Local variability but landscape stability in coral reef communities following repeated hurricane impacts

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ABSTRACT: Coral reef community structure has remained remarkably stable over a 10 yr period within a small protected marine area despite repeated hurricane impacts. Local community dynamics have been highly variable, however. Sites that were destroyed by disease in the 1970s are showing little or no recovery, while sites less than a kilometre away that were devastated by Hurricane Hugo in 1989 are recovering well. Strong coral recruitment has occurred in shallow, exposed areas that showed the greatest hurricane impacts, and these areas are now more species rich than in 1988, although coral cover has not reached pre-hurricane levels. Coral colony survivorship has been high throughout most of the study area. Partial mortality rates were elevated for several years following Hurricane Hugo, but significant whole coral-head mortality only occurred during periods with hurricane impacts and only at the most exposed sites. Overall, the coral community has proved resilient to closely repeated major hurricane impacts. From a single case study we cannot attribute this resilience to the relatively low level of human impacts, but grazing fish populations have apparently remained high enough to keep macroalgae in check despite the mass mortality of the herbivore *Diadema antillarum* in the 1980s.

KEY WORDS: Hurricane impacts · Disturbance · Coral reefs · Community dynamics

INTRODUCTION

Mortality due to natural physical and biological disturbances is a routine process that is vital to the maintenance of diversity in coral reefs and many other systems. However, coral reefs are being degraded on a global scale by a wide range of impacts, including mass bleaching events (Glynn 1993, 1996, Wilkinson 1998), diseases (Lessios 1987, Aronson et al. 1998, Richardson 1998, Harvell et al. 1999), pollution (Pastorok & Bilyard 1985, Lapointe 1997) and many other human activities (Munro 1983, Richmond 1993). We

therefore urgently need to be able to differentiate between situations where disturbance may lead to a deterioration in community structure from those that may promote it. The Intermediate Disturbance Hypothesis predicts that high-diversity systems are promoted under moderate disturbance regimes (Connell 1978, Karlson & Hurd 1993). 'Moderate disturbance' may include severe mortality events such as catastrophic hurricane damage, provided that there is sufficient time between recurrent events to allow for recovery (Rogers 1993). Thus it is difficult to assess the effects of even apparently devastating impacts without a long-term assessment of the community dynamics (Aronson & Precht 1997, Pandolfi 1999).

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Coral reefs are subject to many types of impacts simultaneously, and the influence of different stressors may be synergistic rather than additive (Hughes & Connell 1999). Some human impacts may act in a similar way to natural disturbances, with the cumulative effect being dependent on the severity and frequency of the impacts. In many cases, however, the effects of human impacts are so persistent and pervasive that a functional coral reef community can no longer survive. A well-documented example is the effects of eutrophication resulting from sewage discharges into Kaneohe Bay (Hunter & Evans 1995). In other cases the causes of decline in community structure are more complex, with multiple impacts coinciding to effect a change. In the case of Discovery Bay, Jamaica, the change over 2 decades from a luxuriant coral-dominated reef community to one overrun by fleshy algae has been attributed to the effects of overfishing, the loss of the key herbivore *Diadema antillarum* to disease, effects of land run-off and the impacts of 2 major hurricanes (Liddell & Ohlhorst 1986, Hughes 1994). The hurricanes effectively removed much of the extant coral community, whilst the persistent low grazing pressure due to removal of fish and urchin herbivores and possibly nutrient enrichment from land run-off has promoted algal growth, inhibiting coral settlement and preventing natural recovery. It is unknown whether the community would have gradually declined in the absence of hurricane impacts, and if so over what time scale, but such fundamental 'phase-shifts' are generally associated with large-scale disturbances (Petraitis & Latham 1999).

Declines in community structure are often attributed to the chronic nature of human impacts as opposed to the more acute disturbances brought about by storms, for example (Connell 1997). Many natural disturbances are discrete, periodic events which allow time for recovery between impacts by larval and fragment-mediated recruitment and growth. Most human impacts such as eutrophication and overfishing are by contrast chronic processes, allowing no such time for recovery. However, we have shown that natural chronic processes such as parrotfish grazing, disease and predation may result in greater cumulative mortality over a 2 yr period than even a major hurricane impact (Bythell et al. 1993b). The effect of a given disturbance at the community level may depend on the scope offered to an individual coral colony to either escape from or recover between subsequent impacts. Thus, parrotfish grazing on coral tissue, coral disease and predation may result in chronic mortality within the reef system but are acute, periodic events at the scale of the individual coral colony. Conversely the effects of overfishing, eutrophication and run-off are persistent across the whole system, with little or no scope for individual corals to escape. The former processes allow greater chances for recovery between events whereas the latter may not, resulting in a higher frequency of whole-colony mortality. Clearly, we must assess particular impacts at scales ranging from the individual coral to the whole reef community in order to understand disturbance-mediated control of local community structure (Connell et al. 1997).

