

Ten Years of Disturbance and Change on a Jamaican Fringing Reef

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Abstract. Long-term quantitative monitoring of reef communities enables the documentation of community change, which is typically not observed during the term of most ecological studies and, thus, relegated to anecdotal descriptions. During the interval of 1980-1990, Jamaican north coast fringing reefs experienced several physical and biological disturbance events of large magnitude, including Hurricane Allen in 1980, the catastrophic mortality of the urchin herbivore, *Diadema*, in 1983, Hurricane Gilbert in 1988, and several coral bleaching events. In addition, man has increasingly impacted these reefs, chiefly through overfishing. The cumulative effect of these events has been the transformation of shallow (<30m) reef assemblages from high-diversity communities with high spatial dimensionality (many branching corals) to low-diversity, algal-dominated, and structurally "flat" communities. While these reefs may have "recovered" from naturally-induced disturbance events alone, the combination of natural disturbance and anthropogenic effects appears to have negatively affected their recovery potential.

Introduction

The evolution of the view of coral reefs as nonequilibrium systems, subject to numerous perturbations and variation in recruitment, was one of the most significant conceptual breakthroughs in coral reef science (Sale 1977; Connell 1978). However, over the last decade, the documentation of a

steadily increasing number of disturbance events, from coral bleachings to urchin mass mortalities, and rampant increases in algal biomass, has resulted in fears that reefs may be suffering degradation worldwide, presumably due to the interaction of anthropogenic factors and "natural" disturbance events. The determination of background versus unusual (magnitude and/or frequency) perturbations requires long-term records on sessile epibenthic community composition, herbivore (fish and invertebrate) densities, and environmental parameters, such as sedimentation rates, temperature, and water chemistry.

The present paper presents reef census data for a 15 m site on a north Jamaican reef. Such census data provide much-needed base-line information which can be used to evaluate the effects of natural (storms, mass mortality events) and anthropogenic (resource harvesting, pollution, recreational activities) disturbance on reef systems. The latter becomes of particular importance as coastal areas are increasingly exploited for food, energy, resources, and recreation. Unfortunately, such long-term records are largely lacking for most Caribbean reef localities (exceptions include Bak and Luckhurst 1980; Porter et al. 1981; Dustan and Halas 1987; Hughes et al. 1987; Jaap et al. 1988; and Hughes 1989).

Several disturbance events, most notably Hurricane Allen in August, 1980 (Woodley et al. 1981), the mass mortality of the urchin, *Diadema* in August, 1982 (Hughes et al. 1985, 1987; Liddell and Ohlhorst 1986), and Hurricane Gilbert in September, 1988, have greatly modified the shallower (<30

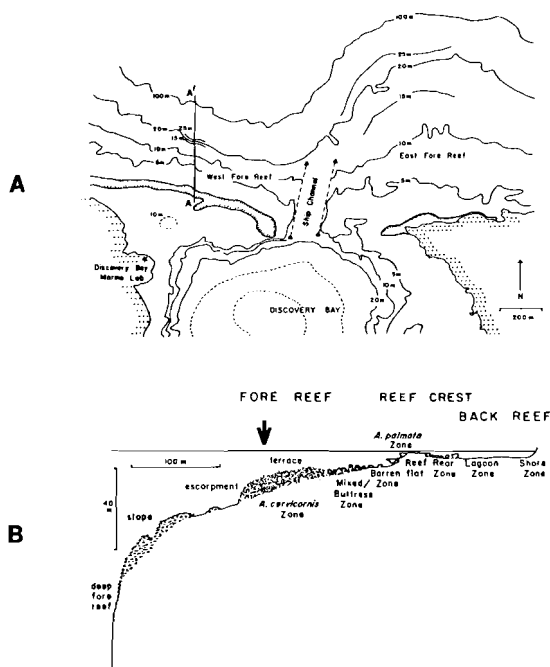


Fig. 1. A. Locality map of Discovery Bay, Jamaica. Study area indicated by line A-A'. B. Profile along line A-A'. Geomorphic features and ecologic zones are displayed. Census site at 15 m is indicated by arrow. Figure modified from Liddell and Ohlhorst (1987).

m) north coast communities. In addition, bleaching events, such as that of July-December, 1987, have also occurred on the Jamaican reefs (Sandeman 1988; Woodley 1988; Gates 1990). Anthropogenic factors in operation over this same time interval include overfishing (Woodley 1979).

