

**IS HERBIVORE LOSS MORE DAMAGING TO REEFS THAN
HURRICANES? CASE STUDIES FROM TWO
CARIBBEAN REEF SYSTEMS (1978-1988)**

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IS HERBIVORE LOSS MORE DAMAGING TO REEFS THAN HURRICANES? CASE STUDIES FROM TWO CARIBBEAN REEF SYSTEMS (1978 - 1988)

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ABSTRACT

Case studies of reefs at Discovery Bay, Jamaica (1978 - 1987) and Teague Bay and Salt River Canyon, St. Croix (1982 - 1988) focus on physical and biotic changes that occurred in forereefs resulting from hurricanes Allen in Jamaica (1980), and David and Frederic in St. Croix (1979) and the Caribbean-wide mass-mortality in the sea urchin *Diadema antillarum* (1983 - 1984).

Severe hurricanes reduce both architectural complexity of reefs and the abundance of living coral by differentially fracturing branching (acroporid) corals. This impact is greatest at shallow depths ($\leq 3\text{m}$) where branching acroporid corals dominate. Abundances of other corals, algae (fleshy and coralline) and herbivores remained unchanged. Hurricane impact is relatively short lived because it can be reversed through the growth and regenerative capacity of corals.

Four years after the urchin die-off, macroalgal biomass remained high at all depths in Jamaica and St. Croix. Macroalgae and reef-building organisms such as corals and coralline algae were inversely correlated at all depths and stations studied. At one 3m site coral abundance declined to zero following the urchin die-off. The sudden loss of sea urchins when subtracted from the fishing-induced decline in megaherbivorous fishes, may have created an unprecedented decline in total herbivory. Without constructive elements for reef growth to counteract bioerosion, reefs will degenerate. Clearly other factors could contribute to the loss of corals but the close temporal correlation seen at two distinct sites argues for herbivory playing a major role in reef growth by facilitating recruitment, growth and survival of reef building organisms.

INTRODUCTION

Case histories of Caribbean reefs may provide the best argument against the outdated concept that diversity begets stability. Highly diverse coral reefs throughout the Caribbean have proven to be highly unstable with large-scale changes in community dominance and physical structure widely observed. Unfortunately, even striking changes in reefs are often difficult to quantify because data for the pre-disturbed state are lacking. My case studies focus on two different reef systems in St. Croix and Jamaica, both of which were affected by two different and unrelated natural events: hurricanes and changes in herbivory.

All reefs were periodically studied between 1978 and 1988 (see Recent Reef Histories). However, the timing of the studies fortuitously gave me an opportunity to evaluate the relative importance of hurricanes and the mass mortality of the herbivore, *Diadema antillarum*. For the purpose of these case studies, I will focus on changes in the reef's architectural complexity, population densities of the dominant grazing sea urchin, *Diadema antillarum*, and resultant changes in algal biomass and the abundances of dominant reef building organisms such as scleractinian corals, *Millapora* sp and encrusting coralline algae. I focus most of my attention on shallow forereef zones because they have the highest organic and calcium carbonate productivity. Further, I show that consequences of the mass mortality in *D. antillarum* could have long-lasting consequences because the subsequent increase in algal biomass may negatively impact the major carbonate producing organisms and thus affect the regenerative capacity of the reef.

METHODS

Recent Reef Histories

The Discovery Bay reef on the north shore of Jamaica was the site of some of the earliest reef research in the Caribbean (Goreau, 1959). My quantitative reef surveys were conducted during July of 1978, 1982 and 1987. Hurricane Allen hit the reef August 1980 (Woodley et al., 1981), and the mass mortality of the sea urchin *Diadema antillarum* occurred July 1983 (Lessios, 1988).

The Teague Bay and Salt River Canyon reefs on the north shore of St. Croix have been intensively studied since the early 1970s (e.g., Sammarco et al., 1974). My quantitative surveys were conducted during April 1982 and 1988. Hurricanes David and Frederic struck St. Croix in August and September of 1979 (Rogers et al., 1982). The mass mortality of *Diadema antillarum* occurred January 1984.