Here we report on a case-study of the effects of 2 recent hurricanes, coupled with 2 major disease epidemics and chronic natural impacts at Buck Island Reef National Monument (BIRNM), St. Croix, US Virgin Islands, in the northeastern Caribbean (Bythell et al. 1993a,b). The island has been under the enforced protection and management of the US National Park Service since 1961 and lies upstream of any local industrial, urban or agricultural sources of pollution. It is therefore a system exposed to relatively low levels of anthropogenic impacts. The site is heavily visited by tourists, but visits are well-managed and concentrated almost entirely within a small 'snorkel trail' at the east end of the island (Gladfelter et al. 1977). Hurricane Hugo (1989) was an extremely intense hurricane (Hubbard et al. 1991), the first to make a direct hit on the island since 1928. Only 6 yr later, in September 1995, 2 hurricanes affected the study site within 2 wk of each other. Hurricane Marilyn made another direct hit on the island and Hurricane Luis affected the island with heavy swells despite passing well to the north. The system has also been subject to 2 region-wide mass mortalities. Epidemic diseases have effectively removed the dominant reef-building coral *Acropora palmata* (early 1970s to present) and the key herbivore *Diadema antillarum* (1983 to 1984) as significant components of the ecological system (Gladfelter 1982, Lessios et al. 1984). We hypothesised that the cumulative effect of these severe natural disturbances, coinciding over such a short period, would result in profound changes to the system, potentially shifting the community to an alternate functional state (Done 1999, Petraitis & Latham 1999).

MATERIALS AND METHODS

Reef community changes. Coral community structure was monitored over time at 3 sites at BIRNM. Within each site replicate determinations were made along 4 fixed, 20 m transects using the well-established chain transect technique. Site locations were previously described by Bythell et al. (1993a). The sites were of distinctly different community composition and topographic structure, broadly described as follows:

- Site 1. Relatively diverse coral community, with moderately high structural relief produced mainly by live colonies of *Montastraea annularis* and *Porites porites*. Moderate coral cover (13 to 29% determined by chain transects). 7 m depth.
- Site 2. Less diverse with very low structural relief; a fairly flat coralline pavement with abundant medium- to large-sized colonies of encrusting *Diploria clivosa* and hemispherical *D. strigosa*. Highest overall coral cover of the 3 sites (32 to 40% determined by chain transects). 4 m depth.
- Site 3. A low diversity, low coral cover site but with high structural relief brought about by mainly dead stands of *Acropora palmata*. Lowest coral cover (0.3 to 6% by chain transect). 3 m depth.

Coral community structure at these sites was analysed by both univariate (percent cover and diversity indices) and multivariate methods (Clarke & Warwick 1994). Multivariate analyses included multidimensional scaling (MDS) analysis of Bray-Curtis similarity measures using double square-root transformations of percent coral cover. Differences between samples were analysed by a 2-way nested ANOSIM without replication, nesting year (1989 to 1996) within transect (n = 4 at each site).

As well as repeated-measures sampling of the permanent transects over time, routine surveys were carried out intermittently at several sites by visual assessment of haphazardly placed 1 m² quadrats. We present here results for only 1 site, on the shallow (2 to 4 m depth) forereef on the south side of the island. This area was by far the most severely damaged during Hurricane Hugo, being virtually razed from the surface to approximately 7 m depth (Hubbard et al. 1991). It is also the area which showed a significant coral recruitment event in 1993, with up to 16 (mean = 7.8) recruits m⁻², consisting of 8 species (Bythell et al. 1993b). Since 1993, densities of recruits (<5 cm diameter) have specifically been monitored during routine surveys in this area by careful visual inspection of 1 m² quadrats subdivided by 10 cm grids.

