Coral Reefs (1993) 12:143–152

Coral Reefs

Chronic and catastrophic natural mortality of three common Caribbean reef corals

J. C. Bythell[1], **E. H. Gladfelter**[2] **and M. Bythell**[1]

[1] Centre for Tropical Coastal Management, Department of Marine Sciences and Coastal Management, University of Newcastle upon Tyne, Newcastle upon Tyne, NE1 7RU, UK
[2] PO Box 26472, Gallows Bay, St. Croix, VI 00820, USA

Accepted 18 January 1993

Abstract. Compared to catastrophic impacts from storms, disease epidemics and bleaching events, little is known about the effects of more routine chronic mortality in reef corals. To monitor this ongoing mortality, monthly visual assessments of the cause of tissue damage were related to mortality rates (changes in planar surface area) of tagged colonies of three common reef corals: *Montastrea annularis*, *Porites astreoides* and *Diploria strigosa* at Buck Island Reef National Monument, St. Croix, US Virgin Islands. During the study Hurricane Hugo, the most powerful cyclone to affect the area in at least 60 y, made a direct impact on the site. Effects of the hurricane were extremely localized, with certain exposed sites being almost completely razed while others showed no detectable changes in community structure. Mortality caused both by the hurricane and by other factors during the 26 month study varied between species and also between site locations around the island. Differences in susceptibility were not dependent solely on gross morphology, because two robust, massive species showed opposite responses to hurricane damage and chronic mortality. *Diploria strigosa* was virtually unaffected by chronic factors, but was heavily damaged at exposed sites during the hurricane. In contrast, mortality from predation and tissue necrosis was high in *Montastrea annularis*, but it largely escaped damage from the hurricane because it was absent from the most severely scoured locations. *Porites astreoides*, with populations dominated by much smaller colonies, was affected by both chronic and hurricane-related mortality. Differences in susceptibility to the various types of natural disturbance among species, coupled with high spatial and temporal variability in the effects of such disturbances, may be critical to the maintenance of species diversity on the reef.

Introduction

Evidence that coral reef community structure is influenced by disturbance has been mounting over the past three decades (Connell 1978; Bak and Luckhurst 1980; Porter et al. 1982; Hughes and Jackson 1985; Hughes 1989; Karlson and Hurd 1993). However, quantifying levels of disturbance at different localities is impeded not only by the diversity of types of disturbance (broadly, biological versus physical), but also by the range of time scales over which they occur. Perhaps more importantly, we have little information on the relative susceptibilities of species to the different types and scale of disturbance. Thus, for example, it has been impossible to rigorously test theories of coral community organization (Slobodkin and Sanders 1969; Connell and Slatyer 1977; Karlson and Hurd 1993), or to objectively determine the significance of anthropogenic impacts on reefs (Brown 1988; Rogers 1988).

Hurricanes and other severe disturbances such as bleaching events and disease epidemics have an immediate and obvious effect on the dynamics of coral reef communities (Highsmith et al. 1980; Woodley et al. 1981; Gladfelter 1982; Porter et al. 1982; Rogers et al. 1982; Harriott 1985; Hughes 1989; Brown and Suharsono 1990; Edmunds and Witman 1991; Rogers et al. 1991; Gleason 1993). Such events, although seemingly deleterious over short time scales, may be necessary to prevent competitive exclusion of species, and therefore to help maintain the diverse community structure typical of many coral reefs (Connell 1978). Even without (or in between) these sporadic impacts, coral populations may be highly dynamic. Chronic events cause death or partial mortality of coral colonies, although larval recruitment, asexual reproduction and growth may be sufficient to offset the losses, resulting in an apparently stable population structure (Bak and Luckhurst 1980; Hughes and Jackson 1985). A wide range of chronic biological disturbances have been identified on coral reefs, including various types of predation (Bak and Steward-van Es 1980; Sammarco 1982; Knowlton et al. 1990) and disease (Antonius 1981a, b). Gates (1990) has also shown that in addition to sporadic, severe bleaching events,

---

Correspondence to: J. C. Bythell

chronic coral bleaching occurs throughout the year in Jamaica. However, the rates of mortality resulting from such events relative to physical damage from storms and sedimentation, and to other biological interactions such as space competition (overtopping and shading or direct aggression; Lang and Chornesky 1990), have not been determined.

The aim of the present study was to define the rates and primary causes of partial and whole colony mortality in an area relatively free of anthropogenic impacts. The study area, surrounding an uninhabited island which lies upstream of any local pollution sources, consists of a mainly shallow water (< 12 m depth) bank-barrier reef (Bythell et al. 1989; Gladfelter et al. 1991). It has been managed by the US National Park Service since 1962 and bans on fishing, collecting and anchoring are strictly enforced. In the early stages of the study (September 17–18, 1989) Hurricane Hugo, a major Category V hurricane (Case and Mayfield 1990), passed directly over the island, the most severe storm to affect the area since 1928 (Hubbard et al. 1991; Gladfelter et al. 1991). We were therefore able to contrast chronic-scale disturbances with a catastrophic event and examine the type and magnitude of their effects on mortality in three species of coral: *Montastrea annularis*, *Porites astreoides* and *Diploria strigosa*.

