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NOTE

Trends in community structure on a Jamaican reef

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ABSTRACT: A quantitative survey of species composition and diversity along depth gradients at Discovery Bay, Jamaica, in 1992 indicated that coral cover was ≤5% at all depths, except at 30 m, where it attained 27%. Percent cover by macroalgae ranged from 44 to 79% over the entire reef, with highest values between 5 and 20 m on the fore reef. Coral diversity increased with depth between a low at reef crest to a maximum of 0.96 (Brillouin's index, H) at 30 m. Total species diversity was highest at the back reef site (2.32). Coral cover at shallow depths (1, 5, and 15 m) was an order of magnitude lower than in 1982. Such striking changes in community structure over the past decade indicate how physical and biological perturbations (e.g. hurricanes, reduced urchin populations and fish grazing) have affected the reef.

KEY WORDS: Algae · Coral · Species diversity · Herbivores · Hurricane · Environmental perturbation

Patterns of reef community structure on the West Fore Reef at Discovery Bay, Jamaica have been described in a series of surveys of large-scale disturbances (Huston 1985, Liddell & Ohlhorst 1986, 1987, 1992, Hughes et al. 1987, Hughes 1994). These disturbances include: Hurricane Allen in 1980, one of the strongest Caribbean storms of this century (Woodley et al. 1981, Kjerfve et al. 1986); mass mortality of the urchin *Diadema antillarum* Phillipi (Lessios et al. 1984, Hughes et al. 1985, Carpenter 1990); Hurricane Gilbert in 1988; and decimation of herbivorous fish populations from overfishing (Munro 1983, Picou-Gill et al. 1991).

Individual reef surveys through time represent 'snapshots' that can be used to assess the importance of various disturbances in community structure. The objective of this study was to quantify how the composition of the sessile reef community has changed as a result of these recent disturbances. Documentation of depth-related trends was made on the Long Term Survey (LTS) buttress of the Discovery Bay West Fore Reef during February and March 1992.

Materials and methods. ***Study site:*** The West Fore Reef of Discovery Bay is located on the north coast of Jamaica (18° 30' N, 77° 20' W; Fig. 1). Depth-related biotic zonation of this reef has been thoroughly described (Goreau 1959, Goreau & Goreau 1973, Lang 1974, Huston 1979, Liddell & Ohlhorst 1987, 1992, Hughes 1994). The LTS reef, which lies within 200 m horizontal distance from study sites used by Huston in March 1977 (Huston 1979) and Liddell & Ohlhorst in May 1980 and August 1982 (Liddell & Ohlhorst 1987), was sampled using line transects (Loya 1978) placed at a depth of 1 m in the back reef, and at depths of 1, 5,

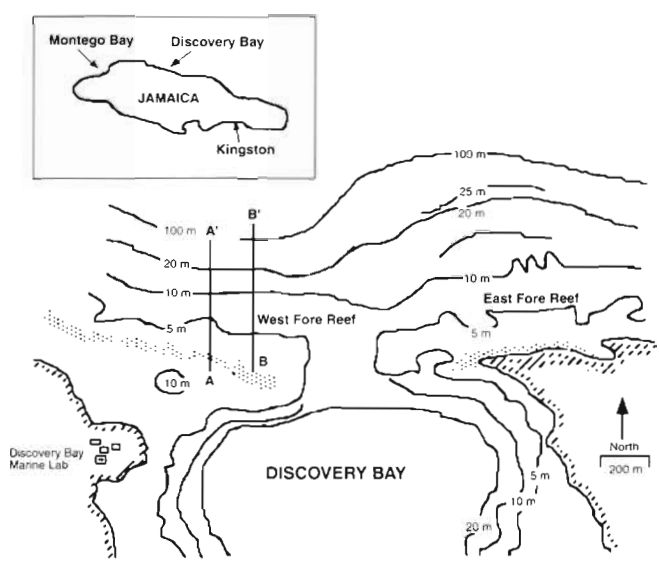

Fig. 1. Map of Discovery Bay, Jamaica (modified from Liddell & Ohlhorst 1987). Census sites in this study were located along the line A–A' Census sites from Huston (1985) and Liddell & Ohlhorst (1987) are shown along line B–B'

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10, 15, 20, and 30 m in the fore reef. Transect lines were placed by an over-the-shoulder blind throw of a 25 m transect tape, marking the transect starting point. The lines did not extend into any major sand channels. The sampling procedure consisted of extending the tape parallel to the depth contour. At 100 randomly located points along the transect tape each sessile organism greater than 5 mm in size beneath the transect point was identified and recorded. Reef substrates were also enumerated as sand or bare hard substrate. The procedure was repeated 4 times per depth yielding approximately 400 data points for each depth contour.