Study Sites and Quantitative Sampling Regime

Both reef locations, Jamaica and St. Croix, were surveyed at distinct depth zones. Nine depth zones were studied in St. Croix at two locations (Teague Bay and Salt River Canyon, site details in Steneck 1983). In St. Croix, shallow sites on the Teague Bay reef between 1 and 5 meters were pooled (i.e., "3 m" zone), and sites at both Teague Bay and Salt River Canyon at 10 m were pooled (i.e.,

"10 m" zone). The deep reef zone at Salt River Canyon pooled stations between 20 and 40m (i.e., "30 m" zone). Two forereef sites were monitored on the Discovery Bay reef in Jamaica (details in Hughes et al., 1987) at depths of 3, and 10m.

Percent cover of reef-dwelling organisms and reef architectural complexity were quantified using linear transects (Rogers et al., 1982, 1983). The "spatial index" represents the meters of substratum measured all reef components following surface contours along the substratum in a plane under a linear meter length stretched straight just over the reef surface. This results in data represented as meters of reef component per linear meter measured. On planar or featureless surfaces the spatial index = 1 but values over 5 m/m were recorded.

Diadema antillarum abundance was recorded at each sampling site by haphazardly tossing a meter square quadrat. Previous work determined that a minimum sufficient sample size for urchin densities is ≥ 20 quadrats per site.

Algal biomasses were determined from substratum samples collected in each zone. Macroalgae were plucked, subdivided by species, dried and weighed. Then substratum was again subsampled to determine the abundance of minute turf algae. For this 13, three mm-wide gouges, each one mm deep and one cm long, were collected for a total sampling area of 3.9 cm². Species-level biomasses were pooled for total fleshy algal biomass.

RESULTS

Hurricane Impacts

Three hurricanes are involved with the two case studies. Jamaica's Discovery Bay reef was most severely hit by Hurricane Allen when it passed within 50 km on 6 August 1980. Maximum winds up to 285 km/h were recorded for this hurricane and 110 km/h winds were recorded on Jamaica. Twelve meter high waves struck the Discovery Bay reef (Woodley et al., 1981). In contrast, the two hurricanes which affected St. Croix in rapid succession, Hurricanes David and Federic, were less intense and had much smaller storm-induced waves. Hurricane David passed 204 km south of St. Croix on 30 August 1979 with winds of 86 km/h and waves up to 5.7 m. Hurricane Federic passed 137 km north of St. Croix on 4 September 1979 with winds of 56 km/hr gusting to 80 km/h and waves up to 3 m.

Jamaica

Reef Architectural Complexity, and Coral Abundance

In 1978, the forereef at Discovery Bay was highly complex (Fig. 1 a). Average spatial indices ranged from 3.8 m/m at 3m to 2.8 m/m at 10m. This translates to 14.8 m² and 7.7 m² of reef surface area per planar m² area for 3m and 10, respectively. High architectural complexity resulted from the abundance of branching acroporid corals. *Acropora palmata* dominated at 3 m (30.9 % cover ± 19.8 standard deviation, hereafter "SD", n = 34) and *A. cervicornis* dominated at 10 m (10.7% ± 13.1 , n = 22). These two species comprised between 80 and 34% of all live coral at 3 and 10m forereef zones, respectively (Fig. 1b).

Hurricane Allen (1979) reduced reef architectural complexity to 1.6 and 1.4 m/m when measured in 1982 at 3 and 10 m, respectively (Fig. 1a). This translated to surface areas of 2.6 and 2.0 m² of reef surface area per planar m² for the 3 and 10m zones respectively. Thus, the 3m site was reduced to less than 18% of the pre-hurricane reef surface area. The nearly flattened 3m zone resulted from damage sustained by the branched coral, *A. palmata*. Architectural complexity remained at post-hurricane levels at both the 3 and 10 m zones through 1987.