Materials and methods

Study area and site selection

The study was carried out at Buck Island Reef National Monument, St. Croix, US Virgin Islands (17°47′N, 64°37′W) as part of a long-term monitoring program of Caribbean region US National Park Service reef sites (Rogers 1988). The three coral species studied, *Montastrea annularis* (Ellis and Solander), *Diploria strigosa* (Dana) and *Porites astreoides* (Lesueuer) are dominant in many areas at Buck Island (Bythell et al. 1989), and represent 22%, 10% and 12% of live coral cover respectively, averaged between zones. Several genetically distinct variants of *M. annularis* have been identified and only the most common type at Buck Island (Morph I; Knowlton et al. 1992) has been included in this analysis. Fifteen study sites were established in December 1988 each containing approximately 25 permanently marked heads of one of the three species. At these sites *M. annularis* and *D. strigosa* have a massive morphology, while *P. astreoides* forms low mounds or plates. Sites were selected in areas of locally high population densities, adjacent to permanently marked cross-reef transects (Gladfelter et al. 1991), and included backreef and forereef locations on both the north and south sides of the island (Fig. 1). Within sites, 25–30 coral heads were selected by swimming a haphazard, roughly circular transect and marking all heads encountered with numbered plastic tags. Tags were attached to the nearby substrate using masonry nails and plastic cable ties. At only one location were all three species found to co-occur in sufficient densities to establish overlapping sites (sites M4, D4 and P4; Fig. 1).

For the purposes of this study, the coral colony was defined as the physiologically isolated tissues which may have arisen either from sexual recruitment or by fission of a parent colony. In addition, what were believed to be genetically identical heads composed of several such colonies were identified in the field by the close proximity of separate tissues and similarities in skeletal morphology and tissue colour. These heads may not have comprised the entire genet, since fragments may be scattered by storms (Highsmith 1982), but it was of interest to determine mortality rates for whole heads as well as individual colonies since this represents a reduction in genetic diversity in the immediate area.

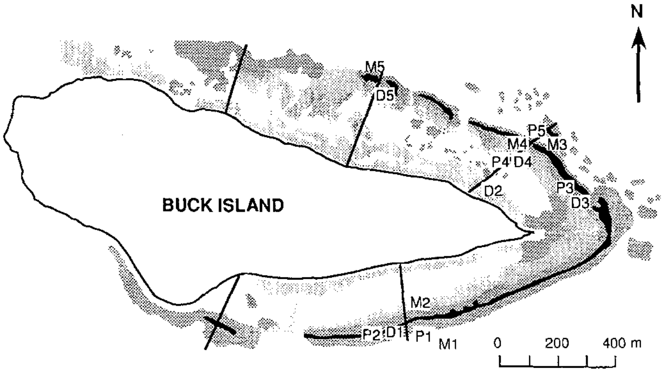


Fig. 1. Location of the fifteen tagged coral sites, five of each species (M1–M5, *Montastrea annularis*; P1–P5, *Porites astreoides*; D1–D5, *Diploria strigosa*). The reef crest zone is shown in black, forereef and backreef zones are shown by darker shading and lagoonal pavement areas by lighter shading. Locations of five permanent transects maintained by the National Park Service (Gladfelter et al. 1991) are indicated by heavy lines radiating out from shore. Sites located in the reef crest/shallow forereef on the south side (D1, P1 and P2) were the only ones severely damaged during the hurriance

Coral colony dynamics

Each tagged coral head was inspected monthly for tissue damage and necrosis. The estimated extent of any damage was categorized into three classes according to total surface area of the individual colony affected (I. < 10%, II. 10–50%, or III. > 50%). Details of larger areas of mortality (> 10% of the colony surface area) were recorded, including the estimated surface area affected and a sketch map of its location within the colony. Laminated photographs of each colony taken from various angles were taken into the field for reference. The reference photographs were repeated after any major mortality event to provide a baseline for subsequent observations. A short-term (58 d) photographic and visual study (Gladfelter et al. 1991) showed that repair rates were similar for the three species. This study also showed that larger areas of tissue loss would not be fully repaired or disguised by fouling algae between monthly observations, although small lesions such as single parrotfish bites could be repaired within as little as five days. Consistency between observers was tested for by comparing assessments made by three observers who monitored the same 30 colonies on the same day and differences were found to be insignificant (Cochran's Q-test, $0.5 > P > 0.1$).

Vertical photographs of all tagged corals were taken between April and July 1989 and repeated 26 months later in 1991. Vertical camera distance was fixed between repeat photographs. Transparencies were projected and digitized (Summagraphics II digitizer with Easydij 7.0 planimetering software). Changes between the 1989 and 1991 photographs were recorded, including the surface area of any tissue loss (partial mortality), total colony mortality, and cases of colony fission and fusion. Specific areas (events) of mortality within each colony were related to the monthly monitoring record to determine the cause and time of change. Occasionally, two or more events of tissue damage of approximately similar magnitude were recorded in the monthly monitoring which could not be distinguished on the photographs. In these cases, surface area losses determined by computer digitization were divided equally among the causes. Errors of less than 5% were found for surface area determinations.