Statistical analyses: Assessment of community characteristics included measurements of species composition of sessile organisms, coral species abundance, percent cover of live macroscopic organisms, coral and total diversity (H; Brillouin 1956) and species richness. Brillouin's index was used to measure diversity because the data set was a finite collection (Pielou 1966). Community structure of sessile organisms was partitioned into 7 functional categories (Steneck & Watling 1982, Morrison 1988) including coral (Scleractinia), macroalgae, coralline algae, filamentous algae, cnidarians (including hydrocorals and soft corals), sponges, living cover, and 2 substrate categories: sand and bare substrate. Macroalgae were grouped as Rhodophyta, Phaeophyta, and Chlorophyta. The percent composition of each species of coral was determined by dividing the number of colonies of an individual coral species by the total number of colonies of all coral species at a given site.

Significant differences ($p < 0.05$) between macroalgae composition, macroalgae percent cover, coral percent cover, total and coral diversity, and total and coral species richness as affected by depth were determined using ANOVA. A Bartlett's test was used to assess normality (data for coral percent cover and coral species number were log-transformed before the test). Based on pooled variance statistics from the ANOVA, Bonferroni tests were used to determine significant differences between means.

Results. ***Living cover:*** For all sites, except the back reef, the cumulative species richness curves (using total species) either leveled-off or increased only slightly, indicating that the sampling area was adequate. Living cover (all categories except sand and bare substrate) was dominated by algae (including macro-, coralline, and filamentous algae) with percent cover ranging from 75 to 94% over the entire reef; the lowest value was at 1 m and the highest at 30 m on the fore reef (Table 1). Coral cover did not exceed 5.0% at all depths except at 30 m where it reached 27%, significantly higher than that at any other depth ($F = 8.36$, $p = 0.0001$; Fig. 2). Macroalgae cover ranged from 44 to 79% over the entire reef with values at 10, 15, and 20 m in the fore reef significantly higher than those at the 1 m fore reef site ($F = 11.48$, $p = 0.0001$; Fig. 3). Rhodophyta comprised 51 and 54% of macroalgae cover at 1 m in the back and fore reefs, respectively; these values were significantly higher than those at all other depths ($F = 44.41$, $p = 0.0001$; Fig. 4). Phaeophyta composition of macroalgae cover was significantly higher from 5 to 20 m in the fore reef than at all other depths (about 60%; $F = 45.65$, $p = 0.0001$; Fig. 4). Chlorophyta coverage ranged from 5.5 to 18% of macroalgae composition over the reef, with its coverage at 1 m in the back reef significantly higher than in

Table 1. Mean percent community composition and diversity (H) from 1 to 30 m on a Discovery Bay (Jamaica) reef as determined by line transects (mean ± SE)

Category	Back reef	Fore reef					
	1 m (397)[a]	1 m (398)	5 m (400)	10 m (400)	15 m (400)	20 m (399)	30 m (274)
Corals	1.5 ± 0.5	3.8 ± 1.2	2.3 ± 0.7	5.0 ± 1.7	3.5 ± 1.2	4.8 ± 0.9	27 ± 7.6
Cnidarians	0.5 ± 0.5	0.5 ± 0.3	0.5 ± 0.3	0.5 ± 0.3	0.3 ± 0.3	0.3 ± 0.3	0.0 ± 0.0
Coralline algae	20 ± 3.5	23 ± 3.0	7.8 ± 1.0	2.0 ± 0.4	2.3 ± 0.5	1.0 ± 0.6	11 ± 2.5
Filamentous algae	5.3 ± 1.3	1.8 ± 0.3	1.3 ± 0.9	1.3 ± 0.6	1.3 ± 0.5	1.8 ± 1.2	3.3 ± 1.5
Macroalgae	50 ± 2.5	44 ± 2.8	70 ± 2.9	79 ± 2.9	74 ± 4.5	78 ± 4.0	52 ± 8.0
Sponges	0.0 ± 0.0	0.1 ± 0.9	0.2 ± 0.9	0.3 ± 0.3	0.3 ± 0.3	0.3 ± 0.3	2.0 ± 0.8
Sand	9.5 ± 4.3	0.0 ± 0.0	2.0 ± 1.2	5.0 ± 1.7	11 ± 2.7	6.5 ± 2.7	2.3 ± 0.9
Bare hard substrate	9.3 ± 1.8	25 ± 2.9	14 ± 1.5	6.8 ± 1.2	6.8 ± 1.1	7.8 ± 0.2	3.5 ± 1.7
Living cover	80 ± 4.8	75 ± 2.9	84 ± 1.2	88 ± 1.7	82 ± 3.6	86 ± 2.7	94 ± 0.9
Total species no.	42	29	22	24	17	23	29
Coral species no.	4	5	4	8	8	7	7
Total diversity (H)[b]	2.32	1.84	1.81	1.63	1.57	1.30	1.88
Coral diversity (H)[b]	0.09	0.34	0.21	0.67	0.50	0.67	0.96

