farm would also enhance the sport and commercial fishery resources of the area, the management officers integrated our transplantation and culture techniques as management strategies to improve the sport fishery resources in the area.

Development of methodology for long distance coral transportation.

Coral transportation is an important step in our protocol. Our first long distance transportation of coral fragments was unsuccessful. Over 50% of the coral fragments died due to water motion within the container. The problem was solved with the design and construction of a livestock coral transportation container with open and close circulation.

Now, a 3 gal./minute water pump (12 volt.) provides water circulation within the container, and coral fragments are held against a specialized plastic plate. More than 400 coral fragments have been transported successfully, using this device. More than 95% of the coral fragments survived the transportation process. Our coral fragments have resisted an average of 3 hours inside the container. The overall survival of *Acropora cervicornis* fragments after 10 months was 86.6% (n=367) (Table 2).

8. Designing specific structure or frame to be used in coral aquaculture.

Because our location is within the Caribbean hurricane trail, all our coral fragments have been attached to specialized structures that we considered to be hurricane resistant. Our first structure designed, a 2x4 feet cement base with an upper rubberize galvanized steel fence, was too heavy to be transported (200 pounds) (Fig 1). The new structures are smaller (80 pounds) and are easily assembled within the reef (Fig 2). Also, the same cement base can be used for different corals species with only slight modifications (i.e. we only modify the shape of the rubberize galvanized steel fence.) On each base we attach 20 fragments of *Acropora sp.*, 20 fragments of *Porites porites* and 30 to 40 fragments of *Madracis mirabilis*. Now we are able to carry an average of twelve cement bases for each trip to the coral farm site.

9. To increase the genetic diversity of local coral population by providing new individuals genetically different. To preserve coral strain for future dispersion.

The main objective of genetic management is to preserve sufficient levels of natural genetic variation to enable populations to adapt to both short- and long-term changes in the environment. This study not only has incremented the local genetic variability with the addition of new coral strains to the reef, but it has also preserved coral strain (on coral nursery) for future dispersion to the natural location or to other nurseries. We collected corals from five reefs to ensure different strains of each culture species (genotypes). Also, within each reef, we collected coral fragments from three different sites.

Results and Discussion

At this moment we can only offer the results from one farming site (Jabón reef) because this is the only one with the proper growth time period to evaluate coral growth rates.

A. Coral Growth

Coral growth results are summarized in Table 1. In these tables, growth is expressed in terms of linear length (length of initial branch plus the length of each branch). In average, the initial branch length of coral fragments, cultured in our platforms, is 14 cm. The overall linear growth, 10 months after transplantation, was 52.2 ± 4.6 cm (N= 318 initial fragments). This highest growth may account 3x more, compared to the initial fragment length. The net overall linear net growth was 38.4 ± 4.5 cm. Fragments originating from San Cristobal Reef, showed lowest linear growth, net growth, and main branch length (Table 1, $p < 0.05$, one way Anova).

B. Fragments' Survival

The overall survival of coral fragments, 10 months after transplanted, was 86.6% (Table 2). The highest survival was observed in coral fragments collected from Margarita Reef (100%) and the

lowest from those collected from San Cristobal Reef (Table 2). We suggest that fragment mortality was associated to genetic basis. For example, coral fragments from two clone collected from San Cristobal Reef (culture device 1061) died the first week after transplantation, while all the fragments from the third clone survived and grew (Table 3). This implies that some coral clones may be adapted to survive and grow in a wide range of environmental conditions while other may be restricted to specific environmental conditions (light regime, sedimentation rate, oxygen concentration, etc.).

C. Branchiness

Branchiness is the number of branches produced by unit of time. These measurements may give us information about the number of fragments that will be harvested after one or two years. The overall branches produced by *A. cervicornis*, 10 months after transplantation, was 7.3 ± 1.8 . To calculate the expected number of corals to be harvested, we multiplied by 7 the number of initial fragments transplanted. However, after 10 months of coral growth, the branch length of those corals were too small to be harvest. From our previous work, we expect that two years of coral growth are needed to harvest the coral branch

Table 1. Growth results of *Acropora cervicornis* transplanted and cultured in the Jabón Reef (ten months of culture).

Collection Sites	N	Colony Linear Growth (cm)	Net Growth (cm) (initial length – final length)	Number of Branches	Main Branch Length (cm)
Jabón Reef	96	54.9 ± 16.6	41.8 ± 16.3	7.3 ± 2.6	22.4 ± 5.3
Mario Reef	90	58.6 ± 28.7	44.1 ± 28.2	7.8 ± 3.9	20.0 ± 8.3
Margarita Reef	40	56.2 ± 14.7	43.1 ± 14.9	8.4 ± 2.9	23.8 ± 4.3
San Cristobal Reef	92	$41.3 \pm 17.6 *$	$27.2 \pm 17.2 *$	6.4 ± 3.0	$17.3 \pm 6.6 *$
Overall	318	52.2 ± 4.6	38.4 ± 4.5	7.3 ± 1.8	20.4 ± 2.6

*Significant difference from other reef ($p < 0.05$)

Table 2. Survival Results of *Acropora cervicornis* transplanted and cultured in the Jabón Reef (ten months of culture).

Collection Sites	N	% of Survival.
Jabón Reef	101	95.0
Mario Reef	106	85.3
Margarita Reef	40	100
San Cristobal Reef	120	72.6
Overall	367	86.6

Table 3. Fragments mortality by clone and reef.

Collection site	Culture device number	Numbers of dead fragments by clone			% Mortality
		Clone A	Clone B	Clone C	
San Cristobal	1092	1	0	0	4.2 (n=24)
San Cristobal	1075	6	3	0	47.4 (n=19)
San Cristobal	1061	7	6	0	65 (n=20)
San Cristobal	1065	0	0	3	15 (n=20)
San Cristobal	1094	2	0	0	5.4 (n=37)
Mario	1100	0	2	6	33.3 (n=24)
Mario	1064	0	0	0	0 (n=20)
Mario	1073	0	0	0	0 (n=22)
Mario	1071	0	0	0	0 (n=20)
Mario	1096	3	0	5	40 (n=20)
Jabón	1062	1	1	1	15 (n=30)
Jabón	1068	1	0	0	5 (n=20)
Jabón	1072	0	0	0	0 (n=21)
Jabón	1066	0	1	0	5.3 (n=19)
Jabón	1069	0	0	0	0 (n=21)
Margarita	1063	0	0	0	0 (n=20)
Margarita	1060	0	0	0	0 (n=20)

REPORT

A.W. Bruckner · R.J. Bruckner

Condition of restored *Acropora palmata* fragments off Mona Island, Puerto Rico, 2 years after the *Fortuna Reefer* ship grounding

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Abstract *Acropora palmata* fragments generated by the *Fortuna Reefer* ship grounding (1997, Mona Island, Puerto Rico) were secured to reef substrate and to dead, standing *A. palmata* skeletons using stainless-steel wire ($n=1,857$). The purpose of this study was to assess fragment survivorship and condition 2 years after the attachment of fragments. Surviving fragments (57%) were larger than dead fragments (26%) and 17% were missing, mostly from shallow water. Live fragments had tissue covering 52% of upper branch surfaces; 23% of the live fragments experienced little or no tissue loss; 27% exhibited proto-branches; 14% had fused to the substrate; and 16% had overgrown the wire. Mortality was greatest in deeper water, especially among fragments secured to *A. palmata* skeletons. Mortality was attributed to overgrowth by *Cliona* spp. and macroalgae, predation by *Coralliophila abbreviata* and *Hermodice carunculata*, disease, and *Stegastes planifrons* territories. Limitations associated with the restoration technique include a low ability of coral tissue to overgrow wire and wire corrosion and breakage. Low rates of natural fusion and continued wire failure may hinder long-term recovery as storms periodically detach and remove restored fragments.

Keywords Habitat restoration · Coral reef · *Acropora palmata* · Elkhorn coral · Ship grounding

Introduction

On 24 July 1997, the *M/V Fortuna Reefer* ran aground on a coral reef located off the southeast coast of Mona Island, Puerto Rico. The 326-ft freighter remained aground in the *Acropora palmata* (elkhorn coral) zone for 8 days. Damage from the grounding and ship removal activities extended approximately 300 m in length by up to 30 m in width, with collateral injuries occurring over a wider area from cables dragged across reef surfaces. Large branches of *A. palmata* were sheared off and entire colonies were dislodged and fractured; brain corals (*Diploria strigosa*) were also shattered by the hull of the vessel and abraded by cables. Overall, damage from the grounding (0.8 ha) and the removal (1.9 ha) impacted a sizeable tract of coral reef (NOAA 1997a).

Physical disturbances caused by hurricanes and ship groundings have profound and long-lasting effects on regenerative processes of coral communities (Stoddart 1962; Woodley et al. 1981; Aronson and Swanson 1997). Destruction of *A. palmata* has resulted in a permanent reduction in the three-dimensional structural complexity of some reefs and has reduced the habitat available to associated organisms (Dennis and Bright 1988; Aronson and Swanson 1997; Lirman 1999). Recovery of elkhorn thickets may be delayed in severely damaged areas due to a loss of adult colonies, limited sexual recruitment and high mortality of fragments (Hughes et al. 1992). Thus, fragment stabilization may enhance survivorship and reduce the time required for the re-establishment of elkhorn thickets.

Acropora palmata is a fast-growing branching coral that typically formed monospecific stands or “thickets” on shallow exposed reefs (Goreau 1959; Almy and Carrion-Torres 1963; Bythell and Sheppard 1993). Although colonies are susceptible to dislodgement and breakage during hurricanes and tropical storms, they are generally adapted to high wave energy through modifications in colony morphology, such as branch orientation and thickness (Glynn et al. 1964; Woodley et al. 1981;

A.W. Bruckner
NOAA/National Marine Fisheries Service,
Office of Protected Resources,
1315 East West Highway,
Silver Spring, Maryland 20910, USA

R.J. Bruckner (✉)
NOAA/National Marine Fisheries Service,
Office of Habitat Conservation,
1315 East West Highway,
Silver Spring, Maryland 20910, USA
E-mail: robin.bruckner@noaa.gov
Tel.: +1-301-713-0174

Gladfelter 1991; Lirman and Fong 1997a). The primary mode of propagation is by colony fragmentation, as this species exhibits low rates of sexual recruitment (Highsmith 1982). Moreover, fusion to the substrate and continued growth of fragments play a significant role in the recovery of damaged elkhorn thickets (Bak and Engel 1979; Highsmith 1982; Rylaarsdam 1983; Rosesmyth 1984; Lirman and Fong 1997b).

Survival, attachment, and continued growth of elkhorn fragments are limited by the substrate type where dislodged fragments land (Fong and Lirman 1995). Fragments deposited in sand are at risk of being abraded or smothered and have no solid substrate for attachment. Because of the heavy swells at the *Fortuna Reefer* grounding site and the large number of fragments that had accumulated in sand channels, NOAA restoration specialists suggested that timely stabilization of fragments could enhance coral survivorship and expedite natural recovery processes. Primary restoration began within 2 months of the incident and involved securing *A. palmata* branches to the reef substrate and to standing elkhorn skeletons using stainless-steel wire (Iliff et al. 1999). The emergency restoration conducted at Mona Island used an innovative technique never before attempted on this scale or with this species.

The purpose of this study was to assess the performance of the *Fortuna Reefer* restoration 2 years after it was completed. We examined the survivorship and growth of coral fragments and relationships among fragment size, orientation, and placement. The effectiveness of the restoration technique was evaluated by examining the percentage of fragments that were lost due to wire breakage, the ability of tissue to grow over the wire and differences in survival between two locations of attachment. This report provides information on the short-term success of a new method to reattach and stabilize elkhorn coral fragments to reef substrate and standing skeletons, which is of potential value when considering future restoration efforts involving *A. palmata*.

Materials and methods

Study site

The *Fortuna Reefer* restoration site ($18^{\circ}03'N$; $67^{\circ}52'W$; Fig. 1) is located off Mona Island, 65 km from the west coast of Puerto Rico. The island forms the top of an underwater ridge separating the Atlantic Ocean from the Caribbean basin and is situated immediately due west of the deep-water Mona Passage. The restoration site ranges from 2–7 m in depth and is often affected by strong currents, heavy swell, and intense wave action from the Atlantic and Caribbean.

Initial restoration

The Commonwealth of Puerto Rico and the National Oceanic and Atmospheric Administration (NOAA) Damage Assessment and Restoration Program (DARP) team conducted a natural resource damage assessment of the grounding site and expedited a settlement amounting to US \$1.25 million for primary and compensatory restoration, which included \$650,000 to conduct an emergency

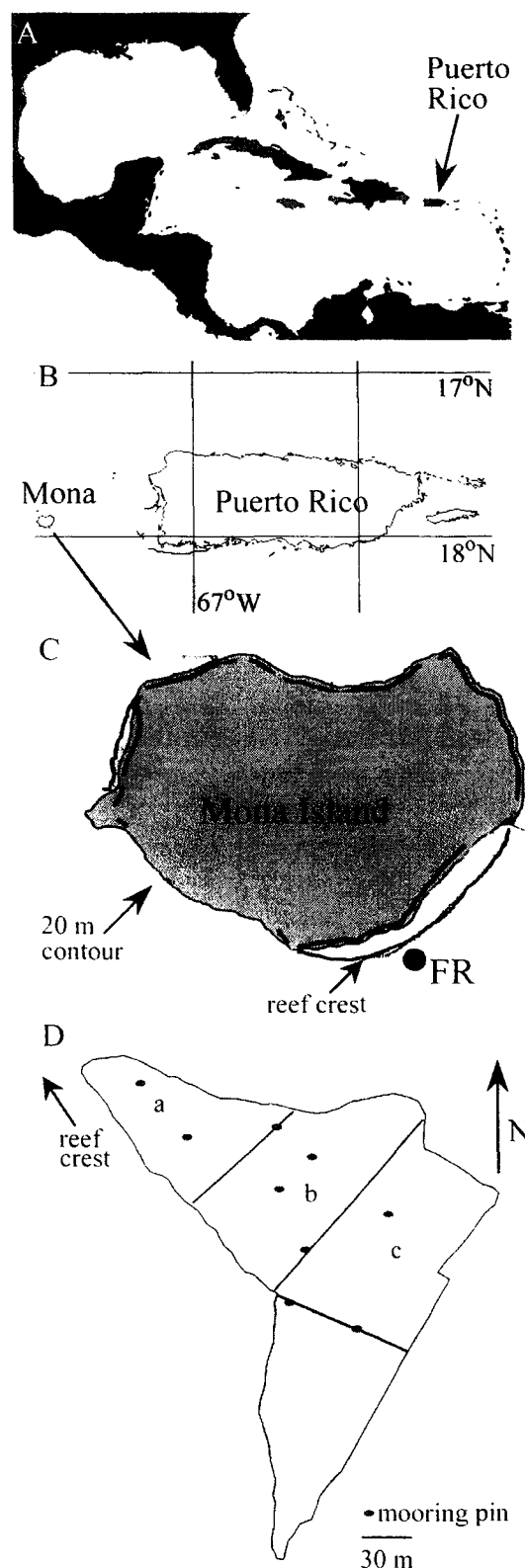


Fig. 1 Location of the *Fortuna Reefer* coral restoration site, Mona Island, Puerto Rico (a–c; $18^{\circ}03'N$; $67^{\circ}52'W$) and schematic diagram of the injured area (d). Mooring pins are indicated by black dots and were used to subdivide the site into smaller quadrants to ensure that fragments were not counted twice; addition, the pins were used to delineate the site into three areas based on depth: a (< 3 m depth), b (3–4 m), and c (> 4 m). Shaded area furthest from the direct impact of the ship was not surveyed

restoration of coral resources injured as a result of the incident (NOAA 1997b). The objectives of the emergency restoration were to re-establish the structural relief of the coral reef community and reduce coral mortality by securing loose *A. palmata* branches to relict reef substrates and standing elkhorn coral skeletons (NOAA 1997a).

Between 24 September 1997 and 14 October 1997, a team of 19 divers including marine engineers and biologists stabilized 1,857 *A. palmata* coral fragments ranging in length from 15 cm to 3.4 m. Fragments were attached either to reef substrate or to dead, standing *A. palmata* skeletons. Stainless-steel wire was used to secure fragments to the reef; wire was extended across a fragment and then wrapped around stainless-steel nails that were cemented into holes drilled in the substrate. Plastic cable ties were used initially to secure smaller fragments to elkhorn coral skeletons, but wave surge loosened the cable ties and these fragments had to be further stabilized with wire (NOAA 1997a; Iliff et al. 1999). Additional fragments were attached to standing skeletons with stainless-steel wire alone. Fragments were reattached in either an upright or downward position (with respect to their original orientation) with the live, unbleached tissue facing upwards.

They were firmly attached so as to withstand normal surge and wave action typical of the conditions where this coral species thrives. Because of heavy swell encountered at the site, coral reattachment using concrete was deemed unfeasible (NOAA 1997a). The authors were not involved in the restoration.

Survey and analysis of restored fragment condition

Approximately 2 years after the injury and restoration we evaluated the condition of restored *A. palmata* fragments at the *Fortuna Reef* restoration site. The survey involved an assessment of the number of fragments that remained attached and their condition, the number that had broken loose and were displaced, and the number that were missing. In addition to recorded data, photographic and video archives were made of the site and of specific fragments. Because of the extensive area of damage and the large number of fragments that were reattached, only a subset of reattached fragments (38%) were assessed in this study. Areas sustaining the greatest damage were surveyed first; the area farthest from the grounding (shaded area in Fig. 1d) was not examined due to time limitations.

For the attached fragments that had remained on the site since they were initially restored in 1997, data were collected in August 1999 on the size (maximum length), orientation (recorded as up, down, or sideways with respect to their orientation prior to fragmentation), location of attachment (reef substrate or standing skeleton), and condition. Each fragment was examined for the presence of new growth, including tissue growth over wire, and/or plastic cable ties, the presence of proto-branches, and natural cementation (fusion) to the substrate. In addition, we estimated the amount of partial or total mortality and recorded the cause of mortality. Partial or total mortality was attributed to overgrowth by *Cliona* spp. or macroalgae, predation by *Coralliophila abbreviata*, *Hermodice carunculata*, or *Sparisoma viride*, disease, presence of *Stegastes planifrons* territories, or was recorded as "unknown".