In calculating frequency of mortality events due to various causes, certain assumptions were made. Frequency of partial mortality events may exceed the number of colonies showing partial mortality, since each colony may be affected by more than one event. However, whole colony mortalities were treated as single events, possibly with multiple causes. It was assumed that if a colony suffered > 10% surface area loss by several factors, each contributed equally to the final demise of the colony. Thus, for example, a colony affected by two separate grazing events and later killed by a disease event was scored 2/3 and 1/3 for grazing- and disease-related whole colony mortality. If the colony had survived, it would have been scored as 2 (grazing) plus 1 (disease) partial mortality events.

Results

Effects of Hurricane Hugo

Hurricane Hugo accounted for 1.8%, 8.3% and 30% mortality (percent of the initial sample planar surface area) in *Montastrea annularis*, *Porites astreoides* and *Diploria strigosa*, respectively. These losses represent 11%, 31% and 97% of the mortality due to all factors combined during the course of the 26 month study (Fig. 2). The extent of hurricane damage was strongly influenced by location (Table 1). Two sites on the south reef crest (P2 and D1) were completely destroyed by burial under a 1-m deep rubble rampart created by the virtual destruction of the shallow forereef on the south side of the island. Site P1 was located on the shallow south forereef and approximately 77% tissue loss was recorded in the tagged *P. astreoides*