Live coral cover decreased significantly following the hurricane (Fig. 1b) due to declines in the relatively delicate *Acropora palmata* and *A. cervicornis* at 3 and 10m, respectively. Coral cover continued to decline between 1982 to 1987 at 3m but remained constant at 10m. This difference in mortality trends between the two depths may reflect the abundance of unbranched corals at 10m. Robust mound forming corals such as *Montastrea annularis*, *M. cavernosa*, *Diploria strigosa*, *D. labyrinthiformis* and *Porites astreoides* were significantly more abundant at 10m and their abundance changed little from 1978 (12.6%) to 1987 (9.8%). The acroporid species never regained their prehurricane abundance and ranged between 0 and 0.5% cover at the 3 and 10m zones in 1987.

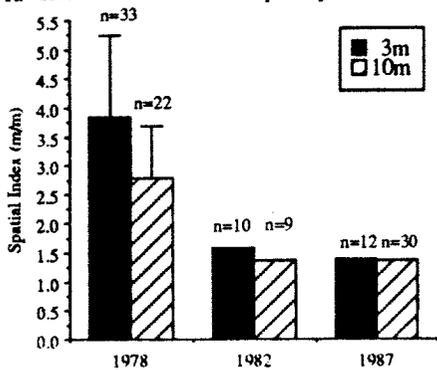
Urchins and Algal Abundance

In 1978, the urchin, *Diadema antillarum*, was abundant at both forereef sites (Fig. 2a). The abundance and depth patterns were virtually unchanged in both zones in 1982, two years after Hurricane Allen. In 1983, the urchins suffered a mass mortality which killed over 98% of the population (see Recent Reef Histories). Four years later (1987) urchin population densities ranged from 0.04/m² (± 0.9 , n = 66 quadrats) at 3m to 0.0/m², (n = 28) at 10m.

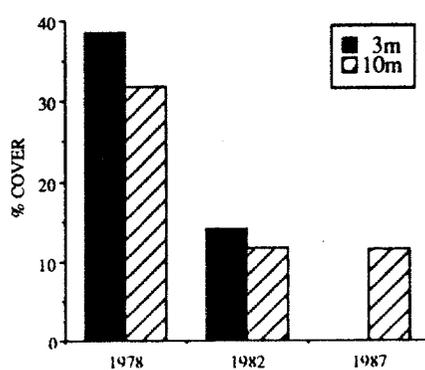
The biomass of fleshy algae (i.e., erect, non-encrusting, turfs and macroalgae; *sensu* Steneck, 1988) were low at both zones from at least 1978 through 1982 (Fig. 2b). Hurricane Allen had little lasting impact on them. However, following the mass

Jamaica

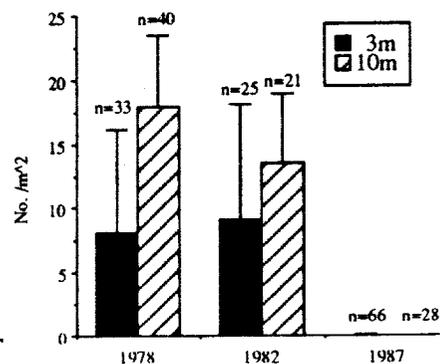
1a Reef Architectural Complexity



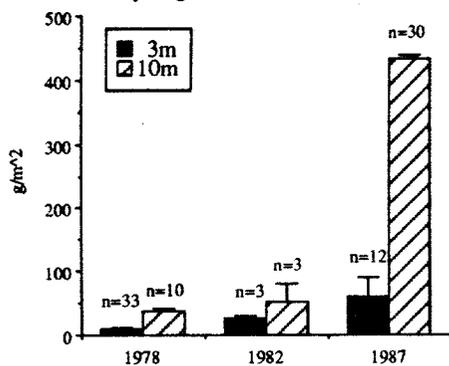
1b Percent Coral



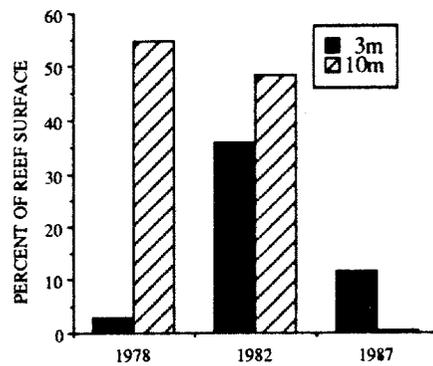
2a *Diadema antillarum* Population Densities