Estimates of remaining tissue and percent recent mortality were made by two divers (the authors) from a planal perspective. All fragments were assumed to initially have 100% of their upper surface covered with tissue. Remaining tissue area and amount of mortality are presented as the percent of the original tissue area remaining on the upper (exposed) surface of the branches and does not include loss of live tissue from the undersides of branches, or tissue associated with proto-branches. For each fragment, a 1-m bar divided into 5-cm increments was oriented along the center of the long axis of the fragment and used as a point of reference to estimate tissue survivorship and loss. For quality control we each measured 35 of the same fragments and compared tissue estimates prior to the actual survey to ensure that our values were consistent; in all cases, estimates for individual fragments differed by 0–5%.

The number of fragments that became detached and subsequently were removed from the site (missing fragments) was determined by tallying groupings of nails to which fragments were no longer attached (for fragments formerly secured to the reef) and counting remnant wire on elkhorn skeletons that was not associated with fragments (for fragments secured to standing skeletons).

Data analyses

Relationships among fragment size (maximum length), fragment orientation (up or down with respect to their original orientation on the colony prior to the ship grounding; sideways fragments were too few in number and are not included), location of attachment (reef substrate or standing skeleton), and depth (pooled into depths of < 3, 3–4, and > 4 m) were examined with respect to fragment survival and the amount of remaining tissue. Length measurements were log transformed and percentages of partial mortality were arcsine square root transformed prior to analyses as necessary. A Student's t-test was used to compare the mean length of living fragments with the mean length of dead fragments. Student's t-tests were also used to compare the mean percent of living tissue on fragments attached to the reef substrate with fragments attached to standing skeletons and the amount of tissue on fragments oriented upright versus fragments oriented downward. Correlation tests (Pearson's product-moment correlation coefficient) were used to examine relationships between fragment length and the numbers of surviving fragments in each 10-cm size class and the amount of partial mortality sustained by these fragments. A single-factor ANOVA was used to examine relationships between the amount of partial mortality and fragment size (fragments were pooled into 10-cm size classes) and also to determine whether fragment size differed among depths. Chi-square analyses of contingency tables were used to test the effects of orientation, location of attachment, and depth on fragment survival. Relationships between survivorship and orientation and survivorship and location of attachment were examined with 2×2 contingency tables; a 2×3 contingency table was used to examine relationships between fragment survival and depth. A two-factor ANOVA was used to examine the effect of depth and location of attachment and the interaction between these variables with respect to amount of tissue mortality.

Results

Condition of fragments

A total of 705 reattachment sites (38% of the original) were examined in August 1999. Of these, 57.5% ($n=405$) had fragments with some live tissue cover, 25.8% ($n=182$) had fragments that experienced total mortality, and fragments were missing at 16.7% ($n=118$) of the sites (Table 1). Most live fragments had lost some tissue during the 2 years since the restoration,

or more of their upper surfaces. A number of fragments had developed vertical features (proto-branches), indicating upward growth. One or more small proto-branches (2–10 cm in height) were observed on 108 (19%) fragments. New upward growth occurred regardless of whether the fragment had fused naturally. Only 10% ($n=58$) had successfully fused to the substrate or the standing skeletons; 11% ($n=66$) had completely overgrown the wire; and 10.6% ($n=62$) had partially overgrown the wire. For 73% ($n=295$) of the surviving fragments, tissue mortality occurred in areas in direct

Table 1 Condition and size of *Acropora palmata* fragments 2 years after the *Fortuna Reefer* restoration, Mona Island, Puerto Rico. Fragments were attached in various orientations to the reef substrate or to dead, standing *A. palmata* skeletons. Percent of live

fragments (% live) was calculated only from remaining fragments. Missing fragments are presented as number and percent of all fragments surveyed in that category

		Live		Dead		Length (cm)		Percent live tissue	Missing	
		No.	(%)	No.	(%)	Mean	SE		No.	(%)
Orientation	Up	267	71	109	29	65.6	2.0	54		
	Down	120	63	70	37	59.4	2.2	47		
	Side	18	86	3	14	87.4	7.6	48		
Location of attachment	Reef	232	73	86	27	77.4	2.8	52	99	(24)
	Skeleton	173	64	96	36	59.5	2.3	51	19	(6.6)
Depth < 3 m	Reef	58	74	20	26	77.2	4.5	56	47	(38)
	Skeleton	64	68	30	32	64.6	3.8	49	9	(9)
3-4 m	Reef	117	77	35	23	74.4	3.9	49	28	(16)
	Skeleton	71	70	30	30	56.3	3.8	60	3	(3)
> 4 m	Reef	59	66	30	34	77.8	4.8	56	24	(21)
	Skeleton	36	49	37	51	57.2	4.8	38	7	(9)
All fragments		405	69	182		64.3	1.5	52	118	(17)

contact with the wire (Fig. 2a). Some fragments had been attached to erect skeletons using plastic cable ties or a combination of cable ties and wire. Fragments appeared to be less negatively affected by the cable ties, as tissue readily overgrew them in 68% of these fragments ($n=28$) (Fig. 2b). In a small percentage of remaining live fragments (8.9%, $n=34$), the wire used to secure them was broken; these fragments remained in place, or had moved 0.5–2 m from the original site of attachment depending on their size.

The only identifiable cause of total mortality was overgrowth by the boring sponge *Cliona* species complex (9% of all restored fragments surveyed, $n=51$; Fig. 2c). Partial mortality was associated with *Cliona* spp. (5% of the living fragments, $n=20$), predation by *Coralliophila abbreviata* gastropods (4%, $n=15$), overgrowth by *Dictyota* spp., other macroalgae, and/or unidentified cyanobacterial mats (3%, $n=11$), *Hermodice carunculata* (fireworm) predation ($n=7$), white-band-type diseases ($n=6$), and *Stegastes planifrons* (damselfish) algal lawns ($n=3$).

Length-related survivorship

Restored fragments identified during this survey ranged in length from 15 to 340 cm. The mean length of fragments was 64 cm (SE = 1.5; median length = 55 cm) and 73% of the fragments ranged from 30–90 cm. Of the original 1,857 fragments reattached during the restoration in 1997, 653 were 15–50 cm in length (estimated to be 50% of the fragments in this size class created during the incident), 869 were 50–100 cm (80% of the total in this size class), and 335 were more than 1 m (all fragments in this size class) (NOAA 1997a). There were no significant differences between the size classes of the fragments in the population restored in 1997 and the restored fragments examined in 1999 (pooled into three size classes, G-test of goodness of fit, $G=4.67$, $p=0.1$),

indicating that the size classes of the fragments examined in 1999 were a representative sample of the fragments reattached in 1997.

Surviving fragments examined in August 1999 were significantly larger (mean = 69.8 cm) than dead fragments (mean = 52.2 cm; $t=6.3$, $df=476$, $p<0.001$). Figure 3 shows the number of fragments in each size class that were alive and the number that had died. More than 75% of the fragments larger than 50 cm survived, while only 46% of those smaller than 50 cm survived, and the number of surviving fragments was correlated with fragment size ($r^2=0.42$, $p=0.001$; 95% confidence limits, $0.26 \leq \rho \leq 0.84$). In addition, the amount of partial mortality differed between size classes (single-factor ANOVA, $F=2.5$, $df=586$, $p<0.001$). There was a positive relationship between fragment size and percent tissue remaining ($r^2=0.42$, $p<0.002$); however, there was a high degree of variability within larger size classes (Fig. 4).

Effect of fragment orientation and location of attachment

Differences in fragment orientation (up or down) and location of fragment attachment (reef substrate or standing skeletons) had minor effects on survivorship and the amount of remaining tissue (Table 1). Approximately 65% of all fragments examined were attached right side up (the original orientation before being dislodged from the parent colony, $n=376$), but there was no difference in fragment length with respect to orientation ($t=1.33$, $df=564$, $p=0.183$). No significant difference was observed in fragment survival with respect to orientation (chi-square analysis of a 2×2 contingency table, $\chi^2=3.25$, $df=1$, $p=0.072$), but there were differences in the amount of tissue remaining on surviving fragments ($t=1.65$, $df=385$, $p=0.035$), with fragments attached right side up having a greater percentage of live



Fig. 2a-c Examples of restored *Acropora palmata* fragments at the Fortuna Reefer coral restoration site photographed in August 1999, approximately 2 years after restoration. **a** Fragment attached to the substrate, illustrating wiring technique used to stabilize it. Partial mortality occurred where tissue was in contact with the wire. Fragment is 104 cm in length. **b** Fragment reattached to an erect *A. palmata* colony using cable ties. This fragment exhibited fusion, growth over cable ties and well-developed proto-branches. Fragment is 82 cm in length. **c** Fragment attached to standing elkhorn skeleton that was colonized by *Cliona* species complex; fragment was subsequently overgrown by the sponge. Fragment is 26 cm in length

tissue (mean = 54%; 95% confidence interval = 50–58%) than those attached upside down (mean = 47%; 95% confidence interval = 40–52%). There was also a significant difference in fragment survival between the two attachment locations (chi-square analysis of a 2x2 contingency table, $\chi^2 = 6.2$, $df = 1$, $p = 0.013$), with a higher proportion of the living fragments found attached to the reef substrate. However, there was no difference in the

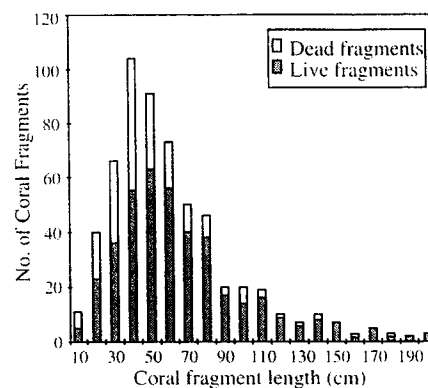


Fig. 3 Size frequency distribution of restored *Acropora palmata* fragments at the Fortuna Reefer coral restoration site. Number of fragments in each size class are shown as stacked bars

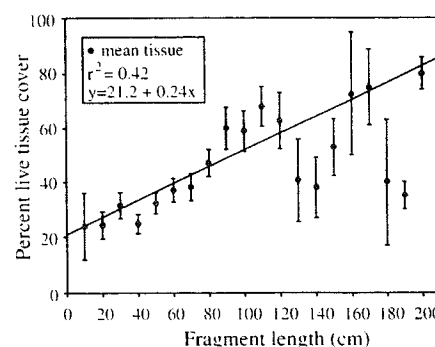


Fig. 4 Mean percent of live tissue ($\pm$ SE) on upper branch surfaces for surviving *Acropora palmata* fragments at the Fortuna Reefer coral restoration site. Data are pooled into twenty 10-cm size classes

amount of tissue remaining on live fragments with respect to attachment location (mean = 52%; $t = 0.47$, $df = 401$, $p = 0.64$; Table 1).

Effect of depth on fragment retention

Restored fragments were located from 2–7 m depth and were pooled into shallow (2–3 m), intermediate (3–4 m) and deep (>4 m or deeper) categories (Table 1). The greatest number of lost fragments were identified in shallow water (25% of the total sample examined in shallow water), followed by those in deep water (16%); fewer fragments from intermediate depths were missing (11%). The number of fragments missing also differed between attachment locations, with 84% of all missing fragments originally attached to the substrate. This may be an artifact of the data, however, as the tallied number of fragments attached to standing colonies and subsequently lost may be an underestimate. Since nails were not used when securing fragments to elkhorn skeletons, the only indication that a fragment previously existed there was the presence of remnant wire.

Effect of depth and location of attachment on fragment condition

The condition of remaining fragments, measured as the percent of surviving fragments and the amount of live tissue, was compared among depths and attachment locations. The length frequency distributions from the three depths did not differ significantly (pooled orientation and attachment location; single-factor ANOVA, $F=1.37$, $df=589$, $p=0.25$). Differences in survivorship were noted among depths (chi-square analysis of a 2×3 contingency table, $\chi^2=11.76$, $df=2$, $p=0.003$). More than 70% of the remaining fragments from shallow and intermediate depths survived, while only 59% of the deep fragments had survived. In addition, differences in the number of fragments that died were noted among depths for fragments attached to standing elkhorn skeletons (chi-square test, $\chi^2=9.26$, $df=2$, $p=0.01$), but not for fragments attached to the reef substrate (chi-square test, $\chi^2=3.33$, $df=2$, $p=0.19$). More than 50% of the fragments reattached to skeletons in deep water had died (Table 1). A two-factor ANOVA comparing the condition of the remaining live fragments with depth and attachment location indicates that no differences exist among depths for the percentage of tissue loss ($F=1.81$, $df=2$, $p=0.165$; Table 2). In addition, the amount of partial mortality on surviving fragments was not significantly different between attachment locations ($F=0.94$, $df=1$, $p=0.333$). In contrast, there was a significant interaction between attachment location and depth ($F=4.94$, $df=2$, $p=0.008$), with the greatest amount of tissue loss (62%) occurring in fragments attached to standing skeletons in deep water.

Discussion

Primary restoration at the *Fortuna Reefer* site was undertaken within 2 months of the grounding incident under the assumption that without rapid reattachment, a high percentage of fragments might die due to sand scouring and other factors, or be removed from the site during periods of high wave action (NOAA 1997a). To maximize the potential for reef recovery, the aim was to restore injured corals to the greatest extent possible. Few unrestored fragments (<2%) were tagged for controls (i.e., fragments created by the incident that were not reattached), because settlement monies from ship groundings and oil and hazardous materials releases may not be used to design and test hypotheses. The absence of data on the survivorship of control fragments provides an incomplete picture of the benefits gained by the considerable investment to secure the fragments. Nevertheless, a broad-scale census of the status of the wired fragments, as gauged by the extent of survivorship and regrowth, provides valuable information on the relative utility of the technique used to secure fragments, the relationships among survivorship and size, orientation, depth, and substrate, as well as information on

Table 2 Two-factor ANOVA examining the condition of surviving fragments from three depths attached either to relict reef substrates or to standing elkhorn skeletons. Condition was determined from amount of tissue remaining, using arcsine transformed percentage. *SS* Sum of squares; *MS* mean square

Source of variation	df	SS	MS	F	p
Depth	2	2,236	1,118	1.81	0.165
Attachment location	1	580	580	0.94	0.333
Interaction	2	6,095	3,047	4.94	0.008
Error	399	243,144			
Total	404	252,055			

potential sources of mortality. This information can be used to enhance future restoration efforts for this coral species and may assist in determining the need for subsequent corrective actions to enhance fragment survivorship.

To become successful recruits, *A. palmata* fragments must fuse to the substrate to prevent removal by wave action. The wiring technique used to stabilize fragments at the *Fortuna Reefer* grounding site was developed with the intent to enhance natural processes of fragment stabilization. It was used as an alternative to cement or epoxy due to the high wave exposure typical at this site and the amount of time required for these materials to harden. In August 1999, both living and dead fragments that were securely attached with wire were observed throughout the restoration site. Broken wire was also common; wire had loosened on some fragments and others had broken free and were carried away. Over 17% of the fragments that were restored originally were identified as missing. Fragment loss was greatest in shallow water, as evidenced by the number of nails, and/or wire without associated fragments. It is likely that more fragments were removed that could not be identified, however. Nails were not used to secure fragments to *A. palmata* skeletons and fragments and wire may have been removed completely, rendering the reattachment site undetectable.

Although wire failure appears to be a significant cause of transplant loss, these losses were relatively low considering that this reef is routinely exposed to severe weather and the site was directly impacted by Hurricane Georges in 1998. Studies that have followed the natural fate of hurricane-generated fragments have reported large losses in the months following the disturbance. In Florida, during an 11-month period in which no additional storms occurred, 57% of the fragments were removed from a hard-bottom substrate (Lirman and Fong 1997b). Similarly, over a 4-year period in Puerto Rico, a tropical storm and two hurricanes removed greater than 96% of *A. palmata* fragments that were generated on an offshore patch reef by a previous storm (Bruckner, unpublished data).

In many cases, the wiring technique appeared to hamper the growth of coral tissue, as evidenced by the absence of tissue directly in contact with the wire. Wire often separated two or more patches of tissue on frag-

ments that otherwise exhibited little or no tissue mortality away from the wire. The wiring technique did not inhibit tissue growth on all *A. palmata* fragments, however, since 16% of the fragments had tissue growing over the wire. Tissue mortality associated with the wire might have been reduced by using plastic-coated stainless-steel wire.

Previous observations of the restoration site indicated that the wire was colonized by filamentous algae and macroalgae and algae were killing tissue in places (E. Weil, personal communication, April 1998); this was less common 3 months later, however (M. Miller, personal communication). During the present survey, algae (primarily filamentous green algae, *Dictyota* spp., and cyanobacterial mats) were observed on the wire associated with a relatively small proportion of the living fragments (3%). The presence of algae did not appear to be selectively affecting the wired fragments during this study, since dense macroalgae also occurred away from the wire and along the margins of unrestored *A. palmata* fragments.

The extent of survival and potential for regrowth may be affected by fragment size. Modular organisms are known to allocate different proportions of their energy and resources to reproduction, with larger colonies of some species investing more energy in reproduction than in growth (Jackson and Hughes 1985). If this is the case for *A. palmata*, smaller fragments potentially have a better chance of survival because they may concentrate their resources on growth, increasing their ability to reattach rapidly. The effect of size on survivorship of *A. palmata* fragments has been studied previously with conflicting results, however. Highsmith et al. (1980) observed a positive correlation between fragment size and survivorship, while Rogers et al. (1982) noted that fragments that survived were smaller overall than those that died. Lirman and Fong (1997b) did not observe any relationship between fragment size and survivorship, possibly because the majority of the fragments were small. In the present study, the mean size of fragments that died was significantly smaller than that of the live fragments, with the highest rate of mortality observed among fragments under 50 cm in length.

Reef-building corals are affected by partial colony mortality due to various factors. Tunnicliffe (1981) noted that Caribbean acroporids exhibit the fastest growth at the distal edges of the colonies and older, basal regions sustained higher rates of mortality. Lirman and Fong (1997b) observed tissue loss in many (73%) of their tagged fragments; fragments lost 61% of their original tissue area over an 11-month period, but surviving fragments had begun to develop vertical growth features. In the present study, surviving fragments had tissue on approximately half of their upper branch surfaces after 2 years. Although reattached fragments on the *Fortuna Reefer* site appear to have fared better than unrestored fragments in Florida and elsewhere in Puerto Rico, differences may be related to specific environmental parameters that vary among locations. In addition,

the amount of tissue remaining on the branch surface may be less important for long-term survivorship than the ability of fragments to reattach and develop new vertical branches. In both studies, fragments had lost a considerable portion of their living tissue, but many were developing proto-branches, indicating that continued growth was occurring.