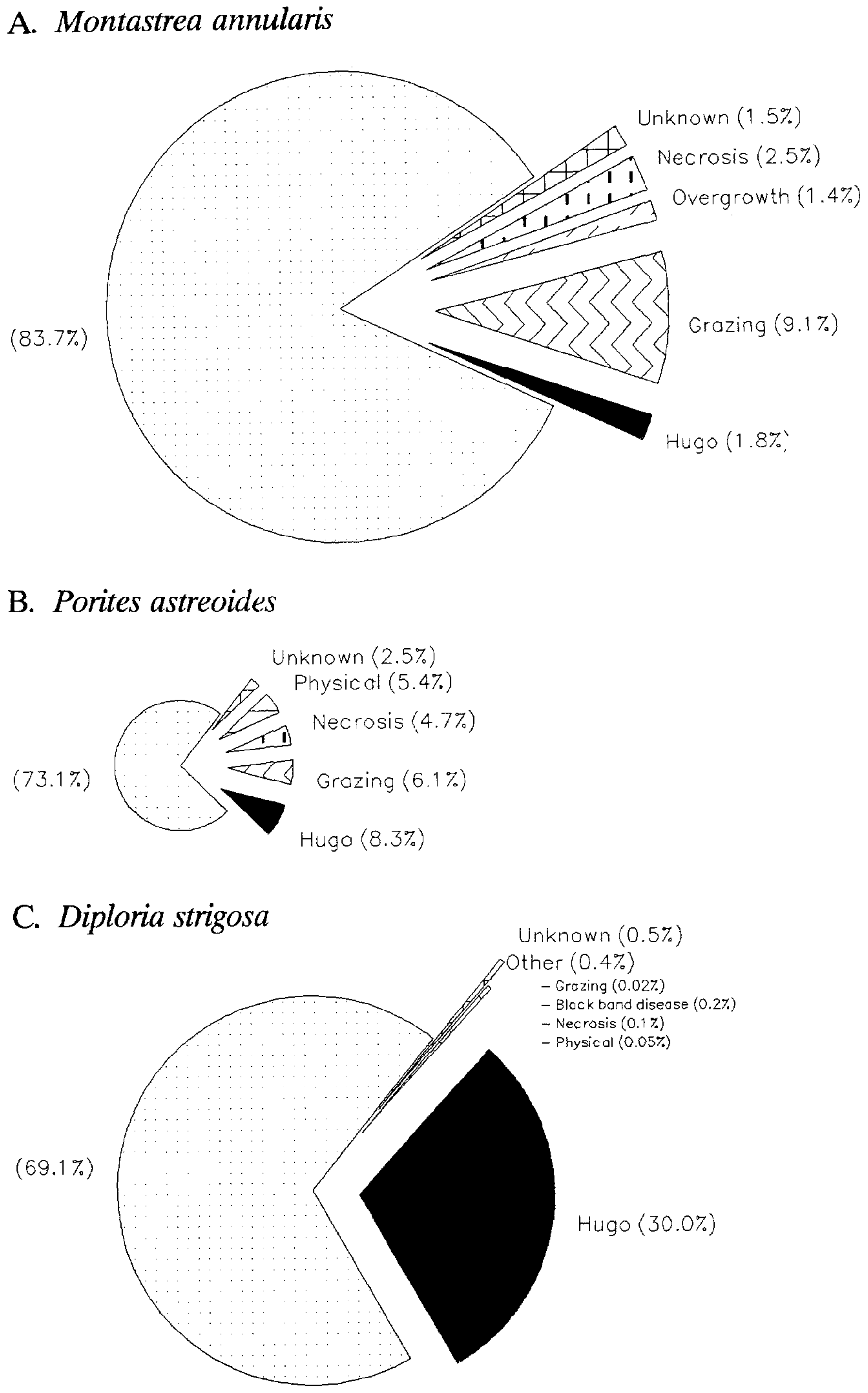


Fig. 2A–C. Pie charts showing the percent surface area mortality due to different factors over the course of the study, based on the initial (1989) surface area of the entire sample. Total area of the pies has been scaled to the median surface area of whole coral heads of each of the three species at Buck Island in order to compare absolute levels of mortality due to each factor. Stippled area represents tissue surface area surviving at the end of the study. See text for explanation of the different causes of mortality such as necrosis (tissue necrosis), overgrowth (algal and invertebrate overgrowth), grazing (parrotfish grazing) and physical (physical breakage or toppling of the colony, other than during the hurricane)

Table 1. Planar surface area losses and frequency of mortality caused by the direct effects of Hurricane Hugo (HUGO) and all other factors (OTHER) during the 26 month study. Surface area losses include both total and partial mortality. TSA = the total initial (1989) sample surface area and, in parentheses, the sum of surface area mortality due to all factors. *n* = number of colonies, with number of cases of partial mortality, followed by number of fatalities due to all causes in parentheses. Total *n* of physiologically isolated tagged colonies analyzed = 978, "–" = no sample; all colonies were destroyed in the hurricane, "*" = small sample size; 74% of colonies were destroyed in the hurricane at P1

Site	Surface area losses		Frequency of partial colony mortality		Frequency of total colony mortality		TSA (cm^2)	*n*
	HUGO (%)	OTHER (%)	HUGO (%)	OTHER (%)	HUGO (%)	OTHER (%)		
A. *Montastrea annularis* ($n = 512$)								
M1	0.3	16.9	0.7	44.4	1.5	6.7	9569 (1648)	135 (61, 11)
M2	0	24.4	0	42.3	0	7.7	802 (196)	26 (11, 2)
M3	3.1	8.3	7.0	12.8	7.0	11.6	1472 (168)	86 (17, 16)
M4	3.9	17.6	9.0	35.0	9.1	17.4	10861 (2337)	234 (103, 62)
M5	0	1.1	0	6.4	0	0	4287 (48)	31 (2, 0)
B. *Porites astreoides* ($n = 323$)								
P1	77.1	5.7*	2.3	4.6*	74.4	4.6*	2956 (2447)	43 (3, 34)
P2	100	–	0	–	100	–	2248 (2248)	38 (0, 38)
P3	0.2	8.9	0	19.8	1.0	16.7	16957 (1554)	96 (19, 17)
P4	1.7	29.0	0	47.6	2.4	9.5	6869 (2107)	42 (20, 5)
P5	0.1	18.7	1.0	33.7	0	15.4	27533 (6913)	104 (35, 16)
C. *Diploria strigosa* ($n = 143$)								
D1	100	–	0	–	100	–	40786 (40786)	37 (0, 37)
D2	0	0.7	0	6.2	0	0	4764 (33)	16 (1, 0)
D3	0	2.2	0	15.0	0	0	27296 (596)	20 (3, 0)
D4	0.4	0.3	17.5	0	15.0	2.5	21350 (156)	40 (7, 7)
D5	0.1	1.1	3.3	23.3	6.7	0	42738 (485)	30 (8, 2)

colonies at this site. Elsewhere, hurricane damage was remarkably light; <4% of the initial sample surface area. At the single location with contiguous sites (M4, P4 and D4), *M. annularis* actually showed slightly greater losses to hurricane damage than the other species, although this was only just significant in comparison with *P. astreoides* (Kolmogorov-Smirnov D = 0.23, $0.05 > P > 0.01$, all other combinations $P > 0.05$). The Kolmogorov-Smirnov two-sample test was used due to the highly non-normal distribution of mortality data; colonies tended to be either undamaged or completely killed by the hurricane (Fig. 3). Although the hurricane resulted in reductions in planar surface area of less than 4% at sites on the north side of the island, this accounted for about 28% of the whole-colony mortalities recorded over 26 months due to all factors combined.

Chronic tissue damage

Outside the three severely impacted sites P1, P2 and D2, chronic mortality over the 26 month study generally accounted for a greater loss of tissue than Hurricane Hugo (Table 1). Frequency of chronic mortality was significantly different between sites for all species (log-likelihood ratio, $P < 0.05$). As might be expected, chronic mortality resulted in a greater frequency of partial versus whole colony mortality, the opposite of the case with hurricane-related mortality (log-likelihood ratio, $P < 0.001$ for all species).