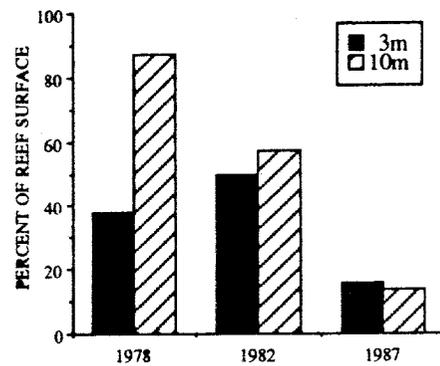
2b Fleshy Algal Biomass



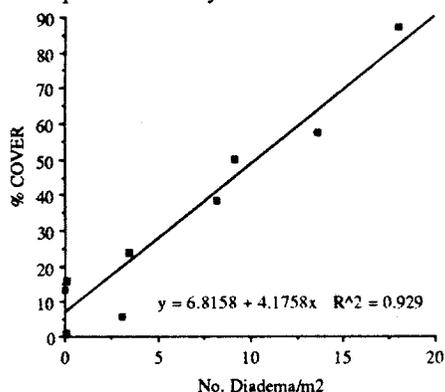
3a Percent Coralline Algae



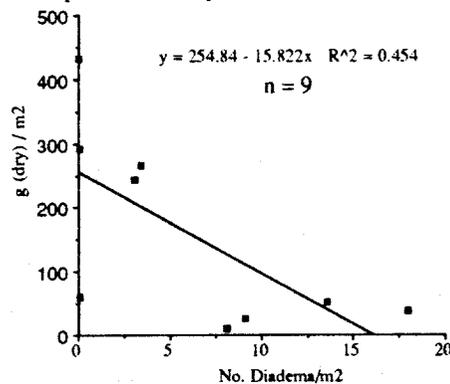
3b Percent Cover of Reef Building Organisms (Coral, Millipora and Coralline algae)



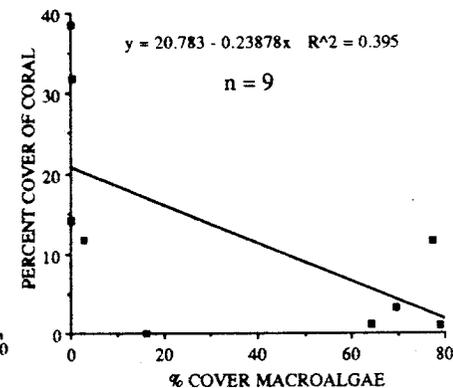
4a Percent Cover of Reef Building Organisms vs Population Density of *Diadema antillarum*



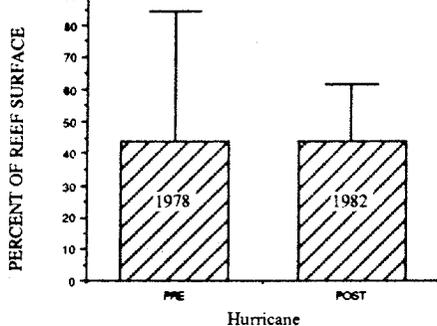
4b Algal Biomass vs Population Density of *Diadema antillarum*



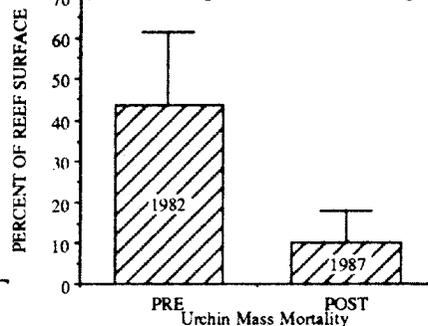
4c Percent Cover of Macroalgae vs Coral



5a Reef Building Organisms (Coral, Millipora and Coralline algae)



5b Reef Building Organisms (Coral, Millipora and Coralline algae)



mortality of *Diadema antillarum*, algal abundance increased at both depths. The increase in algal biomass at the 10 m zone was most conspicuous due to the change in algal dominance from a low canopy algal turf to large stands of macroalgae. Macroalgal abundance rose from 2.4 and 1.8 g/m² in 1978 and 1982 to 400.6 g/m² in 1988. Although the magnitude of increase in algal biomass at 3m was not great, macroalgae which was absent in 1978 and 1982, rose to 46.3 g/m² in 1988.