A critical factor affecting the ability of a fragment to successfully recruit is the substrate type where the fragment is deposited (Lirman and Fong 1997b). Bak and Criens (1981) found that *A. palmata* fragments fuse to other, living elkhorn fragments faster than to any other type of substrate. In Florida, elkhorn fragments landing on rubble substrate had a higher survivorship and a lower percent tissue loss than those deposited on relict reef substrate (Lirman and Fong 1997b). At the *Fortuna Reefer* grounding site, fragments were secured to the relict reef substrate or to dead, standing elkhorn skeletons. Those fragments attached to skeletons were expected to exhibit enhanced survivorship associated with a reduction in scouring, improved water circulation, increased light exposure, and possibly a reduced exposure to benthic predators and pathogens. Contrary to this hypothesis, fragments secured to the reef substrate had a higher survivorship than those attached to elkhorn skeletons. Although fragments on the reef substrate were larger, the percentage of tissue remaining after 2 years on survivors did not differ between the two attachment locations. The differences in survivorship are likely to have resulted from a higher rate of mortality experienced by those fragments placed in contact with the invasive sponge *Cliona* spp., which was found commonly overgrowing elkhorn skeletons and less frequently on the substrate.

It is important to note that elkhorn populations have undergone a regional decline over the last two decades (Gladfelter 1982; Bythell and Sheppard 1993). Large-scale catastrophic losses have been associated with physical disturbance from hurricanes, but a widespread, white-band disease (WBD) epizootic is a contributing factor that has certainly accelerated the decline and continues to afflict elkhorn colonies throughout the region (Gladfelter 1991; Aronson and Precht 2001). Chronic partial mortality from natural stressors like WBD, predation, and other factors not associated with the restoration may be largely responsible for the inability of fragments to successfully fuse to their attachment sites. For instance, the undersides of branches on intact colonies such as those previously affected by WBD often lack live tissue. Should they become fragmented, they may be unable to reattach without tissue in direct contact with the substrate (Bruckner, unpublished data).

In this study, recent signs of mortality including WBD were observed on a small proportion of the restored fragments, as well as on several surrounding *A. palmata* colonies that were unaffected by the ship grounding. Given a widespread occurrence and a presumed increase in the prevalence of coral disease,

predators, and other stressors affecting acroporids in Puerto Rico (Bruckner et al. 1997; Williams et al. 1999), it is unlikely that mortality of restored fragments is exclusively related to the restoration. It is possible that stabilization of *A. palmata* fragments may be an activity that has only slowed an inevitable monotonic mortality process. Nonetheless, studies in Puerto Rico and Florida have shown that unrestored fragments continue to grow, but even sizeable fragments in good condition are lost during periods of high wave energy if they do not have a secure connection to the substrate (Lirman and Fong 1997b; Bruckner, unpublished data). Results to date from the *Fortuna Reefer* site emphasize the importance of a timely restoration. Without intervention, this site might have mirrored other locations in Puerto Rico, where almost complete removal of fragments occurred during subsequent storms due to low levels of natural fusion (Bruckner, unpublished data).

Adaptive management may be particularly valuable as this coral species has been declining throughout its range since the late 1970s, and innovative techniques that enhance survivorship may be critical in promoting localized recovery of elkhorn populations. In anticipation of the continued degradation of the stainless-steel wire which begins to corrode at points of crimping and twisting and given the large number of fragments that were unable to fuse to the substrate, corrective action to maintain the remaining fragments on the site may increase the overall effectiveness of initial restoration efforts. Recommendations for altering the original technique include the use of Portland cement or two-part marine epoxy (Hudson and Diaz 1988; Gittings et al. 1994), in conjunction with heavy-gauge monofilament line, nylon or Teflon-coated wire, or plastic cable ties for short-term fragment stabilization while the adhesive sets. It is imperative that those fragments exhibiting high rates of growth and fusion should not be included in corrective restoration efforts. Corrective action for the remainder will continue to maintain restored fragments on site, providing additional time for recovery and enhancing the long-term success of the initial restoration. This technique would benefit from the coordinated efforts of a multi-task team to remove the wire from loose fragments, scrape and clean the undersides of fragments and the reattachment sites to remove algae and other encrusting organisms, apply the cement or epoxy, and temporarily secure the fragments to allow the adhesive to set. Furthermore, a portion of the fragments restored in 1997 should be left unmanipulated in order to allow an assessment of the benefits gained by a mid-course correction and the potential value of future restoration efforts.

Restoration is a relatively new science that soon may need to be applied on a larger scale to mitigate effects of hurricanes, bleaching events, and disease outbreaks (Precht 1998). Current research is focusing on methods to enhance coral recruitment, restore the natural balance of herbivores and maintain coral nurseries to rescue and rehabilitate fragments generated by physical distur-

bances, for use as transplants for degraded areas. The application of new technologies like those used in the *Fortuna Reefer* restoration can continue to advance the science. Emphasis must be placed on scientifically based approaches needed to assess the outcome of restoration efforts and improve techniques to restore, rehabilitate, and replace damaged corals.

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Introduction to the U.S. Endangered Species Act

A.W. Bruckner, NOAA/NMFS Office of Protected Resources, Silver Spring, MD.

Background

The purposes of the Endangered Species Act are to provide a means to conserve ecosystems upon which endangered species and threatened species depend, to provide a program for the conservation of endangered and threatened species, and to take appropriate steps to recover a species.

Species' Listings Under the Endangered Species Act

The National Marine Fisheries Service (NMFS) is responsible for determining whether marine species, subspecies, or distinct population segments are threatened or endangered under the Endangered Species Act of 1973, as amended, 16 U.S.C. 1531 et seq. (ESA). To be considered for listing under the ESA, a group of organisms must constitute a "species," which is defined under section 3 of the ESA to include "any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." NMFS has determined that, to qualify as a distinct population segment (DPS), a population (or group of populations) must be substantially reproductively isolated and represent an important component in the evolutionary legacy of the biological species. A population (or group of populations) meeting these criteria is considered to be an "evolutionarily significant unit" (ESU) (56 FR 58612, November 20, 1991). In its listing determinations to date, NMFS has treated an ESU as the equivalent of a DPS under the ESA.

Section 3 of the ESA defines an endangered species as "any species which is in danger of extinction throughout all or a significant portion of its range" and a threatened species as one "which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range." The statute lists factors that may cause a species to be threatened or endangered (ESA section 4(a)(1)), but it does not provide further guidance on how NMFS is to determine the risk of extinction or the likelihood of endangerment.

Section 4(b)(1)(A) of the ESA requires NMFS to make listing determinations based solely on the best scientific and commercial data available after conducting a review of the status of the species and after taking into account efforts being made to protect the species. Accordingly, in making its listing determinations, NMFS first determines whether a population group constitutes a "species" under the ESA, and determines the species' status and the factors that have led to its decline. The status review provides background information on the species including taxonomy and biology, current and historic range, population information, habitat requirements, a summary of the threats faced by the species, a review of existing conservation measures, and a discussion of the activities that would be affected if the species were listed.

The process for determining whether a species should be listed is based solely on scientific information on the status of a species and specifically excludes potential economic impacts. The status is determined from an assessment of factors that may be contributing to decline including 1) habitat destruction or modification, 2) overexploitation, 3) disease or predation, 4) inadequacy of existing regulatory mechanisms, 5) other factors affecting survival of the species. NMFS also assesses protective efforts being made to determine if they mitigate risks to the species.

Invertebrate listings

An amendment to the ESA in 1978 allows us only to list distinct populations of vertebrates. Marine invertebrates must be threatened or endangered throughout their range to be listed, because they are thought to have greater ranges and fecundity, and a greater resilience to exploitation and environmental change than vertebrate species. Since most benthic invertebrates produce pelagic larvae with the potential for long-distance dispersal, these species are assumed to exhibit a high degree of interconnectivity through water circulation, and it is thought that a distant population in good condition can serve as a source of recruits to rehabilitate degraded populations.

Even though we are required to list all populations of an invertebrate species if we determine

that they are threatened or endangered, the degree or type of protection these species receive can vary, depending on whether a species is listed as threatened or endangered. If we were only to list one or both of these corals as threatened we would subsequently issue regulations through a rule-making process that would specify what measures were necessary for the conservation of the species and where these measures would apply. In some cases these rules would only affect the species in state or territorial waters if the state has a cooperative endangered species agreement and the state feels that those measures are beneficial for the species. In contrast, if we were to list one or both of the corals as endangered all of the provisions of the ESA automatically apply, regardless of whether the species is in federal waters, or in state and territorial waters. So a threatened listing gives us much greater flexibility.

What does it mean to be listed

A. Critical Habitat

When we publish a final decision to list a species on the ESA we are required to designate critical habitat - Critical habitat includes specific areas that contain the physical, biological and environmental factors necessary to support the species, as well as areas that are not occupied by the species, but are essential for its conservation - for corals, this could include other reef environments, as well as mangroves and grassbeds.

B. Protective measures

By listing a species, we are required to protect that species and recover it to its former abundance or range, concentrating on areas that are critical to the species based on unique genetic diversity, areas with a documented high abundance, populations that may provide a significant source of recruits to other areas and populations at the geographic limits of the species. The ESA also provides us with the tools to protect the habitat occupied by a listed species by prohibiting any activities that are funded, authorized or carried out by the federal government if those activities are likely to contribute to the degradation of the habitat and jeopardize the survival of the species (section 7). For coral reefs, this measure would require permits for any activities involving dredging, coastal development projects, sand extraction and discharge of sediment near coral reef environments. The ESA (section 9) also makes it illegal to "harass, harm, pursue, shoot, wound, kill, trap, capture, or collect or engage in commerce in listed animals except by permit for conservation or scientific purposes. Harm has been defined to include "significant habitat modification or degradation where it actually kills or injures wildlife by significantly impairing essential behavioral patterns including breeding, feeding or sheltering". A Listing will also increase federal aid to state and commonwealth conservation agencies with cooperative endangered species agreements. Most importantly, The ESA requires that we develop and implement a recovery program.

C. Recovery Programs

A recovery program includes a summary of information on a species and its life history, including information on taxonomy, population discreteness, population size and trends (including past and present size and future projections based on current trends), reproduction and recruitment rates, sources and rates of mortality, diet and feeding habits, movement patterns, habitat use patterns and critical habitat requirements. The threats affecting the species should be described in detail, as well as the overall objective of the recovery plan, the type of recovery actions, and an implementation schedule to achieve these actions. The goals of the recovery program are to determine actions necessary to reduce or eliminate the threats affecting the species and protect critical habitat essential for the survival of that species. The recovery program must also identify measurable criteria that will be used to down-list a species once it has recovered, and an analysis of the time and cost required for full recovery.

Proactive management for conservation of *Acropora cervicornis* and *Acropora palmata*: application of the U.S. Endangered Species Act

A.W. Bruckner¹ and T.F. Hourigan²

Abstract *Acropora palmata* and *Acropora cervicornis* are important framework-building corals that provide a critical structuring role on shallow Caribbean reefs. In recent decades both species have declined from white-band disease and other factors. To increase awareness about their decline, the National Marine Fisheries Service in June 1999 identified *A. palmata* and *A. cervicornis* as candidate species for the United States Endangered Species Act (ESA). Candidate status does not add legal protection, but is designed to promote efforts to obtain reliable information on the species and to encourage voluntary conservation strategies for the protection of remaining populations. Application of the ESA to marine invertebrates presents several challenges. While distinct vertebrate populations can be listed, a marine invertebrate must be threatened throughout its range. Both *Acropora* spp. are widespread, however a survey of available information revealed gaps that prevent a synoptic overview of their status. Furthermore, measures of rarity have been developed for individuals, and may not be applicable to clonal organisms that rely on asexual fragmentation as a primary mode of propagation. An ESA listing requires implementation of a recovery plan and action by Federal agencies to conduct conservation programs, and to promote research, restoration and protection for these species, thereby benefiting associated coral reef organisms and the ecosystems upon which they depend.

Keywords *Acropora palmata*, *Acropora cervicornis*, reef-building coral, US Endangered Species Act, candidate species listing

Introduction

There are over 110 species of *Acropora* of which only three, *A. cervicornis* (staghorn coral), *A. palmata* (elkhorn coral) and *A. prolifera* (fused staghorn coral), are found in the Caribbean

(Wallace and Willis 1994). *Acropora cervicornis* and *A. palmata* are the most common of the Caribbean species, forming monospecific, high relief assemblages (thickets) at shallow and intermediate depths in environments occupied by few other corals. Both are key structural components, and play a critical role in the maintenance of healthy, productive reefs by providing vital habitat for a large number of associated organisms (Gladfelter and Gladfelter, 1978). Because of their dominance in shallow water and their rapid rate of growth, they contribute significantly to reef growth (Adey 1975; Gilmore and Hall 1976; Gladfelter 1982; Tunnicliffe 1983). Thickets of *A. palmata* form a buffer zone that protect coastal communities from storm waves. Storms have caused considerable damage to *Acropora* assemblages, but populations often exhibit rapid recovery due to a high survivorship of fragments and rapid tissue regeneration (Glynn et al. 1964; Highsmith 1982; Bak 1983). Accumulations of storm-generated *Acropora* rubble also contribute to the formation of coastal ramparts and islands (Williams et al. 1999).

Until the late 1970s, Caribbean reefs displayed a zonation pattern dominated by three common scleractinian corals, *A. palmata*, *A. cervicornis* and *Montastraea annularis* (Jackson 1992). Populations of *A. cervicornis* and *A. palmata* underwent a region-wide decline during the 1980s and 1990s, with losses of 95% or more in some areas (Gladfelter 1991; Bythell et al 1993; Aronson and Precht 2001). The loss of these species may lead to an increased dominance of macroalgae, reduced rates of reef accretion, and erosion of the reef framework, associated cays, and coastal environments (Williams et al. 1999; Aronson and Precht 2001).

Despite growing threats to reef-building corals and their associated ecosystems, few coral species are actively managed, and none are fully protected throughout their range (Laist et al. 1986). The

¹ A. Bruckner: NOAA/National Marine Fisheries Service, 1315 East West Highway, Silver Spring, Maryland, USA. andy.bruckner@noaa.gov

² T. Hourigan: NOAA/National Marine Fisheries Service, 1315 East West Highway, Silver Spring, Maryland, USA

purpose of this paper is to discuss the application of the U.S. Endangered Species Act (ESA) to reef-building corals, and whether this mechanism could help protect populations of *A. cervicornis* and *A. palmata*. We discuss the ESA listing process, criteria used to classify a species as threatened or endangered, difficulties in applying the ESA to clonal marine invertebrates, and gaps in the available information for acroporids that must be fulfilled to justify an ESA listing. Finally, the advantages of the ESA as a strategy to conserve these species and their habitat are summarized.

Existing mechanisms to protect corals

In recent years, significant progress has been achieved towards protecting coral reefs and promoting sustainable use of reef resources, and a range of international initiatives and agreements support coral reef conservation. Internationally, the non-binding *Framework for Action* developed under the International Coral Reef Initiative (ICRI) includes key strategies to improve management, capacity building, monitoring and targeted research to protect, restore and sustain coral reefs. Parties to the Convention on the International Trade in Endangered Species of Wild Fauna and Flora (CITES) recognized that unregulated harvest of corals for international trade may be detrimental to their survival in the wild. A CITES Appendix II listing for stony corals authorizes international trade only if corals are sustainably harvested. However, in most of the Caribbean, including U.S. reefs, it is illegal to damage, remove or collect scleractinian corals. Installation of moorings and navigational buoys is helping reduce damage associated with anchoring and vessel grounding, and the establishment of marine protected areas, including no-take areas offer further protection by reducing fishing pressure and other extractive activities. Management measures have reduced the potential for physical damage from human activities, but anthropogenic pollutants and sediment remain a significant threat. To our knowledge, no protections exist that take into account the vulnerabilities of selected species, even ones that are as important as *Acropora* spp.

The U.S. Candidate Species Program

An effective program for the conservation of a species requires a means of identifying species not yet listed on the ESA that face immediate, identifiable risks. A candidate species listing provides a red flag to warn management authorities and the public of the concern for a

particular species before that species becomes threatened with extinction. The candidate species listing helps 1) identify species that may need protective measures under the ESA; 2) increase public awareness about the species; 3) stimulate voluntary conservation efforts for these species by Federal agencies and other parties; and 4) identify uncertainties associated with their status.

Based on the large losses sustained by Caribbean acroporids, NMFS proposed that *A. cervicornis* and *A. palmata* may warrant listing on the ESA and identified them as candidate species in June 1999. These and eight other corals were tentatively listed as candidate species in 1991; although individual populations had declined, they were removed from the candidate list in 1997 because no species was identified as threatened throughout its range. Since 1973, the only other marine invertebrates proposed for listing on the ESA were two abalone species.

*Applying the U.S. Endangered Species Act to *Acropora* spp.*

A species may be proposed for listing through a formal petition process or through a candidate species assessment process. Within 90 days of receiving a petition, NMFS must make a finding as to whether there is sufficient scientific and commercial data to warrant listing. If the preliminary finding supports listing, a status review is conducted. This includes an analysis of criteria that may contribute to decline of the species, including: 1) habitat destruction or modification; 2) overutilization for commercial or recreational purposes; 3) disease or predation; 4) inadequacy of existing regulatory mechanisms; or 5) other natural or man-made factors affecting its continued existence. For a species of particular concern, a listing proposal is drafted that contains information on its biological characteristics, population status, range, and habitat requirements; a summary of the threats affecting the species; and examples of available conservation measures and types of activities that would be prohibited. This document is published in the *Federal Register*, undergoes public comment and peer review, and is followed by publication of a final rule containing the listing decision. A recovery strategy must be developed and implemented for listed species within one year of listing.

Decline in acroporid populations: the degree of threat

Acropora palmata and *A. cervicornis* are distributed throughout the wider Caribbean. In

the United States, they occur in the U.S. Virgin Islands, Puerto Rico, Navassa Island and Florida, including the Florida Keys and Biscayne National Park; *A. cervicornis* also extends up the east coast of Florida to Boca Raton. A growing list of threats is contributing to widespread reductions in living cover, abundance and condition of *A. cervicornis* and *A. palmata* and a disappearance of characteristic monospecific thickets (Fig. 2).



Fig. 1 Reports of white-band disease published between 1979-1999, indicated by open squares.

White-band disease outbreaks are believed to be the most important factor responsible for the decline of these species (Fig. 3). Localized destruction has also been associated with hurricane damage, predation, hyper- and hypothermic stress, siltation and pollution associated with runoff, overgrowth by macroalgae, bioerosion, boat groundings and anchor damage, and other factors (Table 1). Harvest for building materials, curios and aquarium specimens was common in the 1960s and 1970s, but coral extraction no longer presents a significant threat. Isolated recruitment has occurred in recent years, but populations have failed to recover to their former abundance, and continued degradation from anthropogenic and natural factors is occurring. Based on the decline criteria used in the ESA, both corals appear to qualify for listing.