[a]Total no. of transect points (4 lines); [b]Brillouin 1956

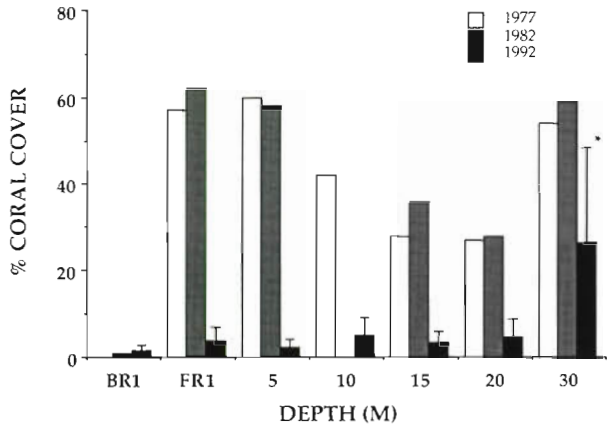

Fig. 2. Percent coral cover in 1977 (Huston 1985; fore reef only), 1982 (Liddell & Ohlhorst 1987; all depths except 10 m on the fore reef), and 1992 (this study) on the West Fore Reef at Discovery Bay. BR refers to back reef, all other depths are on the fore reef (FR). Bars denote 95% confidence intervals. *Lower confidence interval is less than upper; coral cover at 30 m is significantly different from all other depths ($p < 0.0001$, $df = 20$)

the fore reef at 1 m depth only ($F = 3.66$, $p = 0.012$; Fig. 4). Coralline algae coverage peaked at the reef crest (approx. 20%, 1 m depth, back and fore reefs) and at 30 m (11%) in the fore reef. Cover of filamentous algae was 5.3% or less at all depths.

Percent cover of sponges was low over the entire reef, reaching a peak of 2% at 30 m on the fore reef. Cnidarian coverage, which included the hydrocorals (*Millepora alcicornis* Linnaeus and *M. complanata* Lamarck) and soft corals (*Erythropodium* sp.), was ≤0.5% at all depths. Sand cover was highest in the

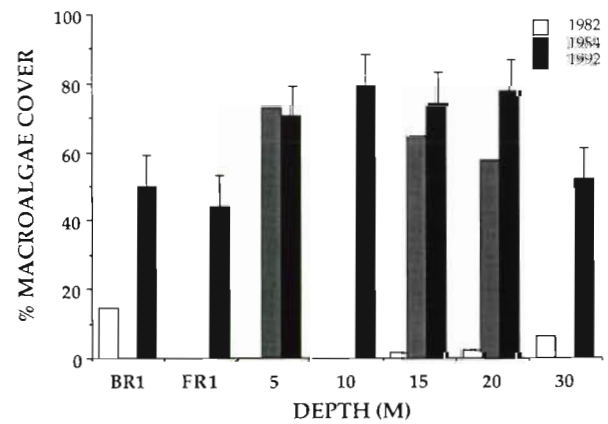

Fig. 3. Percent macroalgae cover in 1982 (Liddell & Ohlhorst 1987; all depths except 10 m on the fore reef), 1984 (Liddell & Ohlhorst 1986; 5, 15, 20 m only), and 1992 (this study) on the West Fore Reef at Discovery Bay. BR refers to back reef, all other depths are on the fore reef (FR). Bars denote 95% confidence intervals