Patterns of abundance among encrusting coralline algae (Fig. 3a) were opposite those of erect algae (Fig. 2b). Corallines were significantly more abundant at 10 m in 1978 and 1982 than in 1987 (Fig. 3a). There they declined most precipitously (Fig. 2b) following the mass mortality in urchins (Fig. 2a).

Abundance of Reef-building Organisms with Herbivores and Hurricanes

The abundance of all major reef-building organisms (i.e., scleractinian corals, *Millapora* spp. and encrusting coralline algae), remained relatively constant between 1978 and 1982 but declined in 1987 at both the 3 and 10m zones (Fig. 3b). Taken together, over all years and both zones, the percent cover of all calcareous reef-building organisms correlates directly with *Diadema* densities (Fig. 4a). In contrast, *Diadema* and algal biomass are inversely correlated (Fig. 4b), as are macroalgae and coral abundance (Fig. 4c). Reef-building organisms were not reduced in abundance two years after Hurricane Allen (Figs. 3b, 5a)

The percent cover of reef-building organisms compared before and after Hurricane Allen (Fig. 5a), were unchanged. The same analysis with respect to the mass mortality in *Diadema* indicated a strong effect. (Fig. 5b)

Fish grazing rates were relatively low in Jamaica (i.e., compared with St. Croix) but the highest values were recorded at 3m. At both depths fish grazing rates increased after the mass mortality in sea urchins. Grazing by herbivorous fishes was monitored using visual bite-rate counts (methods in Steneck, 1983). Fishes with the greatest impact include the "scraping" parrotfish (*Scarus* and *Sparisoma*), and the "denuding" tangs (*Acanthurus*) and some damselfish such as the yellow-tail damsel (*Microspathodon chrysurus*) (scraping and denuding designations in Steneck 1988). In 1982 at 3m, grazing rates were 0 for denuding fishes and 215 bites/m²/h for parrotfishes. In that zone, following the mass mortality of *Diadema*, fish grazing rates increased to 50.6 for denuding grazers and 364.5 for the scraping parrotfishes. Grazing rates were lower at 10 m and 0 and 98.4 bites/m²/h were recorded for denuding and scraping fishes. These rates increased to 12.5 and 155 bites/m²/h in 1988.

St. Croix

Reef Architectural Complexity and Coral Abundance

Hurricanes Federic and David passed near St. Croix in rapid succession in August and September of 1979 but had little impact on the architectural complexity of the Teague Bay reef. Surveys conducted by Rogers et al. (1982) immediately after the hurricanes in November of 1979 recorded relatively high architectural complexity for the Teague Bay reef (i.e., 2.7 m/m spatial index, Rogers et al 1982). In 1982 I recorded a lower architectural complexity (i.e., 1.7 m/m, Fig. 6a) at the 3 m zone which may reflect the patchy nature of the hurricane disturbance on the Teague Bay reef (Rogers et al., 1982). Linear transects in 1988 recorded reef architectural complexity at 3m of 2.5 m/m (Fig. 6a).

The percent cover of live coral was 33.6 to 20.7% at 3 and 10 m, respectively in 1982 (Fig. 6b). This was more than twice the 10% reported just following the hurricanes by Rogers et al. (1982) and supports their conclusions that coral regeneration was rapid on the Teague Bay reef. At greater depths and over both sampling periods, the percent of live coral averaged between 14 and 20%. Coral morphologies were zoned with depth. The branching *Acropora palmata* dominated at 3 m, mound corals (e.g., *Montastrea cavernosa*, *Dichocenia stellaris*, and *Diploria* spp.) dominated at 10 m and platy corals (e.g., *Agaricia* spp) dominated zones between 20 and 40 m.