Predation by grazing parrotfishes was the most serious cause of chronic coral tissue loss (Table 2), although *Diploria strigosa* was notable for being largely unaffected by chronic factors. Larger queen and stoplight parrotfish (*Scarus vetula*, *Sparisoma viride*) were observed to be the main grazers, producing an obvious scar or groove recognizable for several weeks after the event, particularly on

Table 2. Mortality rates (percent of the initial 1989 surface area of tissue for the entire sample) due to factors other than the hurricane, attributed to specific causes. See Table 1 for sample sizes. * Tissue necrosis may have been caused by several factors (see text). "Unknown" factors, i.e. mortality not detected during monthly observations, were probably caused by a cumulative loss of small amounts of tissue over time, since only mortality events > approx. 10% of the colony surface area were recorded and specified by cause from visual surveys

Cause	*Montastrea annularis* (%)	*Porites astreoides* (%)	*Diploria strigosa* (%)
Biological			
Predation – parrotfishes	9.06	6.09	0.02
Predation – damselfishes	0.07	0	0
Overgrowth – algae	1.35	0	0
Overgrowth – other invertebrates	0.03	0	0
Tissue necrosis*	2.45	4.72	0.10
Black band disease	0	0	0.18
Subtotal	12.96	10.81	0.30
Physical			
Toppling followed by scouring and/or burial	0	5.36	0.05
Unknown	1.47	2.50	0.49
Total	14.43	18.67	0.84

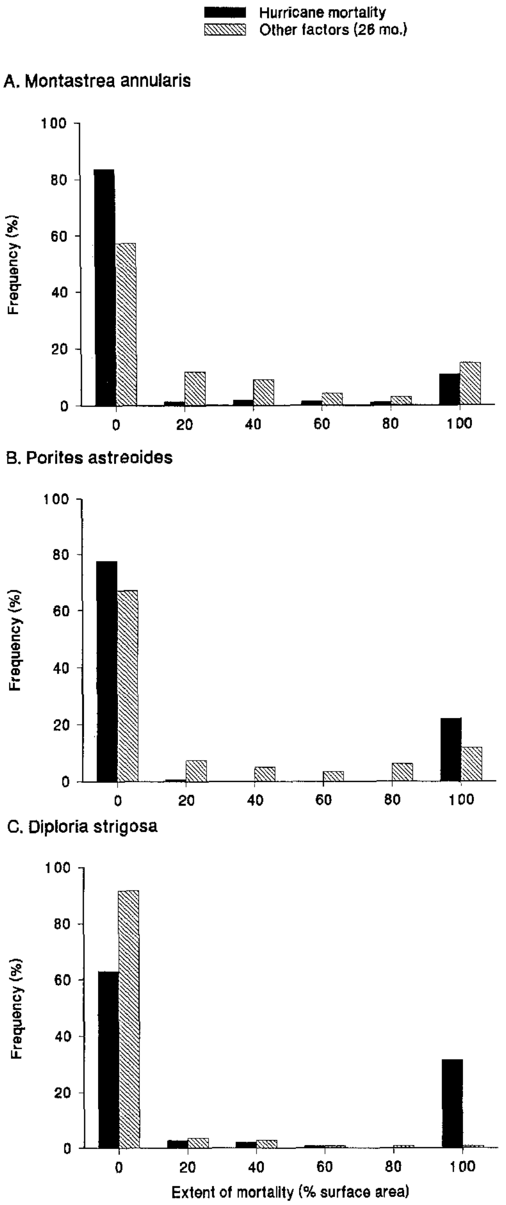


Fig. 3A–C. Frequency distributions for the degrees of mortality (percent surface area loss) due to the hurricane and due to all other factors during the study. Sample sizes were 512, 329 and 143 for *Montastrea annularis*, *Porites astreoides* and *Diploria strigosa*, respectively

the larger areas of grazing (> 10% surface area) recorded during visual assessments. Damselfish grazing caused tissue loss without obvious skeletal damage, but all such losses within the tended algal mat were attributed to the damselfish. Tissue necrosis was also a frequent occurrence, but this condition was produced by various causes: tissues were occasionally seen sloughing off the skeleton, possibly due to disease or "stress-related necrosis" (Antonius 1981b). Necrosis was also seen to occur in close association with clumps or mats of filamentous cyanobacteria. Invertebrate grazing, for example by the gastropod *Coralliophilia abbreviata*, may cause tissue loss of similar appearance, but was not observed at any site during the study (*Coralliophila* population densities were too low to be detected by random 1 m^2 quadrats [$n = 450$]; Bythell et al. 1989). Coral bleaching and sedimentation did not cause a significant amount of mortality during the study. As with hurricane damage, *M. annularis* and *P. astreoides* colonies tended to either escape from damage by chronic factors or be completely killed, whereas *D. strigosa* showed little whole colony mortality due to factors other than the hurricane (Fig. 3). All species showed significant differences in the distribution of degrees of mortality related to the hurricane versus other factors over the 26 month study (Kolmogorov-Smirnov; $P < 0.01$ for *D. strigosa* and *M. annularis*, $0.05 > P > 0.01$ for *P. astreoides*).