Coral population dynamics. Three massive coral species were studied, *Montastraea annularis* (Ellis and Solander), *Diploria strigosa* (Dana) and *Porites astreoides* Lesueuer, which are dominant in many reef zones at BIRNM. Fifteen sites, each with approximately 25 permanently marked colonies of 1 of the 3 species, were established in December 1988 (n = 517) and monitored monthly for 26 mo (Bythell et al. 1993b). These corals were also photographed from various angles in spring 1989 and subsequently re-photographed approximately biannually. In this study, photographs were taken in 1996 post-Hurricane Marilyn/Luis, and the entire photographic archive was examined to determine rates of mortality, fission and fusion over 3 periods, including each of the hurricane periods (Hugo = 1988/89 to 1990/91 and Marilyn/Luis = 1993/94 to 1996/97) as well as the intervening period (1990/91 to 1992/93). The periods were approximately 3 yr each, but exact periods for individual coral heads varied because not all colonies could be relocated at each sampling interval. Cases of mortality, fission and fusion were recorded for each individual lobe (physiologically isolated colony) forming part of each coral head. Mortality was also recorded for the whole coral head and was further subdivided into physical removal or burial versus intact but dead. The former usually occurs due to storm damage, whereas the latter is an indicator of biologically mediated mortality such as parrotfish grazing, disease or overgrowth (Bythell et al. 1993b).

RESULTS

Coral community dynamics

At the 3 long-term monitoring sites where coral community structure was surveyed annually, we have seen different degrees of impact from the hurricanes and fundamentally different dynamics following these impacts (Fig. 1). The sites are all within a few hundred metres of each other. At Site 1 there was significant mortality from Hurricane Hugo, and this has been followed by sustained increases in both species richness and cover. The less intense hurricane impacts (Marylin and Luis) in 1995 appear to have had little effect on the recovery process. Species richness was higher at the end of the study than pre-Hurricane Hugo, whereas coral cover had not reached pre-hurricane levels. At Site 2, initially a low diversity area dominated by 2 species, hurricane impacts were minimal, and there has been no concomitant increase in diversity associated with low recruitment. However, coral cover has increased steadily, indicating that colonisable space was available. It appears that the increase in cover is simply due to growth of coral colonies in place at the start of the study. At Site 3, both coral cover and diversity were initially very low and have remained so throughout the study, again showing low recruitment success. This site was previously dominated by elkhorn coral *Acropora palmata* (Bythell et al. 1989), and it appears that a coral community never regenerated in this area following the mass mortality of this species due to white band disease in the mid-1970s (Gladfelter 1982). At no site has mean cover of fleshy algae exceeded ca 10% throughout the study (Fig. 1), so algal overgrowth and competition cannot account for the lack of recruitment success at Site 2. Although mean algal abundance was also low at Site 3, there was high spatial variability (indicated by large error bars; Fig. 1), indicating that competition and overgrowth by ephemeral algae may be much higher than indicated by the mean.
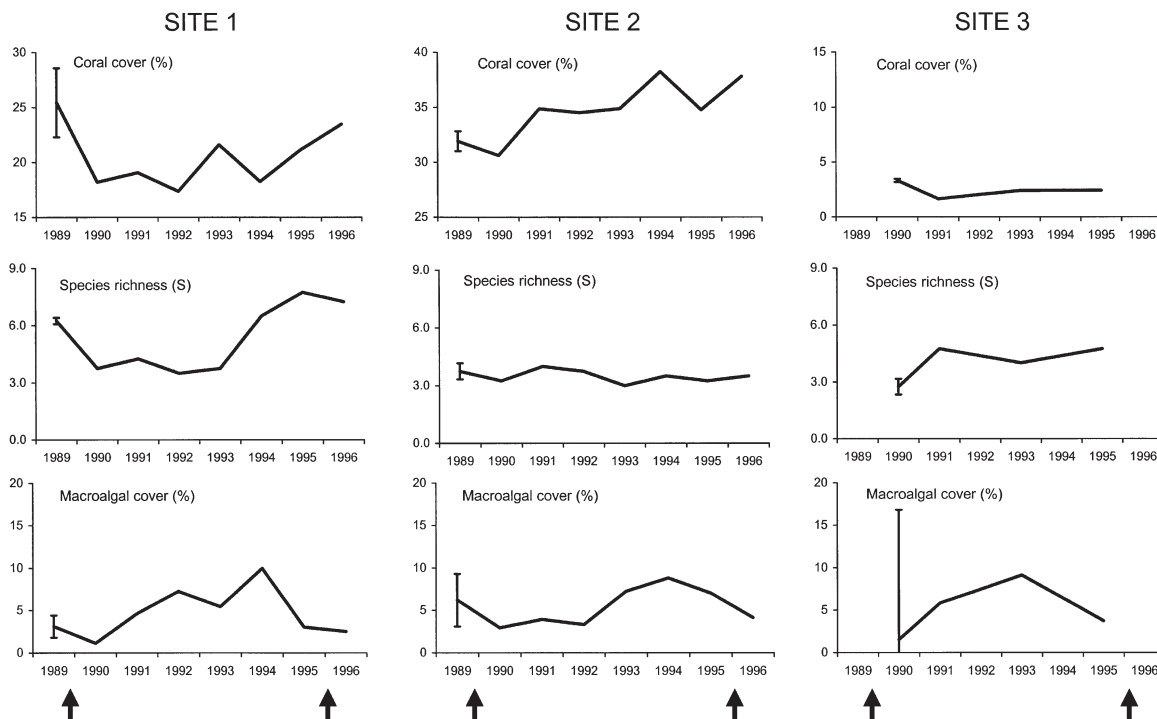
Fig. 1. Changes over time in mean coral cover (%), species richness (S) and macroalgal cover (%) at 3 sites at Buck Island. Permanently marked 20 m line transects were monitored annually at each site. Times of impact of Hurricane Hugo (1989) and Marylin/Luis (1995) are indicated by arrows; 95% confidence limits are shown for repeated measurements of each transect taken on the same day at the beginning of the study