Urchins and Algal Abundance

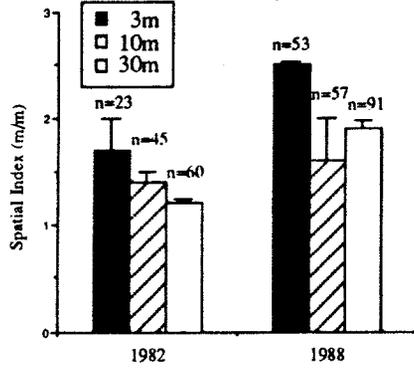
Diadema antillarum population densities were greatest at 3 m and lowest below 20 m in 1982 (Fig. 7a). Populations declined dramatically following the mass mortality in 1984. They remained low four years later in 1988 when they reached their maximum abundance again at 3m but it was only 2.5% of their original population density.

Algal biomass was low at all depths in 1982 but increased significantly by 1988 (Fig. 7b). The most dramatic increase occurred at 10 m depth. Most of the change was due to increases in the abundance of macroalgae (primarily *Dictyota* spp, *Laurencia*, sp. and *Lobophora* sp.) which were virtually nonexistent in 1982.

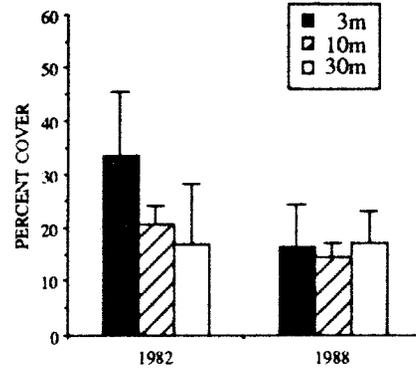
Encrusting coralline algae dominated the 3m zone at Teague Bay in 1982 but decreased to less than half that abundance in 1988 (Fig. 8a). Only slight changes occurred at 10 and 30 m.

St. Croix

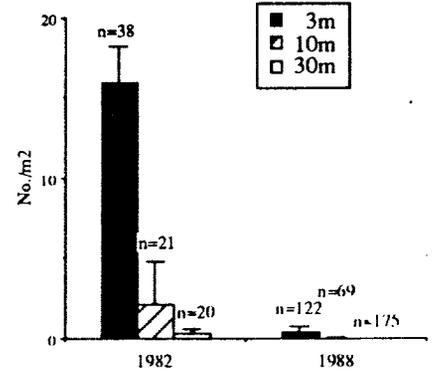
6a Reef Architectural Complexity



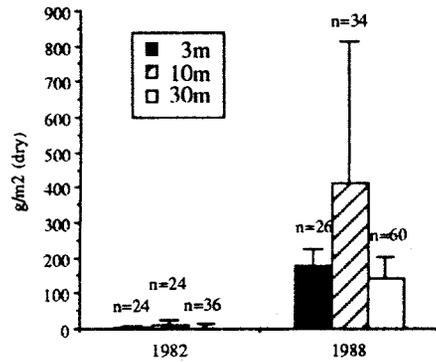
6b Percent Coral



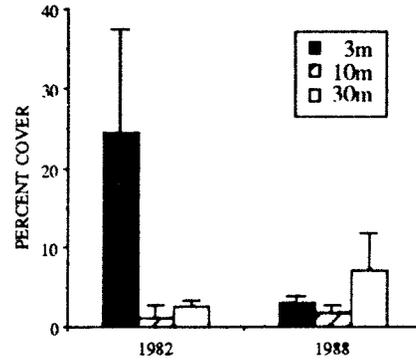
7a *Diadema antillarum* Population Densities