Effect of colony size on mortality

Montastrea annularis and *P. astreoides* showed size-frequency distributions dominated by the smallest size-classes, while *D. strigosa* appeared to have a more even distribution throughout its size range (Fig. 4). When data for whole coral heads were examined, however, *M. annularis* had a very similar distribution to *D. strigosa*. Mortality rates decreased with colony size in *M. annularis* and *P. astreoides* (Fig. 5A, B). The probability of a colony being damaged by chronic factors increases with colony size (Fig. 5A, B; centre panels), but the likelihood of the damage resulting in whole colony mortality decreases with size (Fig. 5A, B; left and right panels). *Porites astreoides* showed higher colony mortality rates due to the hurricane than *M. annularis*, and the decrease in mortality with size was not as pronounced. Mortality rates were not apparently dependent on size-class in *D. strigosa* (Fig. 5C; log-likelihood ratio $P > 0.5$ except partial mortality due to the hurricane, $P = 0.001$). Colony losses to chronic factors were so low in *D. strigosa* that no relation with colony size was evident (a single colony was killed out of a sample of 143). Although *M. annularis* showed high colony mortality rates, the colonies were all lobes forming part of a larger genet, and no whole heads were killed during the study (i.e. 0 out of 68 heads believed to represent separate genets), whereas both the other species sustained considerable loss of whole heads (*P. astreoides*: 71/193, *D. strigosa*: 37/107).

Temporal variation in chronic tissue damage

Frequencies of parrotfish grazing damage and tissue necrosis, defined as the occurrence (%) of colonies newly affected during monthly surveys, were in general slightly higher post-hurricane than pre-hurricane (Fig. 6A, B). Frequencies of both conditions varied significantly between time periods (log-likelihood ratio; $P < 0.01$), except for grazing in *D. strigosa* and tissue necrosis in *P. astreoides*. The different levels of parrotfish grazing in the three species is striking (Fig. 6A), with *M. annularis* consistently having the highest incidence rates and *D. strigosa* the lowest.

