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Quantification of Loss and Change in Floridian Reef Coral Populations

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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 Criens, 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
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 ¼" in diameter were driven into ⅛" 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 $0.50 \times 0.75$ m at the plane of the frame, but because of the phenomenon of parallax, a photograph actually includes an area greater than $0.50 \times 0.75$ 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
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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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Ball Buoy Reef</th>
<th>Triumph Reef</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rel. abund.</td>
<td>Rel. abund.</td>
</tr>
<tr>
<td></td>
<td>haphazard photos</td>
<td>photostation</td>
</tr>
<tr>
<td>Stephanocenia michelini</td>
<td>3.0</td>
<td>7.0</td>
</tr>
<tr>
<td>Acropora palmata</td>
<td>82.2</td>
<td>82.2</td>
</tr>
<tr>
<td>Agaricia agaricites</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Agaricia fragilis</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Siderastrea siderea</td>
<td>0.4</td>
<td>1.4</td>
</tr>
<tr>
<td>Porites porites</td>
<td>0.2</td>
<td>0.2</td>
</tr>
<tr>
<td>Porites astreoides</td>
<td>5.1</td>
<td>6.8</td>
</tr>
<tr>
<td>Montastrea cavernosa</td>
<td>0.1</td>
<td>0.7</td>
</tr>
<tr>
<td>Montastrea annularis</td>
<td>0.2</td>
<td>0.1</td>
</tr>
<tr>
<td>Favia fragum</td>
<td>0.1</td>
<td>0.1</td>
</tr>
<tr>
<td>Diploria clivosa</td>
<td>1.9</td>
<td>2.5</td>
</tr>
<tr>
<td>Diploria labyrinthiformis</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Diploria strigosa</td>
<td>0.4</td>
<td>0.1</td>
</tr>
<tr>
<td>Colophyllia natans</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Dichocenia stokesi</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Dichocenia stellaris</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Meandrina meandrites</td>
<td>0.1</td>
<td>0.0</td>
</tr>
<tr>
<td>Mycetophyllia lamarkiana</td>
<td>0.0</td>
<td>0.1</td>
</tr>
<tr>
<td>Millepora alcicornis</td>
<td>2.2</td>
<td>2.3</td>
</tr>
<tr>
<td>Millepora complanata</td>
<td>6.6</td>
<td>3.2</td>
</tr>
<tr>
<td>Total</td>
<td>100.0</td>
<td>100.0</td>
</tr>
</tbody>
</table>

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 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.

<table>
<thead>
<tr>
<th>Reef site</th>
<th>Projected surf. area initial year (cm²)</th>
<th>Projected surf. area 1991 (cm²)</th>
<th>Change in projected surf. area (cm²)</th>
<th>Percent change in projected surf. area (%)</th>
<th>Wilcoxon signed rank test P value</th>
</tr>
</thead>
<tbody>
<tr>
<td>*Ball Buoy Reef (BP01)</td>
<td>32,291.3</td>
<td>42,029.3</td>
<td>9,737.9</td>
<td>30.2%</td>
<td>0.0003</td>
</tr>
<tr>
<td>Triumph Reef (BP02)</td>
<td>2,224.5</td>
<td>2,056.8</td>
<td>−167.7</td>
<td>−7.5%</td>
<td>0.1845</td>
</tr>
<tr>
<td>† Carysfort Reef (CR01)</td>
<td>14,945.9</td>
<td>10,071.4</td>
<td>−4,874.5</td>
<td>−32.6%</td>
<td>0.0581</td>
</tr>
<tr>
<td>Carysfort Reef (CR02)</td>
<td>29,843.2</td>
<td>27,676.0</td>
<td>−2,167.1</td>
<td>−7.3%</td>
<td>0.7670</td>
</tr>
<tr>
<td>*Looe Reef (LR01)</td>
<td>29,683.0</td>
<td>16,644.8</td>
<td>−13,038.2</td>
<td>−43.9%</td>
<td>0.0001</td>
</tr>
<tr>
<td>*Looe Reef (LR02)</td>
<td>27,601.4</td>
<td>23,955.3</td>
<td>−3,646.1</td>
<td>−13.2%</td>
<td>0.0037</td>
</tr>
</tbody>
</table>

* P ≤ 0.05; statistically significant at the 0.05 level.
† 0.05 < P ≤ 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 × 0.75 m; dates are indicated within each photograph.


The fifth pair of photographs, “I LR 3” (LR01, frame 3), shows the complete disappearance of a colony of *Acropora palma*; 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,
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.
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
Leaf Area Index

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.

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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); 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 nutrification (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 photo-stations survived intact.

REFERENCES