ESA listing requirements for vertebrates and invertebrates

Individual populations of a vertebrate species can be listed on the ESA, provided that they are reproductively isolated from other populations, and they represent important components of the evolutionary legacy of the species. Distinct population segments are defined based on 1) the discreteness of the population relative to the rest of the species; 2) the significance of the population segment to the species; and 3) whether

the population segment is threatened when treated as if it were its own species.

In contrast, marine invertebrates qualify for listing only if threatened throughout their range. Invertebrates are exploited locally and are impacted by localized threats, but most species have life cycles that are presumed to be relatively resilient to exploitation, and are unlikely to be threatened with biological extinction because of their wide distribution and high fecundity. Even though many invertebrates are sedentary as adults, those with pelagic larvae have the potential for long-distance dispersal, and species are presumably interconnected by water currents.

The requirement that a species must be threatened throughout its range to qualify for ESA listing may not be the best conservation strategy for reef-building corals. First, it is impractical and very unlikely that sufficient information on the status of acroporids can be obtained from every reef where they occur. In addition, acroporids cross international boundaries, but U.S. legislation cannot be applied in other countries. Also, Caribbean acroporids may be less resilient to emerging threats because of 1) low levels of sexual recruitment and limited genetic exchange among populations; 2) a reliance on asexual reproduction; and 3) special habitat requirements.



Fig. 2 Characteristic thicket of *Acropora palmata*



Fig. 3 Colony of *Acropora cervicornis* with white-band disease (WBD)

Population parameters

The degree of species endangerment is related to population size and intrinsic variability in population growth rates. For most animals, trends in abundance are based largely on differences between birth and death rates, and populations can persist only if the rate of increase is equal to or greater than zero. Age at sexual maturity, birth interval, annual reproductive rate, and survival rate of different age classes provides an indication of population dynamics in most animals, but it is difficult to apply these criteria to clonal organisms such as *Acropora* spp.

Acropora palmata, *A. cervicornis*, and other corals can be affected by partial mortality at any time during their lifespan and colonies can survive physical separation through fragmentation. A clonal mode of life has important implications for genetic diversity, dispersal capabilities, responses to environmental perturbations, and the ability of populations to persist under changing environmental conditions. There is evidence suggesting that patterns of mortality are related to colony size, and that partial mortality may affect reproductive potential (Hughes and Jackson 1985). Thus, colony size and extent of mortality may be more relevant than age when estimating the potential for population expansion and recovery.

Reproduction and genetic exchange

Marine organisms are often described as short-lived and opportunistic, or as long-lived, persistent species. Opportunistic species produce large numbers of small offspring at an early age, and these often exhibit high rates of recruitment. Large bodied, long-lived animals often delay reproduction and produce fewer offspring, but offspring receive a high degree of parental care and have a greater potential for survival. *Acropora cervicornis* and *A. palmata* can be long-lived, they may reach a large size, and they reproduce annually, with large colonies broadcasting millions of gametes into the water (Bak and Engel 1979). However, colonies delay reproduction until reaching a certain size (approx 20-50 cm diameter) and sexual recruits are rarely observed, suggesting low survivorship of larvae. Colonies are also frequently damaged during storms and reproduction may cease in fragmented colonies (Highsmith 1982; Rylaarsdam 1983; Szmant 1986). The widespread decline of these species further compromises sexual reproduction as acroporids are now rare, and population density

may be too low to ensure high fertilization success (Aronson and Precht 2001).

Colonies of *A. cervicornis* and *A. palmata* are widely distributed, but they occupy very specific habitats within their range. Nevertheless, these species are opportunistic in that they monopolized large areas of reef, which is achieved primarily through fragmentation. Growth in *Acropora* spp. is potentially indeterminate, but it may be constrained due to water depth or degree of wave exposure. Periodic pruning associated with storms allows the biomass of a genotype to increase beyond an individual's physical limits by the constant formation of fragments. This may promote dispersal to new areas, with colonization occurring more rapidly than by sexual recruitment, and in habitats not conducive to sexual recruitment (Tunncliffe 1981). The continued growth and fragmentation of remaining colonies may facilitate localized recovery. However, a reliance on fragmentation as the primary reproductive strategy may retard recovery after large-scale disturbances, such as a severe hurricane that removes most colonies from an area.

Another consequence of fragmentation is that it promotes reduced genetic variability. In light of emerging disturbances, this may lower the potential for adaptation to changing environmental conditions, and this may have been a key factor contributing to the regional spread of white-band disease, and the near total loss of these corals. However, fragmentation may allow adaptation to new conditions, through the retention of resistant clones to replace those lost to disease or other environmental perturbations.

Benefits of an Endangered Species Act listing

The ESA provides a means for conserving species that are threatened or in danger of extinction, and for the conservation of the habitats upon which those species depend. Once listed, the ESA mandates implementation of a recovery program capable of restoring a species in its natural habitat to a level at which it can sustain itself without further legal protection. The goals of the recovery program are to 1) identify the ecosystems and organisms that face the highest degree of threat; 2) determine actions necessary to reduce or eliminate the threats; and 3) implement strategies to recover the species. A recovery program involves activities associated with resource management and can include research, monitoring, habitat acquisition, and strategies to

Table 1. Degree of threat to *Acropora palmata* and *A. cervicornis* using criteria established for the ESA

ESA Criteria	source of decline	degree of threat
Habitat destruction or modification	dredging, vessel groundings, anchor damage, pollution and sedimentation from shoreline development and land use	moderate; localized
Overutilization	collection for curios, aquarium specimens and building materials	high during the 1970s; collection now prohibited in most locations
Disease	white-band disease, new coral syndromes	high; disease epizootics occurred throughout the region in the 1970s-1990s; disease remains a significant threat
Predation	Corallivorous gastropods, polychaetes, parrotfish, damselfish	moderate; regional; corallivores populations have increased presumably in response to reduced predation pressure
Existing regulatory mechanisms	water quality	high; localized near population centers
Other natural threats	bleaching, hurricanes, temperature extremes	high; localized, may be regional

maintain, propagate and/or transplant the species.

The ESA requires that protective measures are applied to the habitats supporting a listed species, with emphasis on areas that are critical to the persistence of the species. Recovery programs target areas with a unique genetic diversity or a high abundance, populations that may provide a significant source of recruits to other areas, or populations at the geographic limits of the species. Also, federal activities can not contribute to the degradation of the habitat utilized by a listed species. For instance, protection under the ESA could prevent dredging or discharge of sediment near coral reef environments.

Discussion

Coral reefs are resilient ecosystems that can rebound to a healthy state through better management decisions, improved water quality, habitat protection and proactive conservation. Management regimes have begun to focus on ecosystem-based conservation measures, instead of a species-by-species approach. One strategy involves zoning of reefs for different activities.

including the establishment of no-take marine protected areas (MPAs). MPAs are designed to restore depleted fisheries and protect biodiversity from extractive activities, and they may also help maintain a high diversity and abundance of species outside of the reserve. While recent efforts are promoting conservation of biodiversity through non-destructive, sustainable management of resources, more efforts need to be directed towards land-based strategies to reduce anthropogenic pollutants and sediments, as these may be much more substantial factors exacerbating coral mortality.

Living marine resources include many sessile species with distributions that cross geographical boundaries, complicating management regimes. Thus far, there are no regional management schemes for conserving corals and there has been no systematic overview of the status of key species such as *A. palmata* and *A. cervicornis*. Only limited information exists on the abundance and condition of Caribbean acroporids, and the degree of genetic differentiation among and within populations is poorly understood. The ESA is the most powerful environmental protection law in the U.S. that can help fill gaps in our understanding of these species. An ESA listing would ensure that additional resources are allocated towards research and monitoring. It can also assist in the

implementation of strategies to reduce habitat degradation and avoid impacts from future activities, including coastal modifications that may affect water quality.

Acropora palmata and *A. cervicornis* are the first coral species to be listed as candidates for the ESA. Proactive conservation through the candidate species program minimizes the cost of recovery and allows management flexibility to stabilize or restore these species and their habitat. However, a candidate species listing alone provides no legal protection. In contrast, a full ESA listing would require the development and implementation of a recovery plan thereby reducing the likelihood of extinction by alleviating threats affecting these species and promoting strategies to increase population size. Key research and management strategies applied in the U.S. can be utilized in other countries, thereby promoting the recovery of acroporid corals throughout the region. By protecting declining coral species such as *A. cervicornis* and *A. palmata* through the ESA, unique species assemblages dependent on reefs will also benefit.

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Federal Communications Commission.

John A. Karousos,
Chief, Allocations Branch, Policy and Rules
Division, Mass Media Bureau.

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DEPARTMENT OF COMMERCE

National Oceanic and Atmospheric Administration

50 CFR Part 226

[Docket No. 991116305-9305-01; I.D. No. 110599D]

RIN 0648-AL82

Designated Critical Habitat: Re- proposed Critical Habitat for Johnson's Seagrass

AGENCY: National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), Commerce.

ACTION: Proposed rule; notice of hearing; request for comments.

SUMMARY: NMFS re-proposes to designate critical habitat for Johnson's seagrass (*Halophila johnsonii*) pursuant to section 4 of the Endangered Species Act (ESA). Johnson's seagrass is found on the east coast of Florida from Sebastian Inlet to central Biscayne Bay. Within this range, 10 areas are proposed for critical habitat: a portion of the Indian River Lagoon, north of the Sebastian Inlet Channel; a portion of the Indian River Lagoon, south of the Sebastian Inlet Channel; a portion of the Indian River Lagoon near the Fort Pierce Inlet; a portion of the Indian River Lagoon, north of the St. Lucie Inlet; a portion of Hobe Sound; a site on the south side of Jupiter Inlet; a site in central Lake Worth Lagoon; a site in Lake Worth Lagoon, Boynton Beach; a site in Lake Wyman, Boca Raton; and a portion of the Biscayne Bay Aquatic Preserve.

The designation of critical habitat provides explicit notice to Federal agencies and the public that these areas and features are vital to the conservation of the species.

DATES: Comments on this proposed rule must be received by January 3, 2000. A public hearing on this proposed action is scheduled for Thursday, December 16, 1999, from 7:00 p.m.-9:00 p.m.

ADDRESSES: Written comments on this proposed designation of critical habitat should be addressed to Mr. Charles Oravetz, Assistant Regional Administrator, Protected Resources Division, NMFS, Southeast Regional

Office, 9721 Executive Center Drive North, St. Petersburg, Florida 33702-2432. Comments may be sent via facsimile (fax) to 727-570-5517. Comments will not be accepted if submitted via e-mail or Internet. A public hearing on this proposal will be held at the South Florida Water Management District auditorium, 3301 Gun Club Road, West Palm Beach, Florida, 33416-4680 (see DATES).

FOR FURTHER INFORMATION CONTACT: Layne Bolen, Southeast Region, Protected Resources Division, NMFS, 727-570-5312, layne.bolen@noaa.gov or Marta Nammack, Office of Protected Resources, NMFS, 301-713-1401, marta.nammack@noaa.gov.

SUPPLEMENTARY INFORMATION:

Background

NMFS published a proposed rule to list Johnson's seagrass as a threatened species on September 15, 1993 (58 FR 48326) and a proposed rule to designate critical habitat on August 4, 1994 (59 FR 39716). A public hearing on both the proposed listing and critical habitat designation was held in Vero Beach, Florida, on September 20, 1994. As a result of public input during the comment period, NMFS postponed further action on listing. NMFS reopened the comment period for the proposed listing on April 20, 1998 (63 FR 19468). In order to update the original status report (Kenworthy, 1993) and to include information from new field and laboratory research on species distribution, ecology, genetics and phylogeny, NMFS convened a workshop on the biology, distribution, and abundance of *H. johnsonii*. The results of this workshop were summarized in the proceedings (Kenworthy, 1997) submitted to NMFS on October 15, 1997. The final rule to list Johnson's seagrass as a threatened species was published by NMFS on September 14, 1998 (63 FR 49035).

On February 23, 1999, NMFS established and convened a recovery team to prepare a recovery plan and develop recommendations for critical habitat for Johnson's seagrass. Based on these recommendations and the best available scientific data on the distribution, ecology and genetics of this species, NMFS has developed a new proposal to designate critical habitat for Johnson's seagrass. A draft recovery plan for Johnson's seagrass is anticipated by January 2000.

The proposed designation identifies those physical and biological features of the habitat that are essential to the conservation of the species and that may require special management

consideration or protection. The economic and other impacts resulting from designating critical habitat, over and above those that result from listing the species, are expected to be minimal.

NMFS has completed a conference opinion with the U.S. Army Corps of Engineers (COE) on maintenance dredging which will be used to fulfill the ESA section 7 consultation requirement. NMFS expects that normal maintenance dredging activities and routine operations on ports will not be negatively impacted by this proposed critical habitat designation.

Critical Habitat

Section 4(a)(3)(A) of the ESA requires that, to the maximum extent prudent and determinable, NMFS designate critical habitat concurrently with a determination that a species is endangered or threatened. NMFS has determined that sufficient information exists to propose designating critical habitat for Johnson's seagrass currently listed as threatened under the ESA. NMFS will consider all available information and data in finalizing this proposal.

The use of the term "essential habitat" within this document refers to critical habitat as defined by the ESA and should not be confused with the requirement to describe and identify Essential Fish Habitat pursuant to the Magnuson-Stevens Fishery Conservation and Management Act, 16 U.S.C. 1801 *et seq.*

Definition of Critical Habitat

Critical habitat is defined in section 3(5)(A) of the ESA as "(i) the specific areas within the geographical area occupied by the species * * * on which are found those physical or biological features (I) essential to the conservation of the species and (II) which may require special management considerations or protection; and (ii) specific areas outside the geographical area occupied by the species * * * upon a determination by the Secretary of Commerce (Secretary) that such areas are essential for the conservation of the species." The term "conservation", as defined in section 3(3) of the ESA, means " * * * to use and the use of all methods and procedures which are necessary to bring any endangered species or threatened species to the point at which the measures provided pursuant to this Act are no longer necessary."

In designating critical habitat, NMFS must consider the requirements of the species, including: (1) space for individual and population growth, and for normal behavior; (2) food, water, air,

light, minerals, or other nutritional or physiological requirements; (3) cover or shelter; (4) sites for breeding, reproduction, or rearing of offspring; and, generally, (5) habitats that are protected from disturbance or are representative of the historic geographical and ecological distributions of the species (50 CFR 424.12(b)).

In addition, NMFS must focus on and list the known physical and biological features (primary constituent elements) within the designated area(s) that are essential to the conservation of the species and that may require special management considerations or protection. These essential features may include, but are not limited to, food resources, water quality or quantity, and vegetation and sediment types and stability (50 CFR 424.12(b)).

Consideration of Economic and Other Factors

The economic, environmental and other impacts of a designation must also be evaluated and considered. NMFS must identify present and future activities that may adversely modify the proposed critical habitat or be affected by a designation. An area may be excluded from a critical habitat designation if NMFS determines that the overall benefits of exclusion outweigh the benefits of designation, unless the exclusion will result in the extinction of the species (16 U.S.C. 1533(b)(2)).

The impacts considered in this analysis are only those incremental impacts that specifically result from designating critical habitat above the economic and other impacts attributable to listing the species or resulting from other authorities. These incremental impacts are expected to be minimal (see Significance of Designating Critical Habitat section). In general, the designation of critical habitat highlights geographical areas of concern and reinforces the substantive protection resulting from the listing itself.

Impacts attributable to listing include those resulting from the "take" prohibitions under section 9 of the ESA and associated regulations. The term "take", as defined in the ESA, means "to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct." (16 U.S.C. 1532(19)). Harm can occur through destruction or modification of habitat (whether or not designated as critical) that significantly impairs essential behaviors, including breeding, feeding, rearing or migration (64 FR 60727; November 8, 1999).

Section 9 of the ESA prohibits certain activities that directly or indirectly

affect endangered species. These prohibitions apply to all individuals, organizations, and agencies subject to U.S. jurisdiction. Section 9 prohibitions apply automatically to endangered species; as described here, this is not the case for threatened species. Section 4(d) of the ESA directs the Secretary to implement regulations "to provide for the conservation of [threatened] species" that may include extending any or all of the prohibitions of section 9 to threatened species.

Section 9(a)(2)(E) of the ESA also prohibits violations of protective regulations for threatened species of plants implemented under section 4(d). NMFS may issue protective regulations pursuant to section 4(d) for Johnson's seagrass in a future rulemaking.

Impacts attributable to listing also include those resulting from the responsibility of all Federal agencies under section 7 of the ESA to ensure that their actions are not likely to jeopardize endangered or threatened species. An action could be likely to jeopardize the continued existence of a listed species through the destruction or adverse modification of its habitat, whether or not that habitat has been designated as critical.

As indicated above, NMFS has completed a conference opinion with the COE on maintenance dredging. This conference opinion included an analysis of the effects of maintenance dredging on proposed critical habitat. NMFS concluded that normal maintenance dredging activities and routine operations on ports are not likely to destroy or adversely modify proposed critical habitat.

Significance of Designating Critical Habitat

The designation of critical habitat does not, in itself, restrict state or private activities within the area or mandate any specific management or recovery actions. A critical habitat designation contributes to species conservation primarily by identifying important areas and describing the features within those areas that are essential to the species, thus alerting public and private entities to the importance of the area. Under the ESA, the only regulatory impact of a critical habitat designation is through the provisions of section 7. Section 7 applies only to actions with Federal involvement (e.g., authorized, funded, or conducted by a Federal agency) and does not affect exclusively state or private activities.

Under the ESA section 7 provisions, a designation of critical habitat would require Federal agencies to ensure that

any action they authorize, fund, or carry out is not likely to destroy or adversely modify the designated critical habitat. Activities that destroy or adversely modify critical habitat are defined as those actions that "appreciably diminish the value of critical habitat for both the survival and recovery" of the species (50 CFR 402.02). Regardless of a critical habitat designation, Federal agencies must ensure that their actions are not likely to jeopardize the continued existence of the listed species. Activities that jeopardize a species are defined as those actions that "reasonably would be expected, directly or indirectly, to reduce appreciably the likelihood of both the survival and recovery" of the species (50 CFR 402.02). Using these definitions, activities that are likely to destroy or adversely modify critical habitat would also be likely to jeopardize the species. Therefore, the protection provided by a critical habitat designation generally duplicates the protection provided under the section 7 jeopardy provision. Critical habitat may provide additional benefits to a species in cases where areas outside of the species' current range have been designated. In these cases, Federal agencies are required to consult with NMFS under section 7 (50 CFR 402.14 (a)), when these designated areas may be affected by their actions. The effects of these actions on designated areas may not have been recognized but for the critical habitat designation.