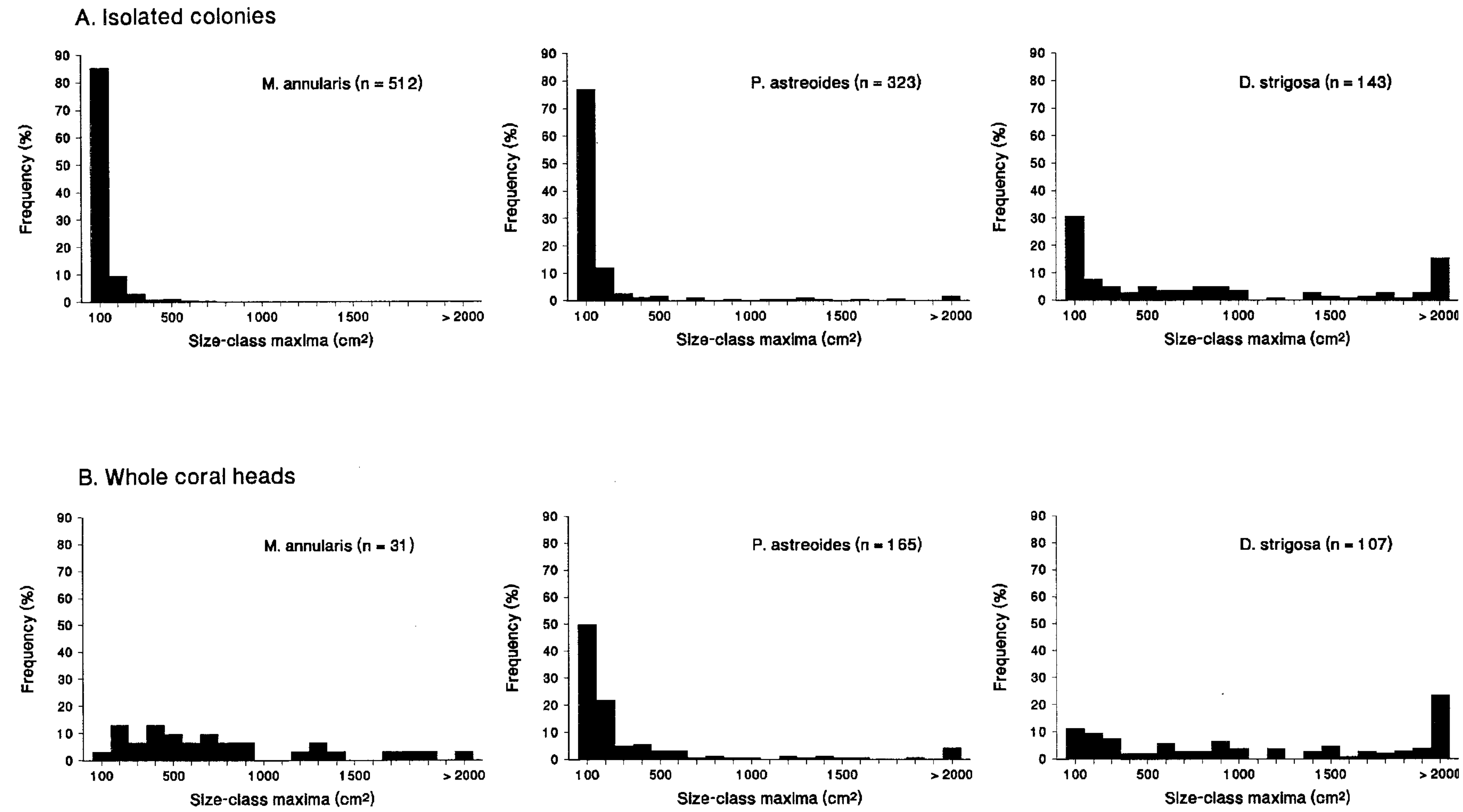
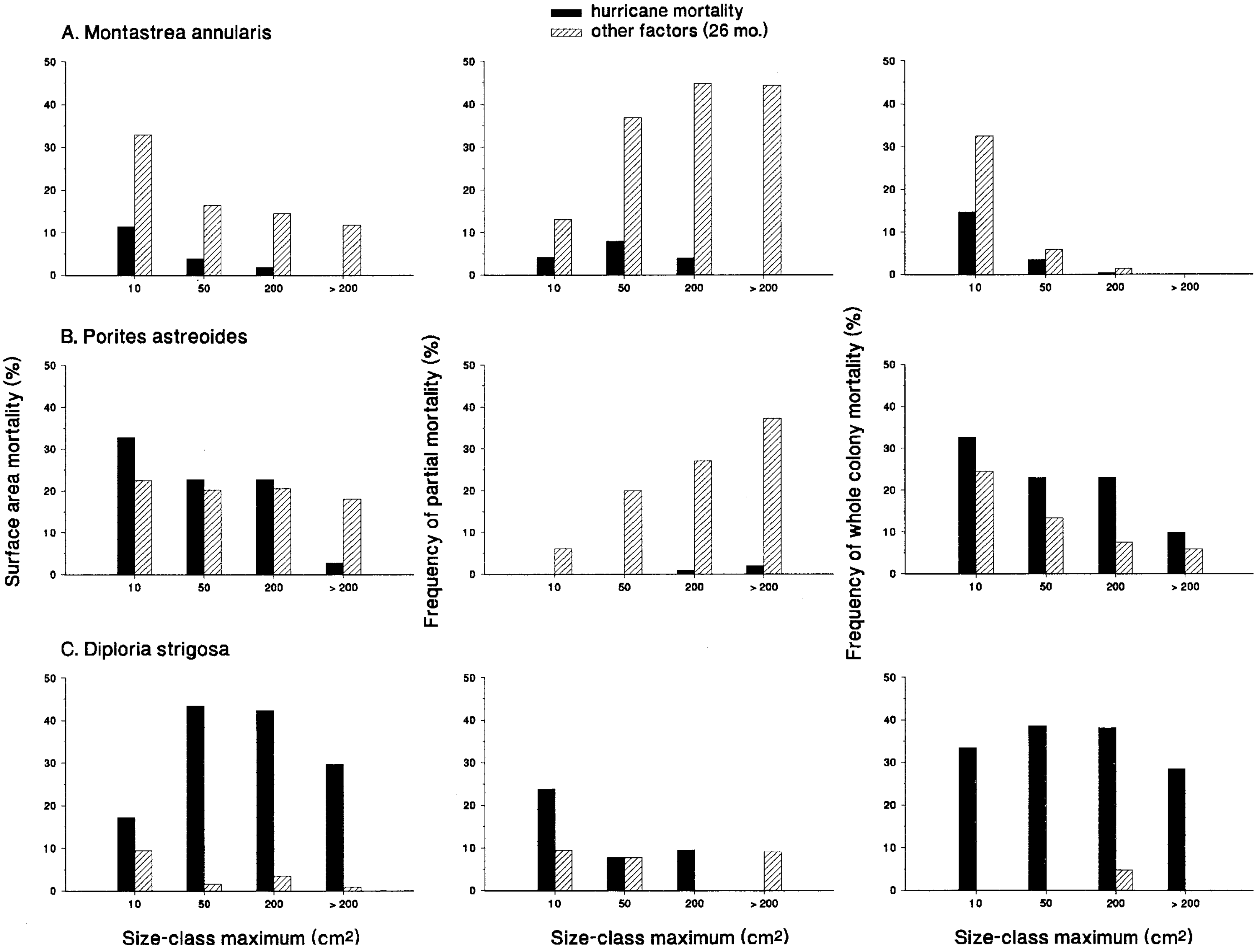


Fig. 4A, B. Size-frequency distributions for the three species based on (**A**) isolated colony surface areas and (**B**) whole coral head surface areas. Coral heads were believed to represent whole genets

