

Changes in the coral reefs of San Blas, Caribbean Panama: 1983 to 1990

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Abstract. Between 1983–1990 large changes in abundances of corals and macroalgae occurred on shallow (1–5 m) lagoonal reefs in the San Blas Islands of Panama. In 1983 these reefs were dominated by the vertical plate forms of the coral genera *Agaricia* and *Millepora*. By 1990 we observed the following major changes: (1) loss of approximately one-half of the initial live coral cover, primarily during 1983–1986, and almost completely due to a decline in the abundance of *Agaricia*. Corals only occupied 12–26% of the reef area by 1990. (2) Macroalgae (mostly *Dictyota* and *Halimeda*) increased from ~2% cover in 1983 to 28% cover in 1990. (3) Microalgal cover increased two to ten-fold between 1983 and 1986, then declined to 50% greater than the initial values by 1990. There are at least three contributors to these changes in the benthic community: (1) a coral bleaching event in 1983, which disproportionately affected *Agaricia*; (2) the mass mortality of *Diadema antillarum* in 1983, which led to decreases in grazing pressure on algae; and (3) possible increases in sediment and nutrient loads due to runoff from deforested mountainsides. Temporal patterns and observations of interactions suggest that the decrease in *Diadema* herbivory is a major factor in this shift in coral and algal populations.

storms (hurricanes/typhoons), coral bleaching events, fishing/mining, sedimentation and nutrient enrichment (reviewed in Wells 1988). Other disturbances are restricted to particular regions: outbreaks of the predatory starfish *Acanthaster planci* in the tropical Pacific (Moran 1986), and mass mortality in the sea urchin *Diadema antillarum* in the tropical western Atlantic (Lessios et al. 1984b). These disturbances have led to a number of reports that coral reefs are in decline, both globally and in the tropical Western Atlantic in particular (e.g. Hallock et al. 1993). However, relatively few long-term, quantitative studies on coral reefs in this region have been published, so the nature and extent of changes in the ecological structure of reefs have been difficult to evaluate.

Here we present data on changes in major components of the benthic community structure on shallow patch reefs at Punta San Blas on the Caribbean coast of Panama between 1983–1990. We address the following questions: (1) how have abundances of corals and algae changed; (2) what factors may be responsible for observed changes; and (3) how do changes in the reefs at Punta de San Blas compare with other reefs of the tropical western Atlantic?

Materials and methods

This study was done along the Caribbean coast of Panama, at Punta de San Blas (9°34'N; 78°58'W). Reef names and numbers used here follow Robertson (1987). We studied five patch reefs that were dominated by vertical plate forms of the scleractinian coral *Agaricia* (*A. agaricites* and *A. tenuifolia*) and the hydrocoral *Millepora* (*M. complanata* and *M. alcicornis*). Three of the reefs (Point 23, Wichubhuala 24, Wichubhuala 14) were shallow (<2 m depth), one (Porvenir 26N) was deeper (5 m depth) and one (Wichubhuala 17) was mid-depth (3–4 m depth). These reefs were typical of patch reefs of 0–5 m depth in the 10 km², semi-enclosed lagoon formed by reefs that fringe the shallow submarine extension of Punta de San Blas. Deeper reefs in this area are dominated by an entirely different set of coral species and associated biota.

Our study began following the die-off of the ecologically important sea urchin, *Diadema antillarum*, in early 1983 (Lessios et al. 1984a, b), which resulted in the death of 95% of the San Blas population

Introduction

The ecological stability of coral reefs has increasingly become a subject of concern as various types of chronic and catastrophic disturbances have affected reefs around the globe (Ginsburg and Glynn 1994; Hughes 1994a; Sebens 1994). Some natural and human-caused disturbances occur in all the major tropical oceanic regions: cyclonic

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(Lessios et al. 1984a). The reefs discussed here were used as controls and "no-*Diadema*" treatments in an experimental study of sea urchin-damselfish interactions (Shulman and Robertson, in preparation). On the "no-*Diadema*" reefs (Wichubhuala 14, Porvenir 26N), *D. antillarum* were removed every 1–6 months throughout the period of this study. No experimental manipulations were performed on the control reefs (Point 23, Wichubhuala 24, Wichubhuala 17). The numbers of *D. antillarum* on the control and "no-*Diadema*" reefs were very low and did not differ significantly from one another during the study (t-tests; $P > .05$). Therefore, the results from all five reefs were grouped and treated as unmanipulated areas.

Permanent quadrats were established on four reefs (Wichubhuala 14, Wichubhuala 24, Porvenir 26N, and Point 23) in June 1983; study was begun on a fifth reef (Wichubhuala 17) in December 1985. The reefs were then censused about every 6 months until the end of 1987. Three of the five reefs were censused again in September 1988 and June 1990. Monitoring of Wichubhuala 14 and Porvenir 26N was discontinued after 1987 due to experimental manipulations and a ship grounding.

On each of the five study reefs, we established 5 permanent, 2m × 2m quadrats. Quadrat sites were located to (1) minimize variation in depth; (2) avoid the edges of the patch reefs; and (3) maintain the maximum distance (range 2–20 m) possible between quadrats. Within each quadrat, the following data were collected:

1. Point-intercept transect: the sessile animal or alga occurring under each of 100 randomly located points along transect lines placed along the diagonals of the quadrat was identified. Cnidarians were identified to genus or species, other animals (mainly sponges) were primarily identified to phylum. Small, filamentous algae were grouped into the category "microalgae", larger, erect fleshy algae (e.g. *Halimeda*, *Dictyota*) were categorized as "macroalgae", while coral-line algae were classified as articulated or crustose.

2. Measurements of macroalgae: each individual or clump of macroalgae with a diameter greater than 2 cm was identified to genus and the longest diameter and its perpendicular measured. A formula for the area of an ellipse was used to estimate areal coverage.

Results

Changes in coral cover

In June, 1983, total coral cover on the 3 shallow reefs ranged from 43–45% (Fig. 1A). In the following 2 to 3.5 y, coral cover declined to 12–23% on the shallow reefs, a decrease of ~10% cover per y. Coral cover then appeared to stabilize at these lower values. On the deeper reef, coral cover was initially 31%, but decreased over the following 3.5 years to about 15% (a rate of decline of ~5%/y). When the mid-depth reef was first censused in December, 1985, coral cover was close to 35%; it showed little change until the final year, when it dropped to 26%.

Agaricia (*A. agaricites* and *A. tenuifolia*) is the most abundant coral genus on these reefs, having an initial cover of 29–35% on the shallow reefs and 22% on the deeper reef in June 1983 (Fig. 1B). This genus showed dramatic declines in abundance: by the end of 1987, cover was 6–10% on the shallow reefs and 8% on the deeper reef. Thus, *Agaricia* was reduced to one-quarter (shallow-reefs) and one-third (deeper reef) of its original abundance. The mid-depth reef had 25% cover by *Agaricia* in late 1985 and this value did not change significantly through 1990.

Millepora (mainly *M. complanata*) is the second most common coral (stony hydrozoan) genus (Fig. 1C). *Millepora* showed no change in abundance on the shallow reefs, a slight decline on the deeper reef, and a marked drop

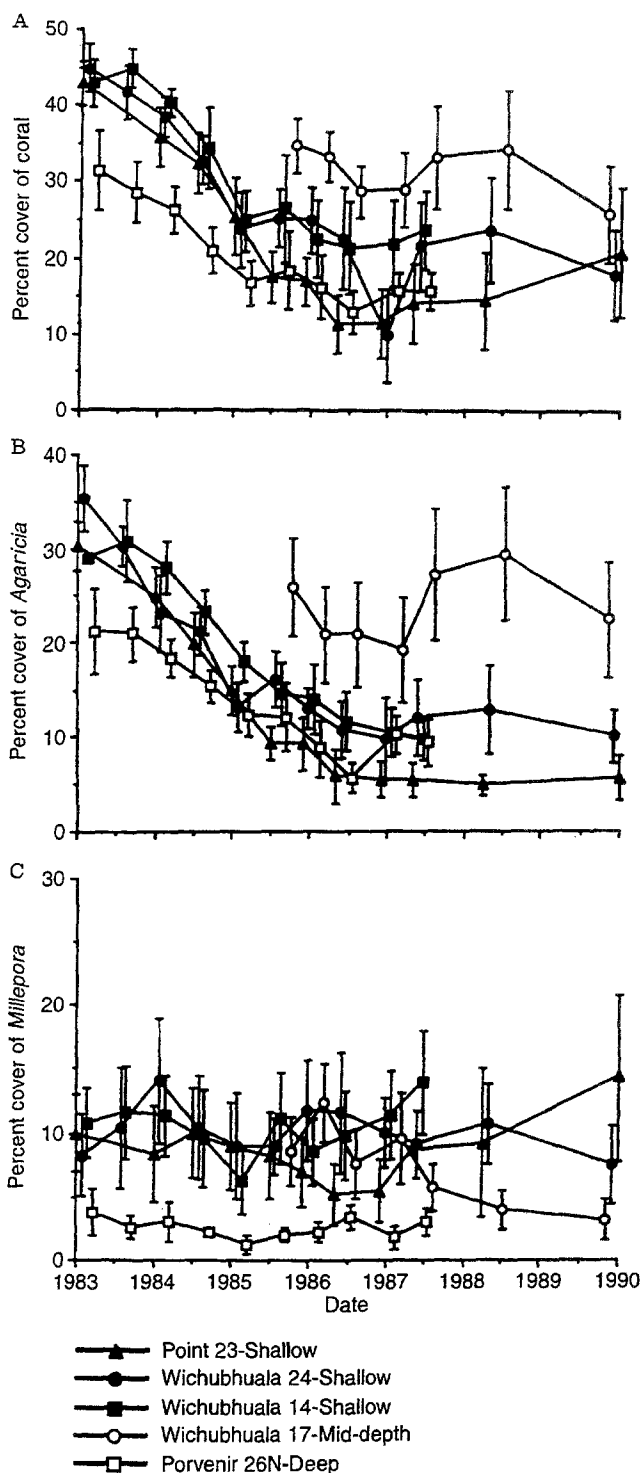


Fig. 1A–C. Change in percent cover ($\bar{X} \pm 1SE$) of corals on five monitored reefs during the period June, 1983 through June, 1990. A Total percent cover for all corals; B percent cover of *Agaricia* spp.; C percent cover of *Millepora* spp. Closed symbols represent the three shallow (<2 m depth) reefs; the open circle symbol represents the mid-depth (3–4 m depth) reef; and the open square symbol represents the deeper (5 m depth) reef

from 9% coverage in 1985 to 3% in 1990 on the mid-depth reef.

A rarer coral, *Porites furcata*, declined in percent cover on both shallow and deeper reefs. Initially having 1–1.6%

cover on shallow reefs and 3% cover on the deeper reef, it declined to 0–0.6% and 0.6% respectively. A congener, *Porites astreoides*, was found only on the shallow reefs. On two of these reefs it declined from an initial abundance of 1.4% cover to less than 0.5% cover.

Changes in algal abundance

In 1983, fleshy (non-coralline) algal cover on the shallow reefs was relatively low (11–24%). It rose through 1988 to maximums of 32–70% (Fig. 2A). On one of these reefs, fleshy algal coverage declined from a maximum of 70% down to 50% in 1987–1990. The deeper reef showed a similar pattern: initially low (5%), rising to a very high value (58%) in 1987 and then declining (to 39%) during the last census in 1990. The mid-depth reef had a 17% coverage of fleshy algae during the first census in late 1985; fleshy algal coverage then rose to a value of 54% in 1990.

The increases in fleshy algal cover were due to increases in both micro- and macroalgae. The percent cover of microalgae increased about 50% on each of the shallow reefs; these increases, which occurred over the first 3 to 3.5 years, were then followed by declines on two of the three shallow reefs (Fig. 2B). The deeper reef showed a more dramatic increase in microalgae. In 1983, microalgae covered only 5% of the area, but rose to a high of 50% before declining to 39% in the last census in 1987 (Fig. 2B). Microalgae increased in coverage by 125% on the mid-depth reef between 1985 and 1990.

Macroalgal abundances showed marked increases on all reefs during the study (Fig. 2C). In 1983, macroalgae covered less than 2% of the area of any reef. On the shallow reefs, macroalgal abundances increased fairly steadily to 10–28% by 1990. On the deeper reef, macroalgal abundance also increased, but to a lesser extent (maximum of 8%). Macroalgal coverage on the mid-depth reef increased from 10% in 1985 to 36% in 1990.

Increases in micro- and macroalgae were not accompanied by any consistent changes in the percent cover of encrusting coralline algae. Abundances varied throughout the 7 year census period, but did not show any upward or downward trend.

The two most common genera of fleshy macroalgae on these reefs were *Dictyota* and *Halimeda*; together they accounted for about 50% percent of the total area covered by macroalgae. Both genera increased over time (Fig. 3A, B). *Dictyota*, initially very rare, rose to a maximum cover of 1–10% on the shallow reefs and 2% on the deeper reef (Porvenir 26N). Percent cover of *Dictyota* remained high through to the end of the study; however, on the deeper reef, the last census showed a decline to near the original value. *Dictyota* was relatively rare on the mid-depth reef throughout the study.

Both the initial abundances and patterns of increase of *Halimeda* differed enormously among reefs (Fig. 3B). On two shallow reefs with initial cover < 0.5%, abundance rose to highs of 1.3–3% cover. On one of these reefs the *Halimeda* cover rose continuously throughout the study, while the other reef only showed an increase in the last two years. On the third shallow reef, an initially high *Halimeda*

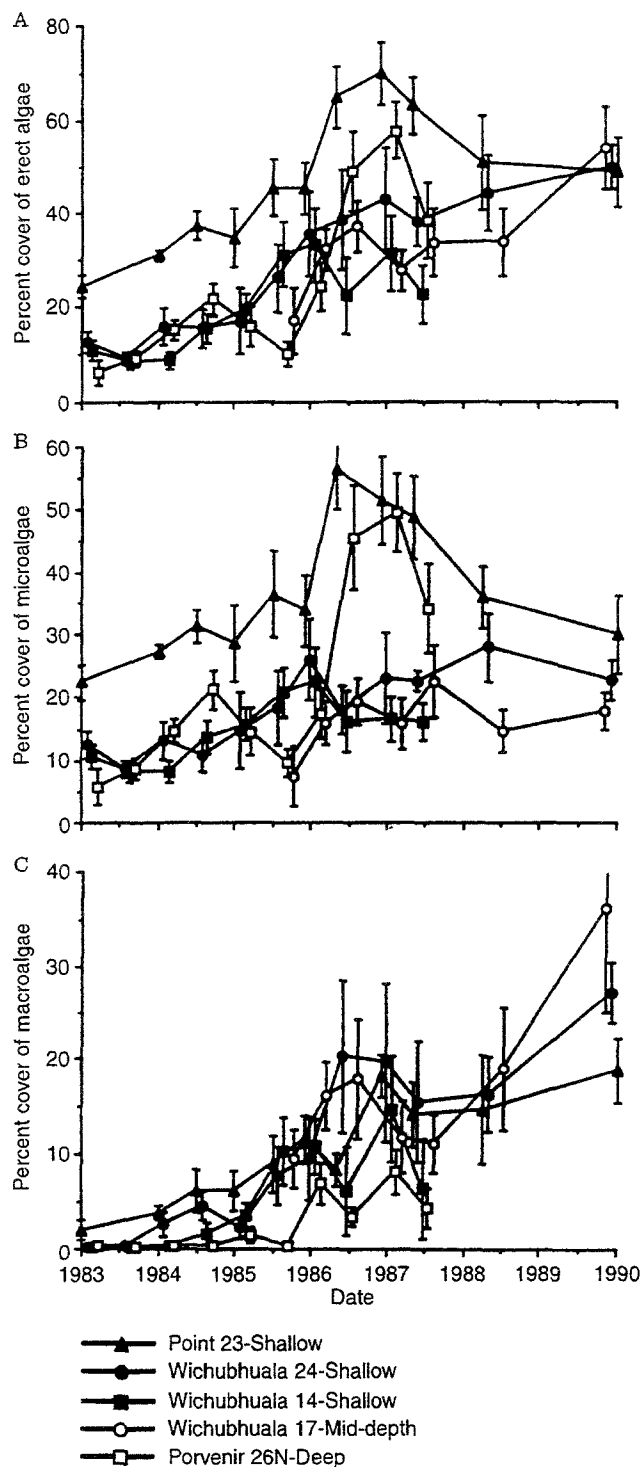


Fig. 2A–C. Change in percent cover ($\bar{X} \pm 1$ SE) of erect (non-encrusting) algae on five monitored reefs during the period June, 1983 through June, 1990. A Total percent cover for all erect algae; B percent cover of microalgae; C percent cover of macroalgae

density (3% cover) tripled over the following 7 years. *Halimeda* was virtually absent from the deeper reef in 1983; by 1988 it had a cover of 0.3%, most gained in the final two years. *Halimeda* showed a very large increase on the mid-depth reef, increasing by over a factor of 10 between 1985 and 1990.

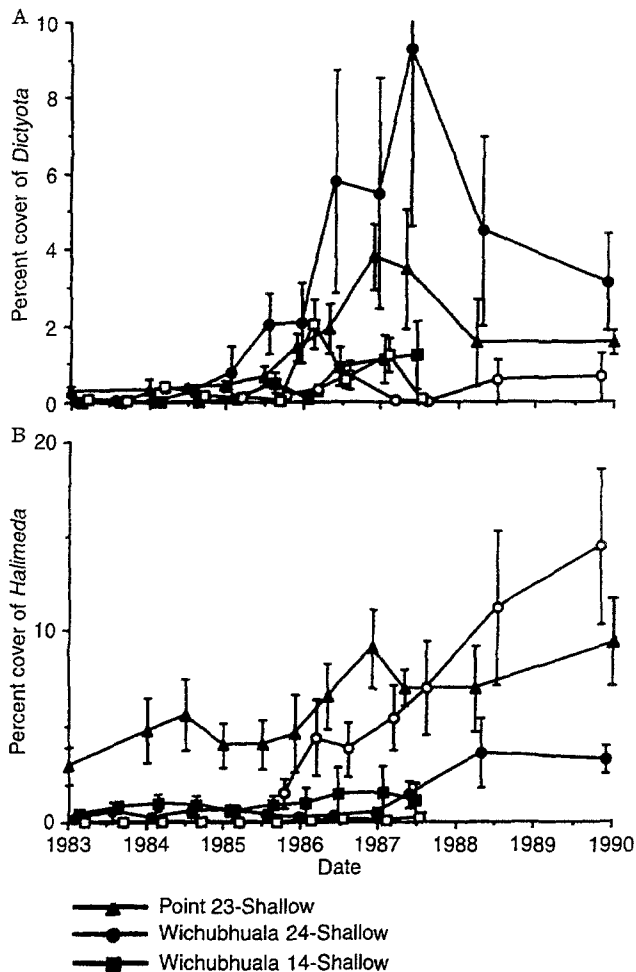


Fig. 3A,B. Change in percent cover ($\bar{X} \pm 1SE$) of two genera of macroalgae on five monitored reefs during the period June, 1983 through June, 1990. A Percent cover of *Dictyota*; B percent cover of *Halimeda*.

Although both *Dictyota* and *Halimeda* generally increased in abundance throughout the study (Fig. 3A, B), the relative abundances (percentage of all macroalgae) of each did not remain the same. On the shallow reefs, the relative abundance of *Dictyota* increased from initial values of 0–10% to highs of 30–60%. Most of this increase took place during 1985–1987, and was followed by a partial decrease to final values of 20–30%. *Halimeda*, initially highly dominant (20–90% initial relative abundance) showed a decline to 10–40% in relative abundance, especially through the middle years, and then regained some of its dominance in the last two years. The deeper reef exhibited quite a different pattern. The relative abundance of *Dictyota* showed two cycles of increase and decrease, with an overall decline in relative abundance from 60% in 1983 to 20% in 1987. *Halimeda*, initially absent, increased in relative abundance to a high of 30% by the end of the study. The mid-depth reef showed a pattern similar to the deeper reef: a decline in the relative abundance of *Dictyota* (which was scarce on this reef throughout the study) and a dramatic increase in dominance of *Halimeda*.

Articulated coralline algae were initially rare on all of the reefs but increased enormously to about 5% on one of the shallow reefs (Point 23). The other reefs showed changes in abundance over time, but with no clear trend. Other macroalgal taxa were either too rare or too spatially patchy to adequately analyze patterns of increase or decrease.

Discussion

The following major changes were observed on San Blas reefs between 1983–1990: (a) a decline in coral from initial values of 31–45% to 12–26% by 1987–1990, almost completely attributable to a decline in the abundance of *Agaricia*; (2) an increase in macroalgal cover (mostly *Dictyota* and *Halimeda*) from initial values of about 2% to final values of 28%; and (3) a two to ten-fold increase in microalgal cover during the period 1983–1986, followed by declines to final values in 1990 that were about 50% greater than initial values. Large changes in coral and algal cover have also been noted on other San Blas reefs. Ogden and Ogden (1994) compared qualitative observations, made in 1971 and 1991 on a range of reefs in our study area and found large decreases in the abundance of not only *Agaricia* spp., but also *Porites porites*, *Acropora palmata* and *A. cervicornis*. They noted that shallow areas that had previously been dominated by these corals were later dominated by a variety of macroalgae.

What are the causes of these changes observed on the San Blas study reefs? During the 1980s, there were several major ecological events that may be responsible for declines in coral and increases in macroalgae.

(1) Coral bleaching. There have been several coral bleaching episodes within the Caribbean over the past decade (Williams and Bunkley-Williams 1990). The cause(s) of natural bleaching events is (are) not completely understood, although elevated water temperature is implicated in some instances (D'Elia et al. 1991; Brown and Ogden 1993).

Relatively severe coral bleaching occurred in San Blas in June–August 1983 (Lasker et al. 1984). *Agaricia* spp. were particularly affected by this event, with partial mortality occurring in 55% of the marked colonies. Lasker et al. (1984) found that, on two reefs studied (different from those in this study), *Agaricia* cover declined to 58% and 38% of initial values in the 6 months following bleaching. Our reefs also showed declines (though not as great) in *Agaricia* cover for that same period (Fig. 1B); however this decline continued for at least 2 more years. Several minor bleaching events that occurred in the years after 1983 (D. R. Robertson, personal observations) may have contributed to the continuing mortality.

(2) Sedimentation and nutrient enrichment due to deforestation in coastal watersheds. Corals are known to be adversely affected by increased sediment concentration in the water (Coffroth 1985; Rogers 1990). Nutrient enrichment has been hypothesized to increase growth of benthic algae, possibly increasing their ability to outcompete corals for space (D'Elia and Wiebe 1990; Hallock et al. 1993). Deforestation on the coast around our study area

occurred at a low rate both before and throughout our study period.

(3) Mass mortality of the sea urchin *Diadema antillarum*. In 1983–1984, the sea urchin *D. antillarum* experienced a mass (95–99%) mortality event throughout the tropical Western Atlantic (Lessios et al. 1984b). This die-off occurred in Punta San Blas in early 1983 (Lessios et al. 1984a). Small-scale experimental studies have shown that *Diadema* preferentially feeds on micro- and macroalgae, and that, in the absence of *Diadema*, micro- and macroalgae increase in abundance and overgrow the competitively inferior corals (Sammarco et al. 1974; Carpenter 1981; Sammarco 1982a, b). Studies at several locations within the Caribbean indicate that the mass mortality of *Diadema* produced the results predicted by those studies (Liddell and Ohlhorst 1986; de Ruyter van Steveninck and Bak 1986; Hughes et al. 1987; Carpenter 1988, 1990). Algal biomass or percent cover increased 25–500% in shallow water, with lesser effects observed in deep water.