MDS analysis showing similarity in coral species community composition over time at Site 1 (Fig. 2) clearly showed the effects of Hurricane Hugo. Up to 1993, it appeared that community composition remained in the post-hurricane condition for 2 to 3 yr before returning towards (but not reaching) the pre-hurricane condition (cf. Bythell et al. 1993a). However, the introduction of novel species beginning with the
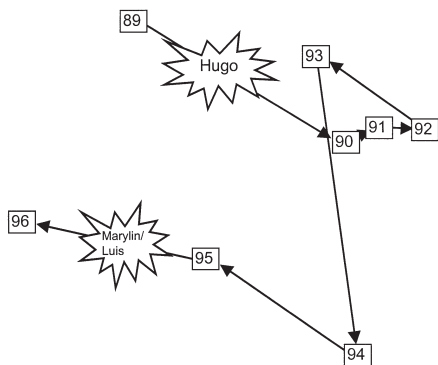

Fig. 2. Multidimensional scaling ordination showing changes in coral species community composition over time. Distances between any 2 samples on the plot represent their approximate similarity in species composition. Stress value for the ordination was 0.03, indicating that the 2D distances between samples is a good representation of their multi-dimensional similarity. Timing of impact of the 2 hurricanes is also shown

recruitment event of 1993 produced a marked shift in the community composition by 1994, which is clearly very different by 1996 to that originally seen in 1988/9. These changes over time at Site 1 were statistically significant, and the community composition of the 4 transects, averaged over years, was also significantly different (2-way nested ANOSIM, R = 0.31, p = 0.006 and R = 0.29, p = 0.019, respectively). There were no significant changes in community composition over time at Site 2 (R = 0.05, p = 0.25) or Site 3 (R = 0.19, p = 0.15), and the MDS plots are therefore not reproduced here. As seen at Site 1, however, there were significant differences between transects at both sites (R = 0.29, p = 0.006 and R = 0.64, p = 0.002, respectively).