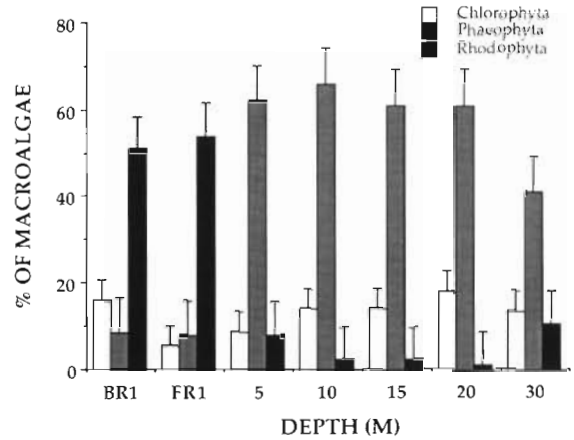

Fig. 4. Percent composition of macroalgae cover (Chlorophyta, Phaeophyta, and Rhodophyta) on the West Fore Reef at Discovery Bay. BR refers to back reef, all other depths are on the fore reef (FR). Bars denote 95% confidence intervals

back reef (9.5%) and at intermediate depths (11%, 15 m fore reef). Bare substrate was highest at the reef crest (25%, 1 m fore reef), but lower in deeper areas (3.5 %, 30 m fore reef).

A total of 16 coral species were found during the survey, with 5 corals (*Agaricia agaricites* Linnaeus, *Diploria strigosa* Dana, *Montastrea annularis* Ellis & Solander, *Porites astreoides* Lesueur, and *Siderastrea siderea* Ellis & Solander) composing 20% or more of the coral at one or more sites. Species replacement occurred in coral along the depth gradient. *P. astreoides* was dominant at the reef crest (1 m of the back and fore reef; 50 and 47%, respectively), *A. agaricites* at intermediate depths (5, 15, and 20 m fore reef; 33, 29, and 37%, respectively), and *M. annularis* at 30 m (54%).

Diversity: Coral diversity increased with depth from the reef crest (1 m) to a maximum at 30 m (Fig. 5) where it was significantly higher than in the back reef and at 5 m in the fore reef ($F = 4.52$, $p = 0.0048$). Coral species richness directly correlated with coral diversity, and was significantly higher at 30 m than at any other depth ($F = 6.50$, $p = 0.001$).

Total diversity was significantly greater at the back reef site than at any other depth ($F = 19.27$, $p = 0.0001$; Fig. 5). Total species richness was also directly related to diversity values, peaking in the back reef and at 30 m. Total species richness at 30 m was significantly greater than species richness from 5 to 20 m on the fore reef ($F = 12.08$, $p = 0.0001$).

Discussion. Community structure of the shallow West Fore Reef at Discovery Bay has changed over the past 15 yr from being dominated by coral to being dominated by algae (Hughes 1989, Goreau 1992, Liddell & Ohlhorst 1992, Hughes 1994). In our study, algae

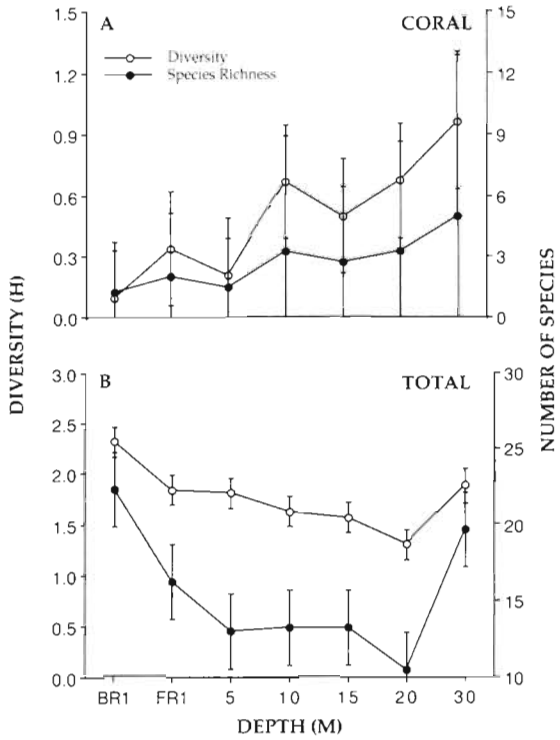

Fig. 5. (A) Relationship of coral diversity and species richness to depth on the West Fore Reef at Discovery Bay. (B) Relationship of total diversity and species richness to depth on the West Fore Reef at Discovery Bay. BR refers to back reef, all other depths are on the fore reef (FR). Bars denote 95% confidence intervals

comprises more than half of the live cover on the buttress. Coral composition is high (27%) only at 30 m, where *Montastrea annularis* is the predominant coral species. In 15 yr, coral has declined from 30–60% of reef coverage in 1977 (Huston 1985) to 5–25% in 1984, after the *Diadema antillarum* die-off (Liddell & Ohlhorst 1986), to 5–15% in 1986 (Gates 1990), to approximately 5% coverage above depths of 30 m in 1992.