A designation of critical habitat provides Federal agencies with a clearer indication as to when consultation under section 7 of the ESA is required, particularly in cases where the action would not result in direct mortality, injury, or harm to individuals of a listed species (e.g., an action occurring within the critical habitat area when or where Johnson's seagrass is not present). The critical habitat designation, in describing the essential features of the habitat, also helps determine which activities conducted outside the designated area are subject to ESA section 7 (i.e., activities that may affect essential features of the designated area). For example, disposal of waste material in water adjacent to a critical habitat area may affect an essential feature of the designated habitat (water quality) and would be subject to the provisions of section 7 of the ESA.

A critical habitat designation also assists Federal agencies in planning future actions because the designation establishes, in advance, those habitats that will be given special consideration in ESA section 7 consultations. This is particularly true in cases where there

are alternative areas that would provide for the conservation of the species and the success of the action. With a designation of critical habitat, potential conflicts between Federal actions and endangered or threatened species can be identified and possibly avoided early in the agency's planning process.

Another indirect benefit of designating critical habitat is that it helps focus Federal, state and private conservation and management efforts in those areas. Recovery efforts may address special considerations needed in critical habitat areas, including conservation regulations that restrict private as well as Federal activities. The economic and other impacts of these actions would be considered at the time regulations are proposed, and, therefore, are not considered in the critical habitat designation process. Other Federal, state and local laws or regulations, such as zoning or wetlands protection, may also provide special protection for critical habitat areas.

Process for Designating Critical Habitat

Developing a proposed critical habitat designation involves three main considerations. First, the biological needs of the species are evaluated and essential habitat areas and features are identified. If alternative areas exist that would provide for the conservation of the species, such alternatives are also identified. Second, the need for special management considerations or protection of the area(s) or features is evaluated. Finally, the probable economic and other impacts of designating these essential areas as critical habitat are evaluated. After considering the requirements of the species, the need for special management, and the impacts of the designation, a notification of the proposed critical habitat is published in the *Federal Register* for comment. After considering all comments and any new information received on the proposal, the final critical habitat designation is published. Final critical habitat designations may be revised, using the same process, as new data become available.

A description of the critical habitat, need for special management considerations, and impacts of designating critical habitat for Johnson's seagrass and the proposed action, are described in the following sections.

Critical Habitat of Johnson's Seagrass

The biology of Johnson's seagrass is discussed in the final rule to list the species as threatened (63 FR 49035, September 14, 1998) and includes information on the current status of the

species, its life history characteristics and habitat requirements, as well as projects, activities and other factors affecting the species. The physical habitat that supports Johnson's seagrass includes both shallow intertidal as well as deeper subtidal zones. The species prospers and is able to colonize and maintain stable populations either in water that is clear and deep (2–5 m) or in water that is shallow and turbid. In tidal channels, it inhabits coarse sand substrates.

Based on published reports and discussions with seagrass experts, the distributional range of Johnson's seagrass is limited to the east coast of Florida from central Biscayne Bay (25°45' N. lat.) to Sebastian Inlet (27°51' N. lat.). There have been no reports of healthy populations of this species outside the presently known range. Although the species occurs throughout the Indian River Lagoon and Lake Worth, the 10 specific areas proposed for critical habitat encompass the largest known contiguous populations of Johnson's seagrass, those known to have persistent populations, those populations known to have persistent flowering, those populations found to have unique genetic variability, and/or populations that include the northern and southern limits of the species' range.

The species is distributed in patches within its range. The dimensions of patches range from a few square centimeters to approximately 327 square meters (sq.m.). The survival of the species likely depends on maintaining its existing viable populations, especially the areas where the larger patches are found. The Sebastian Inlet population is believed to be the northern limit of its distribution and includes flowering patches that have a known persistence of at least 10 years. Ft. Pierce Inlet and Jupiter Inlet are also found to have persistent and flowering populations. The other areas proposed for critical habitat designation represent the core range of the species where Johnson's seagrass is found to be abundant compared to other parts of its range, exhibits unique genetic make-up, or comprises the southern limit of its range. Spread of the species into new areas is limited by its reproductive potential. Johnson's seagrass possesses only female flowers; thus vegetative propagation, most likely through asexual branching, appears to be its only means of reproduction and dispersal. If an established community is disturbed, regrowth and reestablishment are extremely unlikely. If extirpated from an area, it is doubtful that the species would be capable of repopulation. This

species' method of reproduction impedes the ability to increase distribution as establishment of new vegetation requires considerable stability in environmental conditions and protection from human-induced disturbances.

Based on the best available information, general physical and biological features of the areas proposed for critical habitat designation include adequate water quality, salinity levels, water transparency, and stable, unconsolidated sediments that are free from physical disturbance. The specific areas occupied by Johnson's seagrass are those with one or more of the following criteria: (1) Locations with populations that have persisted for 10 years; (2) locations with persistent flowering populations; (3) locations at the northern and southern range limits of the species; (4) locations with unique genetic diversity; and (5) locations with a documented high abundance of Johnson's seagrass compared to other areas in the species' range. Explanations for these criteria are:

1. Persistent populations. Surveys of *H. johnsonii* distribution and abundance in the Indian River Lagoon indicate that populations fluctuate dramatically. In some areas populations disappear and re-appear on both intra- and inter-annual time scales (Virnstein *et al.*, 1997). Some populations have disappeared and not returned. Since sexual reproduction and seed dispersal are unknown, this species may rely on vegetative fragmentation for recruitment and establishment of new populations. Recruitment from fragmentation and migration are random processes which do not guarantee the persistence of the species in any one location. Perennial populations which have persisted for 10 years exist in several locations, including Sebastian Inlet, Fort Pierce Inlet, Jupiter Inlet and Hobe Sound. Environmental characteristics of these sites appear favorable to the species, while in other locations in the lagoon, populations have disappeared. Locations where populations have persisted should receive critical habitat consideration.

2. Persistent flowering populations. The existence of male flowers or recruitment by seed have not been documented for *H. johnsonii*. These observations suggest that this species does not reproduce sexually, and if it does, it is a very rare event. Yet, large clones of mature female plants flower prolifically at several locations, including Sebastian Inlet, Fort Pierce Inlet, Jupiter Inlet and Lake Worth Lagoon. The environmental conditions at these sites appears to be suitable for

flowering, and if there are any males present, these would be likely habitats for successful reproduction. Locations where there are persistent flowering populations should receive critical habitat consideration.

3. Northern and southern ranges of the populations. The geographical limits of the distributional range of a species can indicate a reduction or expansion of the species' range. Greater adaptive stresses can occur at the limits of the species' range. If the range extension were shrinking, the edges should be protected to prevent further loss. Second, the distribution limits may be a point where the populations are expanding and invading new environments. The unique phenotypic and genotypic characteristics of these populations could be an important reservoir for characteristics resistant to extinction and conducive to survival and growth. The northern and southern ranges of Johnson's seagrass are defined as Sebastian Inlet and central Biscayne Bay, respectively. These limits to the species' range should receive critical habitat consideration.

4. Populations with unique genetic variability. The Boca Raton and Boynton Beach sites have populations which are distinguished by a higher index of genetic variation than any of the central and northern populations examined to date. These two sites possibly represent a genetically semi-isolated group which could be the reservoir of a large part of the overall genetic variation found in this species. Information is lacking on the geographic extent of this genetic variability. Locations with populations that have unique genetic variability should receive critical habitat consideration.

5. Areas of abundance. The Lake Worth Lagoon and Palm Beach County seagrass populations represent an abundant core of *Halophila* species, including Johnson's seagrass. Previously a freshwater lake, Lake Worth, was transformed into a lagoon beginning in 1877 when an ocean inlet was stabilized. With dredging of the Intracoastal Waterway, shoreline development, and sewage disposal, the lagoon was permanently altered. Presently, there are about 2000 acres of seagrass in the lagoon covering 35 percent of the bottom. It is estimated that between 20 and 25 percent of the seagrass coverage is comprised of mixed assemblages of *H. decipiens* and *H. johnsonii*. This is proportionately more *Halophila* coverage than occurs elsewhere along the southeast coast of Florida. Presently, conditions within Lake Worth Lagoon and in Palm Beach County in general appear to be

conducive to the survival of *H. johnsonii*. Locations within Lake Worth and Palm Beach County should be considered as critical habitat.

The area proposed for critical habitat in Lake Worth Lagoon, near Bingham Island, consists of the largest recorded contiguous patch of Johnson's seagrass: a 30-acre meadow of Johnson's seagrass intermixed with sparse coverage of *H. decipiens* and *Halodule wrightii* (Smith and Mezich, 1991 and 1999).

Need for Special Management Consideration or Protection

NMFS has determined that the essential areas and features described here are at risk and may require special management consideration or protection. Special management may be required because of the following activities: (1) Vessel traffic and the resulting propeller dredging and anchor mooring; (2) dredging; (3) dock, marina, and bridge construction and shading from these structures; (4) water pollution; and (5) land use practices including shoreline development, agriculture, and aquaculture. Activities associated with recreational boat traffic account for the majority of human use associated with the proposed critical habitat areas. The destruction of the benthic community due to boating activities, propeller dredging, anchor mooring, and dock and marina construction was observed at all sites during a study by NMFS from 1990 to 1992. These activities severely disrupt the benthic habitat, breaching root systems, severing rhizomes, and significantly reducing the viability of the seagrass community. Propeller dredging and anchor mooring in shallow areas are a major disturbance to even the most robust seagrasses. This destruction is expected to worsen with the predicted increase in boating activity. Trampling of seagrass beds, a secondary effect of recreational boating, also disturbs seagrass habitat. Populations of Johnson's seagrass inhabiting shallow water and water close to inlets, where vessel traffic is concentrated, will be most affected.

The constant sedimentation patterns in and around inlets require frequent maintenance dredging, which could either directly remove essential seagrass habitat or indirectly affect it by redistributing sediments, burying plants and destabilizing the bottom structure. Altering benthic topography or burying the plants may remove them from the photic zone.

Permitted dredging of channels, basins, and other in-and on-water construction projects cause loss of Johnson's seagrass and its habitat

through direct removal of the plant, fragmentation of habitat, and shading. Docking facilities that, upon meeting certain provisions, are exempt from state permitting also contribute to loss of Johnson's seagrass through construction impacts and shading. Fixed add-ons to exempt docks (such as finger piers, floating docks, or boat lifts) have recently been documented as an additional source of seagrass loss due to shading (Smith and Mezich, 1999).

Decreased water transparency caused by suspended sediments, water color, and chlorophylls could have significant detrimental effects on the distribution and abundance of the deeper water populations of Johnson's seagrass. A distribution survey in Hobe and Jupiter Sounds indicates that the abundance of this seagrass diminishes in the more turbid interior portion of the lagoon where reduced light limits photosynthesis.

Other areas of concern include seagrass beds located in proximity to rivers and canal mouths where low salinity, highly colored water is discharged. Freshwater discharge into areas adjacent to seagrass beds may provoke physiological stress upon the plants by reducing the salinity levels. Additionally, colored waters released into these areas reduce the amount of sunlight available for photosynthesis by rapidly attenuating shorter wavelengths of Photosynthetically Active Radiation.

Also, continuing and increasing degradation of water quality due to increased land use and water management threatens the welfare of seagrass communities. Nutrient over-enrichment caused by inorganic and organic nitrogen and phosphorous loading via urban and agricultural land run-off stimulates increased algal growth that may smother Johnson's seagrass, shade rooted vegetation, and diminish the oxygen content of the water. Low oxygen conditions have a demonstrated negative impact on seagrasses and associated communities.

Special consideration and protection for these and other habitat features are evaluated in the ESA section 7 consultation process. Special management needs and the protection of these habitat features are being addressed in the development and implementation of the recovery plan.

Activities That May Affect Critical Habitat

A wide range of activities funded, authorized or carried out by Federal agencies may affect the essential habitat requirements of Johnson's seagrass. These include authorization by the COE for beach nourishment, dredging, and

related activities including construction of docks and marinas; bridge construction projects funded by the Federal Highway Administration; actions by the U.S. Environmental Protection Agency and the COE to manage freshwater discharges into waterways; regulation of vessel traffic by the U.S. Coast Guard; management of national refuges and protected species by the U.S. Fish and Wildlife Service; management of vessel traffic (and other activities) by the U.S. Navy; approval of changes to Florida's coastal zone management plan by NOAA's National Ocean Service, and management of commercial fishing and protected species by NMFS.

Expected Impacts of Designating Critical Habitat

This designation will identify specific habitat areas that have been determined to be essential for the conservation of Johnson's seagrass and that may be in need of special management considerations or protection. It will require Federal agencies to evaluate their activities with respect to the critical habitat of this species and to consult with NMFS pursuant to section 7 of the ESA before engaging in any action that may affect the critical habitat.

As discussed in the section on activities that may impact essential habitat and features, the Federal activities that may affect critical habitat are the same activities that may affect the species itself. For plants, this is particularly true when analyzing the impacts of designating critical habitat. For example, the activities that affect water quality, an essential feature of critical habitat, will also be considered in terms of how they affect the species itself.

Should this proposed designation of critical habitat be adopted, Federal agencies will continue to engage in ESA section 7 consultations to determine if the actions they authorize, fund or carry out are likely to jeopardize the continued existence of Johnson's seagrass; however, with designation, they would also need to address explicitly impacts to the species' critical habitat. This is not expected to affect materially the scope of future consultations or result in greater economic impacts, since most impacts to Johnson's seagrass habitat will already be considered in ESA section 7 consultations.

The economic costs to be considered in a critical habitat designation are the incremental costs of designation above the economic impacts attributable to listing or attributable to authorities

other than the ESA. NMFS has determined that there are few, if any, incremental net costs for areas within the species' current distribution, and no areas outside the current range are proposed for critical habitat designation.

Proposed Critical Habitat; Geographic Extent

Based on available information, NMFS proposes to designate critical habitat that is considered essential for the survival and that may require special management consideration or protection. The critical habitat designation proposed by this rule includes: (1) Locations with populations that have persisted for 10 years; (2) locations with persistent flowering populations; (3) locations at the northern and southern range limits of the species; (4) locations with unique genetic diversity; and (5) core locations with a documented high abundance of Johnson's seagrass compared to other areas in the species' range.

NMFS is not including in the proposed designation any areas outside the species' currently known geographical area. NMFS has concluded that, at this time, proper management of the essential features of the areas around Sebastian and Ft. Pierce Inlet, Hobe Sound, Jupiter Inlet, Lake Worth, Boca Raton, and northern Key Biscayne will be sufficient to provide for the survival and recovery of this species. NMFS may reconsider this evaluation and propose additional areas for critical habitat at any time. Johnson's seagrass occurs in numerous locations throughout its range in areas outside of those currently being proposed for critical habitat. Information on genetic variability and persistence of Johnson's seagrass is currently lacking in these areas. Future research, however, involving genetic studies and comprehensive, long-term field surveys, could identify additional areas that are essential to the conservation of the species and require special management considerations, and would, therefore, warrant designation as critical habitat. Also, if a male flower of Johnson's seagrass is identified in an area, this area should be designated as critical habitat.

The 10 areas proposed for critical habitat designation include:

(1) A portion of the Indian River, Florida, north of Sebastian Inlet Channel, defined by the following coordinates:

Northwest corner: 27°51'15.03"N,
80°27'55.49"W
Northeast corner: 27°51'16.57"N,
80°27'53.05"W
Southwest corner: 27°51'08.85"N,
80°27'50.48"W

Southeast corner: 27°51'11.58"N,
80°27'47.35"W

(2) A portion of the Indian River, Florida, south of the Sebastian Inlet Channel, defined by the following coordinates:

Northwest corner: 27°51'01.32"N,
80°27'46.10"W
Northeast corner: 27°51'02.69"N,
80°27'45.27"W
Southwest corner: 27°50'59.08"N,
80°27'41.84"W
Southeast corner: 27°51'01.07"N,
80°27'40.50"W

(3) A portion of the Indian River Lagoon in the vicinity of the Fort Pierce Inlet. This site is located on the north side of the entrance channel just west of a small mangrove vegetated island where the main entrance channel bifurcates to the north. The area is defined by the following coordinates:

Northwest corner: 27°28'06.00"N,
80°18'48.89"W
Northeast corner: 27°28'04.43"N,
80°18'42.25"W
Southwest corner: 27°28'02.86"N,
80°18'49.06"W
Southeast corner: 27°28'01.46"N,
80°18'42.42"W

(4) A portion of the Indian River Lagoon, Florida, north of the St. Lucie Inlet, from South Nettles Island to the Florida Oceanographic Institute, defined by the following coordinates:

Northwest corner: 27°16'44.04"N,
80°14'00.00"W
Northeast corner: 27°16'44.04"N,
80°12'51.33"W
Southwest corner: 27°12'49.70"N,
80°11'46.80"W
Southeast corner: 27°12'49.70"N,
80°11'02.50"W

(5) Hobe Sound beginning at State Road 708 (27°03'49.90"N, 80°07'20.57"W) and extending south to 27°00'00.00"N, 80°05'32.54"W.

(6) Jupiter Inlet at a site located just west of the entrance to Zeek's Marina on the south side of Jupiter Inlet and defined by the following coordinates (note a south central point was included to better define the shape of the southern boundary):

Northwest corner: 26°56'43.34"N,
80°04'47.84"W
Northeast corner: 26°56'40.93"N,
80°04'42.61"W
Southwest corner: 26°56'40.73"N,
80°04'48.65"W
South central point: 26°56'38.11"N,
80°04'45.83"W
Southeast corner: 26°56'38.31"N,
80°04'42.41"W

(7) A portion of Lake Worth, Florida, just north of Bingham Island defined by the following coordinates:

Northwest corner: 26°40'44.00"N,
80°02'39.00"

Northeast corner: 26°40'40.00"N,
80°02'34.00"W

Southwest corner: 26°40'32.00"N,
80°02'44.00"W

Southeast corner: 26°40'33.00"N,
80°02'35.00"W

(8) A portion of Lake Worth Lagoon, Florida, located just north of the Boynton Inlet, on the west side of the Intracoastal Waterway, defined by the following coordinates:

Northwest corner: 26°33'28.00"N,
80°02'54.00"W

Northeast corner: 26°33'30.00"N,
80°03'04.00"W

Southwest corner: 26°32'50.00"N,
80°03'11.00"W

Southeast corner: 26°32'50.00"N,
80°02'58.00"W

(9) A portion of northeast Lake Wyman, Boca Raton, Florida, defined by the following coordinates:

Northwest corner: 26°22'27.00"N,
80°04'23.00"W

Northeast corner: 26°22'27.00"N,
80°04'18.00"W

Southwest corner: 26°22'23.00"N,
80°04'22.00"W

Southeast corner: 26°22'23.00"N,
80°04'19.00"W

(10) A portion of Northern Biscayne Bay, Florida, defined by the following: The northern boundary of Biscayne Bay Aquatic Preserve, N.E. 163rd Street, and including all parts of the Biscayne Bay Aquatics Preserve as defined in 18-18.002 of the Florida Administrative Code (F.A.C.) excluding the Ortega River beyond its mouth, and all Federal navigation channels at the Port of Miami, not including the Intracoastal Waterway, to the currently documented southern-most range of Johnson's seagrass, Central Key Biscayne (25°45'N).

Maps are provided for reference purposes to guide Federal agencies and other interested parties in locating the general boundaries of the proposed critical habitat. They do not constitute the definition of the boundaries of critical habitat. Persons must refer to the regulations at 50 CFR 226.91 for the actual boundaries of the designated critical habitat. Figures 1 through 9 illustrate the ten areas proposed as critical habitat for Johnson's seagrass.

Request for Comments

NMFS is soliciting information, comments and/or recommendations on

any aspect of this proposal from all interested parties. NMFS will consider all information, comments and recommendations received before reaching a final decision.

The public hearing on this proposed action has been scheduled for Thursday, December 2, 1999. Interested parties will have an opportunity to provide oral and written testimony at the public hearing.

Special Accommodations

This meeting is physically accessible to people with disabilities. Requests for sign language interpretation or other auxiliary aids should be directed to Layne Bolen (see ADDRESSES).

References

The complete citations for the references used in this document are available upon request (see FOR FURTHER INFORMATION CONTACT).

Classification

NMFS has determined that Environmental Assessments or an Environmental Impact Statement, as defined under the authority of the National Environmental Policy Act of 1969, need not be prepared for this critical habitat designation. See *Douglas County v. Babbitt*, 48 F.3d 1495 (9th Cir. 1995), cert. denied, 116 S.Ct. 698 (1996).

NMFS proposes to designate 10 areas in the range of Johnson's seagrass as critical habitat. This designation will not impose any additional requirements or economic effects upon small entities beyond those which may accrue from section 7 of the ESA. Section 7 requires Federal agencies to ensure that any action they carry out, authorize, or fund is not likely to jeopardize the continued existence of any listed species or to result in the destruction or adverse modification of critical habitat (ESA section 7(a)(2)). The consultation requirements of section 7 are nondiscretionary and are effective at the time of species' listing. Therefore, Federal agencies must consult with NMFS and ensure that their actions do not jeopardize a listed species, regardless of whether critical habitat is designated.

In the future, should NMFS determine that designation of additional habitat areas in the species' range and/or outside the species' current range is necessary for conservation and recovery, NMFS will analyze the incremental

costs of the action and assess its potential impacts on small entities, as required by the Regulatory Flexibility Act.

Accordingly, the Chief Counsel for Regulation of the Department of Commerce has certified to the Chief Counsel for Advocacy of the Small Business Administration that the proposed critical habitat designation, if adopted, would not have a significant economic impact on a substantial number of small entities, as described in the Regulatory Flexibility Act.

The Assistant Administrator for Fisheries, NOAA, has determined that the proposed designation is consistent to the maximum extent practicable with the approved Coastal Zone Management Program of the State of Florida. This determination has been submitted for review by the responsible State agency under section 307 of the Coastal Zone Management Act.

The Assistant Administrator for Fisheries, NOAA, has determined this rule is not significant for purposes of E.O. 12866.

This proposed rule does not contain a collection-of-information requirement for purposes of the Paperwork Reduction Act.

In accordance with E.O. 13132, NMFS has prepared the following federalism summary impact statement. When NMFS issued a proposed rule to designate critical habitat for Johnson's seagrass in 1994, NMFS began consulting with the State of Florida. While the State expressed support for protection of Johnson's seagrass, it also expressed concern over the possible economic impacts of a critical habitat designation. NMFS understands the concerns of the State regarding timely maintenance of state and federal navigation channels, ports, and inlets, and NMFS' goal is to protect the species with minimal effects to these activities. Concerns regarding possible economic impacts of a critical habitat designation are addressed in the preamble to this rule. In addition, NMFS has completed a conference opinion with the COE on the effects of maintenance dredging on Johnson's seagrass and its proposed critical habitat. NMFS expects that operations on ports will not be negatively impacted by this proposed critical habitat designation.

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International Inc. also withdrew its request for an administrative review. Pursuant to 19 CFR 351.213(d)(1), the Department will rescind an administrative review, in whole or in part, if a party that requested a review withdraws the request within 90 days of the date of publication of notice of initiation of the requested review. The Secretary may extend this time limit if the Secretary decides that it is reasonable to do so. There were two requests for administrative review and both have been withdrawn. Although Direct Source International Inc. withdrew its request after the 90-day deadline, given that the review has not progressed substantially and there would be no undue burden on the parties or the Department, we have determined that it is reasonable to grant the request to withdraw the original review requests. Therefore, we are rescinding this review. This rescission of the administrative review and notice are in accordance with section 751 of the Tariff Act of 1930, as amended (the Act) and 19 CFR 351.213(d).

The cash-deposit rates will remain at 46.01 percent for ZLIP and 126.94 percent for Zhou, the rates established in the most recently completed segment of this proceeding (59 FR 51168, October 7, 1994). This notice is in accordance with section 777(i) of the Act.

Dated: June 9, 1999.

Richard W. Moreland,
Deputy Assistant Secretary for Import
Administration.

[FR Doc. 99-15998 Filed 6-22-99; 8:45 am]

BILLING CODE 3510-DS-P

DEPARTMENT OF COMMERCE

National Oceanic and Atmospheric Administration

[I.D. 061699A]

Endangered and Threatened Species; Revision of Candidate Species List Under the Endangered Species Act

AGENCY: National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), Commerce.

ACTION: Notice of modification of list of candidate species.

SUMMARY: NMFS identifies marine and anadromous species as candidates for possible addition to the List of Endangered and Threatened Species. NMFS is soliciting information concerning the status of these species. This notice is not a proposal for listing, and the involved species do not receive substantive or procedural protection

under the Endangered Species Act of 1973 (ESA). The candidate species list serves to notify the public that NMFS has concerns regarding these species/vertebrate populations that may warrant listing in the future, and it facilitates voluntary conservation efforts. NMFS encourages Federal agencies and other appropriate parties to take these species into account in project planning.

DATES: This updated list is effective on June 23, 1999.

ADDRESSES: Reliable documentation for these additions to the candidate species list should be sent to the Chief of Endangered Species, NMFS, Office of Protected Resources, 1315 East-West Highway, F/PR3, Silver Spring, MD 20910.

FOR FURTHER INFORMATION CONTACT: Marta Nammack or Terri Jordan at (301)713-1401.

SUPPLEMENTARY INFORMATION: The ESA requires determinations of whether species of wildlife and plants are endangered or threatened, based on the best available scientific and commercial data. "Species" includes any species or subspecies of fish, wildlife, or plant, and any distinct population segment of any vertebrate species that interbreeds when mature (vertebrate population). NMFS and the U.S. Fish and Wildlife Service share responsibilities under the ESA. With some exceptions, NMFS is responsible for species that reside all or the major portion of their lifetimes in marine or estuarine waters. The regulations implementing Section 4 of the ESA (49 FR 38900, October 1, 1984) define "candidate" as "any species being considered by the Secretary for listing as an endangered or a threatened species, but not yet the subject of a proposed rule." As resources permit, NMFS conducts a review of the status of each candidate species to determine if it warrants listing as endangered or threatened under the ESA.

Species/vertebrate populations may be added to the candidate species list based on consideration of their biological status. Biological status is determined by both demography and genetic composition of the species/vertebrate population. If there is evidence of demographic or genetic concerns that would indicate that listing may be warranted, the species/vertebrate population should be added to the candidate species list.

Demographic concerns would occur when there is a significant decline in abundance or range from historical levels that would indicate that listing may be warranted. This could result from overharvest, habitat degradation, disease outbreaks, predation, natural climatic conditions, and hatchery

practices that lead to competition with natural stocks or depletion of natural fish for use as hatchery broodstock.

Genetic concerns that would indicate that listing may be warranted include outbreeding and inbreeding depression resulting from poor hatchery practices or substantially reduced numbers of natural individuals.

On July 14, 1997, NMFS revised its candidate species list (62 FR 37561). On January 15, 1999, NMFS published notification soliciting comments and reliable documentation on species it was considering to add to the candidate species list (64 FR 2629). NMFS considered all comments received and all available information in updating the candidate species list.

This document adds 14 new species to the list of candidate species for which reliable information is available to NMFS meeting the previously stated criteria (Table 1). As resources permit, NMFS intends to conduct status reviews on candidate species, collect further documentation on them, and make appropriate amendments to the accompanying table during the next revision.

In addition to these new species, changes to the candidate status of Pacific salmon as a result of status reviews have been noted in Table 1 to this document. In some cases, even when NMFS determines that listing a species under the ESA is not warranted, it may add the species to the candidate species list because some concerns about its status still remain. Chum, sockeye, and chinook salmon are no longer candidate species, though the Hood Canal summer-run and Columbia River chum salmon evolutionarily significant units (ESU), the Ozette Lake sockeye salmon ESU, and the Upper Columbia River spring-run, Puget Sound, Lower Columbia River, and Upper Willamette River chinook salmon ESUs were listed as threatened or endangered (64 FR 14308, March 24, 1999; 64 FR 14508, March 25, 1999; 64 FR 14517, March 25, 1999; 64 FR 14528, March 25, 1999). NMFS designated three more steelhead ESUs (Northern California, Klamath Mountains Province, and Oregon Coast) as candidate species (63 FR 13347, March 19, 1998) and listed the former candidate species, Middle Columbia River steelhead ESU, and the Upper Willamette River steelhead ESU, as threatened (64 FR 14517; March 25, 1999). NMFS also listed the former candidate species, Oregon Coast coho salmon ESU, as threatened in August 1998 (63 FR 42587; August 10, 1998), leaving only two coho salmon ESUs on

the candidate species list. After conducting a coastwide status review of sea-run cutthroat, NMFS proposed to list the Southwestern Washington/ Columbia River ESU as threatened and designated the Oregon Coastal sea-run cutthroat trout ESU as a candidate species (64 FR 16397; April 5, 1999).

In addition, though NMFS determined that the Gulf of Maine population of harbor porpoise's status did not warrant listing under the ESA, the population has been added to the candidate species list because concerns on its status still remain.

It is important to note that the candidate species list is limited by the

information available. Therefore, it does not encompass all declining marine and anadromous species that may warrant listing in the future. Moreover, inclusion of a species on the candidate list does not create a higher listing priority for that species. As appropriate, NMFS may initiate a status review for any species or vertebrate population of concern, regardless of whether it is a candidate species, and the public may petition to list any species or vertebrate population. Inclusion in the candidate species list is intended to stimulate voluntary conservation efforts, which, if effective, can result in a lower likelihood of an ESA listing.

In Table 1, Revised list of candidate species, the common name appears as the first entry followed by the scientific name, the family name, and the area of concern. This area denotes the general geographic boundaries of the species or the vertebrate population for which concern has been expressed. Ongoing or future biological status reviews may narrow the geographic area or population of concern in the future.

Dated: June 15, 1999.

Hilda Diaz-Soltero,

Director, Office of Protected Resources,
National Marine Fisheries Service.

Table 1 - Revised list of candidate species

Common Name	Scientific Name	Family	Area of Concern ³
Marine Mammals			
beluga whale	<i>Delphinapterus leucas</i>	Monodontidae	AK (Cook Inlet population).
harbor porpoise	<i>Phocoena phocoena</i>	Phocoenidae	ME - NC (Gulf of Maine population).
Fishes			
dusky shark	<i>Carcharhinus obscurus</i>	Carcharhinidae	Atlantic; Gulf of Mexico; Pacific.
sand tiger shark	<i>Odontaspis taurus</i>	Odontaspidae	Atlantic; Gulf of Mexico.
night shark	<i>Carcharhinus signatus</i>	Carcharhinidae	Atlantic; Gulf of Mexico.
smalltooth sawfish*	<i>Pristis pectinata</i>	Pristidae	Atlantic; NC to Gulf of Mexico.
largetooth sawfish*	<i>Pristis pristis</i>	Pristidae	Atlantic; TX, FL.
barndoor skate*	<i>Raja laevis</i>	Rajidae	Atlantic; Cape Hatteras, NC to Newfoundland, Canada.
Atlantic sturgeon	<i>Acipenser oxyrinchus oxyrinchus</i>	Acipenseridae	Atlantic, anadromous.
Pacific herring*	<i>Clupea pallasii</i>	Clupeidae	Puget Sound.
Alabama shad	<i>Alosa alabamiae</i>	Clupeidae	AL, FL, anadromous.
searun cutthroat trout	<i>Oncorhynchus clarki clarki</i>	Salmonidae	Pacific, anadromous. Oregon Coastal ESU.
coho salmon	<i>Oncorhynchus kisutch</i>	Salmonidae	Pacific, anadromous. Puget Sound/Strait of Georgia and Southwest WA/Lower Columbia River ESUs ¹
steelhead trout	<i>Oncorhynchus mykiss</i>	Salmonidae	Pacific, anadromous. Northern CA, Klamath Mountains Province, and OR Coast ESUs.
Atlantic salmon	<i>Salmo salar</i>	Salmonidae	Atlantic, anadromous. Gulf of Maine DPS ²
Pacific cod*	<i>Gadus macrocephalus</i>	Gadidae	Puget Sound.
Pacific hake*	<i>Merluccius productus</i>	Gadidae	Puget Sound.
walleye pollock*	<i>Theragra chalcogramma</i>	Gadidae	Puget Sound.
mangrove rivulus	<i>Rivulus marmoratus</i>	Aplocheilidae	FL, estuarine.
saltmarsh topminnow	<i>Fundulus jenkinsi</i>	Cyprinodontidae	TX, LA, MS, AL, FL.
Key silverside	<i>Menidia menidia</i>	Atherinidae	Florida Keys.
opossum pipefish	<i>Microphis brachyurus lineatus</i>	Syngnathidae	Florida, Indian River Lagoon.
brown rockfish*	<i>Sebastes auriculatus</i>	Scorpaenidae	Puget Sound.
copper rockfish*	<i>Sebastes caurinus</i>	Scorpaenidae	Puget Sound.
quillback rockfish*	<i>Sebastes maliger</i>	Scorpaenidae	Puget Sound.
bocaccio*	<i>Sebastes paucispinis</i>	Scorpaenidae	Pacific, CA to OR.
speckled hind	<i>Epinephelus drummondhayi</i>	Serranidae	NC to Gulf of Mexico.
jewfish	<i>Epinephelus itajara</i>	Serranidae	NC southward to Gulf of Mexico.
warsaw grouper	<i>Epinephelus nigritus</i>	Serranidae	MA southward to Gulf of Mexico.
Nassau grouper	<i>Epinephelus striatus</i>	Serranidae	NC southward to Gulf of Mexico.
Mollusks			
white abalone	<i>Haliotis sorenseni</i>	Haliotidae	CA, Baja CA.
black abalone*	<i>Haliotis cracherodii</i>	Haliotidae	OR, CA, Baja CA.
Anthozoans (Corals)			
elkhorn coral*	<i>Acropora palmata</i>	Acroporidae	western Atlantic; Caribbean.
staghorn coral*	<i>Acropora cervicornis</i>	Acroporidae	western Atlantic; Caribbean.

*addition to list

¹ ESU = evolutionarily significant unit. Pacific salmon populations can only be listed under the ESA if they are "evolutionarily significant", per NMFS policy (56 FR 58612).

² DPS = distinct population segment

³ Defines the general geographic area or populations of concern for the species.

organizations to discuss subjects that relate to the field of weights and measures technology and administration.

Pursuant to 15 U.S.C. 272 B, the National Institute of Standards and Technology acts as a sponsor of the National Conference on Weights and Measures in order to promote uniformity among the States in the complex of laws, regulations, methods, and testing equipment that comprises regulatory control by the States of commercial weighing and measuring.

DATES: The meeting will be held January 31–February 4, 1999, 8:00 a.m.–5:00 p.m.

LOCATION OF MEETING: Sheraton Old Town Hotel, 800 Rio Grande Boulevard, N.W., Albuquerque, New Mexico 87104.

FOR FURTHER INFORMATION CONTACT: Dr. Gilbert Ugiansky, Chief, NIST, Office of Weights and Measures, 100 Bureau Drive Stop 2350 Gaithersburg, Maryland 20899–2350. Telephone: (301) 975–4004, or E-mail: owm@nist.gov.

Dated: January 8, 1999.

Robert E. Hebner,

Acting Deputy Director.

[FR Doc. 99–899 Filed 1–14–99; 8:45 am]

BILLING CODE 3510–13–M

DEPARTMENT OF COMMERCE

National Oceanic and Atmospheric Administration

[I.D. 011199C]

Endangered and Threatened Species; Request for Information on Candidate Species List Under the Endangered Species Act

AGENCY: National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), Commerce.

ACTION: Request for information for revision of candidate species list.

SUMMARY: NMFS solicits information on marine and anadromous species that may qualify as candidates for possible addition to the List of Endangered and Threatened Species, including information on the status of species currently classified as candidate species. This notice is not a proposal for listing; candidate species do not receive substantive or procedural protection under the Endangered Species Act of 1973 (ESA). The goal of the candidate species program is to identify marine and anadromous species as candidates for possible addition to the List of Endangered and Threatened Species and encourage voluntary efforts to help prevent listings.

DATES: Comments will be accepted until April 15, 1999.

ADDRESSES: Comments and documentation for these and any recommended additions or deletions to the candidate species list should be sent to Chief, Endangered Species Division, Office of Protected Resources, NMFS, 1315 East-West Highway, Silver Spring, MD 20910.

FOR FURTHER INFORMATION CONTACT: Marta Nammack or Terri Jordan at (301) 713–1401.

SUPPLEMENTARY INFORMATION: The ESA requires determinations of whether species of wildlife and plants are endangered or threatened, based on the best available scientific and commercial data. "Species" includes any species or subspecies of fish, wildlife, or plant, and any distinct population segment of any vertebrate species that interbreeds when mature (vertebrate population). NMFS and the U.S. Fish and Wildlife Service share responsibilities under the ESA. With some exceptions, NMFS is responsible for species that reside all or the major portion of their lifetime in marine or estuarine waters. The regulations implementing Section 4 of the ESA (49 FR 38900, October 1, 1984) define "candidate" as "any species being considered by the Secretary for listing as an endangered or a threatened species, but not yet the subject of a proposed rule."

The four main purposes of the candidate species list are to (1) Increase public awareness about these species; (2) identify those species that may be in need of protective measures under the ESA, and if possible, recover them before listing under the ESA becomes necessary; (3) stimulate voluntary conservation efforts by Federal agencies and other appropriate parties with regard to these species; and (4) identify uncertainties associated with the status of the species. As resources permit, NMFS conducts a review of the status of each candidate species to determine if it warrants listing as endangered or threatened under the ESA. Sometimes, even though NMFS may determine after conducting a status review that a species does not warrant listing under the ESA, NMFS may retain the species on the candidate species list due to remaining concerns or uncertainties. NMFS believes it is important to highlight species for which listing may be warranted so that Federal and state agencies, Native American tribes, and the private sector are aware of which species could benefit from proactive conservation efforts. Agencies and other appropriate parties can take candidate species into account in project planning,

which may lower the likelihood of an ESA listing.

NMFS has developed specific criteria for determining which species/vertebrate populations should be included on the NMFS candidate species list. These criteria are based on the requirement for reliable information on the biological status of a species or vertebrate population.

Biological status is determined by both demography and genetic composition of the species/vertebrate population. If there is evidence of demographic or genetic concerns that would indicate that listing may be warranted, the species/vertebrate population should be added to the candidate species list. Demographic concerns would occur when there is a significant decline in abundance or range from historical levels that would indicate that listing may be warranted. This could result from activities such as over-harvest, habitat degradation, disease outbreaks, predation, natural climatic conditions, and hatchery operations that negatively impact natural stocks. Genetic concerns that would indicate that listing may be warranted include outbreeding and inbreeding depression resulting from poor hatchery practices or substantially reduced numbers of natural individuals.

If you wish to propose that a species/vertebrate population be designated as a candidate species, please submit available information, including: (1) Taxonomic validity of the species, subspecies or vertebrate population; (2) life history; (3) historic and current population size and distribution; (4) assessment of confirmed and likely threats and declines; (5) existing laws, regulations, agreements and other protective mechanisms; and (6) documentation of information used to justify their proposal.

The previous list was published on July 14, 1997, (62 FR 37560). NMFS intends to consider the results of ongoing status reviews and all data received in response to this notice to make appropriate amendments to the list. Some of the species NMFS is considering adding to the candidate species list are the largemouth sawfish (*Pristis pristis*), smalltooth sawfish (*Pristis pectinata*), barndoor skate (*Raja laevis*), elkhorn coral (*Acropora palmata*), staghorn coral (*Acropora cervicornis*), and four gastropods that are possibly extinct: "*Collisella edmitchelli*", *Lottia alveus alveus*, *Cerithidea fuscata*, and *Phyllaplysia smaragda*.

It is important to note that the candidate species list is limited by the information available. Therefore, it does

not encompass all declining marine and anadromous species that may warrant listing in the future. Moreover, inclusion of a species on the candidate species list does not create a higher listing priority for that species. As appropriate, NMFS may initiate a status review for any species or vertebrate population of concern, regardless of whether it is a candidate species, and the public may petition to list any species or vertebrate population.

Dated: January 12, 1999.

Ann D. Terbush,

*Acting Director, Office of Protected Resources,
National Marine Fisheries Service.*

[FR Doc. 99-1011 Filed 1-14-99; 8:45 am]

BILLING CODE 3510-22-F

DEPARTMENT OF COMMERCE

National Oceanic and Atmospheric Administration

[I.D. 011199B]

North Pacific Fishery Management Council; Public Meetings

AGENCY: National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), Commerce.

ACTION: Notice of public meetings.

SUMMARY: The North Pacific Fishery Management Council (Council) and its advisory committees will meet in Anchorage, AK, the week of February 1, 1999.

DATES: 1. The Scientific and Statistical Committee (SSC) will meet beginning at 8:00 a.m. on Monday, February 1, continuing through at least Tuesday, February 2, 1999.

2. The Advisory Panel (AP) will begin meeting at 8:00 a.m. on Monday, February 1, and continue through Thursday, February 4, 1999.

3. The Council will meet jointly with the Alaska Board of Fisheries beginning at 9:00 a.m. on Tuesday, February 2, and begin their regular plenary session at 8:00 a.m. on Wednesday, February 3, continuing through a portion of Monday, February 8, 1999.

Other workgroup or committee meetings may be held during the week. Notices of these meetings will be posted at the hotel. All meetings are open to the public with the exception of Council executive sessions, which may be held during the noon hour during the meeting week, if necessary, to discuss personnel, international issues, or litigation.

ADDRESSES: The meetings will be held at the Anchorage Hilton Hotel, 500 W. Third Avenue, Anchorage, AK.

Council address: North Pacific Fishery Management Council, 605 W. 4th Ave., Suite 306, Anchorage, AK 99501-2252.

FOR FURTHER INFORMATION CONTACT: Council staff, phone: 907-271-2809.

SUPPLEMENTARY INFORMATION: The agenda for the Council's joint meeting with the Alaska Board of Fisheries will include reports and discussion of the following subjects: halibut, groundfish and crab management issues, limited entry for the scallop fisheries off Alaska, progress on a shark management plan, Steller sea lion protection measures, and the American Fisheries Act.

The agenda for the Council's plenary session will include the following issues. The Council may take appropriate action on any of the issues identified.

1. Reports from NMFS on the current status of the groundfish fisheries off Alaska, from the International Pacific Halibut Commission on 1999 halibut quotas and from Groundfish Forum on the results of an experimental fishery to test gear to minimize bycatch.

2. NOAA Legal Counsel will provide a briefing on the new recusal regulations for Council members.

3. Receive a report on the implementation of emergency rules to protect Steller sea lions, review necessary actions for 1999 and review alternatives and options for implementation of additional or alternative measures in 2000.

4. Discuss progress on implementation of fishery management measures in 1999 required by the American Fisheries Act as well as discuss development of further amendments for 2000 and beyond. The Council will also review the disapproval of emergency rules by NMFS and consider a Council response.

5. Review of a discussion paper of proposed management measures for the Alaska halibut charterboat fleet, and review of proposals received by the Alaska Board of Fisheries for halibut local area management plans.

6. Receive status reports on the multi-species community development quota (CDQ) program, the individual fishing quota (IFQ) fee program, and the IFQ weighmaster program.

7. Review alternative management measures to reduce bycatch of seabirds in the groundfish fisheries.

8. Receive reports and discuss further development of issues related to ecosystems management and the

gathering of social and economic data for fishery management actions.

9. Identify research priorities to forward to NMFS.

10. Groundfish amendments scheduled for action are as follows:

a. Final action on revisions to the prohibited species catch allocations for Bering Sea and Aleutian Islands (BSAI) chinook salmon.

b. Discussion of total catch measurement in the groundfish fisheries.

c. Final action on an amendment to address retention of demersal shelf rockfish in the Gulf of Alaska IFQ fisheries.

d. Final action on an amendment to the improved retention/utilization (IR/IU) program; review progress on report to Congress on IR/IU.

e. Receive status report on a pilot halibut avoidance program from the Vessel Bycatch Allowance/Halibut Mortality Avoidance Program Committee.

f. Discuss the differences between the Federal and state definitions of "pelagic trawl" and determine whether revisions are necessary.

11. Final action on license limitation program for the scallop fisheries off Alaska.

12. Progress report on a rebuilding plan for *bairdi* crab in the BSAI.

13. Review the overfishing definition for the Salmon Fishery Management Plan and determine appropriate action.

Although other issues not contained in this agenda may come before this Council for discussion, in accordance with the Magnuson-Stevens Fishery Conservation and Management Act, those issues may not be the subject of formal Council action during the meeting. Council action will be restricted to those issues specifically identified in the agenda listed in this notice.

Special Accommodations

These meetings are physically accessible to people with disabilities. Requests for sign language interpretation or other auxiliary aids should be directed to Helen Allen, 907-271-2809, at least 7 working days prior to the meeting date.

Dated: January 12, 1999.

Richard W. Surdi,

Acting Director, Office of Sustainable Fisheries, National Marine Fisheries Service.

[FR Doc. 99-1013 Filed 1-14-99; 8:45 am]

BILLING CODE 3510-22-F

DEPARTMENT OF THE INTERIOR**Fish and Wildlife Service****DEPARTMENT OF COMMERCE****National Oceanic and Atmospheric Administration****Policy Regarding the Recognition of Distinct Vertebrate Population Segments Under the Endangered Species Act**

AGENCIES: Fish and Wildlife Service, Interior; National Marine Fisheries Service, NOAA, Commerce.

ACTION: Notice of policy.

SUMMARY: The Fish and Wildlife Service and the National Marine Fisheries Service (Services) have adopted a policy to clarify their interpretation of the phrase "distinct population segment of any species of vertebrate fish or wildlife" for the purposes of listing, delisting, and reclassifying species under the Endangered Species Act of 1973, as amended (16 U.S.C. 1531 *et. seq.*) (Act).

ADDRESSES: The complete record pertaining to this action is available for inspection, by appointment, during normal business hours at the Division of Endangered Species, U.S. Fish and Wildlife Service, in Room 452, Arlington Square Building, 4401 North Fairfax Drive, Arlington, Virginia.

FOR FURTHER INFORMATION CONTACT: E. LaVerne Smith, Chief, Division of Endangered Species, U.S. Fish and Wildlife Service at the above address (703/358-2171), or Russell Bellmer, Chief, Endangered Species Division, National Marine Fisheries Service, 1335 East-West Highway, Silver Spring, Maryland 20910 (301/713-1401).

SUPPLEMENTARY INFORMATION:**Background**

The Endangered Species Act of 1973, as amended (16 U.S.C. 1531 *et. seq.*) (Act) requires the Secretary of the Interior or the Secretary of Commerce (depending on jurisdiction) to determine whether species are endangered or threatened. In defining "species," the Act as originally passed included, "* * * any subspecies of fish or wildlife or plants and any other group of fish or wildlife of the same species or smaller taxa in common spatial arrangement that interbreed when mature." In 1978, the Act was amended so that the definition read "* * * any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which

interbreeds when mature." This change restricted application of this portion of the definition to vertebrates. The authority to list a "species" as endangered or threatened is thus not restricted to species as recognized in formal taxonomic terms, but extends to subspecies, and for vertebrate taxa, to distinct population segments (DPS's).

Because the Secretary must "* * * determine whether any species is an endangered species or a threatened species" (section 4(a)(1)), it is important that the term "distinct population segment" be interpreted in a clear and consistent fashion. Furthermore, Congress has instructed the Secretary to exercise this authority with regard to DPS's "* * * sparingly and only when the biological evidence indicates that such action is warranted." (Senate Report 151, 96th Congress, 1st Session). The Services have used this authority relatively rarely; of over 300 native vertebrate species listed under the Act, only about 30 are given separate status as DPS's.

It is important in light of the Act's requirement to use the best available scientific information in determining the status of species that this interpretation follows sound biological principles. Any interpretation adopted should also be aimed at carrying out the purposes of the Act (i.e., "* * * to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, to provide a program for the conservation of such endangered species and threatened species, and to take such steps as may be appropriate to achieve the purposes of the treaties and conventions set forth in subsection (a) of this section" (section 2(b)).

Available scientific information provides little specific enlightenment in interpreting the phrase "distinct population segment." This term is not commonly used in scientific discourse, although "population" is an important term in a variety of contexts. For instance, a population may be circumscribed by a set of experimental conditions, or it may approximate an ideal natural group of organisms with approximately equal breeding opportunities among its members, or it may refer to a loosely bounded, regionally distributed collection of organisms. In all cases, the organisms in a population are members of a single species or lesser taxon.

The National Marine Fisheries Service (NMFS) has developed a Policy on the Definition of Species under the Endangered Species Act (56 FR 58612-58618; November 20, 1991). The policy applies only to species of salmonids

native to the Pacific. Under this policy, a stock of Pacific salmon is considered a DPS if it represents an evolutionarily significant unit (ESU) of a biological species. A stock must satisfy two criteria to be considered an ESU:

- (1) It must be substantially reproductively isolated from other conspecific population units; and
- (2) It must represent an important component in the evolutionary legacy of the species.

This document adopts an interpretation of the term "distinct population segment" for the purposes of listing, delisting, and reclassifying vertebrates by the U.S. Fish and Wildlife Service (FWS) and NMFS. The Services believe that the NMFS policy, as described above, on Pacific salmon is consistent with the policy outlined in this notice. The NMFS policy is a detailed extension of this joint policy. Consequently, NMFS will continue to exercise its policy with respect to Pacific salmonids.

The Services' draft policy on this subject was published on December 21, 1994 (59 FR 65885) and public comment was invited. After review of comments and further consideration, the Services adopt the policy as issued in draft form.

Summary of Comments and Recommendations

The Services received 31 letters from individuals and organizations commenting on the draft policy. In addition, since publication of the draft policy, the National Academy of Sciences, National Research Council (NRC), has published a report titled "Science and the Endangered Species Act," prepared by a committee appointed by the Academy at the request of several members of Congress. This report in part examines the definition of "species" under the Act, and endorses the recognition of scientifically identified evolutionary units for conservation purposes. It discusses the recognition of DPS's in terms of "distinctiveness," which is consistent with the concept of "discreteness" as presented in the draft policy except that it would not recognize an international political boundary to delimit a DPS. The committee noted that: "Although there can be good policy reasons for such delineations, there are not sound scientific reasons to delineate species only in accordance with political boundaries." The Services agree that the inclusion of international boundaries in determining whether a population segment is discrete is sometimes undertaken as a matter of policy rather than science. Although the committee

The following principles will guide the Services' listing, delisting and reclassification of DPS's of vertebrate species. Any proposed or final rule affecting status determination for a DPS would clearly analyze the action in light of these guiding principles.

Policy

Three elements are considered in a decision regarding the status of a possible DPS as endangered or threatened under the Act. These are applied similarly for addition to the lists of endangered and threatened wildlife and plants, reclassification, and removal from the lists:

1. Discreteness of the population segment in relation to the remainder of the species to which it belongs;
2. The significance of the population segment to the species to which it belongs; and
3. The population segment's conservation status in relation to the Act's standards for listing (i.e., is the population segment, when treated as if it were a species, endangered or threatened?).

Discreteness: A population segment of a vertebrate species may be considered discrete if it satisfies either one of the following conditions:

1. It is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may provide evidence of this separation.
2. It is delimited by international governmental boundaries within which differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms exist that are significant in light of section 4(a)(1)(D) of the Act.

Significance: If a population segment is considered discrete under one or more of the above conditions, its biological and ecological significance will then be considered in light of Congressional guidance (see Senate Report 151, 96th Congress, 1st Session) that the authority to list DPS's be used " * * * sparingly" while encouraging the conservation of genetic diversity. In carrying out this examination, the Services will consider available

scientific evidence of the discrete population segment's importance to the taxon to which it belongs. This consideration may include, but is not limited to, the following:

1. Persistence of the discrete population segment in an ecological setting unusual or unique for the taxon.
2. Evidence that loss of the discrete population segment would result in a significant gap in the range of a taxon.
3. Evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range, or
4. Evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics.

Because precise circumstances are likely to vary considerably from case to case, it is not possible to describe prospectively all the classes of information that might bear on the biological and ecological importance of a discrete population segment.

Status: If a population segment is discrete and significant (i.e., it is a distinct population segment) its evaluation for endangered or threatened status will be based on the Act's definitions of those terms and a review of the factors enumerated in section 4(a). It may be appropriate to assign different classifications to different DPS's of the same vertebrate taxon.

Relationship to Other Activities

The Fish and Wildlife Service's Listing and Recovery Priority Guidelines (48 FR 43098; September 21, 1983) generally afford DPS's the same consideration as subspecies, but when a subspecies and a DPS have the same numerical priority, the subspecies receives higher priority for listing. The Services will continue to generally accord subspecies higher priority than DPS's.

Any DPS of a vertebrate taxon that was listed prior to implementation of this policy will be reevaluated on a case-by-case basis as recommendations are made to change the listing status for that distinct population segment. The appropriate application of the policy will also be considered in the 5-year

reviews of the status of listed species required by section 4(c)(2) of the Act.

Effects of Policy

This guides the evaluation of distinct vertebrate population segments for the purposes of listing, delisting, and reclassifying under the Act. The only direct effect of the policy is to accept or reject population segments for these purposes. More uniform treatment of DPS's will allow the Services, various other government agencies, private individuals and organizations, and other interested or concerned parties to better judge and concentrate their efforts toward the conservation of biological resources at risk of extinction.

Listing, delisting, or reclassifying distinct vertebrate population segments may allow the Services to protect and conserve species and the ecosystems upon which they depend before large-scale decline occurs that would necessitate listing a species or subspecies throughout its entire range. This may allow protection and recovery of declining organisms in a more timely and less costly manner, and on a smaller scale than the more costly and extensive efforts that might be needed to recover an entire species or subspecies. The Services' ability to address local issues (without the need to list, recover, and consult rangewide) will result in a more effective program.

Author/Editor: The editors of this policy are Dr. John J. Fay of the Fish and Wildlife Service's Division of Endangered Species, 452 ARLSQ, Washington, DC 20240 (703/358-2105) and Marta Nammack of the National Marine Fisheries Service's Endangered Species Division, 1335 East-West Highway, Silver Spring, Maryland 20910 (301/713-2322).

Authority: The authority for this action is the Endangered Species Act of 1973, as amended (16 U.S.C. 1531 *et seq.*).

Dated: February 1, 1996.

John G. Rogers,
Acting Director, Fish and Wildlife Service.

Dated: February 1, 1996.

Nancy Foster,
Deputy Assistant Administrator for Fisheries,
National Marine Fisheries Service.

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Caribbean Acroporid Workshop Participant List

Name	Agency	Address	Contact information
Dr. Richard Aronson	Dauphin Island Sea Lab	101 Bienville Boulevard Dauphin Island, AL 36528 6704 Dorchester Drive, Mobile, AL 36695	raronson@disl.org voice: 251-861-7567 fax: 251-861-7540
Carlos Bacheco	Guanica Dry Forest	Department of Natural Resources Forest Service Area P. O. Box 5887- Puerta de Tierra San Juan, Puerto Rico 00906	menqui@hotmail.com P: 787-821-5706 F: 787-821-5707
Dr. Rolf Bak	Netherlands Institute for Sea Research	NIOZ P.O. Box 59 1790 AB Den Burg, Texel The Netherlands	rbak@nioz.nl tel 31 222 369 451 fax 31 222 319 674
Iliana Baums	University of Miami	RSMAS-MBF 4600 Rickenbacker Causeway Miami, FL 33149	ibaums@rsmas.miami.edu Phone 305.361.4642 Fax 305.361.4600
Dr. Stephania Bolden	Protected Resources NMFS/SERO	National Marine Fisheries Service 9721 EXECUTIVE CTR DR NORTH ST PETERSBURG FL 33702-2439	Stephania.Bolden@noaa.gov PH: (727) 570-5312
Rafe Boulon	Chief of Resource Management	Virgin Islands National Park PO Box 710 Cruz Bay Saint John, V.I. 00830	rafe_boulon@nps.gov P: 340/693-8950 x 224 F: 340 693-9500
Andy Bruckner	NOAA/NMFS	Office of Protected Resources 1315 East West Highway Silver Spring, MD 20910	andy.bruckner@noaa.gov P: 301-713-2319 x 140 F: 301-713-0376
Dr. John Bythell	University of Newcastle	Department of Marine Science Newcastle NE1 7RU, United Kingdom	j.c.bythell@ncl.ac.uk P: 44 191 222 6659 Fax: 44-191-2227891

Miguel Canals	Guanica Dry Forest	Department of Natural Resources Forest Service Area P. O. Box 5887- Puerta de Tierra San Juan, Puerto Rico 00906	menqui@hotmail.com P: 787-821-5706 F: 787-821-5707
Dr. Mark Chiappone	National Undersea Research Center	University of North Carolina at Wilmington Florida Keys Research Program 515 Caribbean Drive Key Largo, FL 33037	lina@shadow.net
Richard Curry	Biscayne National Park	Biscayne National Park 9700 SW 328 th St. Homestead, FL 33033	richard_curry@nps.gov P: 305-230-1144x3010 F: 305-230-1190
Dr. Barry Devine	Chief Scientist	Eastern Caribbean Center / Conservation Data Center University of the Virgin Islands #2 John Brewer's Bay St. Thomas, USVI 00802	bdevine@uvi.edu P: 340-693-1038 F: 340-693-1025 340-693-5409 Home
Dr. Juan Manual Diaz	INSTITUTO DE INVESTIGACIONES MARINAS Y COSTERAS	INVEMAR Programa BEM (Biodiversidad y Ecosistemas Marinos) Zona Portuaria (A. Aéreo 1016) - Santa Marta, Colombia	jmdiaz@invemar.org.co P: (575)-421-4774 (1380) F: (575)-421-1377 (5181)
Cara H. Dickman	National Center for Caribbean Coral Reef Research (NCORE)	Rosenstiel School of Marine and Atmospheric Science (RSMAS) University of Miami 4600 Rickenbacker Cswy. Key Biscayne, FL 33149	cdickman@rsmas.miami.edu ph. 305.361.4824 fax. 305.361.4910
Elizabeth Fairey	Coral Reef Conservation Program	Office of Habitat Conservation National Marine Fisheries Service 1315 East-West Highway, SSMC#3 Silver Spring, MD 20910	liz.fairey@noaa.gov Phone (303) 713-2325 x191 Fax (303) 713-1043

Robin P. Fortuna	National Center for Caribbean Coral Reef Research	Rosenstiel School of Marine & Atmospheric Science University of Miami 4600 Rickenbacker Causeway Miami, FL 33149-1098	rfortuna@rsmas.miami.edu Phone: 305.361.4820, Fax 305.361.491
Jaime Garzon-Ferreira	NSTITUTO DE INVESTIGACIONES MARINAS Y COSTERAS	INVEMAR Programa BEM (Biodiversidad y Ecosistemas Marinos) Zona Portuaria (A. Aéreo 1016) - Santa Marta, Colombia	jgarzon@invemar.org.co P: (575)-421-4774 (1380) F: (575)-421-1377 (5181)
Toby Gardner	University of East Anglia	Centre for Ecology, Evolution and Conservation School of Biological Sciences University East Anglia Norwich NR4 7TJ	t.gardner@uea.ac.uk Tel: 01603 610340
Francisco Geraledes	Centro de Investigaciones de Biología Marina Universidad Autonoma de Santo Domingo	PO Box 748 Santo Domingo, Dominican Republic mailing address: Aristides Fiallo Cabral 105 Santo Domingo, Dominican Republic	mamma@codetel.net.do Tel/fax: 809-688-0922 cel 809-729-1184
Dr. Elizabeth Gladfelter	Marine Policy Center	Woods Hole Oceanographic Institution Marine Policy Center, #41 Woods Hole, MA 02543	egladfelter@whoi.edu P: (508) 289-3446 F: (508) 547-2146
Peter W. Glynn	Coral Reef Research Group - RSMAS	RSMAS University of Miami 4600 Rickenbacker Cswy Miami FL 33149	pglynn@rsmas.miami.edu P: (305) 361-4134 F: (305) 361-4600
Edwin Hernandez	Coral Reef Research Group	University of Puerto Rico Department of Biology P.O. Box 23360 San Juan, P.R. 00931-3360	coral_giac@yahoo.com P: (787)764-0000 x-4855 F: 787-764-2610
Zandy Hillis-Starr	Chief of Resource Management, Buck Island National Monument	Buck Island Reef NM 2100 Church Street, #100 Christiansted St. Croix Virgin Islands 00820-4611	Zandy_hillis-starr@nps.gov, P: 340-773-1460 x 35 340-690-0655 cellular 340-773-2950 fax

Dr. Dennis Hubbard	Oberlin College	Dept. of Geology- Oberlin College 52 W. Lorain St. Oberlin OH 44074	dennis.hubbard@oberlin.edu (440) 775-8346 (voice) (440) 775-8038 (FAX)
Richard Hubbard	Institute of Marine Affairs	Institute of Marine Affairs Hilltop Lane, Chaguaramas Trinidad and Tobago	director@ima.gov.tt rhubbard@ima.gov.tt P: (868)634-4291-4 Fax (868)634 4433
Walt Jaap	State of Florida	Division of Marine Resources Florida Marine Research Institute 100 8th Ave. SE St. Petersburg FL 33701	Walt.jaap@fwc.state.fl.us wkjaap@worldnet.att.net P: 727-896-8626 F: 727 823-0166
Dr. Eric Jordan-Dahlgren	CARICOMP-Estacion Puerto Morelos	Apartado Postal 833, Cancun 77500 Quintana Roo, Mexico	jordan@mar.icmyl.unam.mx P: 52-987-10139 F: 52-987-10138
Dr. Brian Keller	FKNMS	NOAA/NOS Florida Keys National Marine Sanctuary PO Box500368 Marathon, FL 33050	brian.keller@noaa.gov P:305-743-2437 x 25 F:305-743-2357
Dr. Phil Kramer	AGRRA	MGG/RSMAS University of Miami 4600 Rickenbacker Cswy Miami, FL 33149	Pkramer@rsmas.miami.edu P: (305) 361-4768 or 4664 F: 305-361-4632
Dr. Diego Lirman	RSMAS	Center for Marine and Environmental Analyses RSMAS University of Miami 4600 Rickenbacker Cswy Miami FL 33149	Dlirman@rsmas.miami.edu Tel: 305-361-4168 Fax: 305-361-4077
Christy Loomis	Eastern Caribbean Center	Eastern Caribbean Center / Conservation Data Center University of the Virgin Islands #2 John Brewer's Bay St. Thomas, USVI 00802	cloomis@uvi.edu P: 340-693-1038 fax 340-693-1025

Christy Loomis	Eastern Caribbean Center	Eastern Caribbean Center / Conservation Data Center University of the Virgin Islands #2 John Brewer's Bay St. Thomas, USVI 00802	cloomis@uvi.edu P: 340-693-1038 fax 340-693-1025
Anne McCarthy	Environmental Specialist III	Florida Department of Environmental Protection FDEP/FKNMS Lower Region 216 Ann Street Key West, Florida 33040	anne.mccarthy@noaa.gov 305/304-4432 cell phone 305/292- 0311 office voice 305/292-5065 office fax
Dr. John McManus	NCORE	RSMAS University of Miami 4600 Rickenbacker Cswy Miami, FL 33149	jmcmanus@rsmas.miami.edu u P:305-361-4824 F:305-361-4910
Jeff Miller	National Park Service	1300 Cruz Bay Creek St. John, USVI 00830	jeffmiller@islands.vi P: 340 693 8950 ext 227 F:340 693-9500
Dr. Margaret Miller	NOAA/NMFS	National Marine Fisheries Service Southeast Science Center 75 Virginia Beach Dr, Miami, FL 33149	P: 305-361-4561 F: 305-361-4562 margaret.w.miller@noaa.gov
Dr. Steven Miller	Director National Undersea Research Center	University of North Carolina at Wilmington Florida Keys Research Program 515 Caribbean Drive Key Largo, FL 33037	Smiller@gate.net
Dr. Erich Mueller	Mote Marine Lab	Center for Tropical Research 24244 Overseas Highway (US 1) Summerland Key, Fl 33042	emueller@mote.org phone: (305) 745-2729 FAX: (305) 745-2730

Michael Nemeth	Leader, Coral Monitoring Project	Division de Recursos Marinos, Dept de Recursos Naturales y Ambientales, PO Box 906600, San Juan, PR 00906-6600	Michaelnemeth@hotmail.com Fax: 787-723-2805
Antonio Ortiz	University of Puerto Rico	Department of Marine Sciences P.O. Box 908 Lajas, PR 00667	Alortiz9@hotmail.com P:787-899-2048 F:787-899-5500
Bill Precht	Ecological Sciences Program Manager	PBS&J 2001 NW 107 th Avenue Miami, FL 33172	bprecht@pbsj.com Phone: 305) 592-7275 x488 Fax: (305) 594-9574 1-800-597-7275
Dr. Caroline Rogers	National Park Service	USGS Carribean Field Station 1300 Cruz Bay Creek St. John, USVI 00830 USA	Caroline rogers@usgs.gov Phone: 340 693-8950 ext 221 Fax 340 693-9500
Paula Rueda	Marine Ecology Research Group	Faculty of Environmental Studies. Universidad Javeriana. Cra 7a N.40-60 Ed. 67 Bogotá, Colombia	rueda_paula@hotmail.com P: (57-1) 8617419 F: (57-1) 8637771
Hector J. Ruiz Torres	University of Puerto Rico	Department of Marine Sciences PO Box 908 Lajas, PR 00667 permanent address: Box 1126 Hormigueros, P.R. 00660	astreoides@hotmail.com Phone: 787-899-2048 Fax:787-899-5000
Dr. Kathleen Sullivan	Associate Professor	University of Miami PO Box 249118 Coral Gables, FL 33124	sullivan@benthos.cox.miami.edu P: 305-284-3013 F: 305 284-3039
Dr. Jim Thomas	National Coral Reef Institute (NCRI)	NSU Oceanographic Center 8000 N. Ocean Drive Dania Beach, FL 33004	thomasjd@nova.edu Phone: (954) 262-3661 Fax: (954) 262-4098
Dr. Bernardo Vargas-Angel	National Coral Reef Institute (NCRI)	NSU Oceanographic Center 8000 N. Ocean Drive	vargasb@nova.edu Phone: (954) 262-3677

		Dania Beach, FL 33004	Fax: (954) 262-4027
Dr. Mark Vermeij	NMFS	Cooperative Institute for Marine and Atmospheric Studies (CIMAS)/ NOAA Fisheries 75 Virginia Beach Dr. Miami FL 33149	markv08@attglobal.net mark.vermeij@noaa.gov Tel 305-361-4320 Fax 305-361-4562
Steve Vollmer	Palumbi Lab	Harvard University, Biological Laboratories, Box 90 16 Divinity Ave. Cambridge, MA 02138	svollmer@oeb.harvard.edu ph: 617.496.8667 fax: 617.495.1958
Dr. Ernesto Weil	Department of Marine Sciences	University of Puerto Rico Department of Marine Sciences PO Box 908, Lajas, PR 00667	eweil@caribe.net P:787-899-2048x241 F:787-899-5500
Fritz Wettstein	Environmental Administrator	FKNMS, Lower Keys Region Florida Department of Environmental Protection 216 Ann St. Key West FL 33040	fritz.wettstein@noaa.gov 305/304-0178 cell phone 305/292- 0311 office voice 305/292-5065 office fax
Dr. Dana Williams	NOAA/NMFS	National Marine Fisheries Service Southeast Fisheries Science Center 75 Virginia Beach Dr, Miami, FL 33149	dana.williams@noaa.gov P: 305-361-4561 F: 305-361-4562
Additional participants for the first day only			
Mike R. Johnson,		NMFS Habitat Conservation Division, Miami	Mike.r.johnson@noaa.gov
Audra Livergood,		NMFS Restoration Center, Miami	audra.livergood@noaa.gov
Abby Renegar	Nova Southeastern University	Ft. Lauderdale, Florida	
Megan Berkle	Nova Southeastern University	Ft. Lauderdale, Florida	zennnnwoman@hotmail.com

Heather Halter	Nova Southeastern University	Ft. Lauderdale, Florida	
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STATUS & TRENDS Working Group

Working Group Chair: Phil Kramer

Committee members:

Rich Aronson
Rolf Bak
Miguel Canals
Mark Chiappone
Liz Fairey
Jaime Garzon-Ferrera
Francisco Geraldès
Robert Ginsburg
Edwin Hernandez
Walt Jaap
Patricia Kramer
Caroline Rogers
Kathleen Sullivan
Dana Williams

Goal: develop a comprehensive report on the regional condition of *Acropora palmata* and *Acropora cervicornis* populations, with a specific focus on U.S. waters

A) Puerto Rico, Virgin Islands, Florida, and regional white papers

- Historic abundance, total extent of decline, recent rate of decline
- Patterns of recovery
- Threats affecting populations
- List of locations where information is available from and type of information
- Data sources

B) Relationship with ESA

- Support for listing (based on population decline, ESA threats)
- Proposed Category for listing (none, threatened, endangered)

C) Information needs

- Understanding and addressing threats
- Monitoring and assessment of population dynamics



BIOLOGY/ECOLOGY Working Group

Working Group Chair: Diego Lirman

Committee members:

Iliana Baums
John Bythell
Eric Jordan-Dahlgren
Elizabeth Gladfelter
Peter Glynn
Erich Mueller
Antonio Ortiz
Paula Rueda
Bernardo Vargas
Mark Vermeij
Steve Vollmer
Ernesto Weil

Goal: evaluate the genetic, phenotypic and life history characteristics of these species and relationships to population viability, recovery potential and USG concept of an evolutionary significant unit (ESU) or distinct population segment.

- A) Reproduction - fragmentation versus sexual reproduction
 - benefits and disadvantages of fragmentation from the perspective of endangerment, recovery and degree of genetic differentiation
 - importance of sexual reproduction; how likely is a population to recover through sexual reproduction/recruitment from distant reefs?
- B) Degree of genetic separation among and within populations
 - What does genetic information tell us regarding the importance of individual populations in the persistence of the species?
 - Can populations in certain locations/reefs be considered distinct populations?
 - What are appropriate "management units" for conservation?
- C) Relationship with ESA
 - Invertebrates must be threatened/endangered throughout their range. How does the reproductive strategy or the genetic nature of populations affect this requirement?
 - What additional distinctions can be made of a clonal invertebrate like a coral?
 - Discussion of why the life history/genetics/ecology would support protection at a more localized level
 - Benefits of protecting individual populations or populations in certain areas (i.e. Florida Keys, east coast of Puerto Rico etc.) and the relationship with:
 - Water circulation patterns that prevent recruitment from distant locations; -
 - Populations at geographic limit of the species;
 - Unusually healthy populations that may provide recruits to new areas)
- D) Research and Information Needs
 - What is needed to address gaps in our understanding of the biology/ecology and genetics?



a)

**INFORMATION
NEEDS Working
Group**

Working Group Chair: John McManus

Committee members:

Carlos Bacheco
Barry Devine
Juan Manuel Diaz
Toby Gardner
Dennis Hubbard
Christy Loomis
Jeff Miller
Steven Miller
Bill Precht
Hector Ruiz
Jim Thomas

Goal: Expanded use of existing tools and application of new tools to identify and quantify critical habitat, quantify current and historical extent and changes over biological time periods and determine geological extent and stability of populations and factors that influence this.

- A) Remote sensing, aerial photography and GIS mapping
 - What type of information can we get on critical habitat, historical distribution and extent of Acroporid populations, and extent of decline?
 - Can these tools be applied to deeper (e.g., fore reef *A. cervicornis*) populations?
 - Where is this being applied?
 - What new technologies are needed to improve the utility of these efforts?
- B) Coring
 - How have populations of these corals changed over the last 10,000 years?
 - Is the recent decline unprecedented?
 - When gaps in the geologic record are identified, how can we determine the causative agents?
 - Existing information and proposed or ongoing research
- C) Strategies to enhance recovery
 - Propagation and transplantation/restoration
 - Improved sexual recruitment
 - Mitigation of threats
 - Other strategies
- D) Research and monitoring needs
 - Monitoring approaches for standing colonies, fragments and new recruits
 - What is the likelihood of developing and applying new, effective, cost efficient restoration strategies?
 - What measurable criteria can be used to determine the effectiveness of future actions taken to enhance recovery?



a) **MANAGEMENT
Working Group**

Working Group Chair: Brian Keller

Committee members:

Stephania Bolden
Rafe Boulon
Richard Curry
Zandy Hillis-Star
Richard Hubbard
Walt Jaap
Anne McCarthy
Michael Nemeth
Hazel Oxenford
Fritz Wettstein

Goal: evaluate existing legislation, regulations, statutes and other conservation strategies for coral reef ecosystems that specifically address reef-building corals to determine the adequacy of these measures and the need for additional measures.

A) Existing mechanisms to protect corals (Federal, state, territorial, country, regional)

B) Proposed new conservation, management and education and outreach strategies to address the decline in these corals.

C) Evaluation of ESA and benefits to Acropora

- Specific management parameters - adequacy of existing protective measures and new measures that would supercede the need for additional protective measures under ESA
- Conservation benefits of an ESA listing- what and where
- Benefits/disadvantages of protecting specific populations under the ESA rather than all populations throughout US waters
- Site specific management actions that would enhance conservation and survival of the species
- What type of existing and future activities would be affected by an ESA listing
- What would be needed in a recovery plan, should these species be listed

E) Management needs

- Regional approaches to conservation
- Country/State/Territorial management approaches
- Tools other than ESA that could help mitigate threats, enhance conservation and promote recovery of populations in U.S. waters
- Monitoring and research priorities to address management needs