When species similarity data are averaged between transects and examined by MDS for all 3 sites over time, it is evident that coral species community composition has remained fundamentally unchanged throughout the course of the study (Fig. 3). The variation between sites is substantially greater than the variation over time, even accounting for the significant changes at Site 1. Thus although local community dynamics are highly variable on the scale of a few hundred metres (Fig. 1), and there were significant differences in community composition over the scale of a few metres (between transects), the landscape community composition appears to have remained stable.
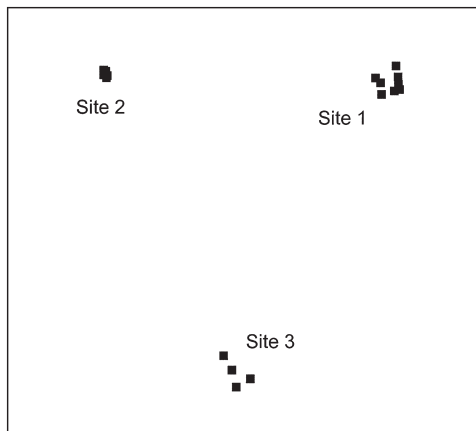
Fig. 3. Multidimensional scaling ordination showing changes in coral species community composition for the 3 sites from 1989 to 1996. Stress value for the ordination was 0.01, indicating that the 2D distances between samples is a good representation of the multidimensional similarities
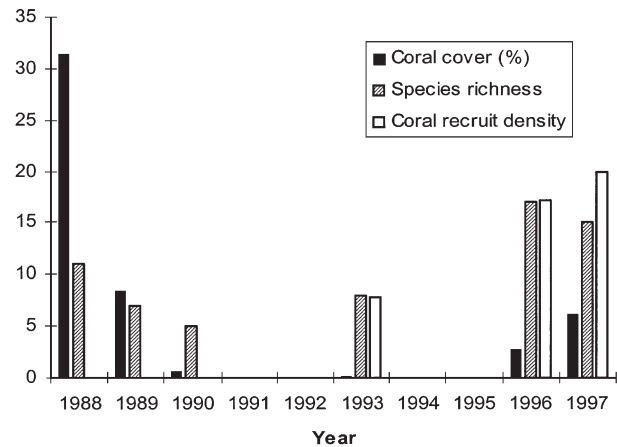

Fig. 4. Changes in coral cover, coral species richness and coral recruitment at a shallow (3 to 4 m) forereef site on the south side of Buck Island, which was heavily damaged during Hurricane Hugo. Data are derived from haphazardly placed 1 m^2 quadrats (n = 11 to 15) within the depth contour and 20 m either side of a fixed transect line. Only the first 11 quadrats were used to estimate species richness between sample times. Standard deviation ranged from 1.4% (1996) to 9.9% (1989) for coral cover and 3.5 m^{-2} (1993) to 10.9 m^{-2} (1996) for recruit density

Not all areas have remained fundamentally unchanged, however. The shallow forereef (<7 m depth) on the south side of the island was almost completely razed by Hurricane Hugo in 1989. Routine surveys using visually assessed 1 m^2 quadrats show that the area has recovered substantially, with coral diversity now greater than it was pre-hurricane in 1988 (Fig. 4). These surveys also show that the area was not completely destroyed during Hurricane Hugo, but that there was a significant period of further decline, with coral cover not reaching a minimum until 1993. Significant and sustained recruitment since then has resulted in coral species richness increasing dramatically to 136% of pre-hurricane levels, although mean coral cover has only reached 20% of the pre-hurricane level. This area which was most severely impacted by hurricane disturbance has shown the greatest improvement in community composition of all sites studied.

Table 1. Frequency of mortality (%) of whole coral heads during the course of the study. Hugo = the period 1989–1991, which included Hurricane Hugo; Intermission = the period 1991–1993; and Marylin/Luis = the period 1993–1996, which included the impacts of Hurricanes Marylin and Luis. Sample sizes shown in parentheses. There were highly significant differences between species (1-way chi-squared, p < 0.001) and between time periods, given species differences (2-way chi-squared, p < 0.001). Note however that the interval including Marylin and Luis was a year longer than the previous two and therefore exaggerates the effects of these hurricanes somewhat

Species	Hugo	Intermission	Marylin/Luis	Total
Porites astreoides	36 (238)	7 (153)	11 (143)	46 (238)
Diploria strigosa	16 (158)	1 (133)	5 (132)	20 (158)
Montastraea annularis	1 (121)	0 (120)	2 (120)	3 (121)

Coral colony dynamics

Overall survivorship of coral heads has been high despite the hurricane impacts, ranging from 54% in the plating/submassive species *Porites astreoides* to 80% (*Diploria strigosa*) and 97% (*Montastraea annularis*) in the 2 massive species over 8 yr (Table 1). As seen in the transect data, Hurricane Hugo caused far greater individual coral mortality than the less intense hurricanes of 1995. Within coral heads, the frequency of partial mortality shows a period of elevated mortality after Hurricane Hugo (Table 2). In 1 species (*M. annularis*) the mortality rate during this period was actually higher than during either of the hurricane periods. This corresponds with the decline in community structure seen on the south shallow forereef during this period (Fig. 4) and strongly suggests a period of delayed mortality from the 1989 hurricane. Virtually all of the mortality occurring during this period between hurricane events was due to factors such as parrotfish grazing damage and disease (Bythell et al. 1993b), which left the dead coral skeleton in place (Table 3). Mortality associated with physical removal of the colony was only prevalent during Hurricane Hugo.