Methods

Study locality

Discovery Bay lies on the north central coast of Jamaica at Lat. $18^{\circ}30'N$ and Long. $77^{\circ}20'W$. The well-developed fringing reefs occurring along the north central coast of Jamaica display a striking, depth-related biotic zonation which has been the topic of many papers (Goreau 1959; Goreau and Goreau 1973; Kinzie 1973; Lang 1974; Bonem and Stanley 1977; Liddell and Ohlhorst 1981, 1987, 1988; Liddell et al. 1984a, 1984b; Huston 1985; and others). In addition, these reefs have been the location of numerous studies dealing with the physiology, functional morphology, and other aspects of the biology and ecology of the reef organisms.

The study area is located on "Zingorro" reef, which lies on the West Fore Reef, approximately

0.5 km west of the Discovery Bay ship channel (Fig. 1A, line A-A'). The following succession of structural/geomorphic zones are encountered along a transect across the West Fore Reef: reef crest, fore reef terrace, fore reef escarpment, fore reef slope and deep fore reef. The study site occurs at 15 m on the outer portion of the gently-sloping fore reef terrace and at a distance of approximately 200 m seaward from the reef crest (Fig. 1B).

Census methods

Although census data were collected for a number of north Jamaican reef sites between 1976-1989, due to space limitations, we will largely restrict our discussion to one 15 m reef locality. Quantitative data for this site were gathered over the interval of June, 1980 to September, 1989 (Table 1). These data were supplemented by observations made by the authors between March, 1975 and December, 1990. The vagaries of funding and other commitments prevented the collection of data as frequently or as systematically as would be ideal, nonetheless, several major disturbance events were bracketed by this data and an overall picture of reef degradation occurring over the past ten years is preserved (Table 2).

Data were collected by a line transect method in which 10 m lines with points marked every 20 cm were loosely draped over the reef and the identity of every item beneath a transect point recorded (linear point intercept method). Alternatively, transect lines were photographed (April and September, 1989 censuses) and the identity of items occurring beneath transect points noted in the laboratory. Photographic data consisted of color transparencies encompassing 40 cm by 60 cm areas. Objects as small as 1 mm could be observed on the transparencies when projected. Transect lines were placed 1 m apart and oriented parallel to bathymetric contours and were restricted to reef areas (lines did not extend into major sand channels or grooves). Typically 11 lines (approximately 550 points) were surveyed at each time interval. Ninety-five percent confidence intervals were calculated using data from each 10 m transect line as discrete entities. Line methods were considered to be preferable to others, such as the quadrat method, in that they allow for a greater area of reef to be censused per unit of time and, therefore, may be less subject to biasing by heterogeneous distributions of reef benthos.

Transect data were used in the determination of sessile community composition (Table 2). Data were also gathered on the density of the important urchin grazer, *Diadema antillarum* (Sammarco et

al. 1974; Carpenter 1981), by counting those present in 1 m wide strips adjacent to the transect lines (Table 2).

Results

Over the interval of 1980–1989 the 15 m reef study site was greatly altered by a variety of physical, biotic, and, possibly, anthropogenic disturbances (Tables 1–2). The cumulative effect of these was a reduction in coral cover (from 33% to 2%) and an increase in noncrustose algal cover (from 10% to 79%; Table 2; Fig. 2). The reduction in coral abundance corresponds to a change from a highly three-dimensional (many branching corals) to a structurally flat reef surface. An additional, disturbing trend is the reduction in abundance of total calcifying organisms (chiefly corals, encrusting foraminifera, crustose coralline algae, and the calcareous green alga, *Halimeda*) from 45% to 20% cover over the same interval (Table 2; Fig. 3).