Fig. 5A–C. Mortality patterns in relation to colony size in the three species. Mortality is presented as percent surface area losses (*left panels*), frequency of colonies with partial mortality (*centre panels*) and frequency of colonies completely killed (*right panels*) over the course of the study. Sample sizes were 512, 329 and 107 for *M. annularis*, *P. astreoides* and *D. strigosa*, respectively


hurricane mortality
other factors (26 mo.)
A. Montastrea annularis
B. Porites astreoides
C. Diploria strigosa
Surface area mortality (%)
Frequency of partial mortality (%)
Frequency of whole colony mortality (%)
0
10
20
30
40
50
10
50
200
> 200
Size-class maximum (cm2)
Size-class maximum (cm2)
Size-class maximum (cm2)

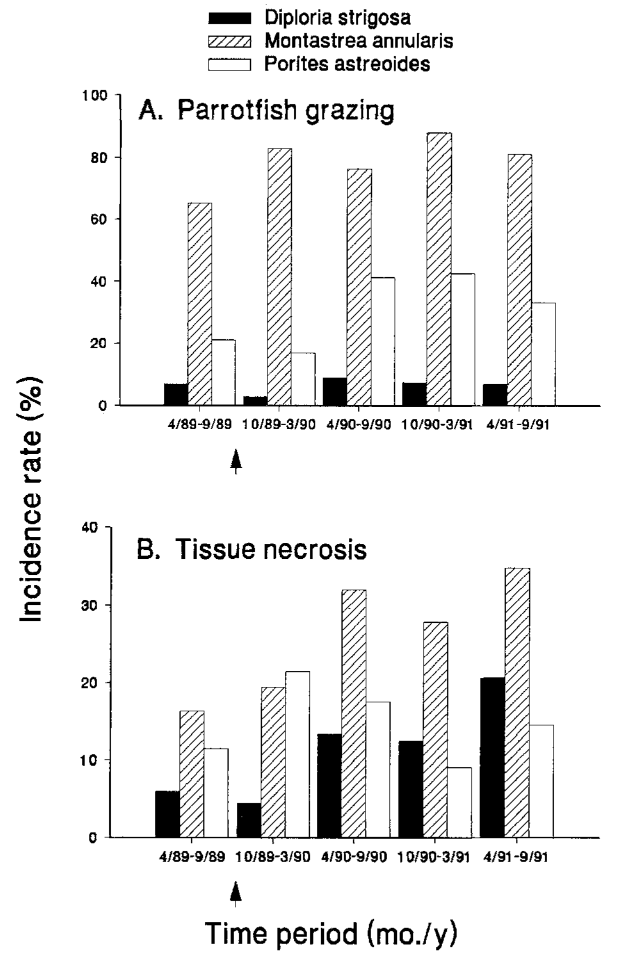


Fig. 6A, B. Six-month incidence rates (percent of colonies) of (**A**) parrotfish grazing and (**B**) tissue necrosis over time. Only new incidences were included, that is, cases of colonies showing the effect which did not show the effect during previous monthly monitoring. Arrows indicate the time of impact of Hurricane Hugo

Tissue turnover rates, colony fission and fusion

Tissue turnover rates were calculated as the time (y) that it would take to lose the entire initial sample surface area at the rates of whole and partial colony mortality, excluding hurricane damage, encountered during the study. Turnover rates were far slower in *D. strigosa* (179 y) than in *M. annularis* (15 y) and *P. astreoides* (13 y), reflecting the low level of damage from chronic mortality in *D. strigosa* and the importance of episodic events.

Table 3. Coral colony population dynamics over the 26 month study. All percentage data are related to the initial (1989) number of colonies in the sample

	M. annularis $n = 512$	*P. astreoides* $n = 323$	*D. strigosa* $n = 143$
Average number of physiologically isolated colonies per coral head (= estimated genet) in 1989	13.0	1.7	1.3
Colony mortality	17.8%	34.1%	32.2%
Fission	18.4%	16.7%	0.7%
Fusion	0.6%	1.8%	1.4%
Net change in number of colonies 1989–1991	0	−19.2%	−32.9%

Colony fission generated many new colonies in *P. astreoides* and *M. annularis* compared with *D. strigosa* (Table 3). Despite this, high mortality rates in *P. astreoides* resulted in an overall reduced population size. Mortality approximately equalled fission in *M. annularis* and population size remained stable. Lower fission rates in *D. strigosa*, coupled with high hurricane-related mortality resulted in a substantially reduced population size. Colony fusion did not play an important role in changing population size in any species (Table 3).

Discussion

This study supports the idea that hurricanes may act as a structuring force on coral community organization (Connell 1978; Woodley et al. 1981; Porter et al. 1982; Hughes 1989). Although strong hurricanes may impact our study site only at 60 + y intervals (Hubbard et al. 1991), populations of both *Montastrea annularis* and *Diploria strigosa* are sufficiently long-lived that they contain many colonies which have survived major hurricanes in the past. *Diploria strigosa*, while being virtually immune to mortality from chronic day-to-day impacts over a 26 month period, suffered extensively during Hurricane Hugo. Conversely, *Montastrea annularis* showed substantial chronic losses, mainly to predation and tissue necrosis (Fig. 2). Hurricane mortality was also significant, but its impact decreased sharply with colony size and did not kill whole genets. