

Long Term Monitoring of the Coral Reef Organisms of Biscayne National Park

Final Report: 1989-1990 Field Seasons

Amendment no. 1,
Subagreement no. 25,
Cooperative Agreement No. CA-5000-4-8005

Between USDI, NPS, & UGA Research Foundation Inc.

Volume 1 (of 8)

Deliverable: Summary Report, Results, and Statistical Analysis

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Volume 1:

Deliverable: Summary Report, Statistical Analysis, and Original Data Base

Volume 2:

Deliverable: First and Second Year Underwater Photo Quadrat Series

Volume 3:

Deliverable: First and Second Year Tracing and Identification from the Quadrat Photographs

Volume 4:

Deliverable: First and Second Year Digitized Maps from the Quadrat Photographs

Volume 5:

Deliverable: First and Second Year Original Data from the Quadrat Photographs

Volume 6:

Deliverable: First and Second Year Line Transect Data and Analysis

Volume 7:

Deliverable: Sampling Protocol Handbook 1:
Line Transect Methods & Software Analysis

Volume 8:

Deliverable: Sampling Protocol Handbook 2:
Photographic and Digitizer Methods & Software Analysis

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Summary Report, Results, and Statistical Analysis

In 1989 a coral reef monitoring project was established in Biscayne National Park in order to measure changes in coral reef community structure over time and to provide information about the natural resource to park management. Two reef sites in Biscayne National Park were chosen for intensive, ongoing study: Ball Buoy Reef, at the southern end of the Park, and Triumph Reef, towards the northern end. Methods employed at each site were: (1) a 1000 m² visual swim survey to assess species richness and the species present in the area; (2) three permanent line transects, 25 m long each, (3) a permanent 13.5 m² photostation, and (4) a 100 m² haphazard photographic survey to test the representativeness of the 13.5 m² photostation. In 1990, we added to each station: (1) two additional permanent 25 m long line transects; and (2) three permanent video transects, utilizing three of the five existing line transects.

This first volume of results and analysis ensuing from this coral reef monitoring project includes a summary text describing data and results, maps of the photostations, locational information for the photostations, summary tables and graphs describing results, and a copy of a publication resulting from this work (Porter and Meier, Amer. Zool. 32:625-640, 1992).

INTRODUCTION

Coral reefs of the Florida Keys stretch for a distance of 580 km from Fowey Rocks on the northern boundary of Biscayne National Park to Loggerhead Reef on the western boundary of the Dry Tortugas National Monument, and encompass an area of more than 3100 km². The best developed reefs lie in a string on the seaward margin, between 3 and 5 km offshore, of the Florida Keys. Reefs have been growing in these locations since the last sea-level inundation some 5,000 years B.P. Coral zonation along the outer margin of reefs in the Keys follows the general Caribbean model (Goreau, 1959; Jaap, 1984), with a shallow *Acropora palmata* zone grading to a deeper *Montastrea* buttress zone. Deep reef and vertical wall communities are rare in the Keys due to the gentle slope of the continental shelf out to the 100 m contour.

The health of coral reefs in the Florida Keys has been the subject of considerable speculation in the popular press (Adler, 1990; Ward, 1990; Caputo, 1991; Fishman, 1991). Dustan and Halas (1987) compared coral cover and diversity under 22 repeatable line transects laid parallel to depth contours from the surface to 40 m in 1979 and 1982. They demonstrated a decline of coral populations at some depths in the Key Largo National Marine Sanctuary and growth at others. These authors point out that, in the absence of baseline data on natural rates of change, speculation about human influence, particularly at system-wide spatial scales, will be impossible.

This report describes the establishment and baseline monitoring of reefs in Biscayne National Park.

METHODS

In 1989 a coral reef monitoring project was established in Biscayne National Park in order to measure changes in coral reef community structure over time and to provide information about the natural resource to park management. Two reef sites in Biscayne National Park were chosen for intensive, ongoing study: Ball Buoy Reef, at the southern end of the Park, and Triumph Reef, towards the northern end. Methods employed at each site were: (1) a one-time 1000 m² visual swim survey to assess species richness and the species present in the area; (2) three permanent line transects, 25 m long each, counted annually, (3) a permanent 13.5 m² photostation, surveyed annually, and (4) a one-time 100 m² haphazard photographic survey to test the representativeness of the 13.5 m² photostation. In 1990, we added to each station: (1) two additional permanent line transects; and (2) three permanent video transects, utilizing three of the five existing line transects.

Each photostation was photographed in 1989 and 1990. Each photograph includes the outline of the camera frame, which carries identifying information on the specific reef site, frame number, and date of the photograph (see Volume 2 of this Report). Coral colony and frame outlines are then traced from prints onto mylar sheets (see Volume 3 of this Report). Coral species are identified and assigned a unique colony number that can be followed through time, the colonies are digitized (see Volume 4), and a value for projected surface area of each colony in each frame is obtained (original data are presented in Volume 5). The photographs have been analyzed for percent cover, colony number, species richness, species diversity, and relative abundance of scleractinean and hydrocoral species present. For more details regarding the photographic method and its analysis, refer to Volume 8 of this Report.

Three 25 m line or chain transects at each photostation were counted in 1989 and 1990; each transect was counted three times and both coral and substrate analyses were performed. Data and analysis from the line transect studies are presented in Volume 6 of this Report. A full exposition of our counting and analytical methods are provided in Volume 7.

The three video transects in each station were first recorded in 1990. Additionally, the photostations were also recorded on video in 1990 in an effort to develop more automated methods of analysis. We are evaluating the results of these methods in the hope that they may provide a rapid means of monitoring and analysis in the future, but they will not be further discussed in this Report.

A map of our monitoring sites in the Florida Keys, including those in Biscayne National Park, is shown in Figure 1. A more detailed map showing the locations of our sites in Biscayne National Park is presented in Figure 2. A very detailed survey map of the layout of the monitoring station at Ball Buoy Reef (designated BP01) is shown in Figure 3. A three-page legend accompanies Figure 3, providing all survey details. Note that the location of the monitoring station at Ball Buoy Reef, according to NOAA Hydrographic Nautical Chart 11462 13th ed. Mar/75, is Latitude $25^{\circ} 18.3' N$, and Longitude $80^{\circ} 11.2' W$. A recent Loran C reading taken by Brian Lockwood of Biscayne National Park locates the station at Ball Buoy Reef at $25^{\circ} 19.108' N$ and $80^{\circ} 11.025' W$. A photomontage of the photostation at Ball Buoy Reef (also known as South Pile Reef), taken from 1989 photographs, is presented in Figure 4. A mapped montage, resulting from digitizing and mapping each individual frame within this photostation, is presented in Figure 5.

A detailed survey map of the layout of our other monitoring station in Biscayne National Park, at Triumph Reef (designated BP02) is shown in Figure 6. Another three-page legend accompanies Figure 6, providing survey details. The location of the monitoring station at Triumph Reef, according to NOAA Hydrographic Nautical Chart 11462 13th ed. Mar/75, is Latitude $25^{\circ} 28.7' N$, and Longitude $80^{\circ} 06.7' W$. The corresponding Loran C reading, taken by Brian Lockwood, locates the station at Triumph Reef at $25^{\circ} 28.325' N$ and $80^{\circ} 06.715' W$. A photomontage of the photostation at Triumph Reef, constructed from 1989 photographs, is presented in Figure 7.

Finally, a reproduction of a photograph showing the the photostation method in progress is provided in Figure 8. Note the placement of the large grid on the stainless steel stakes at a specified height, the placement of the smaller camera framer over and in alignment with the large

grid, the legs that hold the camera at a specified distance above the camera framer, and the label plates on the camera framer itself that are used to identify the site, frame number, and date within each photograph.

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RESULTS

Both reef areas lost coral species between 1989 and 1990. One species was lost from each of the photostations at Ball Buoy Reef and Triumph Reef (Table 1). This loss is equivalent to a total of 7% of the original species richness in each photostation. Between 1989 and 1990, both reefs gained in percent cover of living coral (Tables 1 and 2). The photostation at Ball Buoy Reef gained 7%, and the photostation at Triumph Reef gained almost 10% in percent cover of living coral in one year's time. Measures of species diversity (Shannon-Weiner diversity index, based either on area or on colony number) declined slightly or remained nearly the same between 1989 and 1990 at both sites (Table 1).

The increase in percent cover at Ball Buoy Reef was due primarily to growth in size of some of the *Acropora palmata* colonies, while at Triumph Reef the increased percent cover was primarily in the hydrozoan fire coral, *Millepora alcicornis*, as well as growth observed in one *Montastrea annularis* colony (Table 2). The increase in percent cover at Ball Buoy Reef was accompanied by a small increase in number of colonies, from 194 to 205, a gain of almost 6% of the colonies present in 1989 (Table 3). At Triumph Reef, the increase in percent cover was accompanied by an increase in number of colonies, from 95 to 108, an increase of almost 14% (Table 3). Year-to-year events recorded for individual colonies, summarized in Table 4, show that the number of colonies of *Acropora palmata* at Ball Buoy showed no net change between 1989 and 1990, even though the percent cover of *Acropora palmata* increased. The data in Table 3 confirm that the photostation at Triumph Reef underwent a net gain of 13 *Millepora alcicornis* colonies, the primary species responsible for the increased percent cover of living coral at that reef between 1989 and 1990; most of that gain was due to sexual recruitment (Table 4).

Instances of sexual recruitment - successful settlement, metamorphosis, and survival of coral larvae - were observed at both reefs, but only of "weedy" species or species that are not the primary contributors of reef structure within each reef. Four species at Ball Buoy Reef had sexual recruits between 1989 and 1990: *Agaricia agaricites* (2 colonies), *Favia fragum* (3 colonies),

Millepora alcicornis (6 colonies), and *Porites astreoides* (1 colony) (Table 4). *Mycetophyllia lamarckiana* was completely lost from the photostation at Ball Buoy Reef. At Triumph Reef, sexual recruitment was observed in just two species: *Millepora alcicornis* (14 species) and *Favia fragum* (1 colony). Between 1989 and 1990, *Porites porites* was completely lost from the photostation at Triumph Reef.

A complete set of reproductions of photographs from each reef site, taken during each sampling year, are presented in Volume 2. These may be examined to detect other processes occurring in the coral community over time. For example, evident in the 1989 and 1990 photographs at Ball Buoy Reef is increased growth of *Acropora palmata*, characteristic of that photostation. However, numerous protruding growths on *A. palmata* branches are also visible in 1990; see, for example, frame 8 of Ball Buoy Reef (BP01, or "BNP I") in both years for comparison. It is not known whether these growths result from damselfish nips, or represent "tumors" (*sensu* Peters *et al.*, 1986), or are an infestation of barnacles, polychaetes, or some other invertebrate.

A series of comparisons of photostation data between 1989 and 1990 is presented graphically for Ball Buoy Reef in Figures 9-16, and for Triumph Reef in Figures 17-24. In these figures, the data for each photostation have been treated as having cumulative values over space: from 0.75 m² at frame 1, to 13.50 m² at frame 36. Examining the data in this fashion is useful for assessing not only the differences between the endpoints, but also the adequacy of the sample size of the photostation in describing the parameter in question. For example, a species-area curve of cumulative number of coral species plotted against increasing area sampled should show a logistic curve that reaches a plateau. If instead such a species-area curve were linearly increasing throughout the entire range of the graph, the implication would be that an increase in sample size would result in an increase in species number, and the area sampled is inadequate to describe the community being studied.

The species-area curves for the photostation at Ball Buoy Reef in 1989 and 1990 (Figure 9) does indeed follow the pattern of sampling adequacy that one hopes to achieve, suggesting that, at

least for the common species, the photostation method censuses species richness (S) well. Figure 10, cumulative percent cover of living coral over survey area, also levels off. Cumulative species diversity, the Shannon-Weiner diversity index calculated using the natural log of the area of live coral, is shown in Figure 11. Cumulative species diversity using the Shannon-Weiner index calculated according to the natural log of the number of colonies is shown in Figure 12. Cumulative relative abundance of coral species in 1989 and 1990 at Ball Buoy Reef is shown in Figure 13.

A plot of the difference between number of coral species at Ball Buoy Reef in 1989 and 1990, including standard error bars (Figure 14), suggests that the change in number of species was not significant. Similar plots of the changes in percent cover of living coral (Figure 15) and species diversity (Figure 16) also suggest that these changes between 1989 and 1990 were not significant.

The species-area curves for Triumph Reef in 1989 and 1990 (Figure 17) do not reach a plateau, probably because this is a very low percent cover reef (less than 2% coral cover), and therefore all species within the photostation behave as though they are relatively "rare." Cumulative coral cover at Triumph Reef is shown in Figure 18; very little variation in percent cover between frames is evident. Cumulative species diversity does follow a logistic curve, based either on area (Figure 19) or on number of colonies (Figure 20). Relative abundance of species at Triumph (Figure 21) shows only small shifts for most of the species between 1989 and 1990, again largely because the percent cover of each species is small to begin with.

A plot of the differences and standard errors in coral species within the photostation at Triumph Reef (Figure 22) likewise demonstrates that there was no change between 1989 and 1990. However, a plot of differences and standard errors in percent coral cover (Figure 23) suggests that there was a real increase in coral cover from 1989 to 1990. The same plot for species diversity (Figure 24) shows no significant change between 1989 and 1990.

SURVEY DESIGN

There are several reasons it was decided to use multiple monitoring methods in this study. First, the methods we chose are nested in spatial scale, so that we could test whether our smaller-scale samples were good representations of larger-scale processes. Second, the use of multiple methods allows one to compare results from different survey methods for the same reef areas and same time spans. Summary results of these nested surveys, all of which were performed in 1989, are presented in Table 6 for Ball Buoy Reef. Species lists for the 10,000 m² swim survey, the 100 m² haphazard photo survey, the 13.5 m² photostation, and the 0.75 m² line transect (3 transects x 25 m each x 1 cm, the width of the chain under the line) show 8 coral species in the line transect, 14 species in the photostation, 16 species in the haphazard photo survey, and 28 species in the large swim survey. It is worth noting that there is almost a doubling in species recorded by the photostation as compared to the line transect, but only a small increase from the photostation to the haphazard survey. There is excellent agreement between relative abundance of corals detected by the haphazard survey and the photostation survey (Table 6). The line or chain transect method, however, shows generally similar results, but misses or underestimates many of the less abundant species (Table 6).

These results are similar to those obtained for Triumph Reef, where the line transect contained 10 coral species, the photostation 14 species, the haphazard survey 16 species, and the swim survey 25 species (Table 7). Again there is good agreement in relative abundances of corals as measures by the haphazard and photostation methods; the results of the line transect in some instances departs from the results of the photographic methods. The line transect tends to miss some of the rarer species, and also appears to have overrepresented several species: *Agaricia agaricites*, *Porites porites*, and *Millepora complanata* (Table 7). The *Agaricia* was probably more prevalent in the transect than in the other surveys as a result of random events or stochasticity, but the *Porites* and especially the *Millepora* may have been overrepresented because of the three-

DISCUSSION

While a period of one year between two sampling episodes certainly does not constitute a long-term coral monitoring program, it does constitute the beginning of one: the first step in the proverbial thousand-mile journey. The establishment of these sampling stations was a very labor-intensive process, but the permanent location of the photostations and transects by the use of stainless steel stakes and eyepins should prove invaluable. It will be possible to sample these sites for a substantial number of years into the future. Implanting the stainless steel, while expensive and laborious, fulfilled the intention of rendering these station locations highly corrosion-resistant and, it is expected, virtually hurricane-proof.

Between 1989 and 1990, species richness declined by one species, or 7%, in each photostation. However, both reefs gained in percent cover of living coral by 7-10% in one year. At Ball Buoy Reef, the gain in percent cover was primarily due to growth of *Acropora palmata* colonies, the dominant reef-building coral at that reef; at Triumph the gain in percent cover was due primarily to a net increase in number of colonies of *Millepora alcicornis* as well as growth of existing *M. alcicornis* colonies.

The number of colonies of coral at each station showed net increases between 1989 and 1990. Some of this was due to sexual recruitment, though this was due to recruitment of more "weedy" species, or species with life histories that may be described as more r-selected. At Ball Buoy Reef, there was no sexual recruitment of *Acropora palmata*. Instead, there was some vegetative reproduction: broken branches or pieces of *A. palmata* colonies either originating from within or outside the photostation that may or may not continue to survive and grow. This vegetative reproduction did not, however, replace, in number, all of the *A. palmata* colonies that died between 1989 and 1990. Still, the acroporid reef studied in Biscayne National Park increased by 8% of its initial abundance between 1989 and 1990. This result is in contrast to the large losses identified for the other two acroporid reefs we have studied in the Florida Keys (Porter and Meier, 1992).

Species diversity changed very little in either photostation between 1989 and 1990. It is worth considering, however, why species diversity values based on number of colonies are very similar between the two stations, while species diversity values based on area are much higher at Triumph Reef than at Ball Buoy Reef. In a given year, the same number of species were present at each photostation. Based on area, however, *Acropora palmata* is strongly dominant at Ball Buoy, while there is much more evenness in distribution of species at Triumph, a very low percent cover reef. This difference between the two reefs does not hold when calculating species diversity based on number of colonies. In this sense the two reefs are similar in structure: at each reef there is one species strongly prevalent in number of colonies (*A. palmata* at Ball Buoy, and *M. alcicornis* at Triumph), followed by two species that contain a high-to-intermediate number of colonies (*M. alcicornis* and *Porites astreoides* at Ball Buoy, and *Porites astreoides* and *Agaricia agaricites* at Triumph), followed by low numbers of colonies in the rest of the species.

Other biological processes are well suited to tracking through the photostation method, and we expect to take advantage of this feature with the accumulation of additional years of data. For example, a precisely taken photographic record at relocatable stations enables one to identify and quantify the incidence of fission events and the subsequent destiny of the fragmented colonies, turnover rates of coral species, and phenomena such as coral "tumors", invertebrate infestations, bleaching, and black band disease.

A comparison of the advantages and disadvantages of the swim survey, line or chain transect survey, and photostation survey is presented in Tables 8 and 9. The swim survey is the only method that accurately assesses total species richness (S) of the coral community; the chain transect is the only method of the three to take into account the three-dimensional nature of corals and the reef, and was the only method that assessed the relative abundance of substrates other than live corals; the photostation was the only method that was able to estimate species diversity based on individual colonies (Table 8). Table 9 compares the three methods in terms of set up time, underwater survey time, above water analysis time, and research equipment costs. Clearly each

method has some advantages and some drawbacks. The choice of method, as always, must relate to the specific questions being asked.

Further discussion of results issuing from the two monitoring stations in Biscayne National Park, and two monitoring stations each in the Key Largo and Looe Key National Marine Sanctuaries (now incorporated into the recently created Florida Keys National Marine Sanctuary) are presented in a publication by Porter and Meier (1992) (Appendix 1).

CONCLUSIONS AND IMPLICATIONS

Since corals are declining elsewhere in the Keys, research in Biscayne National Park should continue to monitor the state of its environment and corals. Factors worth observing in the future include: (1) the condition of corals on other reefs in Biscayne National Park; (2) community processes involved in post-disturbance recovery; (3) the role of visitor impact; (4) incidence and impact of bleaching in Biscayne National Park; (5) current or potential incidences and impacts of nutrient enrichment or pollution of water or sediment; (6) factors promoting infection and spread of coral disease; and (7) the status of algae and herbivores, including the sea urchin *Diadema antillarum*, other invertebrate grazers, and herbivorous fish. It is worth noting that unlike other photostations, where coral loss has occasionally been associated with an increase in certain cyanophyte species (the filamentous *Lyngbya*, or *Phormidium corallyticum* in black band disease), these cyanophytes have not been observed in any of our Biscayne National Park stations.

There is a need to monitor these reefs on multiple scales of both time and space. The processes requiring investigation occur on the level of the individual, the population, the community, the ecosystem, and the landscape; these processes have their range of variation on different temporal and spatial scales, and so sampling must occur on multiple temporal and spatial scales. In this case, one needs data of both fine-grained resolution and large scale, and the monitoring program must provide means of acquiring both if the ability to answer the most critical questions is not to be lost.

Interpretation of our results for management purposes will require a longer monitoring period, identification of causes responsible for changes observed on these study reefs, and, ideally, assessment of the rates of change and their causes on other reefs in the Florida Keys.

ACKNOWLEDGMENTS

Many people contributed to the success of this project, and we gratefully acknowledge them for their efforts. From the University of Georgia, we thank Linda Chiang, Thelma Richardson, Ron Davis, Jennifer Tougas, Sarah Lewis, Heather Shannon, and a host of energetic undergraduate students. We also thank the entire staff at Biscayne National Park for their help and cooperation, especially Richard Curry and the rest of the Resources Management staff, and Park Service rangers who helped time and again with logistics.

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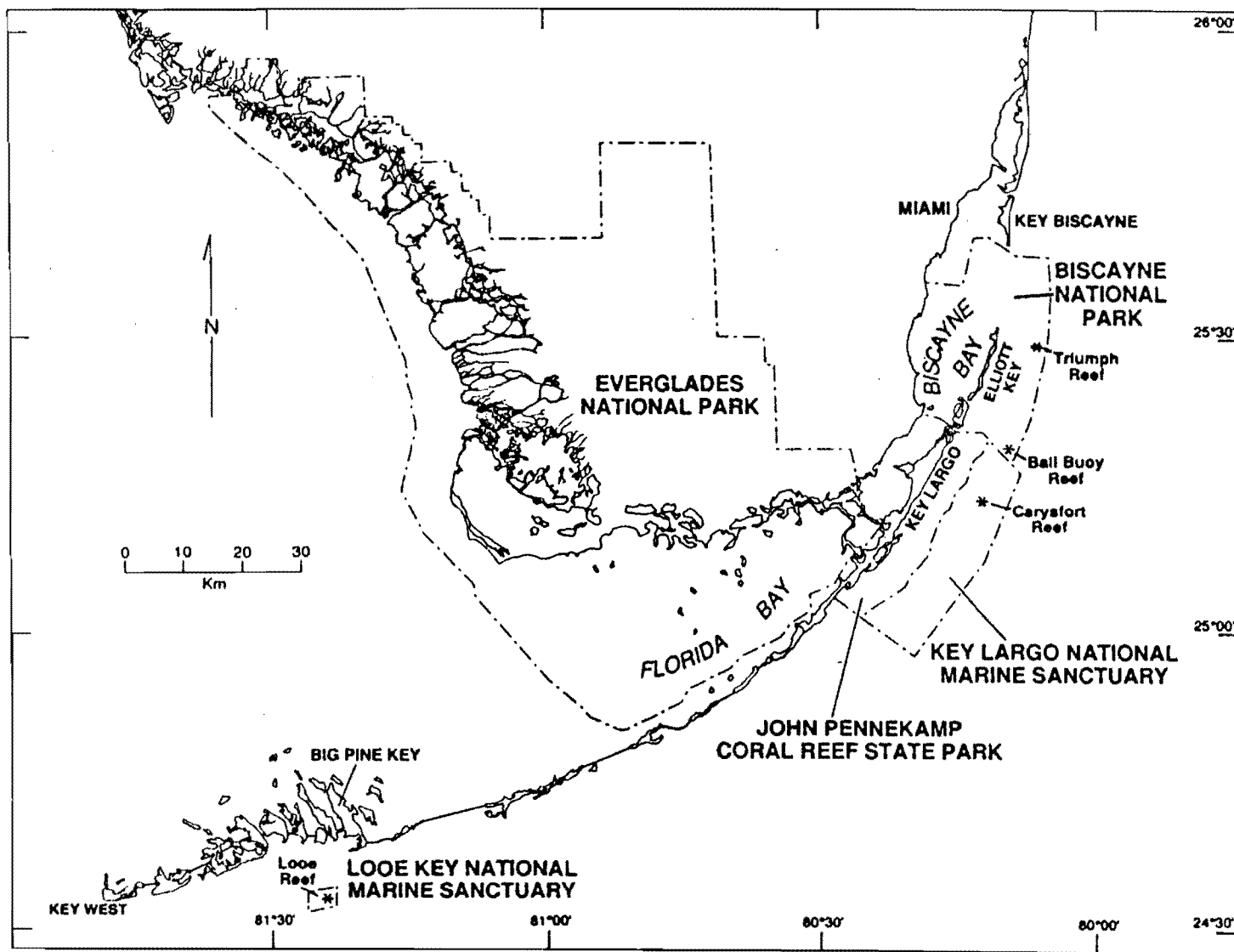


Figure 1.

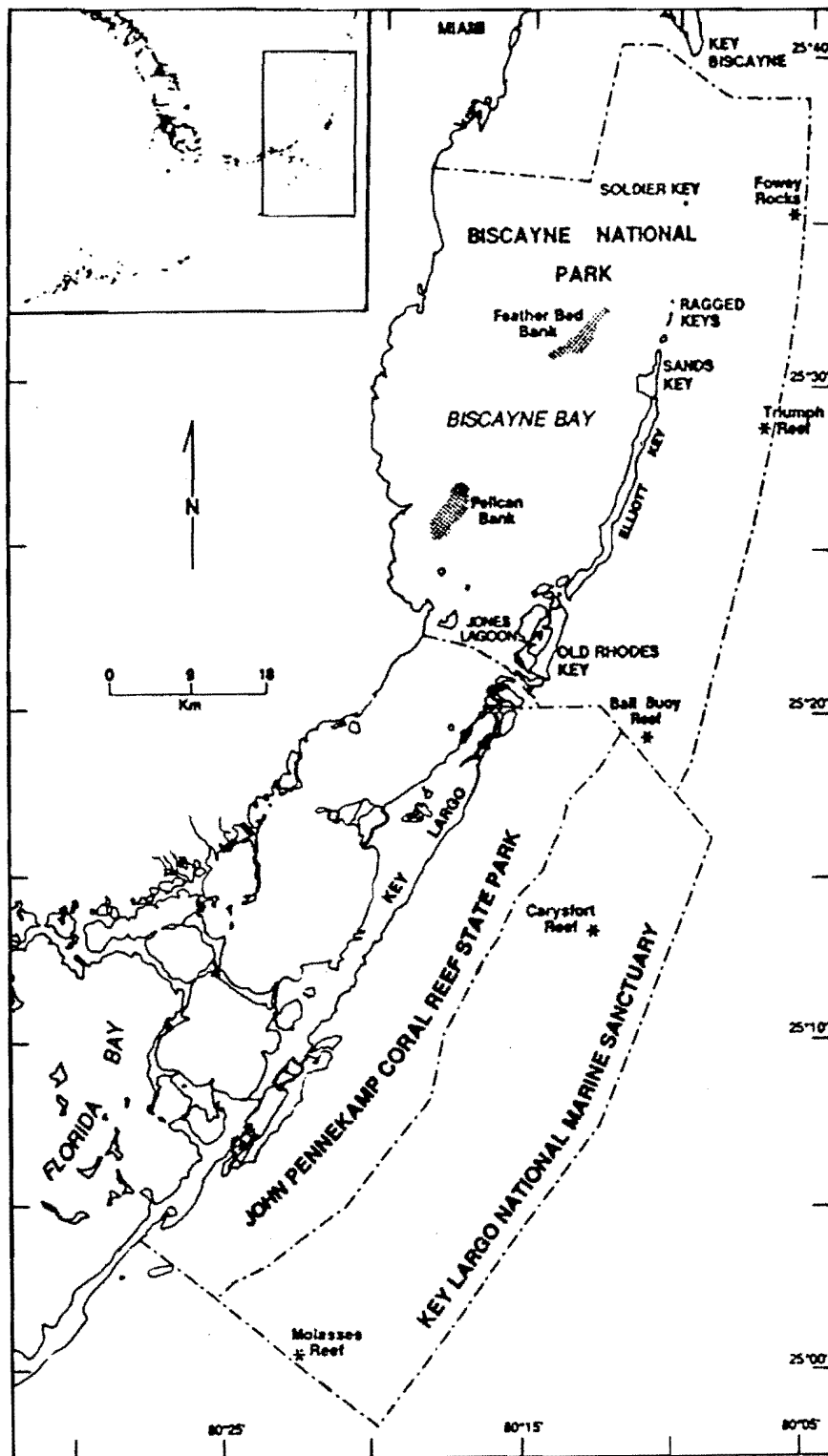


Figure 2.

[REDACTED]

Biscayne National Park Ball Buoy Reef

Photostation 1 Line Transects 1-5

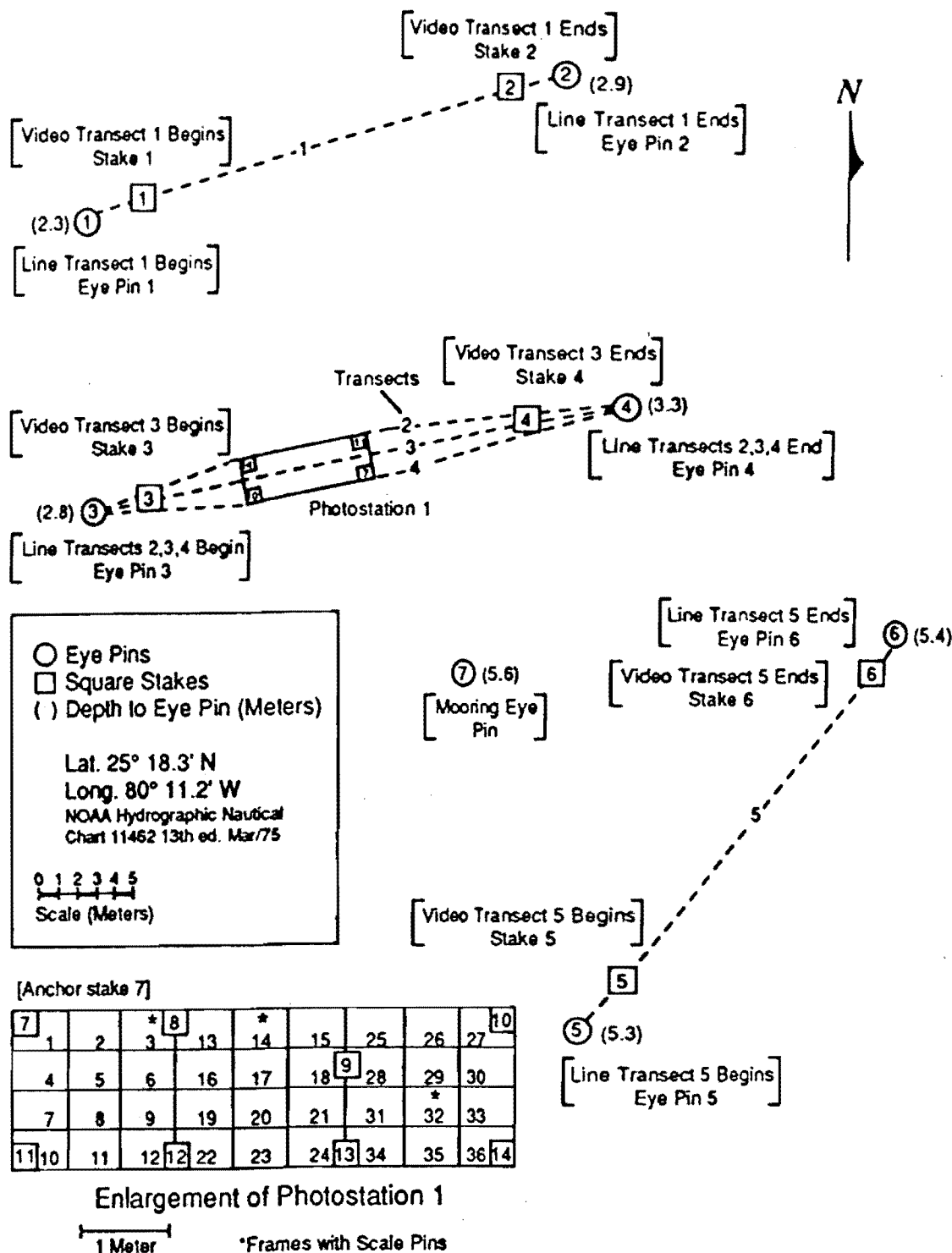


Figure 3.



Geographic Location : Biscayne National Park, Fl. (BP)
 Reef Site : Ball Buoy Reef (01)
 Lat./Long. Location : 25° 18.3'N; 80° 11.2'W
 Year Established : 1989
 Years Data Collected : 1989, 1990, 1991

Line Transect # :	1	2	3	4	5
Line Transect Eye Pin # :	beg	1	3	3	5
	end	2	4	4	6
Depth (m) Eye Pins :	beg	2.3		2.8	5.3
	end	2.9		3.3	5.4
Video Transect # :	1		3		5
Video Transect Stake # :	beg	1		3	5
	end	2		4	6
Depth (m) of Video stakes :	beg	2.3		2.8	5.3
	end	2.9		3.3	5.4
Distance between :	Stake #	Eye Pin #		Distance (m)	
	1	1		3.43	
	2	2		2.45	
	3	3		3.53	
	4	4		4.75	
	5	5		3.75	
	6	6		2.20	
		1, 3		15.20	
		2, 4		17.60	
		4, 7		16.50	
		5, 7		19.50	
	13	3		8.46	
	1, 2			3.52	
	3, 4			3.52	
	5, 6			3.75	
Compass Heading :	Stake #	Eye Pin #		Heading (°)	
	1→2			75	
	3→4			80	
	5→6			40	
		1→3		180	
		2→4		170	
		4→7		210	
		5→7		160	
	14←	3		75	
Distance to Notch :	Stake #	Distance (cm)			
(Photostation)	7	24.0			
	8	16.0			
	9	16.3			
	10	16.0			
	11	12.0			
	12	5.0			
	13	8.0			
	14	3.2			



Scale Pins :

Frame #	Species	Scale Pins #	Distance (cm)
3	P. astroides	1, 2	24.40
		2, 3	24.60
		3, 4	27.15
		4, 1	31.90
		1, 3	43.15
14	P. astroides	2, 4	30.55
		1, 2	19.10
		2, 3	19.55
		3, 4	17.85
		4, 1	16.00
32	D. strigosa	1, 3	19.55
		2, 4	29.60
		1, 2	21.75
		2, 3	35.35
		3, 4	20.80
		4, 1	28.05
		1, 3	36.60
		2, 4	38.25

Photostation Annotations :

- (1) Line Transect # 3 bisects photostation BP01.
- (2) Stake #'s 7 through 14 position the photostation BP01.
- (3) The Anchor Stake (upper left corner of the photostation) is stake # 7.
- (4) Average Depth (m) of Photostation Stakes is 3.3 m.

All photo stakes have a notch filed on all 4 corners at a designated height. This notch establishes the z coordinate of the photo transect. Usually this notch is 3" to 4" from the top and is cut approximately $\frac{1}{4}$ " into the steel. A PVC ring $1\frac{1}{2}$ " thick sits just above the notch and serves as a platform to hold the large framer and prevent it from sliding down the stake. This is a critical part of the photostation design.

The anchor stake, which is upper left hand stake of the photostation has three notches well below the ring notch.

** Annotation to Ball Buoy Reef Survey Data

A mooring Pin (Eye Pin #7) is located between Tr. 4 and Tr. 5. Depth of Mooring Eye Pin is 5.6 m.

Stake #15 is near Eye Pin #4, but is not being used in this survey.

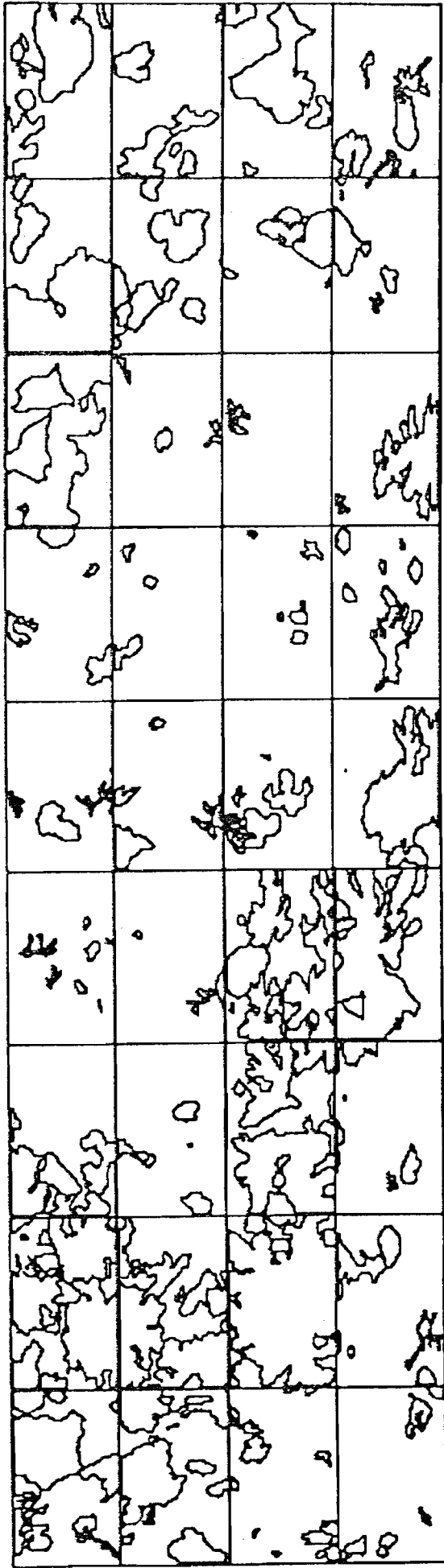
Scale Pin Annotations :

All scale pins are oriented around a coral head. Four pins were placed around a head; a set of four pins exists for every 12 frames of the photostation. Keeping the anchor stake for the whole photostation to the upper left, pins were placed above, below, to the left, and to the right of the selected coral head. Pins are numbered in clockwise fashion: above (1), to the right (2), below (3), and to the left (4) of the coral head. The purpose of the scale pins is to provide an unmoving scale in the photographs to show that the position of the large framer has not shifted since the previous set of photographs; the use of four pins allows the x-axis (defined by pins 2 & 4) and y-axis (pins 1 & 3) to be calibrated independently.



Figure 4.





(Y/N): ☒

Figure 5.



The University of Georgia

Institute of Ecology

November 19, 1993

Dr. Caroline Rogers
Virgin Islands National Park
P.O. Box 710
St. John
U.S. Virgin Islands 00830

Dear Caroline:

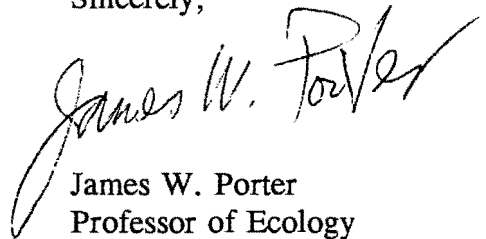
Enclosed is our Final Report for Cooperative Agreement No. CA 5000-4-8005, #25. Per your request, we have removed all reference to work done after December 31, 1990.

Work accomplished between January 1, 1991 and our last sample on September 30, 1992 (post-Hurricane Andrew) will be the subject of an equally massive final report to be submitted in January, 1994.

As I mentioned before, we delayed the submission of the enclosed final report because we viewed the subsequent renewals of this research program as continuation awards, with revised termination dates. However, during this time, the University of Georgia renegotiated its Cooperative Agreement with the National Park Service, and the Department of the Interior then viewed the subsequent renewals as entirely separate work.

It is our understanding that our second final report, covering work accomplished in 1991 and 1992, will complete all phases of this NPS project.

Sincerely,



James W. Porter
Professor of Ecology

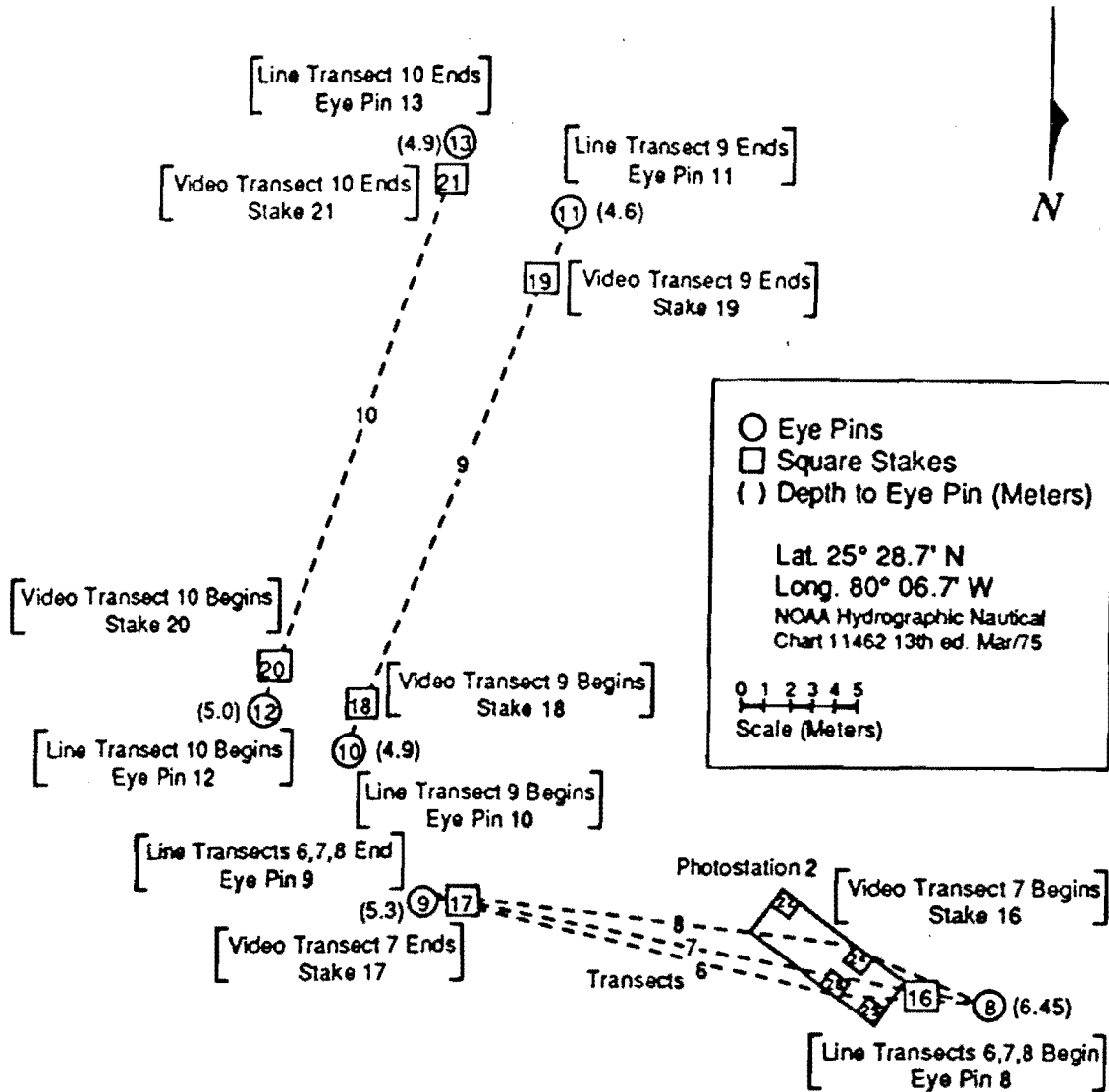
encl. Final Report (8 Volumes)

Additional full copies to: Ms. Priscilla Nalls, National Park Service
 Mr. Richard Curry, Biscayne National Park

Cover letter cc. to: Ms. Linda Allen, UGA Research Foundation
 Dr. C Ronald Carroll, UGA Institute of Ecology
 Mr. Bob McGee, UGA Administrative Services

Biscayne National Park Triumph Reef

Photostation 2 Line Transects 6-10



[Anchor stake 22]

22	1	2	3	13	14	15	25	26	27	25
4	5	6	16	17	18	28	29	30		
7	8	9	19	20	21	31	32	33		
26	10	11	12	27	22	23	24	28	34	35
										29

Enlargement of Photostation 2

1 Meter

*Frames with Scale Pins

Figure 6.

Line Transect # :		6	7	8	9	10
Line Transect Eye Pin # : beg	8	8	8	8	10	12
end	9	9	9	9	11	13
Depth (m) of Eye Pins : beg			6.5		4.9	5.0
end			5.3		4.6	4.9
Video Transect # :			7		9	10
Video Transect Stake # : beg			16		18	20
end			17		19	21
Depth (m) of Video Stakes : beg			6.5		4.9	5.0
end			5.3		4.6	4.9
Distance Between :	Stake #	Eye Pin #	Distance (m)			
	16	8	3.02			
	26	8	6.62			
	27	8	5.61			
	17	9	1.59			
	18	10	1.69			
	19	11	3.16			
	20	12	0.67			
	21	13	1.38			
		9, 10	7.60			
		10, 12	4.15			
		11, 13	5.82			
	16, 17		21.00			
	18, 19		21.50			
	20, 21		23.50			
Compass Heading :	Stake #	Eye Pin #	Heading (°)			
		8→9	100			
		10→11	200			
		12→13	210			
		9→10	150			
		10→12	120			
		11→13	110			
Distance to Notch :	Stake #	Distance (cm)				
	22	6.0				
	23	8.2				
	24	3.0				
	25	4.4				
	26	55.6, 77.0				
	27	3.3, 12.2				
	28	12.6				
	29	3.8				

Scale Pins :

Frame #	Species	Scale Pins #	Distance (cm)
2	P. porites	1, 2	16.80
		2, 3	13.90
		3, 4	13.10
		4, 1	15.75
		1, 3	17.50
		2, 4	24.10
19	S. michelini	1, 2	17.45
		2, 3	15.05
		3, 4	14.90
		4, 1	15.60
		1, 3	19.15
		2, 4	25.05
26	D. stokesii	1, 2	19.00
		2, 3	20.25
		3, 4	16.40
		4, 1	21.00
		1, 3	24.25
		2, 4	29.35

* distances between all pins are distances parallel to the plane of the framer (∴ approximating as closely as possible what the camera will see) - not distances between tops or bottoms of pins, necessarily.

** pin 1 is bent; apparent distance of aerial tip-to-tip is - 19.50cm

Photostation Annotations :

(1) Line Transect # 7 cuts through the lower part of photostation BP02.

(2) Stake #'s 22 through 29 position the photostation BP02.

(3) The Anchor Stake (upper left hand corner of the photostation) is stake # 22.

(4) Average Depth (m) of Photostation Stakes is 6.4 m.

(5) All photo stakes have a notch filed on all 4 corners at a designated height. This notch establishes the z coordinate of the photo transect. Usually this notch is 3" to 4" from the top and is cut approximately $\frac{1}{8}$ " into the steel. A PVC ring $1\frac{1}{2}$ " thick sits just above the notch and serves as a platform to hold the large framer and prevent it from sliding down the stake. This is a critical part of the photostation design.

The anchor stake, which is the upper left hand stake of the photostation has three notches well below the ring notch.

** Annotation to Triumph Reef Survey Data

Stake #24 is actually 2 stakes. The left stake holds the framer for frames 13-24; the right stake holds the framer for frames 25-36.

Stake #29 is 0.2m outside frame 36. The frame is held to the stake by a rubber band.

Stake #28 has been lost from the survey area. This position is marked by a small $\frac{1}{4}$ " stainless steel pin positioned in the lower left hand corner of frame #35.

Scale Pin Annotations :

All scale pins are oriented around a coral head. Four pins were placed around a head; a set of four pins exists for every 12 frames of the photostation. Keeping the anchor stake for the whole photostation to the upper left, pins were placed above, below, to the left, and to the right of the selected coral head. Pins are numbered in clockwise fashion: above (1), to the right (2), below (3), and to the left (4) of the coral head. The purpose of the scale pins is to provide an unmoving scale in the photographs to show that the position of the large framer has not shifted since the previous set of photographs; the use of four pins allows the x-axis (defined by pins 2 & 4) and y-axis (pins 1 & 3) to be calibrated independently.



Figure 7.

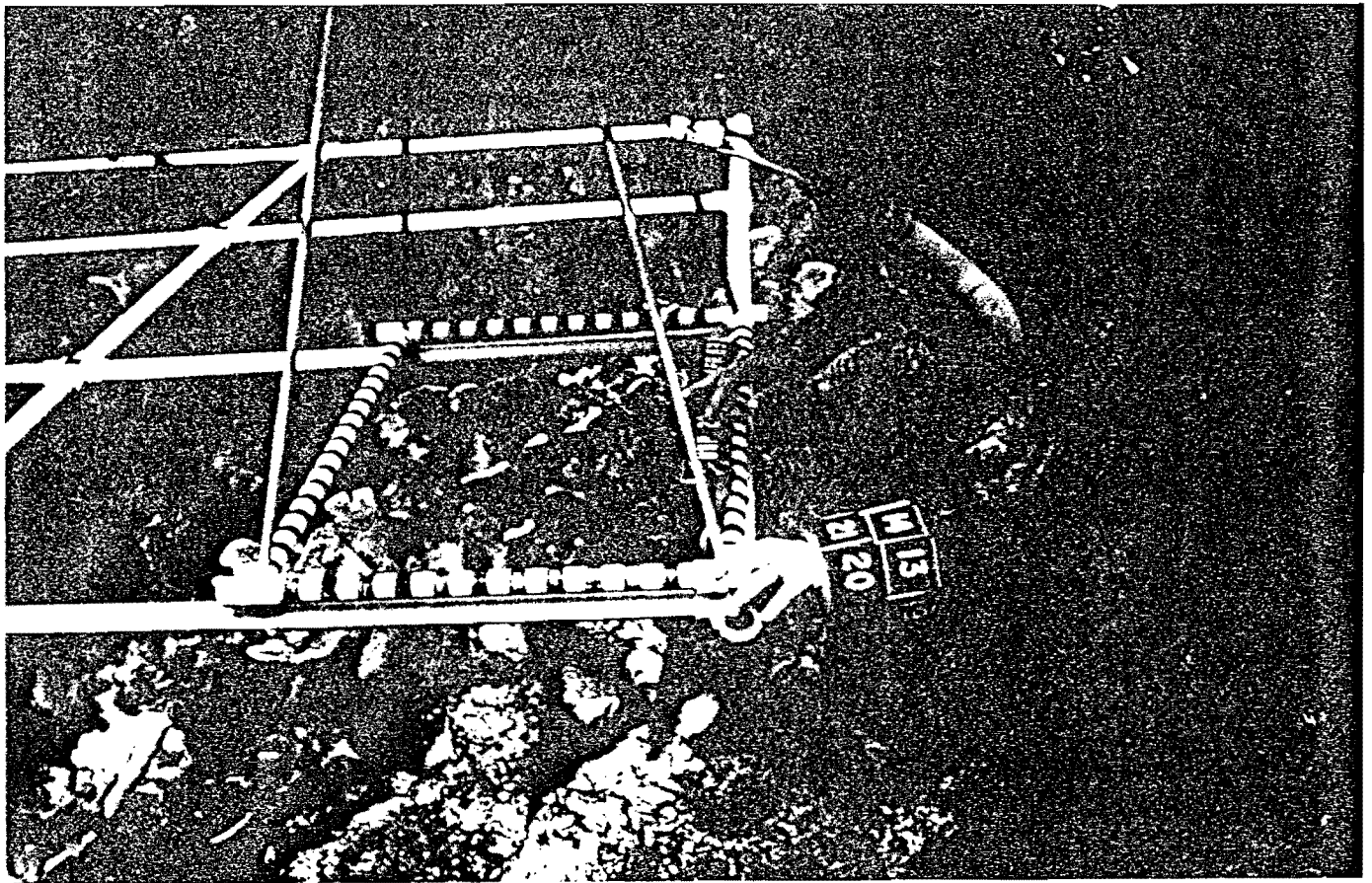


Figure 8.

Table 1. Summary statistics for reefs monitored in Biscayne National Park, 1989-1990.

Reef	BP01 : Ball Buoy Reef	
Year	1989	1990
Percent cover	24.45	26.17
Species richness	14	13
Species diversity (based on area)	0.80	0.77
Species diversity (based on colony number)	1.73	1.74

Reef	BP02 : Triumph Reef	
Year	1989	1990
Percent cover	1.77	1.94
Species richness	14	13
Species diversity (based on area)	2.20	2.17
Species diversity (based on colony number)	1.74	1.62

Table 2. Percent cover of scleractinian and hydrocoral species on reefs monitored in Biscayne National Park, 1989-1990.

Reef	BP01 : Ball Buoy Reef	
Year	1989	1990
Species:		
<i>Acropora palmata</i>	19.78	21.39
<i>Agaricia agaricites</i>	0.01	0.04
<i>Agaricia fragilis</i>	0.00	0.00
<i>Diploria clivosa</i>	0.67	0.66
<i>Diploria strigosa</i>	0.00	0.01
<i>Favia fragum</i>	0.01	0.01
<i>Millepora alcicornis</i>	0.92	1.09
<i>Millepora complanata</i>	0.77	0.77
<i>Montastrea annularis</i>	0.02	0.01
<i>Montastrea cavernosa</i>	0.11	0.09
<i>Mycetophyllia lamarckiana</i>	0.02	-
<i>Porites astreoides</i>	1.78	1.81
<i>Porites porites</i>	0.02	0.01
<i>Siderastrea siderea</i>	0.33	0.28
Total percent cover	24.45	26.17

Reef	BP02 : Triumph Reef	
Year	1989	1990
Species:		
<i>Agaricia agaricites</i>	0.14	0.15
<i>Diploria clivosa</i>	0.03	0.03
<i>Diploria stellaris</i>	0.25	0.24
<i>Diploria strigosa</i>	0.00	0.00
<i>Favia fragum</i>	0.00	0.01
<i>Meandrina meandrites</i>	0.26	0.29
<i>Millepora alcicornis</i>	0.21	0.30
<i>Millepora complanata</i>	0.03	0.01
<i>Montastrea annularis</i>	0.27	0.33
<i>Montastrea cavernosa</i>	0.29	0.28
<i>Porites astreoides</i>	0.17	0.14
<i>Porites porites</i>	0.00	-
<i>Siderastrea siderea</i>	0.02	0.03
<i>Stephanocoenia michelinii</i>	0.11	0.11
Total percent cover	1.77	1.94

Table 3. Number of colonies of scleractinian and hydrocoral species in photostations monitored in Biscayne National Park, 1989-1990.

Reef	BP01 : Ball Buoy Reef	
Year	1989	1990
Species:		
<i>Acropora palmata</i>	72	72
<i>Agaricia agaricites</i>	3	6
<i>Agaricia fragilis</i>	1	1
<i>Diploria clivosa</i>	7	7
<i>Diploria strigosa</i>	1	1
<i>Favia fragum</i>	4	6
<i>Millepora alcicornis</i>	45	50
<i>Millepora complanata</i>	11	11
<i>Montastrea annularis</i>	1	1
<i>Montastrea cavernosa</i>	2	2
<i>Mycetophyllia lamarckiana</i>	1	-
<i>Porites astreoides</i>	42	45
<i>Porites porites</i>	2	1
<i>Siderastrea siderea</i>	2	2
Total number of colonies	194	205
Total percent cover	24.45	26.17

Reef	BP02 : Triumph Reef	
Year	1989	1990
Species:		
<i>Agaricia agaricites</i>	13	10
<i>Diploria clivosa</i>	1	1
<i>Diploria stellaris</i>	4	4
<i>Diploria strigosa</i>	1	1
<i>Favia fragum</i>	1	2
<i>Meandrina meandrites</i>	1	1
<i>Millepora alcicornis</i>	45	58
<i>Millepora complanata</i>	1	1
<i>Montastrea annularis</i>	1	1
<i>Montastrea cavernosa</i>	5	6
<i>Porites astreoides</i>	17	18
<i>Porites porites</i>	1	-
<i>Siderastrea radians</i>	-	-
<i>Siderastrea siderea</i>	2	3
<i>Stephanocoenia michelinii</i>	2	2
Total number of colonies	95	108
Total percent cover	1.77	1.94

Table 4. Events causing addition or loss of coral colonies in photostations monitored in Biscayne National Park, 1989-1990.

Reef	Event	BP01: Ball Buoy Reef 1989-90	BP02: Triumph Reef 1989-90
Species:			
<i>Acropora palmata</i>	- DE	7	
	+ FI	2	
	+ TR	4	
	+ RE	1	
<i>Agaricia agaricites</i>	- DE		2
	- MI		2
	- AW		1
	+ SR	2	
	+ RE	2	2
<i>Favia fragum</i>	- DE	2	
	- MI	1	
	+ SR	3	1
<i>Millepora alcicornis</i>	- DE	1	7
	- AW	5	2
	+ SR	6	14
	+ TR	3	9
	+ UA	2	
	+ RE		1
<i>Montastrea cavernosa</i>	+ UA		1
<i>Mycetophyllia lamarckiana</i>	- DE	1	
<i>Porites astreoides</i>	- DE	1	2
	- MI		3
	+ FI		4
	+ SR	1	
	+ UA	1	
	+ RE	3	2
<i>Porites porites</i>	- DE	1	1

Key to abbreviations:

- DE Loss due to death of colony
- MI "Missing in action": colony possibly present, not visible
- AW "Absent without leave": colony transported out of station
- UD Unknown cause for disappearance
- FU Reduction in colony number due to fusion event
- + FI Increase in colony number due to fission event
- + SR Gain of colony through sexual recruitment
- + TR Colony transported into photostation
- + UA Unknown cause for appearance
- + RE Reappearance of colony previously obscured from view

Table 5. Relative abundance of scleractinian and hydrocoral species on reefs monitored in Biscayne National Park, 1989-1990.

Reef	BP01 : Ball Buoy Reef			
Year	1989		1990	
Species:				
<i>Acropora palmata</i>	80.89	<i>A. palmata</i>	81.72	
<i>Porites astreoides</i>	7.28	<i>P. astreoides</i>	6.93	
<i>Millepora alcicornis</i>	3.78	<i>M. alcicornis</i>	4.17	
<i>Millepora complanata</i>	3.14	<i>M. complanata</i>	2.93	
<i>Diploria clivosa</i>	2.74	<i>D. clivosa</i>	2.53	
<i>Siderastrea siderea</i>	1.34	<i>S. siderea</i>	1.08	
<i>Montastrea cavernosa</i>	0.45	<i>M. cavernosa</i>	0.33	
<i>Porites porites</i>	0.10	<i>A. agaricites</i>	0.16	•
<i>Mycetophyllia lamarckiana</i>	0.09	<i>P. porites</i>	0.05	
<i>Montastrea annularis</i>	0.08	<i>M. annularis</i>	0.04	
<i>Agaricia agaricites</i>	0.04	<i>F. fragum</i>	0.04	
<i>Favia fragum</i>	0.03	<i>D. strigosa</i>	0.02	
<i>Diploria strigosa</i>	0.02	<i>A. fragilis</i>	0.01	
<i>Agaricia fragilis</i>	0.01	<i>M. lamarckiana</i>	-	•
Total percent cover	24.45		26.17	
Number of species	14		13	

Reef	BP02 : Triumph Reef			
Year	1989		1990	
Species:				
<i>Montastrea cavernosa</i>	16.15	<i>M. annularis</i>	16.89	•
<i>Montastrea annularis</i>	14.98	<i>M. alcicornis</i>	15.35	•
<i>Meandrina meandrites</i>	14.73	<i>M. meandrites</i>	15.18	
<i>Diploria stellaris</i>	14.02	<i>M. cavernosa</i>	14.55	•
<i>Millepora alcicornis</i>	11.74	<i>D. stellaris</i>	12.61	
<i>Porites astreoides</i>	9.58	<i>A. agaricites</i>	7.98	
<i>Agaricia agaricites</i>	7.96	<i>P. astreoides</i>	7.27	•
<i>Stephanocoenia michelinii</i>	5.97	<i>S. michelinii</i>	5.69	
<i>Millepora complanata</i>	1.75	<i>D. clivosa</i>	1.72	
<i>Diploria clivosa</i>	1.65	<i>S. siderea</i>	1.63	•
<i>Siderastrea siderea</i>	1.05	<i>M. complanata</i>	0.59	•
<i>Porites porites</i>	0.22	<i>F. fragum</i>	0.29	•
<i>Diploria strigosa</i>	0.11	<i>D. strigosa</i>	0.24	
<i>Favia fragum</i>	0.08	<i>P. porites</i>	-	•
Total percent cover	1.77		1.94	
Number of species	14		13	

• Indicates change in rank order of relative abundance.

Biscayne National Park
Ball Buoy Reef (I), Frs. 1-36

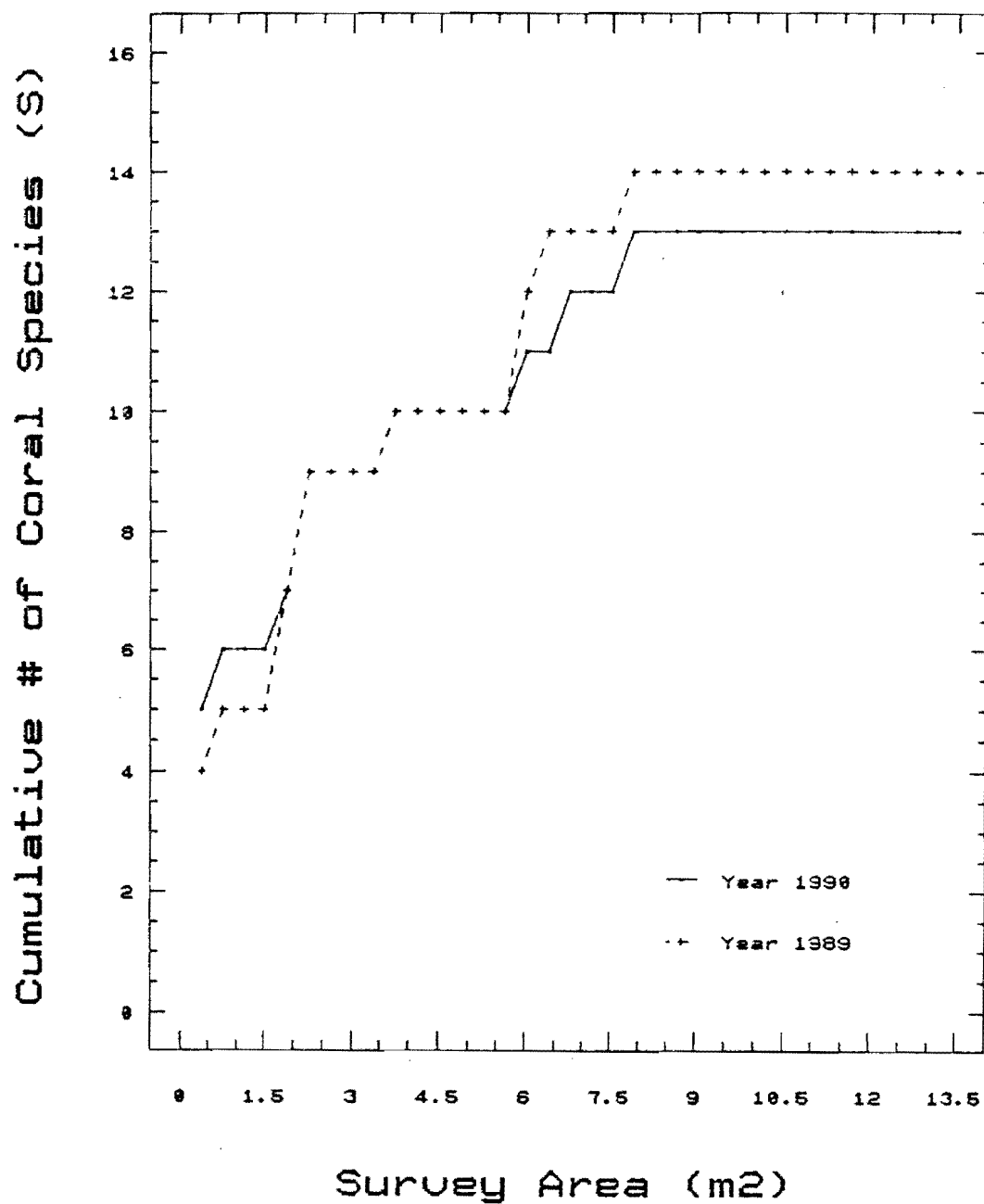


Figure 9.

Biscayne National Park
Ball Buoy Reef (I), Frs. 1-36

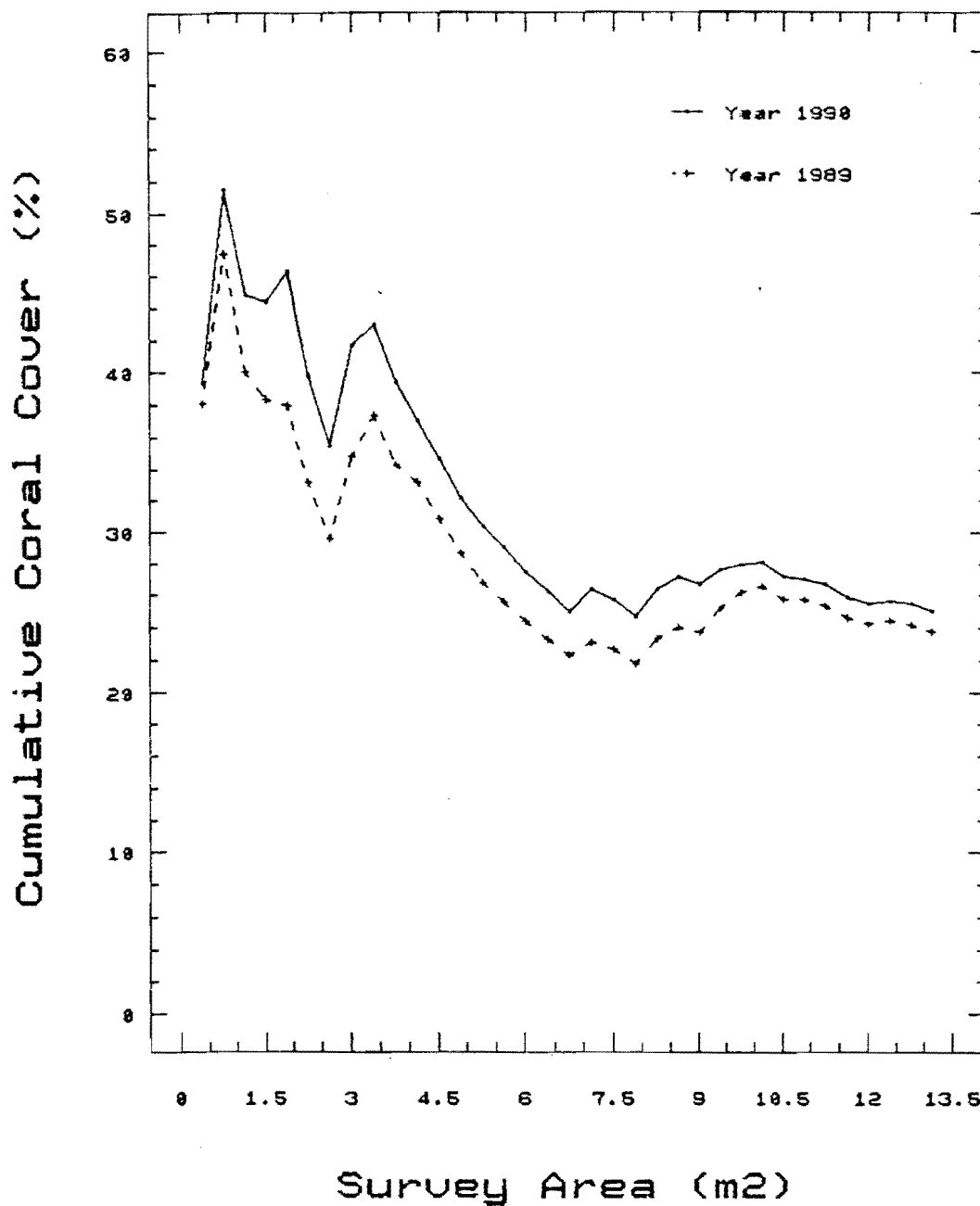


Figure 10.

Biscayne National Park
Ball Buoy Reef (I), Frs. 1-36

Cumulative Species Diversity (H' In Area)

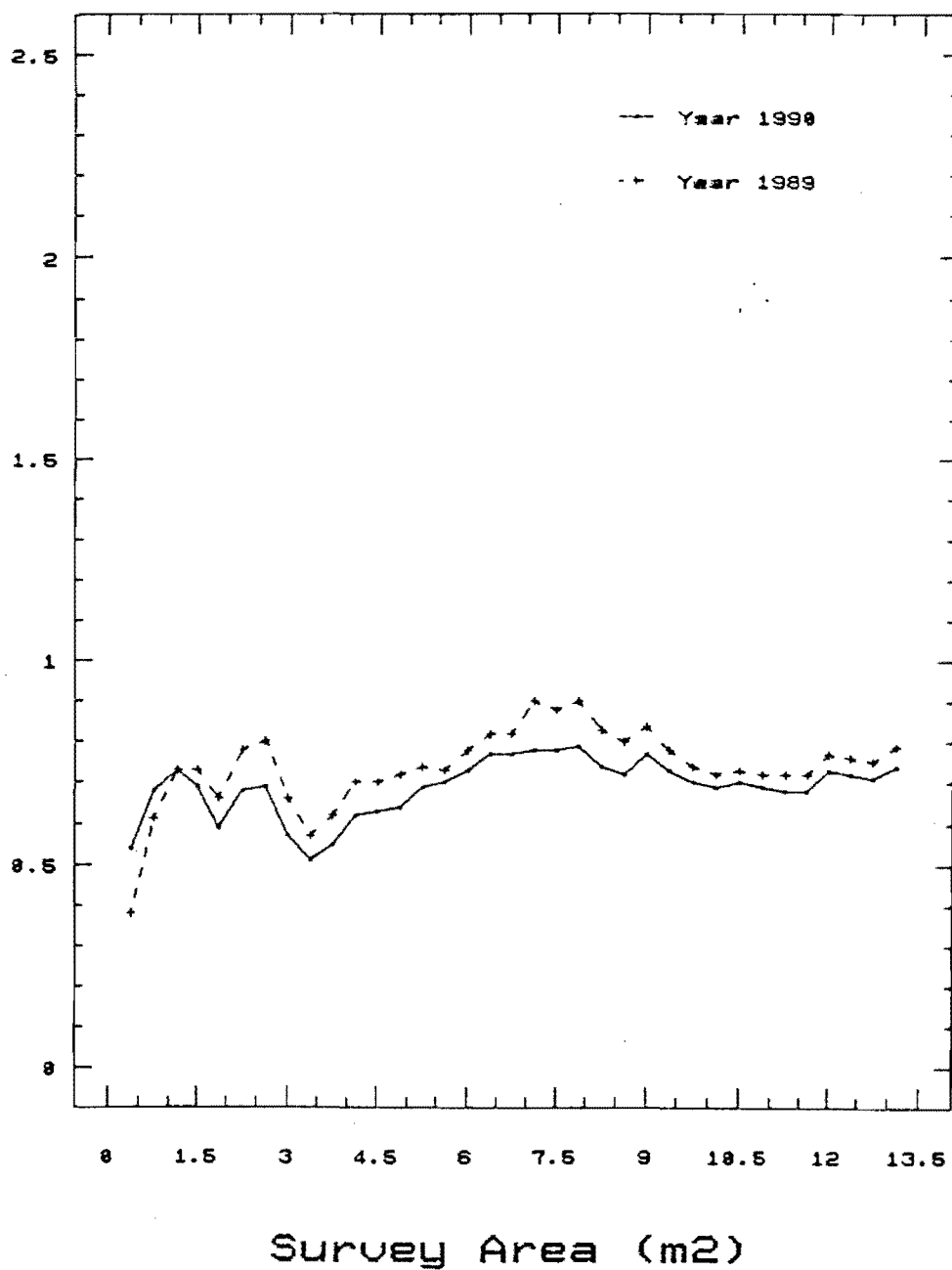
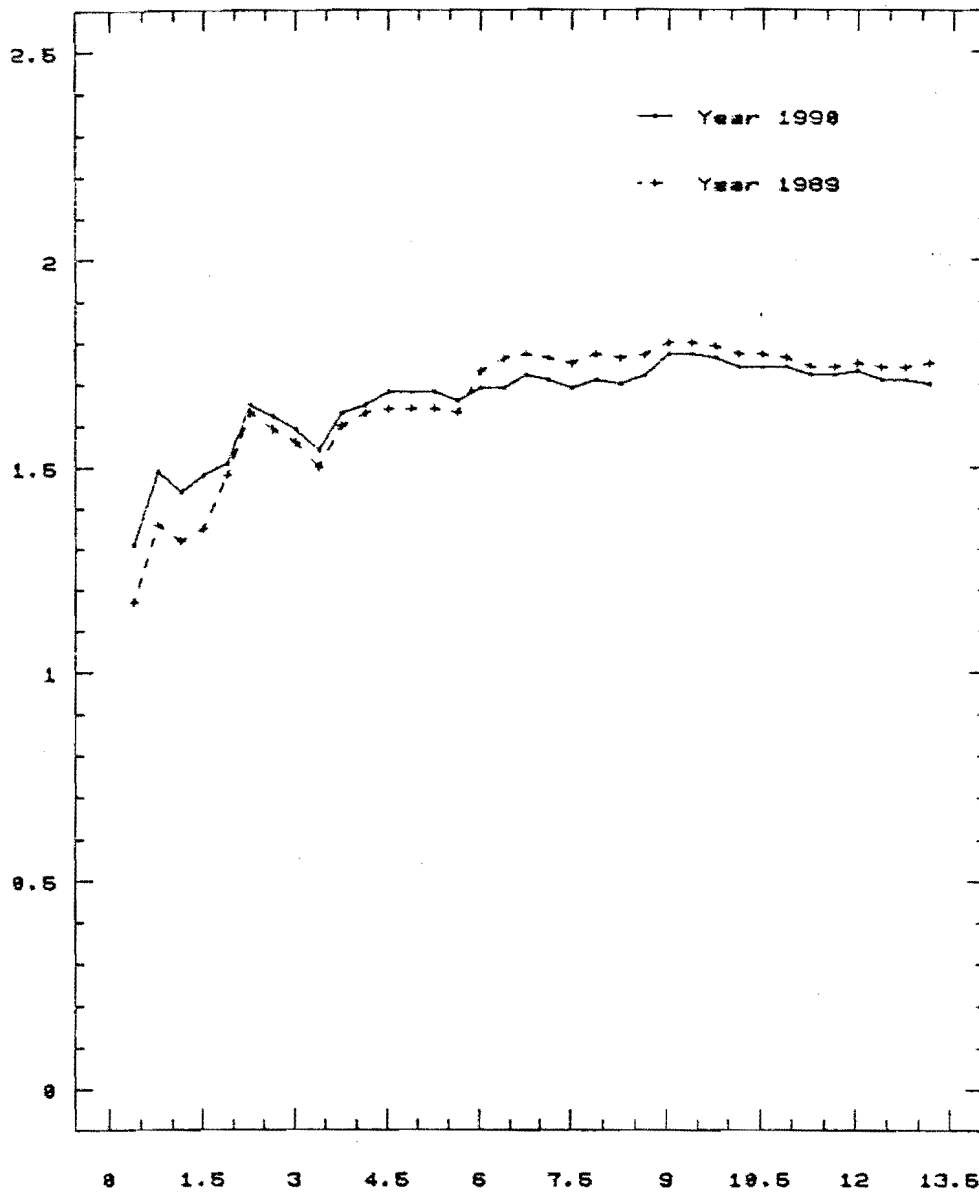


Figure 11.

Biscayne National Park
Ball Buoy Reef (I), Frs. 1-36

Cumulative Species Diversity(H' In Col.)



Survey Area (m2)

Figure 12.

Biscayne National Park
Ball Buoy reef (I), Frs. 1-36

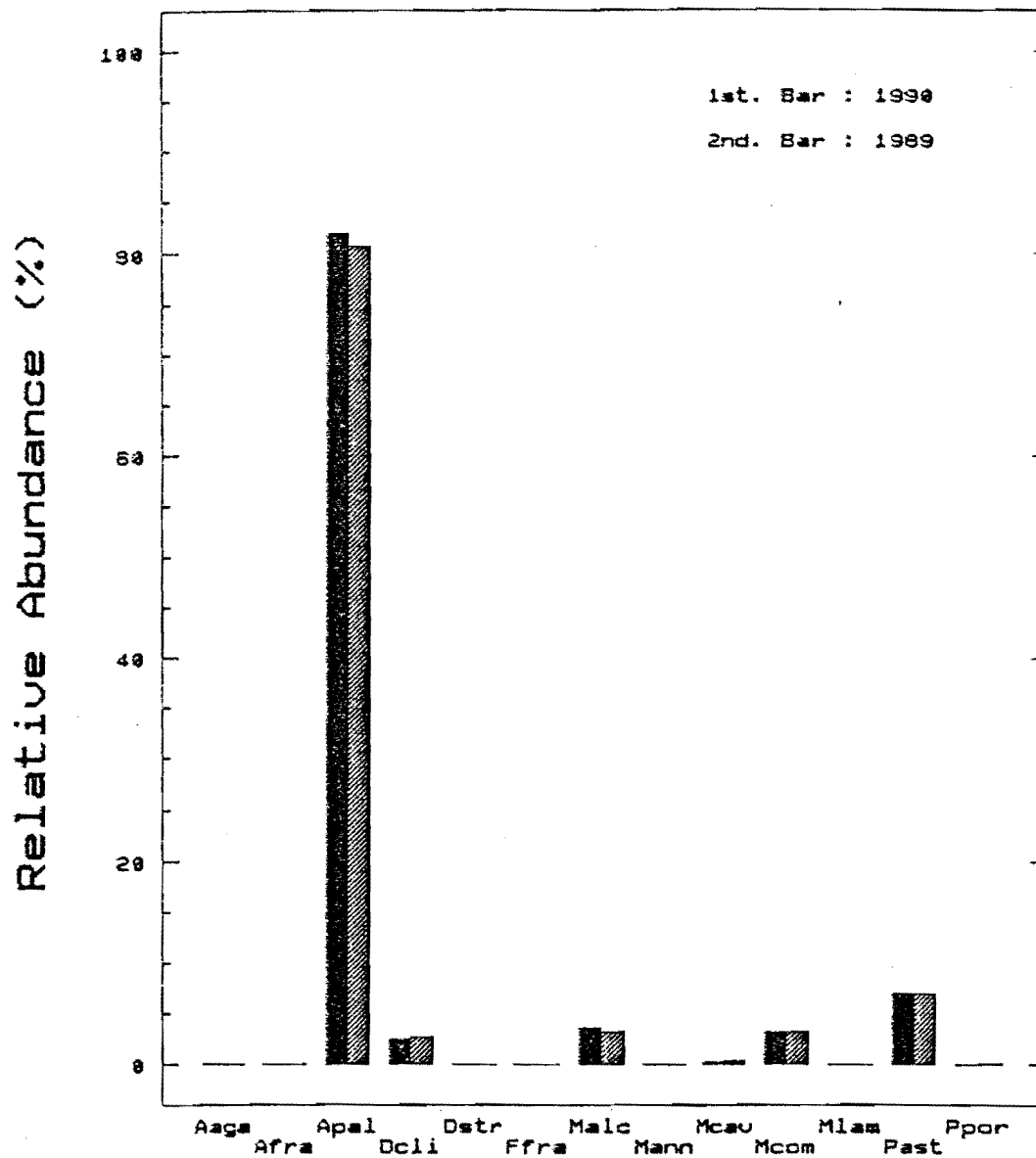
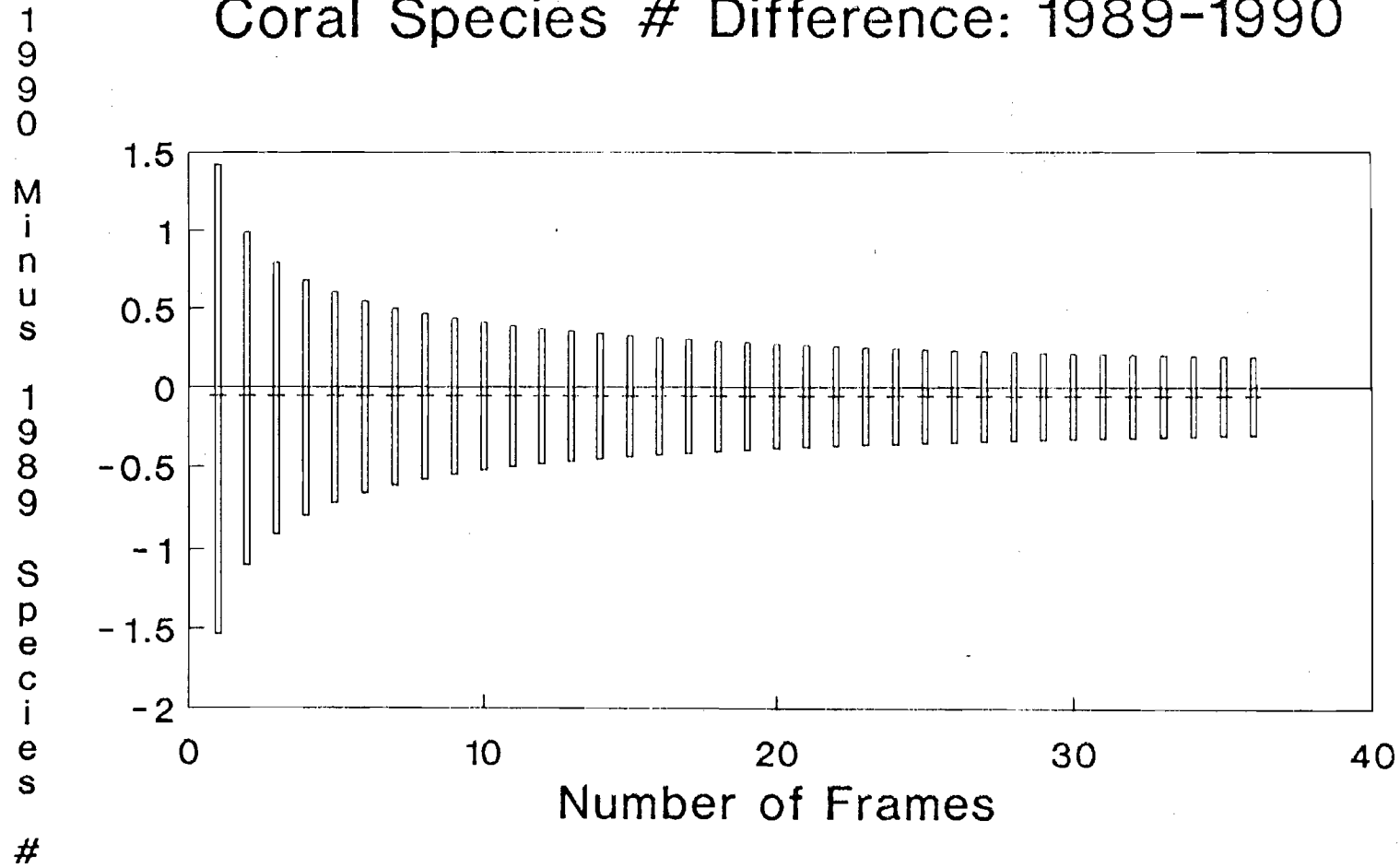


Figure 13.

Biscayne National Park

Coral Species # Difference: 1989-1990



⊞ : Mean Difference +/- 2 S.E.

Ball Buoy Reef

Figure 14.

Biscayne National Park

% Coral Cover Difference: 1989-1990

1
9
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0

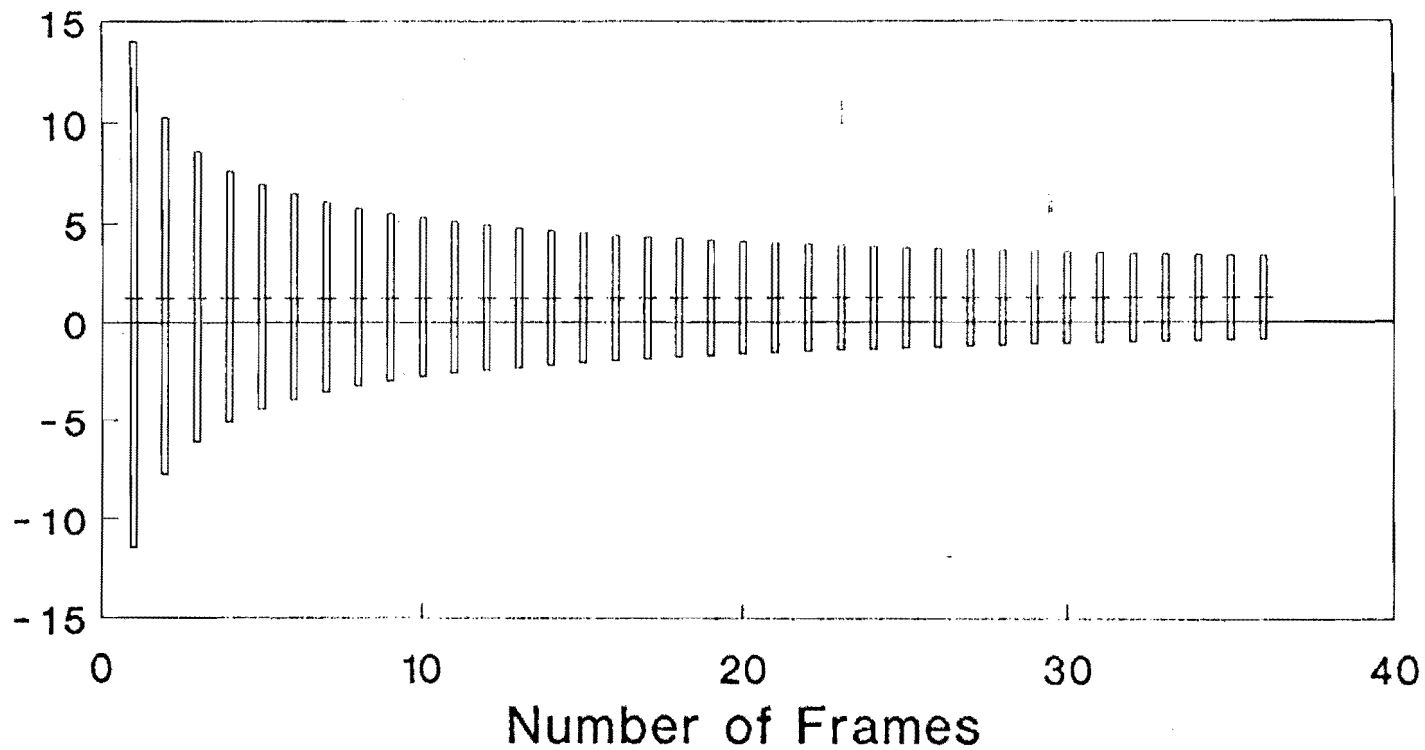
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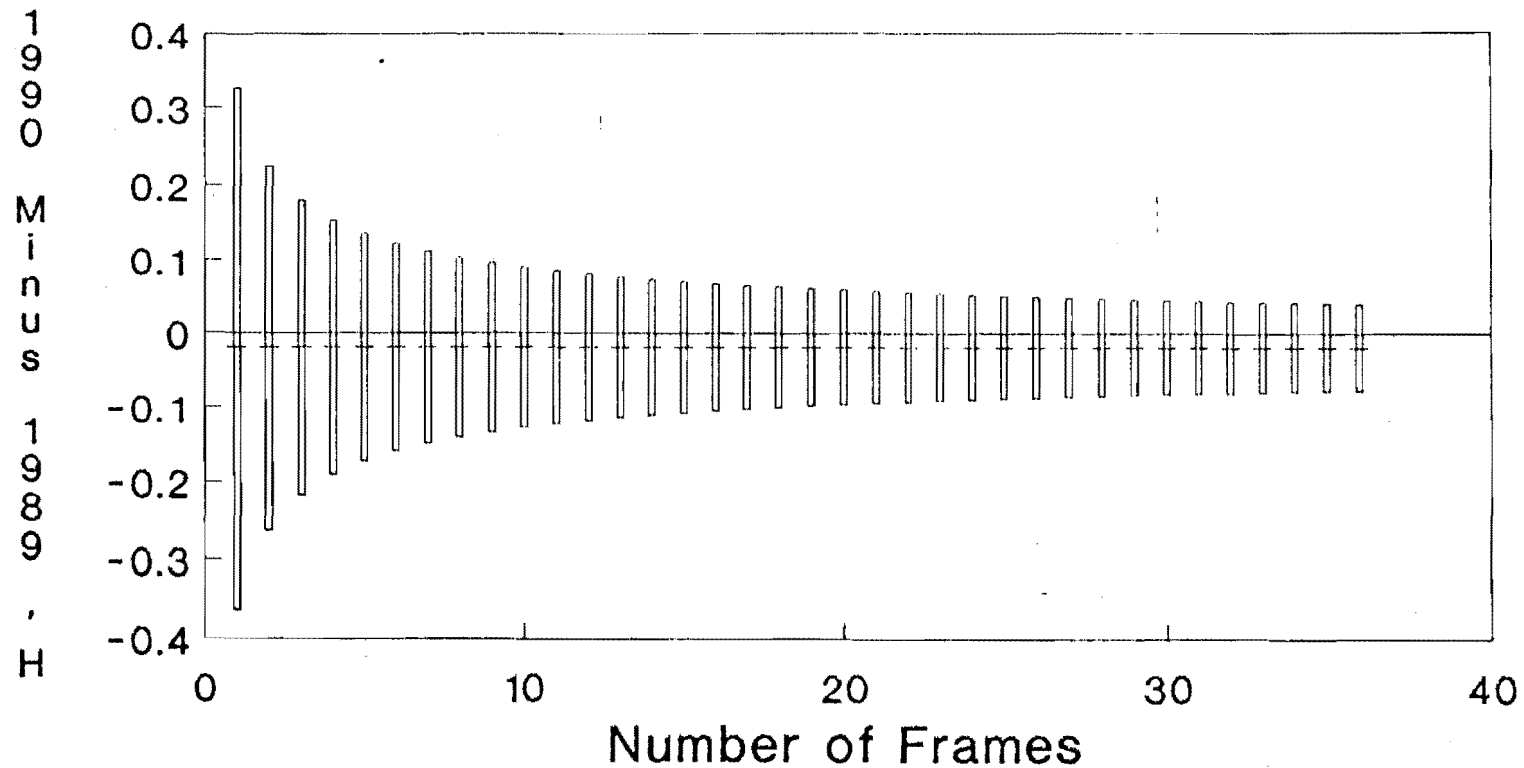
⊞ : Mean Difference +/- 2 S.E.

Ball Buoy Reef

Figure 15.

Biscayne National Park

Species Diversity Difference: 1989-1990



⊞ : Mean Difference +/- 2 S.E.

Ball Buoy Reef

Figure 16.

Biscayne National Park
Triumph Reef (II), Frs. 1-36

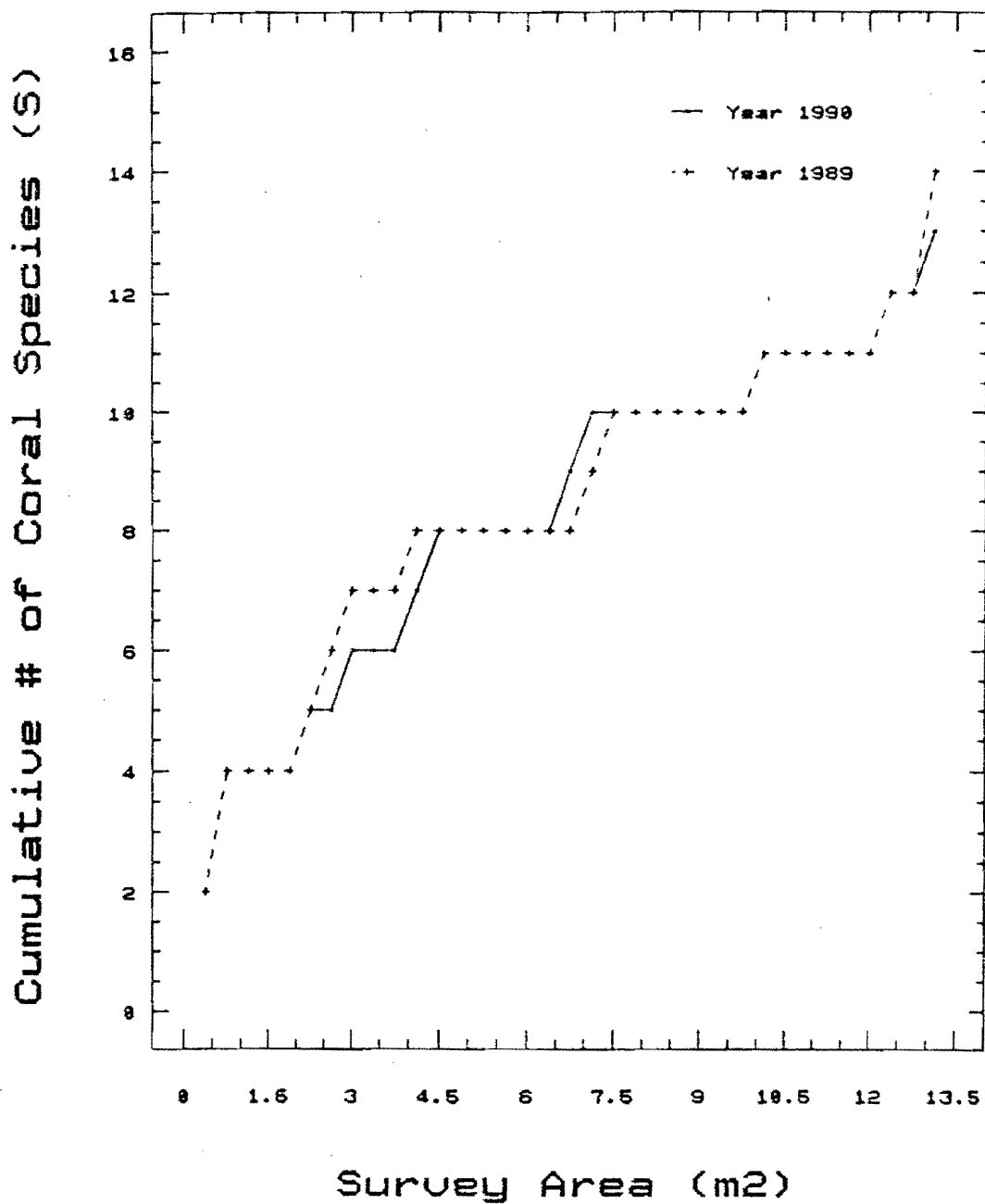


Figure 17.

Biscayne National Park
Triumph Reef (II), Frs. 1-36

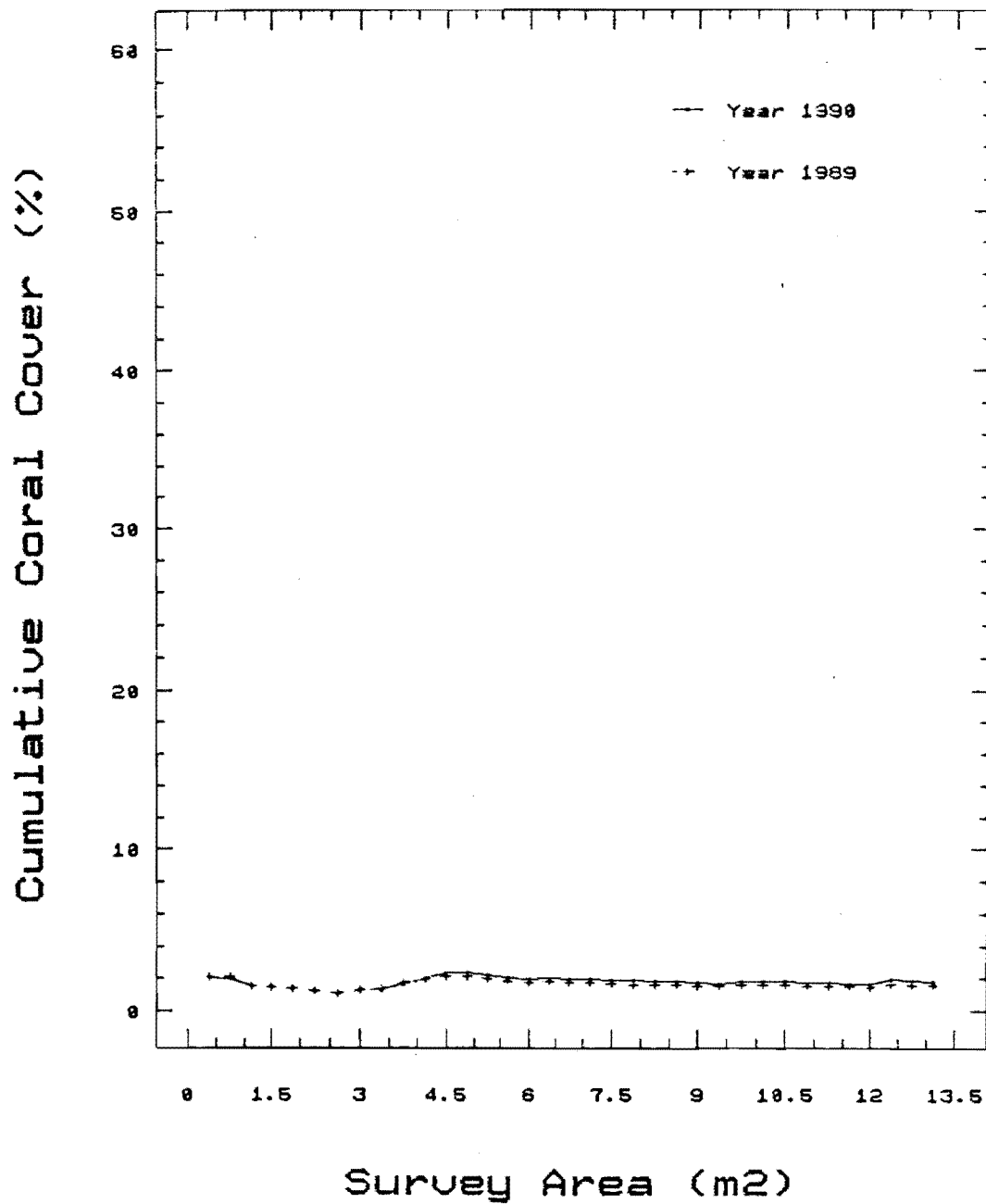


Figure 18.

Biscayne National Park
Triumph Reef (II), Frs. 1-36

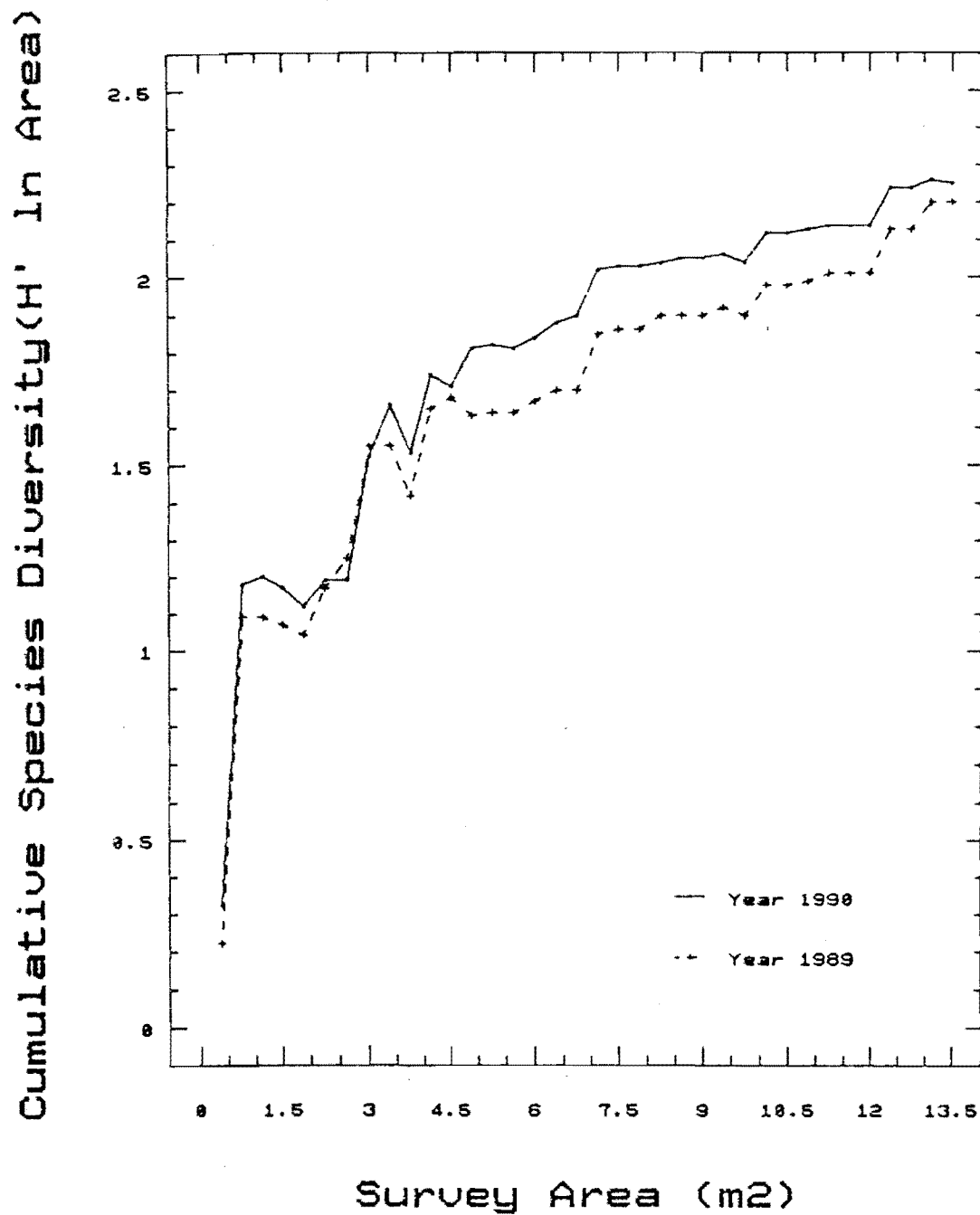


Figure 19.

Biscayne National Park
Triumph Reef (II), Frs. 1-36

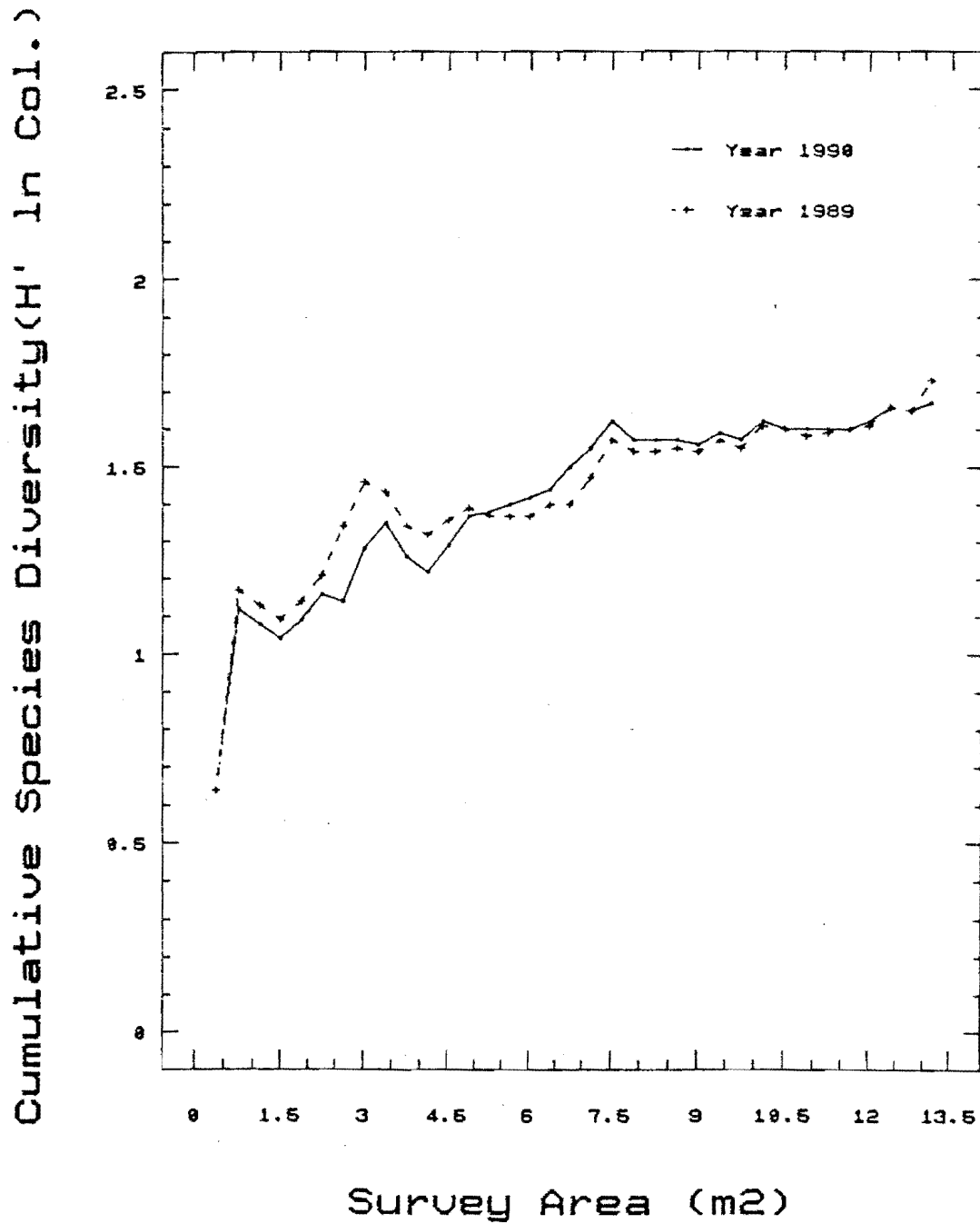


Figure 20.

Biscayne National Park
Triumph Reef (II), Frs. 1-36

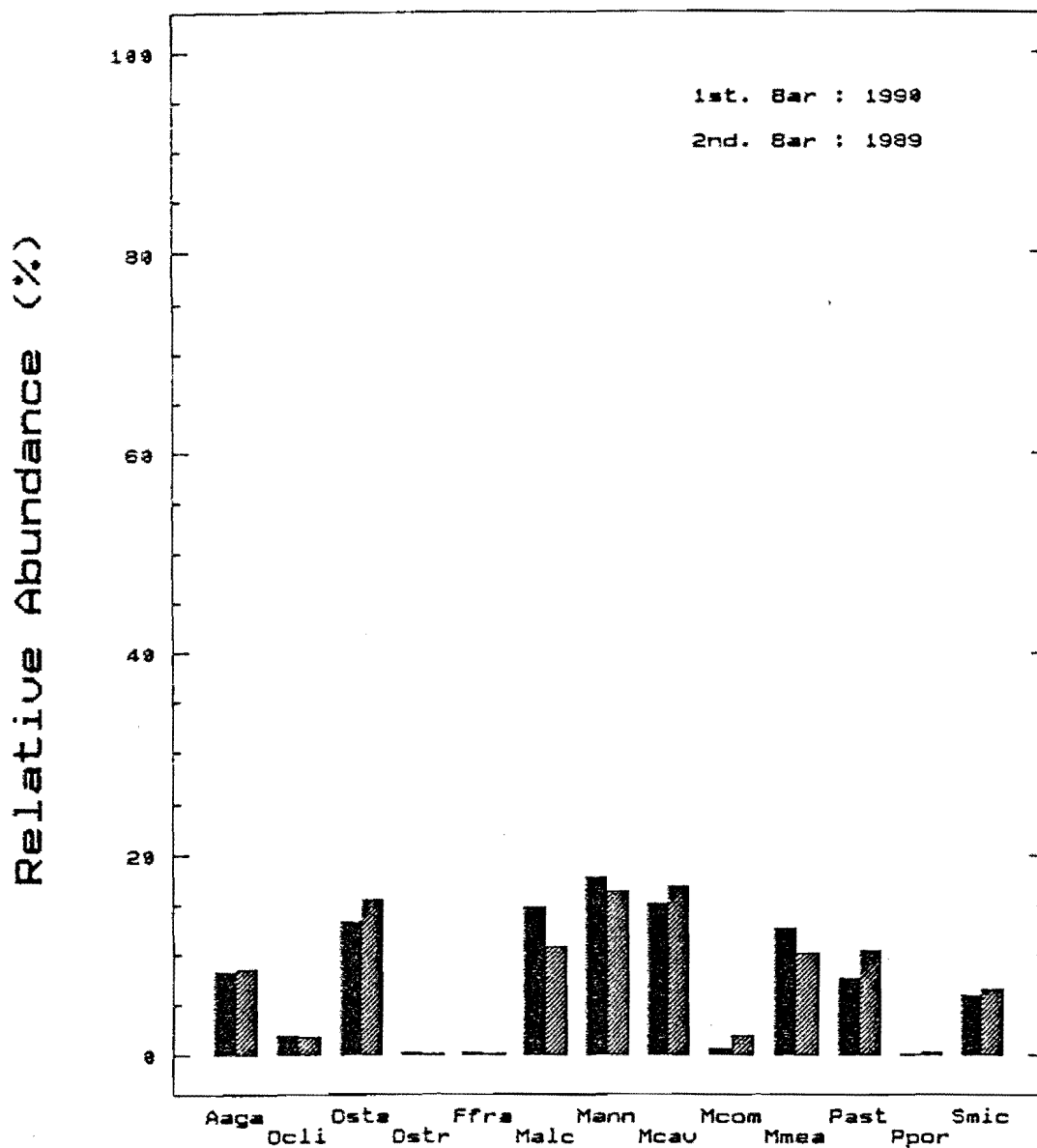


Figure 21.

Biscayne National Park

Coral Species # Difference: 1989-1990

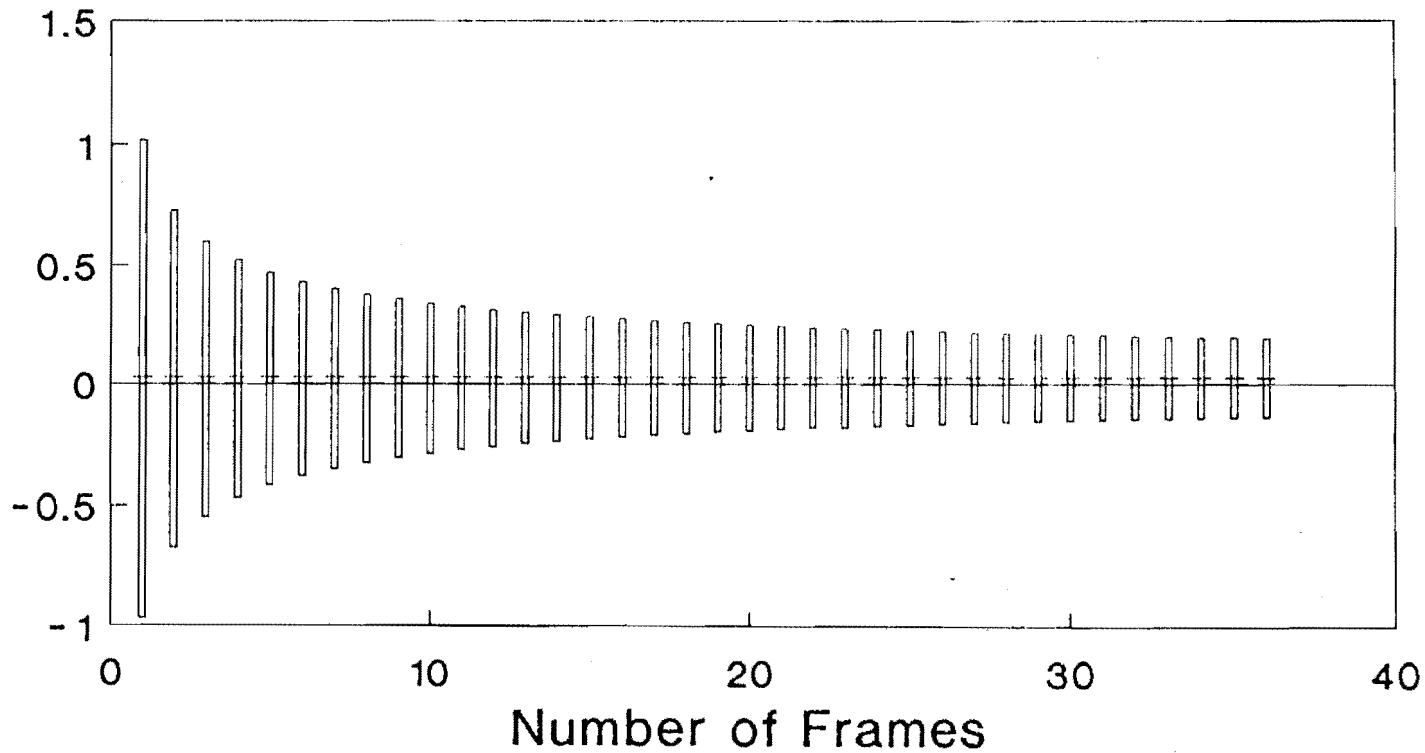
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⊞ : Mean Difference +/- 2 S.E.

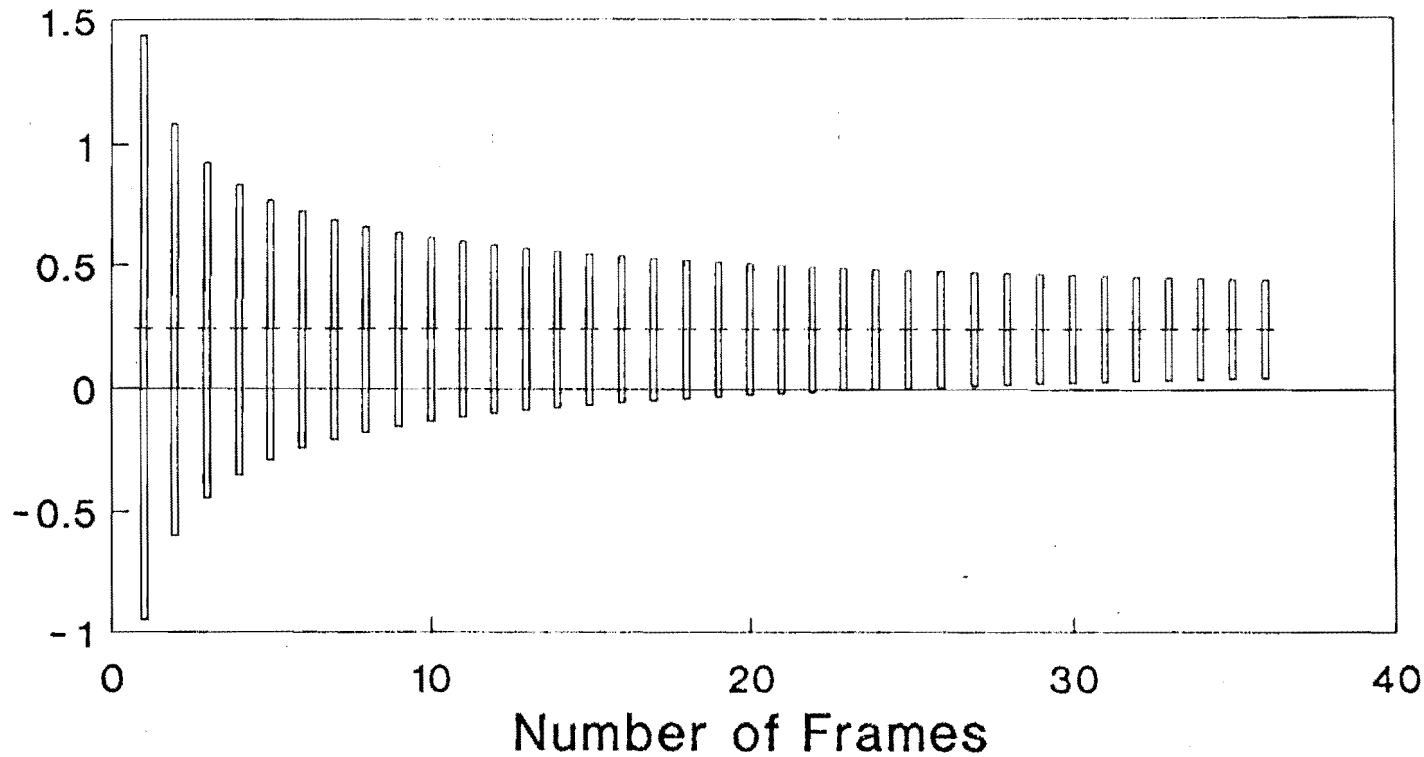
Triumph Reef

Figure 22.

Biscayne National Park

% Coral Cover Difference: 1989-1990

1990
Minus
1989
%
Coral
Cover



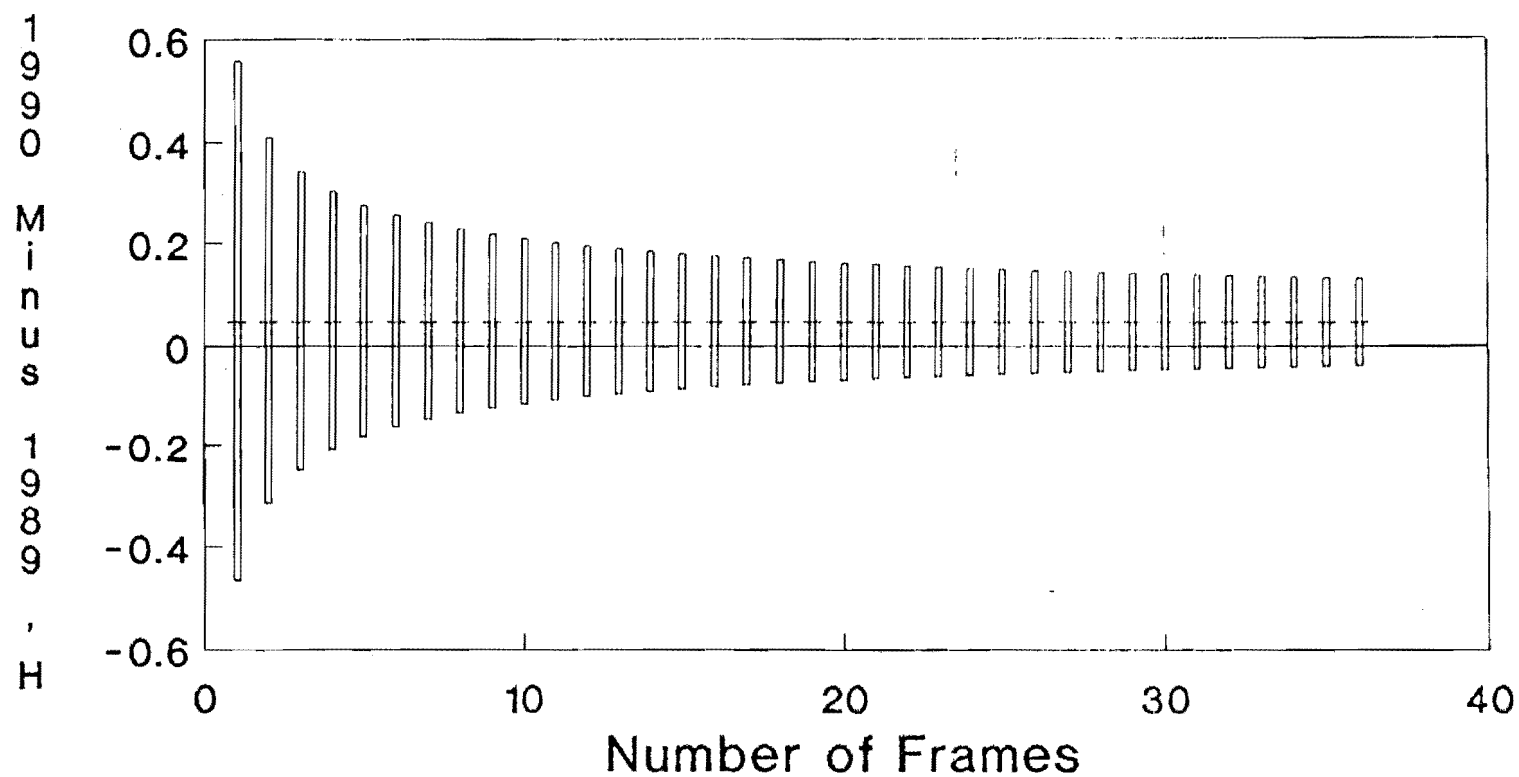
⊞ : Mean Difference +/- 2 S.E.

Triumph Reef

Figure 23.

Biscayne National Park

Species Diversity Difference: 1989-1990



⊞ : Mean Difference +/- 2 S.E.

Triumph Reef

Figure 24.

Table 6.

BISCAYNE NATIONAL PARK
Coral Species List: Ball Buoy Reef (1989)

Species Name	Swim Survey (10,000 m ²)	Haphazard Photos (100 m ²)	Photo Station (13.5 m ²)	Chain Transect (0.075 m ²)	Rel. Abun. Haphazard Photos	Rel. Abun. Photo Station	Rel. Abun. Chain Transect
1. <i>Stephanocoenia michelinii</i>	X	0	0	0	0	0	0
2. <i>Acropora pulnata</i>	X	X	X	X	82.2	82.2	80.5
3. <i>Acropora cervicornis</i>	X	0	0	0	0	0	0
4. <i>Madracis decactis</i>	X	0	0	0	0	0	0
5. <i>Leptoseris cucullata</i>	X	0	0	0	0	0	0
6. <i>Agaricia agaricites</i>	X	X	X	X	0.2	0.2	2.2 --
7. <i>Agaricia fragilis</i>	X	X	X	0	0.1	0.1	0 --
8. <i>Agaricia humilis</i>	X	0	0	0	0	0	0
9. <i>Siderastrea siderea</i>	X	X	X	0	0.4	1.4	0.4
10. <i>Siderastrea radians</i>	X	0	0	0	0	0	0
11. <i>Porites porites</i>	X	X	X	X	0.2	0.2	0.9
12. <i>Porites astreoides</i>	X	X	X	X	5.1	6.8	7.8
13. <i>Montastraea annularis</i>	X	X	X	0	0.2	0.1	0 --
14. <i>Montastraea cavernosa</i>	X	X	X	X	0.1	0.7	0.4
15. <i>Favia fragum</i>	X	X	X	X	0.1	0.1	0.2
16. <i>Diploria clivosa</i>	X	X	X	0	1.9	2.5	0.1 --
17. <i>Diploria labyrinthiformis</i>	X	0	0	0	0	0	0
18. <i>Diploria strigosa</i>	X	X	X	0	0.4	0.1	0 --
19. <i>Colpophyllia natans</i>	X	X	0	0	0.1	0	0
20. <i>Oculina diffusa</i>	X	0	0	0	0	0	0
21. <i>Dichocoenia stokesi</i>	X	0	0	0	0	0	0
22. <i>Dichocoenia stellaris</i>	X	X	0	0	0.1	0	0
23. <i>Meandrina meandrites</i>	X	X	0	0	0.1	0	0
24. <i>Mycetophyllia lamarkiana</i>	X	0	X	0	0	0.1	0 --
25. <i>Scolymia cubensis</i>	X	0	0	0	0	0	0
26. <i>Eusmilia fastigiata</i>	X	0	0	0	0	0	0
27. <i>Millepora alcicornis</i>	X	X	X	X	2.2	2.3	3.2
28. <i>Millepora complanata</i>	X	X	X	X	6.6	3.2	4.3
Total	28	16	14	8	100.0	100.0	100.0

* New state record for Florida

-- Large discrepancy between % cover values measured by the Chain Transect Method versus both Photographic Methods.

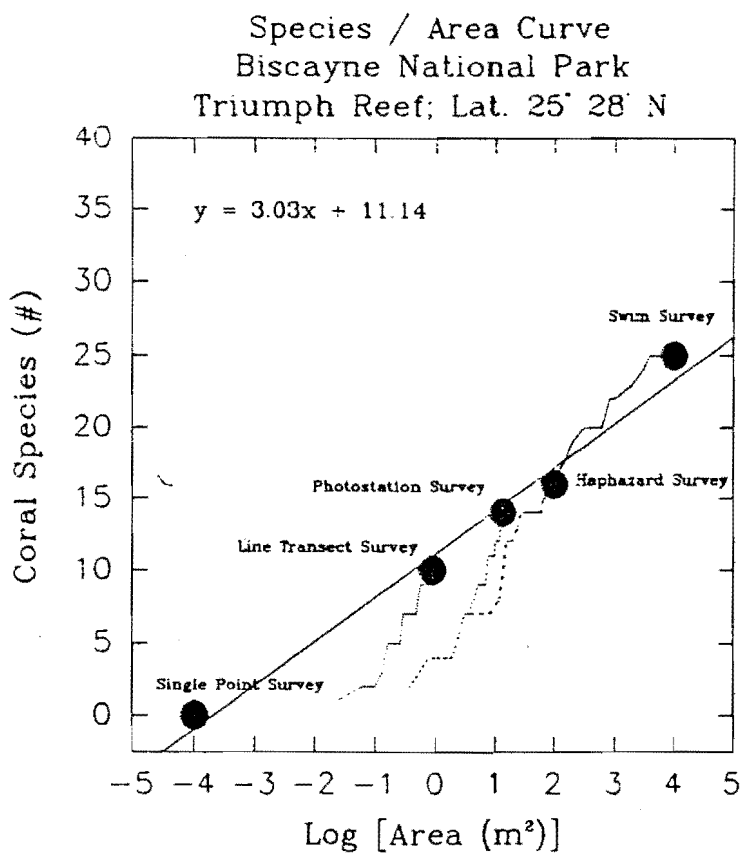
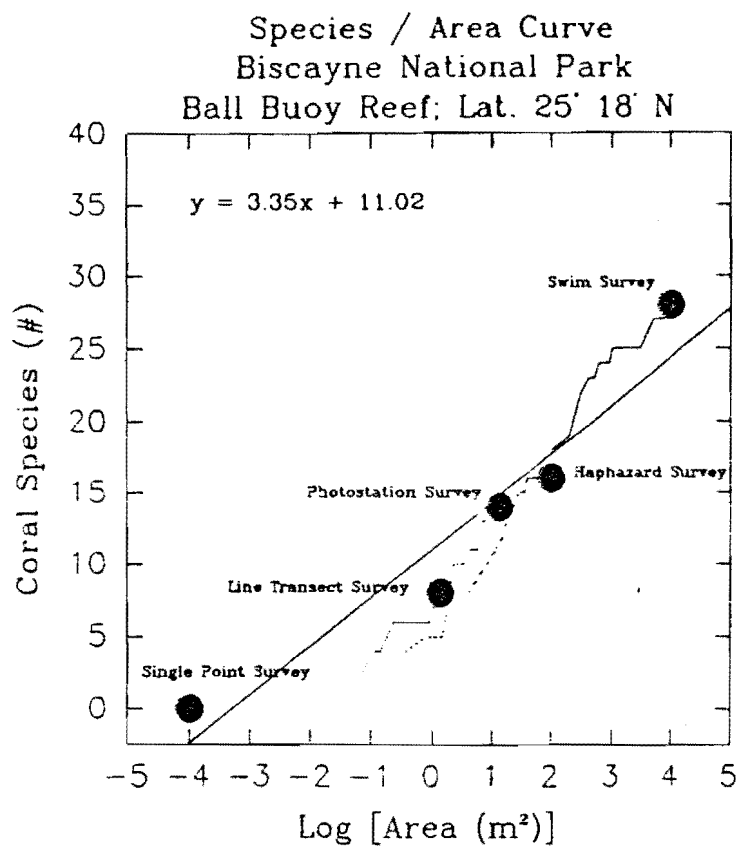


Figure 25.

Table 8.

Coral Reef Monitoring Methods

Parameter	Methods		
	Swim Survey	Chain Transect (75 m)	Photo Station (13.5 m ²)
S	⊕	—	—
3-D	—	⊕	—
% Coral Cover	—	+	+
Rel Ab. (coral).	—	—	+
Rel Ab. (substrates)	—	⊕	—
Sp. Diver. (area/length)	—	+	+
Sp. Diver. (colony)	—	—	⊕
	1	4	4

Table 9.

Coral Reef Monitoring Methods

	Swim Survey	Chain Transect (75 m)	Photo Station (13.5 m ²)
Set up time (Days)	0	6	8
Under water survey time	3	6	1
Above water analysis time	<u>0</u>	<u>4</u>	<u>20</u>
	3	16	29
Research Equipment Cost (Excl. mainframe & software)	\$ 0	\$ 200	\$ 3000

Quantification of Loss and Change in Floridian Reef Coral Populations¹

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SYNOPSIS. Six coral reef locations between Miami and Key West were marked with stainless steel stakes and rephotographed periodically between 1984 and 1991. The monitored areas included two photostations in the Looe Key National Marine Sanctuary, two photostations in the Key Largo National Marine Sanctuary, and two photostations in the Biscayne National Park. Stations were monitored for species number, percent cover, and species diversity of the scleractinian and hydrozoan stony corals. Monitoring began in 1984 for photostations in the National Marine Sanctuaries and in 1989 for stations in the National Park.

All six areas lost coral species between the initial survey year and 1991. Survey areas lost between one and four species; these losses constituted between 13% and 29% of their species richness. Five of the six areas lost live coral cover. Based upon photographs taken repeatedly at these locations, net losses ranged between 7.3% and 43.9%. In the one station showing an increase in coral cover, the increase was only for the canopy branches of *Acropora palmata*; understory branches of this same species lost surface area at the same rate as canopy branches gained area. For most of the common species, there was a reduction in the total number of living colonies in the community, and a diminution in the number of large, mature colonies. Throughout the study period, there was no recruitment to any of the photostations by any of the massive frame building coral species.

Mortality of this magnitude is often associated with hurricane damage, but in this survey the losses occurred during a period without catastrophic storms. Sources of mortality identifiable in the photographs include (1) black band disease and (2) "bleaching"; other potential sources of mortality are also considered. We conclude, for our survey areas, that loss rates of this magnitude cannot be sustained for protracted periods if the coral community is to persist in a configuration resembling historical coral reef community structure in the Florida Keys.

INTRODUCTION

Coral reef community structure is known to be influenced by processes occurring on a range of temporal and spatial scales (Naylor and Hartnoll, 1979; Jackson, 1991). Generally, predation (reviewed by Glynn, 1990; Knowlton *et al.*, 1990) and disease (Antonius, 1981a, b; Bak and Crieens, 1981) may happen quickly on relatively small scales of space and time, whereas epidemic

diseases (Gladfelter, 1982), hurricanes (Stoddart, 1974; Porter *et al.*, 1981; Woodley *et al.*, 1981), and sea level change may occur less frequently, and on larger spatial scales. To quantify controlling influences on community structure, observations and experiments on biologically relevant time scales are needed. At the very least, these appropriate time scales must encompass the lifespan of the dominant members of the community. For coral reefs, structurally important members may live for centuries (Hughes and Jackson, 1985), and important ecological influences may be manifested only on decadal time scales (Done, 1992). While

¹ From the Symposium on *Long-Term Dynamics of Coral Reefs* presented at the Annual Meeting of the American Society of Zoologists, 27-30 December 1991, at Atlanta, Georgia.

the need for long term data sets is obvious (Likens, 1987; D'Elia *et al.*, 1991), no cohesive program for fostering and funding this kind of research has evolved for oceanic environments.

In the absence of long term studies, comparative geographic studies over broad spatial scales suggest that coral reef community structure in the Caribbean is relatively predictable (Goreau, 1959; Ball *et al.*, 1967; Porter *et al.*, 1982; Edmunds *et al.*, 1990). The prevalence in shallow water of the branching species *Acropora palmata* suggests that the processes controlling shallow water coral reef community structure should be amenable to observations on relatively small spatial scales. Coral zonation is more variable at greater depths. Nevertheless, species within the genus *Montastrea* (either *M. annularis* or *M. cavernosa*) frequently dominate, suggesting that the trajectory of community development, even at these depths, will be predictable as well.

Coral growth is indeterminate, with no genetically determined limit to the size of individual colonies (Sebens, 1982). *Acropora palmata* is capable of linear extension rates of up to 10 cm per year (Shinn, 1989). Shinn (1989) calculates that with three uninterrupted branching events per year, a single blade could produce 56 km of branches in ten years. This *potential* growth rate further substantiates the impression that some mechanisms regulating coral reef community structure should be apparent not only on smaller spatial scales, but also on smaller temporal scales, considerably less than the lifetime of an individual investigator.

Coral reefs of the Florida Keys stretch for a distance of 580 km from Fowey Rocks on the northern boundary of Biscayne National Park to Loggerhead Reef on the western boundary of the Dry Tortugas National Monument, and encompass an area of more than 3,100 km². The best developed reefs lie in a string on the seaward margin, between 3 and 5 km offshore, of the Florida Keys. Reefs have been growing in these locations since the last sea-level inundation some 5,000 years B.P. Coral zonation along the outer margin of reefs in the Keys follows the general Caribbean model (Goreau, 1959;

Jaap, 1984), with a shallow *Acropora palmata* zone grading to a deeper *Montastrea* buttress zone. Deep reef and vertical wall communities are rare in the Keys due to the gentle slope of the continental shelf out to the 100 m depth contour.

The health of coral reefs in the Florida Keys has been the subject of considerable speculation in the popular press (Adler, 1990; Ward, 1990; Caputo, 1991; Fishman, 1991). Dustan and Halas (1987) compared coral cover and diversity under 22 repeatable line transects laid parallel to depth contours from the surface to 40 m in 1979 and 1982. They demonstrated a decline of coral populations at some depths in the Key Largo National Marine Sanctuary and growth at others. These authors point out that, in the absence of baseline data on natural rates of change, speculation about human influence, particularly at system-wide spatial scales, will be impossible.

In order to measure change in coral reef community structure, we set up a series of underwater photographic monitoring stations in the Looe Key and Key Largo National Marine Sanctuaries in 1984 (White and Porter, 1985), and in the Biscayne National Park in 1989 (Fig. 1). We quantify vectors of change (both magnitude and direction) for these coral reefs and describe the possible agents of change visible in these photographs. Processes theoretically postulated to influence coral reef community development are compared to processes identified from these data that appear to shape the coral reef community.

METHODS

Monitoring methods

We use several methods to monitor each reef site. In photostation surveys, the primary goal is to identify the species of scleractinian corals and hydrocorals present and quantify their abundance. Chain transect surveys are used to determine the relative abundances of different substrate types as well as coral species. Video surveys of transects and photostations are also recorded to preserve information in digital format. Larger scale haphazard photographic surveys are used to determine whether the photostations are representative of the sur-

rounding reef. Finally, a 1000 m² swim survey on each reef provides a virtually complete list of coral species present on the reef. Most of the data presented here are taken from photostation surveys. A major feature of our photostation method is that the boundaries of the actual areas sampled are permanently marked by stainless steel stakes cemented into holes drilled into limestone substrate so that the stations can be relocated.

Chain transects were established by stretching a 25-m line between two eyepins permanently cemented into the seafloor. Chains are attached to the 25-m line at the beginning of each meter, allowed to drop to the seafloor, and made to conform to the three-dimensional substrate directly below the 25-m line. The number of chain links overlying each different type of substrate are counted and recorded. This process is replicated three times for each transect. The effect is that of "slicing" through the reef and tracing the resulting outline. In this survey, all scleractinian corals and hydrocorals are identified to species. Other categories of organisms and substrate types were recorded, but are not considered in this paper. Three 25-m chain transects have been surveyed annually since 1989 in each of the Biscayne N.P. sites; one 25-m chain transect was surveyed in each of the N.M.S. sites beginning in 1991.

Photostations are set up on a four-stake system, with four stainless steel stakes cemented into the substrate defining the x- and y-coordinates of a 2.00 × 2.25 m (4.5 m²) PVC frame which serves as a positioning grid. Rings to support the grid from underneath are slipped over the stakes and screwed in place at notches filed into the stakes so that the z-coordinates of the grid are defined as well. This grid provides the boundaries and supports for a smaller PVC camera frame) 0.50 × 0.75 m, or 0.375 m²) with a 35 mm Nikonos V camera with a 28 mm underwater lens mounted 1.0 m above the plane of the frame. The camera frame outlines the actual two-dimensional area sampled with each photograph. Twelve photographs, each covering 0.375 m², are required to survey each 4.5 m² area. In each of the photostations at Carysfort and Looe

Reefs, the 4.5 m² grid is laid down twice for a total area of 9.0 m² (24 photographs). In the photostations at Biscayne N.P., the grid is laid down three times for a total area of 13.5 m² (36 photographs).

Before 1991 the placement of the 4.5 m² grid in Carysfort and Looe Reefs was guided by two stakes that defined the corners along one side of the large frame during placement. In 1991 those photostations were improved by the implantation of stainless steel stakes that more precisely and repeatably define the z-axis, thereby bringing all photostations up to the same standard of the four-stake system for future surveys. All data presented here from Carysfort and Looe Reefs were collected from photographs using the two-stake system. The sites in Biscayne N.P. have been based since their establishment upon the four-stake system. The photostations on Looe Reef were surveyed in 1984, 1985, 1986, and 1991; Carysfort Reef photostations were photographed in 1984, 1985, 1986, 1988, and 1991; and Biscayne N.P. photostations were surveyed in 1989, 1990, and 1991.

The 0.50 × 0.75 m camera frame provides a reliable scale within each photograph that is accurate at the level of the frame. In order to create an objective measure of scale at the level of the substrate, in 1991 "scale pins" were added to all photostations: stainless steel rods measuring 1/4" in diameter were driven into 3/16" holes drilled into areas of bare, stable substrate and the distances between pins measured to the nearest 0.5 cm with tree calipers. A set of four pins was established within one frame of each set of 12 photographs.

In order to test whether our photostations are truly representative of the surrounding reef, we have conducted haphazard surveys of the areas in which our photostations are located. Using either a Hasselblad camera mounted on a 4 m² frame, or a Nikonos camera mounted on a 1 m² frame, photographs representing 60 to 100 m² were taken of the reef surrounding each photostation. The corals in these photographs were analyzed and quantified in the same manner as photographs from the photostations. This survey was performed once on each reef site for comparison with the coral composition

of the corresponding photostation for that year, and is not repeated on a yearly basis.

Data analysis

The data collected by the chain transect method consists of an enumeration of coral species and substrate types, their sequence, and their length underneath the chain. Since there is some variation in the placement of the chain under the transect line (due to wave surge, etc.), every transect is counted three times within a one to five day period so that confidence intervals can be calculated for transect results. For each transect we calculate species richness, Shannon-Weiner species diversity, percent cover of coral species, and relative abundance of substrate types. Since we obtain three replicate counts for each transect each year, we are able to statistically compare these values between years. Since the transect length is 25 m, but the distance travelled by the chain over the length of the transect is greater than 25 m, this method also yields information about the three-dimensional topography of the reef, a parameter not directly described by our other sampling methods taken alone.

The photostation surveys are performed using Kodak Tri-X black and white negative film. Each survey is repeated with Kodak Ektachrome color slide film to produce a backup set of color photographs. Each photograph includes the outline of the camera frame, which carries identifying information on the specific reef site, frame number, and date of the photograph (see examples in Fig. 4). Coral colony and frame outlines are traced from prints onto mylar sheets, coral species are identified and assigned a unique colony number that can be followed through time, and the colonies are digitized.

Colony areas in the photographs represent projected surface area: that is, three-dimensional objects projected onto two dimensions in a non-orthographic fashion (objects closer to the camera appear to be larger than objects of the same size but further away from the camera). While orthographic surface area, the result of stereo photo images, would more accurately represent absolute percent cover (Done, 1981),

both methods underestimate the biological surface area of a living coral. This is increasingly the case for colonies with greater three-dimensional relief, especially for a branching coral such as *Acropora palmata* where living tissue on the undersides of branches would not be visible at all, regardless of the photographic system employed. While projected surface area is a reasonable estimate of percent cover, it is true that estimates of change in coral cover by this method will be conservative.

The camera frame defines an area of 0.50×0.75 m at the plane of the frame, but because of the phenomenon of parallax, a photograph actually includes an area greater than 0.50×0.75 m below the plane of the frame down to the sea floor. Adjacent photographs therefore contain overlap. In order to ensure that individual colonies are counted and measured only once, the photographs are corrected for parallax. Areas of overlap in adjacent frames are removed by vertical and horizontal cut lines at the left and bottom edges of each camera frame where they overlap with the right and top edges of adjacent frames.

Cumulative species richness and percent cover are calculated on a frame by frame basis. Percent cover for individual species, cumulative species diversity (based either on the number of colonies of each species or the area covered by each species), and year to year comparisons for percent cover are analyzed on a colony by colony basis.

RESULTS

Adequacy of sampling procedures

One concern is that each photostation should be representative of the reef surrounding it. As an example, relative abundances of coral species for the two reefs in Biscayne N.P. are presented in Table 1. A comparison of results of haphazard surveys and photostation surveys for the same year shows good agreement between relative abundances of species estimated by these two survey techniques. In particular, the dominant species on Ball Buoy Reef, *Acropora palmata*, formed 82.2% of the coral cover in both types of survey. Also, while

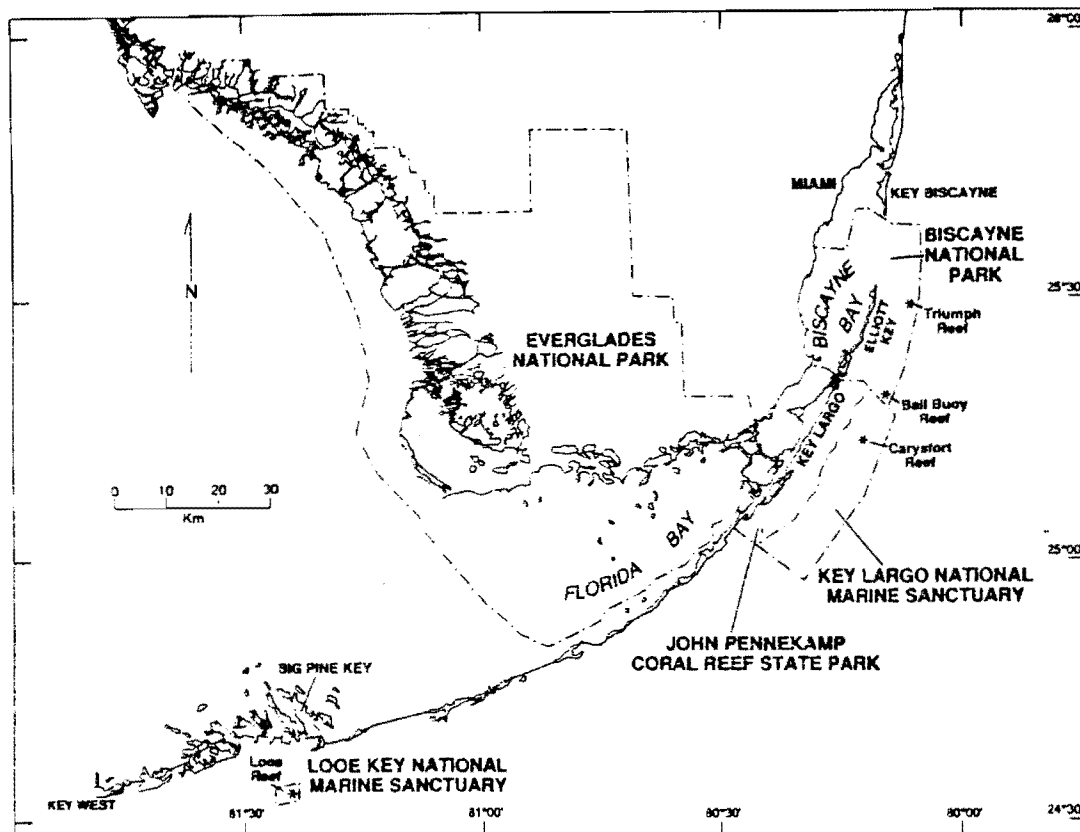


FIG. 1. Reef study sites. The locations and depths of the six photostations in this study are as follows: Biscayne National Park: Ball Buoy Reef (BP01), 3.1 m depth, and Triumph Reef (BP02), 6.0 m; Key Largo National Marine Sanctuary: two sites on Carysfort Reef, (CR01) 4.0 m and (CR02) 14.5 m; Looe Key National Marine Sanctuary: two sites on Looe Reef, (LR01) 5.5 m and (LR02) 7.7 m depth. The sites on Carysfort and Looe Reefs have been monitored since 1984, while the sites in Biscayne National Park have been monitored since 1989.

the photostations in Biscayne N.P. are 13.5 m² in area, or 13.5% of the area covered by each haphazard survey, in both cases the photostations contained 14 of 16, or 87.5% of the species found in the larger 100 m² haphazard surveys.

All photostation comparisons from year to year are made between identical frame positions. Since errors generated by parallax corrections will be the same from year to year for the same frame, measures of *changes* from year to year should be accurate in spite of this potential source of error. Even so, we would like to know how closely our parallax corrections match reality. In order to test the accuracy of these corrections, we compared the distances between scale pins

as they appear in "corrected" photographs to those same distances measured *in situ*. We found that the photographs with cut lines consistently underestimate distances by about 20% at the level of the substrate. Projected surface area of living corals with three-dimensional structure that lies between these two planes overestimates the orthographic surface area of a coral when its surface is close to the frame, and underestimates it when the coral surface is closer to the substrate. Therefore, the difference between orthographic surface area and projected surface area will vary with topographic variation in both the substrate and the coral. No one correction value is accurate for every frame within a photostation, nor even for

TABLE 1. Photostation and haphazard surveys: comparisons of coral relative abundance of coral species. Survey data are from Ball Buoy Reef (BP01) and Triumph Reef (BP02) in Biscayne National Park, 1989. Area covered by each haphazard photo set: 100 m²; area covered by each photostation: 13.5 m².

Species	Ball Buoy Reef		Triumph Reef	
	Rel. abund. haphazard photos	Rel. abund. photostation	Rel. abund. haphazard photos	Rel. abund. photostation
<i>Stephanocoenia michelinii</i>	—	—	3.0	7.0
<i>Acropora palmata</i>	82.2	82.2	—	—
<i>Agaricia agaricites</i>	0.2	0.2	5.0	8.0
<i>Agaricia fragilis</i>	0.1	0.1	—	—
<i>Siderastrea siderea</i>	0.4	1.4	3.0	1.0
<i>Porites porites</i>	0.2	0.2	0.5	1.0
<i>Porites astreoides</i>	5.1	6.8	5.0	9.8
<i>Montastrea cavernosa</i>	0.1	0.7	16.0	18.0
<i>Montastrea annularis</i>	0.2	0.1	18.0	16.0
<i>Favia fragum</i>	0.1	0.1	0.3	0.1
<i>Diploria clivosa</i>	1.9	2.5	5.0	2.0
<i>Diploria labyrinthiformis</i>	—	—	1.0	0.0
<i>Diploria strigosa</i>	0.4	0.1	0.2	0.1
<i>Colpophyllia natans</i>	0.1	0.0	—	—
<i>Dichocoenia stokesi</i>	—	—	1.0	0.0
<i>Dichocoenia stellaris</i>	0.1	0.0	17.0	16.0
<i>Meandrina meandrites</i>	0.1	0.0	16.0	10.0
<i>Mycetophyllia lamarkiana</i>	0.0	0.1	—	—
<i>Millepora alcicornis</i>	2.2	2.3	8.0	9.0
<i>Millepora complanata</i>	6.6	3.2	1.0	2.0
Total	100.0	100.0	100.0	100.0

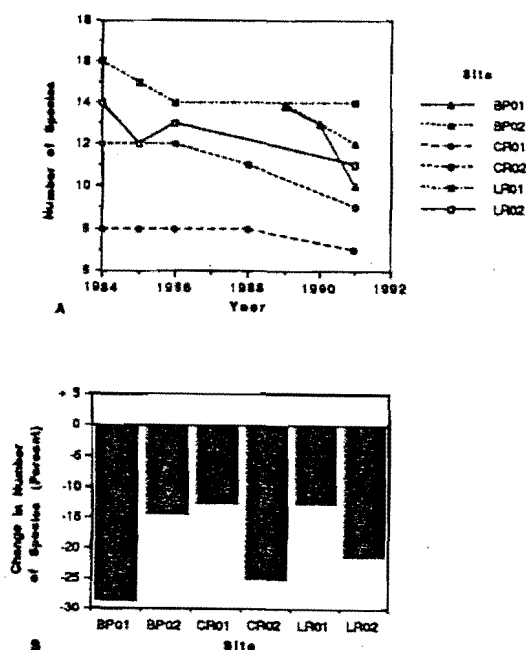


FIG. 2. Changes in species richness: number of species in each photostation during each sampling year (A) and percent change from initial survey year to 1991 (B). The initial survey year was 1989 for BP01 and BP02, and 1984 for all other photostations.

every point within a frame. Given, however, that the errors for individual corals within frames are systematic and will be very similar or identical between years for the same individual corals, measures of relative changes for individual coral colonies will still be relatively accurate. For these reasons, coral area is stated in terms of *projected surface area*. These areas are not to be interpreted as orthographically projected surface area, nor as biological surface area.

Changes in species number

The number of coral and hydrocoral species located in the photostations was lower in 1991 than in the initial year of sampling on every reef (Fig. 2). The rate of loss was usually higher in recent years than in earlier sampling years. The number of species lost varied between one and four; this translates into percentage losses varying between 13% and 29%.

Changes in percent coral cover

Percent cover of living coral declined in five of the six photostations and increased in one photostation between the initial year

of sampling and 1991 (Fig. 3). Between 1989 and 1991, the change in projected surface area of coral in the Biscayne N.P. photostations was +30.2% (BP01) and -7.5% (BP02); in Key Largo N.M.S., coral change between 1984 and 1991 was -32.6% (CR01) and -7.3% (CR02); and in Looe Key N.M.S., coral change between 1984 and 1991 was -43.9% (LR01) and -13.2% (LR02) (Table 2).

Representative pairs of photographs from each reef site, taken in the initial sampling year and in 1991, are presented in Figure 4. The first pair of photographs, labelled "I BNP 5," is frame "5" (of 36) taken in Biscayne N.P. at site one (BP01). Evident in the photographs is increased growth of *Acropora palmata*, characteristic of that photostation alone. However, numerous protruding growths on *A. palmata* branches are also visible in 1991; it is not known whether these growths result from damselfish nips, or represent "tumors" (Peters *et al.*, 1986), or are an infestation of barnacles, polychaetes, or some other invertebrate. Two small bleached areas of *A. palmata* are also visible in the upper portion of frame 5, 1991. In the second pair of photographs, "II BNP 25" (or BP02, frame 25), a small colony of *Stephanocoenia michelinii* is present in the lower right corner in 1989; the dead skeleton of this colony is visible in 1991.

In the third pair of photographs, "I CR 4" (CR01, frame 4), cover of living *A. palmata* decreases greatly from 1984 to 1991. In 1991, bared substrate has been colonized by turf algae, and numerous patches of the

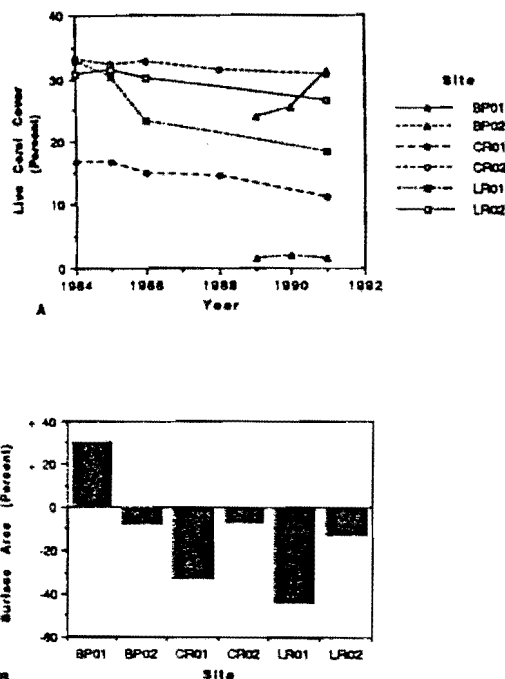


FIG. 3. Changes in percent cover of living coral: cover in each photostation during each sampling year (A) and percent change from initial survey year to 1991 (B). The initial survey year was 1989 for BP01 and BP02, and 1984 for all other photostations.

calcareous alga *Halimeda* are present. A light-colored zoanthid colony (*Palythoa*) is visible in the upper right of both frames. The primary event apparent in the fourth pair of photographs, "II CR 16" (CR02, frame 16), is partial mortality of a large colony of *Montastrea annularis*; photographs from intervening years show that the mor-

TABLE 2. Changes in projected surface area: initial survey year to 1991. For Carysfort Reef and Looe Reef sites, initial survey year was 1984; photostation area was 9.0 m². For Triumph Reef and Ball Buoy Reef, initial survey year was 1989; photostation area was 13.5 m². Photostation designations are shown in parentheses. Wilcoxon Signed Rank Tests are the result of colony by colony comparisons between the initial year and 1991. Total percent cover may be calculated as the ratio of total projected surface area of living coral to the photostation area.

Reef site	Projected surf. area initial year (cm ²)	Projected surf. area 1991 (cm ²)	Change in projected surf. area (cm ²)	Percent change in projected surf. area	Wilcoxon signed rank test P value
*Ball Buoy Reef (BP01)	32,291.3	42,029.3	9,737.9	30.2%	0.0003
Triumph Reef (BP02)	2,224.5	2,056.8	-167.7	-7.5%	0.1845
† Carysfort Reef (CR01)	14,945.9	10,071.4	-4,874.5	-32.6%	0.0581
Carysfort Reef (CR02)	29,843.2	27,676.0	-2,167.1	-7.3%	0.7670
*Looe Reef (LR01)	29,683.0	16,644.8	-13,038.2	-43.9%	0.0001
*Looe Reef (LR02)	27,601.4	23,955.3	-3,646.1	-13.2%	0.0037

* $P \leq 0.05$; statistically significant at the 0.05 level.

† $0.05 < P \leq 0.06$.



FIG. 4. Representative pairs of frames from each photostation: BP01, BP02, CR01 (first plate); CR02, LR01, and LR02 (second plate). The frame dimensions are 0.50 m $\times$ 0.75 m; dates are indicated within each photograph.

tality occurred between 1988 and 1991. This colony "bleached" in 1987, "recovered" in 1988, but suffered partial mortality by 1991 (Fitt *et al.*, 1993).

The fifth pair of photographs, "I LR 3" (LR01, frame 3), shows the complete disappearance of a colony of *Acropora pal-*

mata; the event occurred between 1986 and 1991. Colonies of *Montastrea annularis* and *M. cavernosa* that had been partially hidden by overtopping are visible in the 1991 photograph. The last pair of photographs, "II LR 15" (LR02, frame 15), shows partial mortality of a large *M. cavernosa* colony,



FIG. 4. Continued.

which occurred between 1986 and 1991. A metal guide pin is visible in 1991; this pin was placed in 1984 into a small dead area of the coral head, but the size of the dead area remained stable through 1986, indicating that the placement of the pin was not the cause of mortality.

The map of the photostation with the greatest amount of coral loss (LR01) indicates heavy loss of the elkhorn coral, *Acropora palmata* (Fig. 5), while growth in the only photostation to exhibit overall increase in percent cover (BP01) was due primarily to growth of this same species.

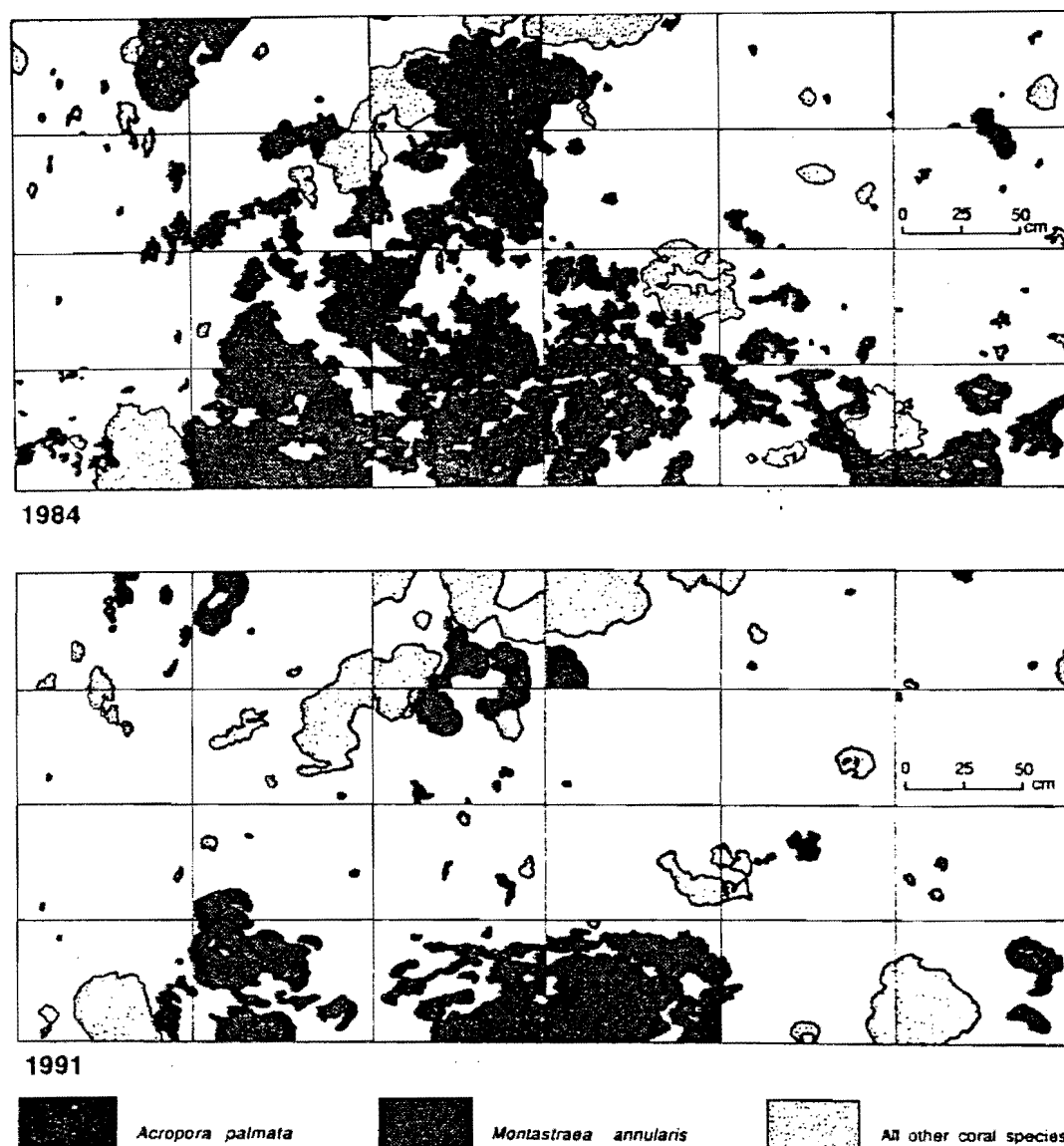


FIG. 5. Montage of projected surface areas of living coral in each frame of photostation LR01, 1984 (top) and 1991 (bottom).

Additional information from chain transects

The increase in projected surface area of *Acropora palmata* on BP01 requires examination in the context of additional information yielded by the chain transects for that site. As a measure of three-dimensional complexity, leaf area index for *A. palmata* was calculated and averaged for each year of the line transect survey on BP01 (Fig. 6). Leaf area index is calculated as the mean

number of links covering living *A. palmata* tissue divided by the total number of chain links counted under meters containing *A. palmata* colonies. There was a significant decrease in leaf area index between 1989 and 1991, indicating a decrease in three-dimensional complexity during that period. Thus, while projected surface area of *A. palmata* increased on BP01 from 1989 to 1991 (Fig. 3), the leaf area index declined (Fig. 6), demonstrating that understory branches

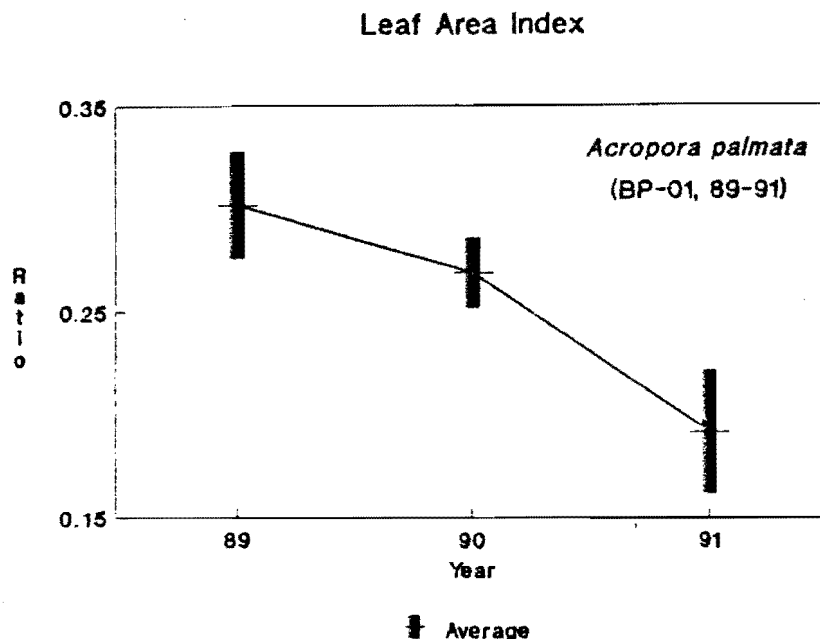


FIG. 6. Leaf area index of *Acropora palmata*, from chain transects in site BP01, 1989 and 1991. The calculation of leaf area index is discussed in text. Error bars represent 95% confidence intervals around the mean for each year.

(those invisible to the camera) were lost. The total number of links covering *A. palmata* did not change during the three surveys, further demonstrating that as the canopy branches grew, the understory branches thinned. Casual observations in 1991 of fragments and broken branches of *A. palmata* lying on the seafloor support this finding.

Changes in size frequency distribution

Plots of the size frequency of selected species from Carysfort and Looe Reefs (Fig. 7) show consistent decreases in the number of large colonies of the most common species between 1984 and 1991. Total projected surface area at these sites of the species figured (*Acropora palmata*, *Montastrea annularis*, and *M. cavernosa*) also declined over this period. In some cases, the number of small colonies of a species increased (Fig. 7C, D), owing not to recruitment but to the death of areas within large colonies that resulted in several isolated smaller colonies. A species by species analysis of changes occurring in our study sites and the detectable events associated with these changes

will be published elsewhere (Meier and Porter, in preparation).

Inverse relationship between algae and Diadema

A final pertinent observation includes the inverse relationship observed between macroalgae, particularly in the genera *Halimeda* and *Dictyota*, and the long-spined sea urchin *Diadema antillarum*. Sea urchins were absent from the photostations and chain transects in Biscayne N.P. in 1989 (0.0/m²), while macroalgae abundance was relatively high, having a mean percent cover of 13.82 ± 1.06 (SD). In 1990, sea urchin density increased to 0.4/m² and mean percent cover of macroalgae decreased significantly, to 4.24 ± 1.22 . Finally, in 1991 sea urchins were again absent (0.0/m²), with a concomitant increase in macroalgal abundance, to 15.03 ± 1.32 percent cover.

DISCUSSION

Loss of species diversity

Changes in species number consistently indicate a loss of species diversity in each of the six reefs studied. In our plots, rare species were much more likely to suffer local

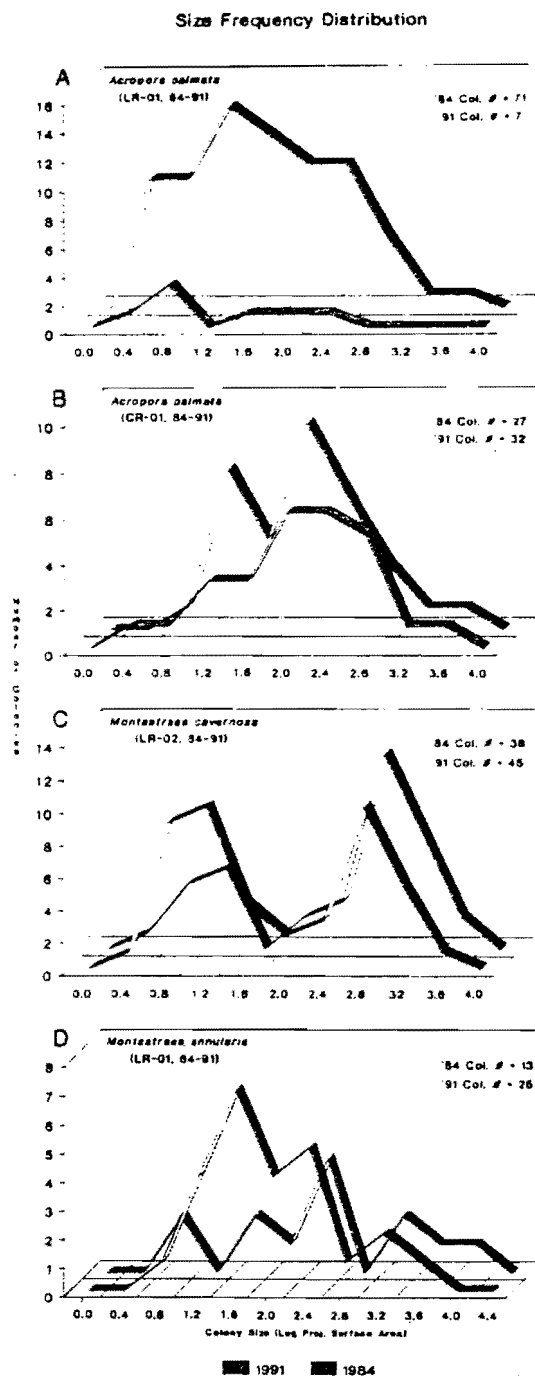


FIG. 7. Size frequency distributions of selected common species, 1984 and 1991. Species, photostation, and number of colonies are designated. No size class data have been omitted in the size frequency ribbon-histograms: straight lines indicate linearity in the fit of the data.

extinction than common species. Since the species lost tended to be those that were relatively less abundant to begin with, their loss did not have a strong impact on total changes in percent cover. Superficially, this finding would appear to agree with models of reef development (Loya, 1976; Maguire and Porter, 1977; Connell, 1978) that predict a loss of rare species as community structure is increasingly dominated by branching corals that overtop and shade out competing understory species. This pattern was observed on shallow water reefs in Jamaica prior to Hurricane Allen (Porter *et al.*, 1981). The problem with this theoretical analysis when applied to the Florida data is that the branching corals were dying at the same time as the rare species were lost (Figs. 2, 4).

Loss of coral abundance

As Figure 3 indicates, shallow water reefs are capable of rapid increases in coral cover. The acroporid reef studied in Biscayne N.P. increased by an average of 15% of its initial abundance each year for the two year duration of the survey. The large losses identified instead for the other two acroporid reefs in the study are in striking contrast to this measured growth potential. The shallow reef surveyed on Looe Key lost 44% of its cover (Fig. 5); its counterpart on Carysfort lost 33% (Table 2). These kinds of losses among the branching coral community are normally associated with hurricanes (Stoddart, 1974; Porter *et al.*, 1981; Rogers *et al.*, 1982; Edmunds and Witman, 1991), but South Florida has been without a direct hit from a major hurricane for more than 26 years. Shinn (1989) points out that the usual frequency for hurricanes in the Keys is on average once every six to seven years. Two minor storms passed by the Florida Keys in 1985, Elena in September and Katie in November, and could have contributed to the elevated loss rates observed between 1985 and 1986. The photographs taken in 1986, however, reveal the presence of dead branches of *Acropora palmata* still standing, but without living tissue on them. The photographs also reveal living *A. palmata* that persisted through 1986 unbroken, including some

large, highly branched colonies. Both of these observations suggest that storm damage was not the cause for coral loss between 1985 and 1986.

At first glance, the loss of understory branches from *Acropora palmata* in Biscayne N.P. (Fig. 6) might seem like the process of "self thinning" observed in plant populations (Harper, 1977). This process, however, has not been identified for calcium carbonate coral branches, and further, unlike trees, large coral branches "dropped" in this fashion could theoretically reattach and regrow, thus reappearing as new coral under the line transect even if invisible to an overhead camera. The line transect counts demonstrate definitively that this did not happen (Fig. 6).

Decline of both adults and juveniles

Changes in the size frequency distributions of colonies of *Acropora palmata* in Florida (Fig. 7A, B) show a decline in both large and small colonies between 1984 and 1991. In the seven years of the study, we have not identified any sexual recruitment of *A. palmata* to the population.

Like *A. palmata*, the head corals *Montastrea annularis* and *M. cavernosa* occur at depths strongly influenced by hurricanes (Woodley *et al.*, 1981; Edmunds and Witman, 1991), but since we did not record any major storms during the study period, the loss of these head corals also cannot be attributed to such physical disturbance. As with *Acropora*, there has been a steady diminution of the number of large colonies, but unlike *Acropora*, there has been an increase in the number of smaller sized colonies (Fig. 7C, D).

Increasing colony number was due entirely to "fission" events and partial mortality among larger coral colonies rather than to the appearance of sexual recruits. Observations of photographs in the sequence of sampling years indicate that most smaller colonies resulting from the breakup of larger colonies continued to decrease in size and eventually die. As with *Acropora*, no sexual recruits to the population were identified for either of the *Montastrea* species in any of our photostations.

Replacement of coral by algae

When living coral is lost from the photostations, it is replaced by substrates dominated by turf algae (Fig. 4). We have no evidence that the algae killed the coral, but rather assume that bared substrate is actively colonized by turf algae. Colonies of the blue-green alga *Lyngbya* were also present in 1991; this is the first time *Lyngbya* has been observed in any of our photostations. Black band disease, caused by another cyanobacterium, *Phormidium corallyticum* (Antonius, 1981a; Rutzler and Santavy, 1983), has also been observed in our photostations, particularly infecting *Montastrea annularis* and *M. cavernosa* colonies. In only one case was recovery from black band disease observed; in all other cases, the disease resulted in complete or partial mortality of the affected colony. Black band was much more prevalent on the southern reefs than on the northern reefs.

CONCLUSIONS AND RECOMMENDATIONS

Five of six reefs monitored declined in percent cover of living coral over the sampling period. All reefs declined in species number during this time. In some cases these losses were very high: the worst losses were 33% and 44% declines in coral cover over a seven-year period, and 25% and 29% declines in combined number of scleractinian and hydrocoral species over a seven- and two-year period, respectively. These rates of loss are obviously not sustainable over a long time period.

All research sites were located in protected areas: one national park and two national marine sanctuaries. That coral losses of the magnitude presented here occurred in protected areas indicates that current methods of protection do not prevent some significant sources of coral mortality. Even the recent expansion of the number of protected reefs with the establishment of the Florida Keys National Marine Sanctuary, for example, is not in itself adequate to halt the declines observed. Arguments for declines that occur with geological periodicity are not adequate to account for the rapid rates of decline mea-

sured here. Clearly, research is needed specifically to determine the cause or causes of coral decline. Such research programs should address: (1) the condition of corals on other reefs; (2) the role of visitor impact; (3) whether nutrient enrichment is occurring, and if so, the sources of the nutrients and their effects; (4) factors promoting infection and spread of coral disease; and (5) the status of algae and herbivores, including the sea urchin *Diadema antillarum*, other invertebrate grazers, and herbivorous fish.

The recent widespread die-off of the long-spined sea urchin, *Diadema antillarum*, (Lessios *et al.*, 1984) as well as anecdotal observations of decreases in herbivorous fish abundance, may be related to increased algal abundance that could compete with corals and their larvae for space (Birkeland, 1977; Sammarco, 1980; Carpenter, 1985). Incidents of bleaching, a response of corals to elevated sea surface temperatures, have been recorded from the Florida Keys during the past decade (including 1983, 1987, 1989, 1990, and 1991) (B. Causey, personal communication), and were occasionally observed in our photographs (Fig. 4, first plate, top); these occurrences did not necessarily result in death of the coral. Black band disease has also been observed in our photographs; this disease usually resulted in complete or partial mortality of the affected coral; in only one instance was recovery of *Montastrea annularis* from black band disease observed. Environmental stress or physical damage to corals may increase a colony's susceptibility to this disease.

Direct and indirect human impact may also be a factor in coral decline (Grigg and Dollar, 1990). Boat groundings, anchor damage, and diver damage to corals are possible sources of coral mortality, but are all controlled, at least to some extent, in our study sites by law enforcement officers and park rangers. Sources of indirect human impact resulting from development and use of the Keys include possible siltation, sediment resuspension pollution from harbors and boats, and potential problems of landfill containment and sewage disposal. The hypothesis of eutrophication (Lapointe and Clarke, 1992) as a source of direct and indirect impact on coral and algal populations

is certainly viable, and deserving of further study.

There is a need to monitor these reefs on multiple scales of both time and space. The processes requiring investigation occur on the level of the individual, the population, the community, the ecosystem, and the landscape; these processes have their range of variation on different temporal and spatial scales, and so sampling must occur on multiple temporal and spatial scales. In this case, one needs data of both fine-grained resolution and large scale, and the monitoring program must provide means of acquiring both if the ability to answer the most critical questions is not to be lost. Ogden *et al.* (1992) describe additional qualities desirable in an effective coral reef monitoring program. Currently even modest monitoring projects are grossly underfunded, and the long-term support essential to the success of a monitoring program is presently not within the operational time frame of funding agencies.

The current state of knowledge is inadequate to determine the long-term effects of the changes in the coral community observed in this study. Recovery times for these species at these locations are not known; neither are the community dynamics underlying processes of change and potential recovery. Though one expects that management decisions take into account information provided by studies such as this, we caution against overinterpretation of our results for management purposes: we have not measured the rates of change on other reefs, and we do not know definitively what causes are responsible for the present changes observed on these study reefs.

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NOTE ADDED IN PROOF

On August 24, 1992, Hurricane Andrew passed through Biscayne National Park, producing some damage to stations BP01 and BP02 in the Park, and to CR01 in the Key Largo National Marine Sanctuary. An analysis of the effects of Hurricane Andrew will be presented elsewhere, but we note here that the loss in percent cover of living coral on some reefs over a period of seven years was much greater than losses experienced by reefs as a result of this class 4 hurricane. Every survey stake and eyepin in our photostations survived intact.

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