Hurricane Allen in 1980 resulted in a reduction in coral cover from 33 to 10% at the 15 m site. The abundance of total calcifying organisms was less affected by the storm, decreasing from 45 to 37%. This was perhaps due to the colonization of storm-generated coral rubble by crustose coralline algae. During the interval of December, 1980 to August, 1982, coral cover increased to 18% and total calcifying organisms to 48% (approximately prehurricane levels for total calcifying). Following the mass mortality of *Diadema* in 1983, both coral and total calcifying organisms have declined while noncrustose algae have increased to present levels. It is of interest to note that increases in noncrustose

algae actually began several years prior to the mass mortality of *Diadema* (Table 2; Figs. 2–3).

While it would be incautious to freely extrapolate the results from one 15 m site to other depths or localities, the above trends are mirrored by shallower sites on Zingorro reef and at other Jamaican localities. For example, at 5 m on Zingorro, coral cover decreased from 58% in 1977 to 5% in 1982, reflecting the impact of Hurricane Allen. Algal abundance increased from 0.5% cover in 1977 to 18% in 1982 to 55% in 1983 following the mass mortality of *Diadema*. In 1989 coral cover was 4% and algal cover 60% at this site (Liddell and Ohlhorst 1986, 1987, unpublished census data of authors).

Hughes (in press) documents similar trends for 7, 10, and 15–20 m sites at Rio Bueno (located 5 km to the west of Discovery Bay). Coral cover at his study sites ranged between 47–70% in the 1970s; in 1990 values were only 5–9%. Algal cover prior to the mass mortality of *Diadema* in 1983 was 1–3%; in 1990 algal cover varied between 61–94%. One interesting difference between the Rio Bueno and Discovery Bay shallow sites is the initially lower algal abundance at Rio Bueno (1–3%) as compared to Discovery Bay (15–31% range for 5, 10, 22 m sites in Aug. 1982), which may have been due to lesser fishing pressure at Rio Bueno (Liddell and Ohlhorst 1986).

Deeper sites on Zingorro reef were, predictably, much less affected by storms than the shallower sites. For example, at 30 m, coral cover prior to and after Hurricane Allen was 51% and 58%, respectively. Noncrustose algal abundance has shown an increase from 9% in 1980 to 12% in 1982 to 45% in 1989, despite the very low numbers (mean 0.1

Table 1. Chronology of censuses and disturbance events.

Date	Event	Interval (months)
1 June, 1980	Census	
August, 1980	<i>Hurricane Allen</i>	2
2 December, 1980	Census	4
3 December, 1981	Census	12
4 August, 1982	Census	8
August, 1983	<i>Diadema Mass Mortality</i>	12
5 August, 1983	Census	0.5
6 December, 1983	Census	4
7 August, 1984	Census	8
8 June, 1987	Census	34
July, 1987	<i>Coral Bleaching</i>	1
September, 1988	<i>Hurricane Gilbert</i>	14
9 March, 1989 ¹	Census	6
September, 1989	<i>Urchin Mortality</i>	6
10 September, 1989 ¹	Census	0
December, 1990	<i>Coral Bleaching</i>	15
December, 1990	Observations	0

¹ Photographic transects, all others *in situ* linear point intercept method.

Table 2. Changes in community composition over time (percentages with 95% confidence intervals in parentheses)