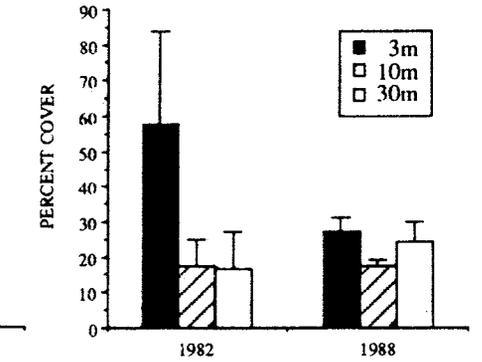
7b Fleshy Algal Biomass



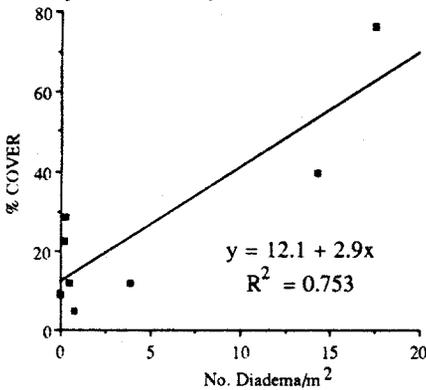
8a Percent Cover of Coralline Algae



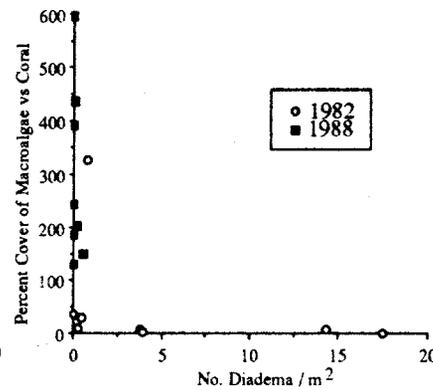
8b Percent Cover of Reef Building Organisms (Coral, Millipora and Coralline algae)



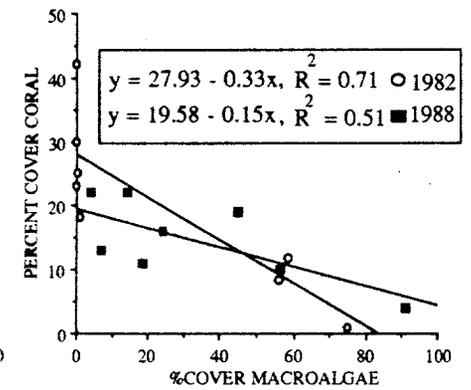
9a Population Density of *Diadema antillarum* vs Reef Building Organism vs % COVER



9b Algal Biomass vs Population Density of *Diadema antillarum* vs Percent Cover of Macroalgae vs Coral



9c Percent Cover of Macroalgae vs Coral



Abundance of Reef-building Organisms with Herbivores and Hurricanes

Reef building organisms declined significantly at 3 m between 1982 and 1988 (Fig. 8b). There were no significant changes at the other depth zones between years. Reef building organisms were also positively correlated with *Diadema antillarum* abundance in 1982 (Fig. 9a). Urchin densities were too low in 1988 to include them in this analysis. Macroalgal biomass was high only where *Diadema* abundance was low (Fig 9 b). Since urchin densities were low in all zones in 1988, macroalgal abundances were high (Figs 9b, 7b). Coral cover was inversely correlated with macroalgal abundance during both sampling periods (Fig. 9c).

Impact of the hurricanes on the St. Croix reefs were relatively minor and short lived. My personal experience on the Teague Bay reef dates back to 1972, and from then to 1982 no conspicuous differences were evident to me. Throughout that period, *Diadema* were annoyingly abundant, macroalgae were rare and coral was conspicuous. Therefore, the 1982 data may indicate long-persistent patterns of reef composition prior to the mass mortality.

Fish grazing was greatest in the 3 m zone in 1982 but increased at 10 m after the mass mortality in sea urchins. Grazing rates of 12.5 bites/m²/h (± 0.7 SD) and 625.8 (± 884 SD) were recorded at 3 m for denuding and scraping fishes, respectively. Following the mass mortality, grazing rates at 3m were 553.0 bites/m²/h (± 242 SD) and 510.0 (± 721 SD) for denuding and scraping fishes, respectively. Although lower values were recorded at 10 m for these two groups of grazing fishes in 1982 (i.e., 9.5 \pm 9.2 SD, 39.5 \pm 55.9 SD), significantly higher values were recorded in 1988 (i.e., 236.5 \pm 87.0 SD, 1913.0 \pm 1224.7 SD). At even greater depths around 30 m, grazing rates were moderately low (8.3 \pm 2.3 SD, 172.3, \pm 151.1 SD) from denuding and scraping herbivores, respectively).