Population dynamics of the cohort of physiologically isolated coral colonies

Table 2. Mortality rate (% yr^{-1}) of physiologically isolated colonies. Mean ±95% confidence intervals calculated from a normal approximation of the binomial distribution (Mason et al. 1989), sample sizes in parentheses. Mortality is expressed per year to control for variation in monitoring periods of individual colonies

Species	Hugo	Intermission	Marylin/Luis
Porites astreoides	15.6 ± 3.8 (356)	12.4 ± 4.4 (217)	3.5 ± 2.5 (201)
Diploria strigosa	12.0 ± 4.3 (214)	2.0 ± 2.3 (141)	0.8 ± 1.4 (163)
Montastraea annularis	6.8 ± 2.4 (418)	8.3 ± 3.3 (266)	3.7 ± 1.9 (382)

reflects not only mortality, but also fusion and fission events, the latter brought about by partial mortality (Hughes & Jackson 1985, Bythell et al. 1993b). Colony fission was common in *Porites astreoides* and particularly *Montastraea annularis* but less common in *Diploria strigosa* (Table 4). However, the frequent partial mortality events in *M. annularis* rarely resulted in whole coral head mortality (Table 1). Colony fusion only occurs during growth and lateral spread of colonies and is clearly more evident during the period between hurricanes (Table 4). The elevated partial mortality during the post-Hurricane Hugo period (Table 2) did not therefore seem to have a strong effect on lateral growth of those colonies which survived.

DISCUSSION

Coral reef systems may be composed of patches that are at different stages of succession depending on the severity of, and time since, the last disturbance (Hughes 1989, Connell et al. 1997). Alternatively, the

Table 3. Frequency of occurrence of mortality (%) of physiologically isolated colonies associated with physical removal of the colony as opposed to *in situ* mortality. See Table 2 for sample sizes and combined mortality rates

Species	Hugo	Intermission	Marylin/Luis
Porites astreoides	52	5	18
Diploria strigosa	74	0	0
Montastraea annularis	5	0	0

different responses seen at Buck Island due to hurricane impacts over the past 10 yr may be due to different mechanisms controlling local community structure. As Karlson & Hurd (1993) assert: 'There is no *a priori* reason why [coral reefs] cannot be viewed as mosaics of species assemblages, some adapted to predictable equilibrial conditions and others to nonequilibrial conditions'. When all samples from the present study are combined, coral species community composition has been remarkably stable. Several authors have suggested that increasing the spatial or temporal scale of observation will lead to increased predictability in community structure (Connell & Sousa 1983, Jackson 1992, Levin 1992, Karlson & Hurd 1993), although Connell et al. (1997) challenge this idea at least for shallow-water, heavily disturbed habitats. Far from showing high levels of disturbance-related mortality, our shallow-water (2 to 12 m) study site has also shown a much lower rate of individual coral mortality than Hughes & Jackson (1985) found for deeper water populations in Jamaica (overall, approximately 28% over 9 yr vs 38% over 3 yr). These findings support broader-scale surveys of the study area which have shown that the substantial loss of coral cover between 1976 and 1990 was virtually entirely due to the loss of *Acropora* species, with other species populations remaining relatively stable (Bythell et al. 1989, Hubbard et al. 1993). Clearly the system has not recovered from the loss of *Acropora* species, notably the major reef-builder *A. palmata*, due to white band disease since the late 1970s. However, the more recent large-scale disturbances of successive hurricane impacts have failed to cause a shift to an alternate state (Done 1992, Knowlton 1992, Hughes 1994, Petraitis & Latham 1999).

The results are consistent with the Intermediate Disturbance Hypothesis as a mechanism for controlling local community diversity (Connell 1978, Sousa 1984, Rogers 1993). In strongly disturbed habitats (e.g. Site 1), which initially showed reduced abundance and species richness, species richness has subsequently increased above the pre-hurricane state due to recruitment of novel species into the area. Several recent

Table 4. Fission and fusion events (% yr^{-1}). Means ±95% confidence intervals calculated from a normal approximation of the binomial distribution (Mason et al. 1989). See Table 2 for sample sizes

Species	Hugo		Intermission		Marylin/Luis	
	Fission	Fusion	Fission	Fusion	Fission	Fusion
Porites astreoides	5.3 ± 2.3	0.4 ± 0.7	4.4 ± 2.7	4.1 ± 2.6	4.1 ± 2.7	0.3 ± 2.8
Diploria strigosa	1.0 ± 1.3	0.2 ± 0.7	1.0 ± 1.6	1.0 ± 1.6	0.8 ± 1.4	1.1 ± 1.6
Montastraea annularis	7.0 ± 2.4	0.6 ± 0.8	7.7 ± 3.2	4.3 ± 2.4	3.4 ± 1.8	0.5 ± 0.7

models suggest that such moderate to high recruitment rates are necessary to maintain the intermediate disturbance principle (Caswell & Cohen 1993, Dial & Roughgarden 1998). Interestingly the community that was not strongly affected by the hurricanes (Site 2) has shown little recruitment, and species richness has remained low and unchanged throughout the study. It is unlikely that coral-coral competition has been responsible for maintaining a low diversity state at these sites. Space competition is widely described as the major controlling factor in the coral reef environment (Connell 1978, Porter et al. 1981, Tunnicliffe 1983, Hughes & Jackson 1985, Lang & Chornesky 1990, Tanner 1997). However, in this case, competition for space has not arisen from corals since coral cover is generally below 30%, and Site 2 showed an increase in coral cover during the study, indicating the availability of free space, but no increase in diversity. Similarly, monitoring of individual coral heads has shown no cases of direct coral-coral interactions (e.g. overgrowth) leading to mortality (Bythell et al. 1993b). The data strongly suggest that low recruitment rates are limiting species diversity in some areas.

Where successful coral recruitment has occurred, it has been shown here to influence the composition of the coral community as profoundly as the disturbance brought about by the hurricane impacts (Fig. 2). Recruitment has been strong on the south side of the island, which showed the greatest physical damage from Hurricane Hugo, and weak on the north side of the island (Wright 1999). In this study, high recruitment success was not dependent on coral mortality alone (i.e. space being made available), since Site 3 had high mortality in the 1970s from white band disease, but has shown no significant recovery. The high recruitment on the south of the island during this study is thus either a coincidence due to high spatial and temporal variability (Wright 1999), or related to the physical disturbance caused by Hurricane Hugo. The implication of the latter is that the disturbance impacted a competitor (or predator) previously limiting juvenile recruitment success. The present study was not able to detect such a competitor. Macroalgal cover (plants >5 cm tall) was not related either spatially or temporally to the areas of high coral recruitment (Fig. 1), nor were any other of the major categories of benthic cover (data not shown). However, further micro-scale studies are clearly needed to assess the mechanisms of competition between benthic organisms and coral recruits and juveniles.

Several of the key findings of this study support those of other long-term (from a human perspective) studies of disturbance in coral communities (Done et al. 1991, Hughes 1994, Hunter & Evans 1995, Connell et al. 1997), namely that coral communities show a range of different levels of impact and trajectories of recovery following impacts. The effects of successive hurricanes are clearly highly variable due to both external factors (e.g. direction of approach and magnitude) and internal factors, including the relative abundance of coral morphs and colony sizes of different susceptibilities to damage (Woodley et al. 1981, Done 1988, Andres & Rodenhouse 1993, Bythell et al. 1993a, Connell et al. 1997, Fong & Glynn 1998) but also historical processes (Tanner et al. 1996).

Whatever the mechanisms it is clear that within this protected area where fishing pressure has been light enough to maintain an adequate algal grazer community, the regional effects of white band disease (Gladfelter 1982) rather than the *Diadema* mass mortality have resulted in the most significant long-term change to local coral community structure. While hurricanes are an important part of the disturbance regime, the high variability in effects over space, over time and between corals with different susceptibilities means that even frequent hurricane disturbance may be 'intermediate' in its effects in promoting system-wide diversity.

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