	Date									
	June 1980	Dec. 1980	Dec. 1981	Aug. 1982	Aug. 1983	Dec. 1983	Aug. 1984	June 1987	March 1989	Sept. 1989
	No. Points (No. Lines)									
	457 (9)	560 (11)	510 (10)	586 (11)	231 (5)	296 (5)	585 (11)	556 (11)	610 (11)	495 (9)
Corals	33.2 (7.7)	9.5 (2.0)	16.1 (2.1)	18.0 (6.4)	9.8 (7.9)	12.8 (4.4)	13.4 (4.3)	8.7 (4.2)	2.8 (2.3)	2.3 (2.0)
Other Coelenterates ¹	3.3 (1.5)	3.4 (1.8)	3.8 (2.5)	0.9 (0.9)	1.9 (2.3)	4.0 (1.6)	0.3 (0.5)	1.4 (0.9)	0.3 (0.5)	0.2 (0.5)
Boring Sponges ²	22.4 (6.8)	34.5 (4.7)	23.2 (4.3)	14.0 (4.7)	9.0 (6.8)	5.2 (3.6)	6.5 (2.9)	3.9 (2.2)	0.0	0.4 (0.6)
Other Sponges ³	1.3 (1.3)	0.0	0.8 (1.0)	0.7 (0.9)	0.0	0.3 (0.9)	0.4 (0.8)	0.4 (0.5)	0.5 (0.8)	0.4 (0.6)
<i>Gypsina</i> ⁴	0.9 (1.1)	3.0 (1.9)	4.2 (1.6)	3.1 (1.5)	0.0	1.0 (1.2)	2.4 (1.1)	0.0	0.0	0.2 (0.5)
Coralline Algae ⁵	11.0 (2.9)	23.0 (5.1)	22.9 (5.1)	24.0 (8.1)	9.8 (5.2)	2.8 (3.4)	4.3 (1.4)	2.1 (1.1)	3.2 (1.7)	9.0 (3.1)
Filamentous Algae ⁶	6.3 (3.5)	6.5 (2.6)	1.5 (1.3)	17.7 (7.0)	27.5 (17.5)	36.3 (5.5)	8.0 (2.2)	14.0 (5.2)	17.9 (5.9)	13.9 (7.3)
Macroalgae ⁷	4.0 (4.3)	14.0 (4.2)	20.5 (5.3)	13.0 (4.7)	27.5 (8.5)	35.3 (6.2)	56.9 (4.2)	62.7 (6.3)	57.3 (7.5)	65.4 (8.0)
Total Living Cover	82.3 (2.1)	93.9 (3.3)	84.5 (19.4)	90.6 (5.3)	85.5 (16.4)	97.7 (3.3)	92.1 (3.2)	93.4 (2.2)	82.0 (6.8)	91.5 (3.7)
Sand	4.6 (3.2)	0.2 (0.4)	1.6 (2.3)	3.5 (4.1)	3.9 (5.6)	0.3 (1.0)	3.4 (2.2)	2.7 (2.2)	13.7 (5.8)	4.4 (2.5)
Hard Substrata	13.2 (3.6)	6.1 (3.3)	5.5 (2.6)	5.1 (2.7)	10.6 (11.3)	2.0 (3.2)	4.4 (1.8)	3.9 (2.4)	4.3 (4.9)	4.0 (2.6)
No. <i>Diadema</i> M ⁻²	3.2 (1.1)	5.2 (1.3)	3.9 (1.4)	6.4 (1.2)	0.0	0.0	0.0	0.0	0.0	0.0
Area for <i>Diadema</i> Surveyed (M ²)	90	110	100	110	110	110	110	110	110	110

¹ Chiefly coralliomorphs and the gorgonians, *Briarium* and *Erythropodium*.² Coral rubble with exhalent oscula of *Cliona*.³ Chiefly *Ircina* and *Agelas*.⁴ Encrusting foraminiferan.⁵ Coral rubble with crustose coralline algae.⁶ Multispecies turfs.⁷ Chiefly *Dictyota*, *Halimeda*, and *Lobofora*.

m²) of *Diadema* at this depth prior to the mass mortality event. By 1989 coral cover had declined to 33%. Similarly at 45 m, coral cover was 43% in 1980, 45% in 1982, but only 13% in 1984. Noncrustose algal abundance increased from 26% in 1980 to 32% in 1982, to 47% in 1984 (Liddell et al. 1984a, b, Liddell and Ohlhorst 1987, unpublished census data of the authors).