DISCUSSION

Reefs grow most rapidly in shallow wave-exposed zones and thus the dynamics occurring there will have the greatest consequences. Reef communities living in shallow water (i.e., ≤ 10 m) have the greatest rates of organic (Adey and Steneck, 1985) and inorganic (i.e., calcium carbonate, Smith and Buddemeier, 1992) production. It is also where herbivory and the potential for physical disturbances are greatest.

Branching coral morphologies often dominate shallow forereef environments and comprise a significant proportion of coral framework in growing reefs (e.g., Adey and Burke, 1976, Macintyre et al., 1977). Further, branching coral morphologies are capable of most rapid growth (Gladfelter et al., 1978) and regeneration (Rogers et al., 1982) but they are also most susceptible to hurricane impacts (Porter et al., 1981).

Hurricane impact appears to be very limited both spatially and temporally. In St. Croix, the north-shore reefs (i.e., Teague Bay and Salt River Canyon) were spared by Hurricanes David and Federic whereas the south shore "Robin" reef suffered a dramatic reduction in architectural complexity (Rogers et al., 1982). Jamaica's Hurricane Allen reduced architectural complexity by more than 80% in the shallowest zones by fracturing the branching acroporid corals (Fig. 1a). However, because acroporids are capable of very rapid growth and regeneration (although this can be delayed by post hurricane diseases [Knowlton et al., 1981]), and because most of the other coral components were unchanged, hurricane impact is likely to be rather short lived. Similar conclusions were reached by Rogers et al., 1982, 1983. Finally, hurricane impacts are limited to shallow reefs of usually less than 10 m (Woodley et al., 1981, Rogers et al., 1982).

The loss of *Diadema* appears to be much more significant than hurricanes because its impact on algal abundance is very widespread (e.g., reviewed in Lessios., 1988) and relatively long-lasting. In Jamaica and St. Croix, algal biomass increased at all depths but to the greatest extent at 10 m (Figs 2b, 7b). Similar reports have been made for these reefs (e.g., Jamaica: Liddell and Ohlhorst, 1986, Hughes et al., 1987; St. Croix: Carpenter, 1990) and other reefs throughout the Caribbean (e.g., St. John, Levitan 1988; Curacao, Ruyter van Steveninck and Bak, 1986). Accumulations of macroalgae have long been known to affect the recruitment (Birkland 1977), and survival of corals (e.g., Figs. 4c, 9c; Fishelson 1973) as well as limit the abundance of encrusting coralline algae (Steneck, 1986, Liddell and Ohlhorst, 1986, Ruyter van Steveninck and Bak, 1986). Thus when considered together, reef building organisms are dependent on and positively correlated with grazers such as *Diadema antillarum* (Fig. 4a, 9a).

Herbivory from fishes may have been much more important before they were harvested by humans. In Jamaica, the fishing pressure on the reef is greater than it is in St. Croix because the human population is great and the reef area small (Stevenson and Marshall, 1974, Smith and Buddemeier, 1992). During the course of the study, only in Jamaica were herbivorous fishes served at local restaurants. I found that not only were herbivore grazing rates lower in Jamaica (see Results), but the fish body sizes were smaller as well. On both islands, fish grazing rates were highest at 3 m and thus the magnitude increase in algal biomass following the mass mortality was lower than it was at 10 m (Figs 2b, 7b). Since herbivorous fishes and *Diadema* compete for the same algal trophic resources (Carpenter, 1990), the loss of abundant, large bodied herbivorous fishes may have been compensated by increases in urchin populations. If so, that reduction in herbivore diversity may have directly contributed to cascading effects that destabilized the structure of Caribbean reefs.

Acknowledgments

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