The corals which currently inhabit the reef are ones that either survived Hurricane Allen and the subsequent rise in coral predation (Knowlton et al. 1990), are post-hurricane survivors, or early successional opportunists which were not competitively displaced by algae. However, because small corals are typically inferior substrate competitors with algae (Sammarco 1980, Liddell & Ohlhorst 1986), and algal cover has increased on the reef since 1983, it is likely that rates of successful recruitment of corals since Hurricane Allen have been extremely low.

In contrast to the decline in coral cover, the abundance of algae has increased. Although the initial decrease in coral cover occurred in 1980 from Hurricane Allen (Porter et al. 1981, Woodley et al. 1981), it was not until 1984, when the abundances of the grazer *Diadema antillarum* and herbivorous fish were both very low, that algae began to greatly increase in abundance. Liddell & Ohlhorst (1986) found that within 1 yr after the mass mortality of the urchin *D. antillarum* on the West Fore Reef algal cover increased up to 4 times its initial level. In addition, reef algal composition has changed. Algae species which accounted for <5.0% cover over the entire reef in 1982, have greatly increased in percent cover since then. For example brown algae species, which have been found to develop both chemical and morphological resistance mechanisms to herbivores (*Dictyota* sp., Norris & Fenical 1982; *Lobophora* sp., Nicotri 1980; *Sargassum* sp., Brock 1979), now make up more than 70% algal composition of the fore reef. As urchin grazing pressure declined in 1983 from urchin mortality, macroalgae unpalatable to herbivorous fishes (but palatable to urchins) became more abundant. Hurricane Gilbert in 1988 probably contributed to the reduction of these algal populations. But, continued low urchin densities and reduced concomitant grazing after the hurricane resulted in the population's recovery.

A steady decline in herbivorous fish populations has resulted in reduced grazing pressure on algal populations. Documentation of fishing pressure on the West Fore Reef of Discovery Bay has shown that the reef is overfished, and that herbivorous fish populations have been declining for at least the past 15 yr (Munro 1983, Picou-Gill et al. 1991). Although it is difficult to quantify the effects of this type of impact, it has undoubtedly had a positive effect on algal abundances on the reef and should be considered in decisions regarding reef maintenance.

Areas of the reef with the highest algal abundance, and most exposed to hurricane disturbance, have the lowest diversity. Total species diversity is highest at both depth extremes of the study area: 1 m in the back reef and 30 m on the fore reef. Coral diversity, however, is high only at 30 m. The high total and coral diversity at the 30 m site is probably a result of reduced competitive displacement (Porter 1972) and less hurricane impact than at shallow fore reef depths (5 to 20 m). Hurricane induced mortality, fluctuations of water temperature, salinity, and wave action may account for lower abundance, small colony size, lower living cover of coral, and possibly lower coral diversity on the reef flat compared with the deep reef. At deeper sites, where variability in physical parameters are low, biological factors, such as specialization (Loya 1972) or lack of competitive superiority (Porter 1972, 1974), have a greater influence on community diversity.

As physical and biological disturbances may vary over a depth gradient, so might the effects of distur-

bances vary from one reef lobe to another across a reef system. The LTS lobe on the West Fore Reef at Discovery Bay is one that may have suffered more from hurricane damage, and subsequent urchin population reduction, than other buttresses. The effects of large disturbances, such as Hurricanes Allen and Gilbert, the *Diadema antillarum* die-off, and heavy fishing pressure, however, are wide spread on the West Fore Reef and into Discovery Bay (J. Woodley pers. comm.). This indicates that such effects are neither localized nor isolated to a specific area on the reef.

The extent to which both physical and biological disturbances have contributed to changes in reef community structure at Discovery Bay are demonstrated in this and in previous reef surveys. The results of this study indicate that, whereas, acute disturbances (e.g. hurricanes, *Acanthaster planci* plagues, *Diadema antillarum* die-off) change community structure, chronic disturbances (e.g. fishing pressure and algal abundance) influence rate and direction of community recovery. It is likely that if *D. antillarum* and herbivorous fish densities had remained similar to pre-hurricane levels, then the marine benthos of the West Fore Reef at Discovery Bay would still be dominated by corals. However, the combination of both short- and long-term disturbances and overfishing have dramatically changed the reef, and the recovery of coral populations is not imminent.

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