Discussion

"Natural" Events

Storms. Hurricane Allen, occurring in August of 1980, was the largest storm to strike Jamaica during this century (Woodley et al. 1981). Its effect upon the shallow (<30 m) reef communities was major (Woodley et al. 1981; Liddell et al. 1984b; Table 2 herein). The overall effect was a decrease in coral abundance, particularly for the branching *Acropora cervicornis*. The loss of branching corals resulted in a reduction in reef structural (habitat) complexity. Reef structural complexity has been cited as a possible determinant of fish community structure (Luckhurst and Luckhurst 1978), although the importance of this factor has been challenged (Sale and Douglas 1984; Lewis and Wainwright 1985). The fragmentation and death of corals yielded hard substrata which were quickly colonized by boring sponges and crustose coralline algae.

Hurricane Gilbert in September of 1988 had a relatively minor effect upon the 15m reef community. This was largely due to the fact that there was little coral remaining on the shallow reefs to destroy (coral cover did drop from 9% to 3%). Although much of the macroalgae were swept away by the storm (JD Woodley, Discovery Bay Marine Laboratory, personal communication), they were quickly reestablished as dominant space-occupiers on the shallow reefs. The April, 1989 census showed a decline in noncrustose algal abundance of only 6% (from 63% to 57%, Table 2).

Mass Mortality Events. The mass mortality of the urchin, *Diadema*, in early August of 1983 had major consequences for the shallow Jamaican reef communities, which are still evidenced today. The removal of this herbivore, in the absence of abundant fish grazers, resulted in explosive increases in noncrustose algal cover (compare Aug., 1982 to Aug., 1983 data, Table 2). This trend has continued and strikingly high noncrustose algal cover (up to 79%) has been maintained to the present (personal observations, December, 1990). Numerous small coral recruits were present on the shallow reefs in

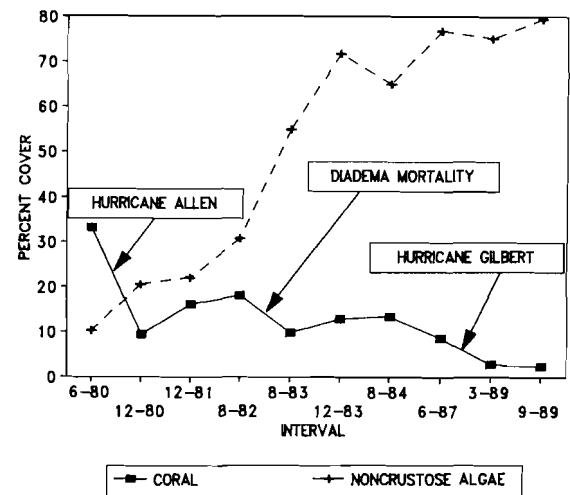


Fig. 2. Change in reef community composition, June, 1980–September, 1989. Noncrustose algae include both macroalgae and filamentous algae.

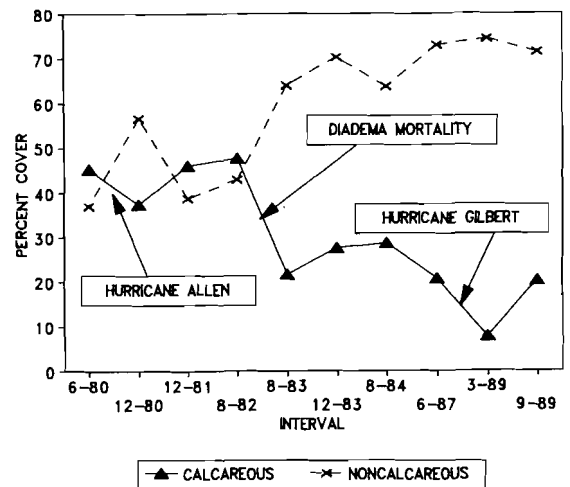


Fig. 3. Change in reef community composition, June, 1980–September, 1989. Calcareous organisms include corals, coralline algae, the calcareous alga, *Halimeda*, and the encrusting foraminiferan, *Gypsina*.