In Panama, coral bleaching, *Diadema* loss, and deforestation have occurred virtually simultaneously and without controls. Therefore, it is difficult to separate their effects on algae and corals. However, temporal patterns can provide some clues. In San Blas, most of the decline in coral cover took place from 1983 through 1986, with little change from late 1986 through 1990. Deforestation continued throughout this entire period. If increases in sediments or nutrients were the driving force behind coral loss and algal increases, it is difficult to understand why the decline in coral cover did not continue after 1986.

Both the loss of *Diadema* and the 1983 coral bleaching event could have contributed to the decrease in coral cover and increase in algae. However, we observed many instances in which macroalgae were overgrowing portions of live coral colonies. Sections of corals that were covered by algae were generally bleached white or very recently dead. The relatively long period of decline in *Agaricia* abundance is also more suggestive of the effects of competition from continuously increasing macroalgae populations. However, even corals that recovered from bleaching may have been weakened and therefore more susceptible to overgrowth by algae or other competitors.

The scleractinian coral *Agaricia* and the hydrocoral *Millepora* exhibited markedly different temporal patterns of change in abundance. The decline in *Agaricia* and the relative stability of *Millepora* could be due to differential susceptibility to algal overgrowth or the effects of bleaching. *Agaricia* was more severely impacted by bleaching (Lasker et al. 1984) and may be a poorer competitor against algae. These differences between the *Agaricia* and *Millepora* have not previously been observed and may be important for predicting future changes on Caribbean reefs.

Declines in coral cover have been observed on other shallow reefs within the western Atlantic: Florida Keys (Porter and Meier 1992); Jamaica (Hughes 1994a, b); St. Croix (Hubbard et al. 1994); Barbados (Stearn et al. 1977; Scoffin 1994); and Netherland Antilles (Bak and Luckhurst 1980; Bak and Nieuwland 1994). In most of these cases, the causes of coral decline are not well understood (Ginsburg 1994), but possibilities include coral diseases, and hurri-

canes, as well as *Diadema* loss, increases in sediment, and nutrients loads, and coral bleaching.

In contrast, the Jamaican reefs are well studied and the chronology of events leading to coral decline has been well described (Hughes 1994a, b). These reefs have been hit by a combination of chronic and catastrophic events: overfishing, two hurricanes, and *Diadema* mass mortality. Coral cover has declined from about 50% in the 1970s to 5% today along much of the coastline. The loss of almost all herbivores (*Diadema* through disease; fishes through overfishing) has resulted in a continuous bloom of algae that outcompete corals and prevent coral larvae from successfully establishing (Hughes 1994a).

The decline in coral cover on the San Blas reefs, though dramatic, has not yet been as great as that observed in Jamaica. The contributory causes also differ in these two areas: (1) the San Blas reefs have not been damaged by hurricanes (they are south of the hurricane belt); (2) coral bleaching, only a very minor factor in Jamaica (Gates 1990; Hughes 1994a), has been an important source of coral mortality in San Blas; and (3) unlike Jamaica, the San Blas reefs have not been extensively fished and have relatively high populations of herbivorous fishes. Thus, the underlying causes of changes in these reefs may be quite different, though a decrease in herbivory due to *Diadema* loss appears to have played an important role in both areas.

Effective protection and management of coral reefs will increasingly require an understanding of both generalized and localized causes of changes in the composition and abundance of coral reef communities. Data available from Caribbean reefs, show widespread declines in coral abundance but the patterns are variable and we do not, as yet, have a general understanding of cause and effect. Widespread Caribbean coral declines may be due to many interacting causes which vary in relative importance among locations.

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