1983, however, following the urchin mortality event, these small corals quickly succumbed to overgrowth by algae (Hughes et al. 1985, 1987; Liddell and Ohlhorst 1986). Along with corals, cover by crustose coralline algae and boring sponges declined as noncrustose algal cover increased (Table 2).

Diadema numbers are still extremely low in fore reef areas (Table 2). The agent for the urchin mortality is unknown (Lessios et al. 1984).

The urchin, *Lytechinus*, also suffered a die-off in September, 1989 at fore reef localities (JD Woodley,

personal communication; also, personal observations). Densities prior to the mortality are not available, although the urchin occurred in much lower numbers than *Diadema* prior to 1983.

Coral Bleaching. Although sporadic and localized bleaching of corals at Jamaica has been observed on several occasions (prior to 1987, observations of JW Porter, noted in Woodley 1988; December, 1990, personal observations of authors), the most significant event in recent years occurred during July-December, 1987. Although at least seven species of scleractinians suffered varying degrees of bleaching, overall mortality was apparently light (Woodley 1988). The occurrence of coral bleaching at Jamaica and elsewhere has been attributed to abnormally high seawater temperatures (Gates 1990) and, possibly, irradiance (Sandeman 1988).

Coral Diseases. Diseases affecting corals, such as black band disease and white band disease, have been occasionally noted on the north Jamaican reefs (personal observations), but only sporadically and in very low frequencies.

Anthropogenic Factors

Overfishing. Human-induced disturbance at Jamaica is poorly documented, yet perhaps extremely significant. Evidence of overfishing at Jamaica (Woodley 1979) and other Caribbean localities has led to speculation that these sites represent greatly disturbed settings as evidenced by an exaggerated dependence upon invertebrate grazers to control algal populations (Hay 1984). Although quantitative data have been lacking until recently, the authors have witnessed a great decline in size of fish and total numbers of fish on the Jamaican reefs over the 1975-1990 interval. Lately, in response to declining catches, many fishermen have resorted to consuming fish "tea" (chowder) in order to utilize catches consisting largely of juvenile fish (Chris Zamora, Canadian Fisheries Project at Discovery Bay Jamaica, personal communication).

The overall increase in algal biomass at all reef sites (including deep sites which never possessed high urchin numbers) and the steady increases in algal abundance at many sites prior to the *Diadema* mortality event indicates that the absence of the urchin is not solely responsible for the observed algal increases. Perhaps these trends reflect the cumulative effects of overfishing on the Jamaican reefs, which were then intensified by the urchin mortality.

Eutrophication. Although base-line data on nutrient concentrations in reef waters are largely lack-

ing, certain indirect lines of evidence suggest that low-level eutrophication may have contributed to the changes occurring on the Jamaican reefs. The increase in large blue-green algal mats in lagoonal areas may be one indication of possible eutrophication (JD Woodley, personal communication). The highly-fractured and dissolved Pleistocene limestone fringing the north coast would provide a ready conduit for the transport of wastes generated by an expanding local population and tourism facilities into the coastal waters. Nitrate-rich groundwater inputs into Discovery Bay have been documented by D'Elia et al. (1981), although they attributed the nitrogen to a natural, rather than anthropogenic source.

Conclusions

It appears that greatly reduced herbivore densities (invertebrate and fish) may have influenced the pattern of succession on Jamaican reefs following physical disturbance events, such as Hurricanes Allen and Gilbert. Presumably this effect was mediated through direct overgrowths of corals and other benthos by algae and/or algal preemption of recruitment (Liddell and Ohlhorst 1986, Hughes 1989). We should caution, however, that documentation of correlation between events does not ensure causality.

Analysis of the degradation of these much-studied reefs is hampered by the lack of long-term data on fish densities and other environmental parameters. Such considerations underscore the importance of the establishment of reef monitoring programs at this and other Caribbean localities. In addition to collecting base-line data on the composition of the reef benthos, the structure of the fish communities, sedimentation rates, and water chemistry must also be considered in order to evaluate the interaction of these diverse factors.

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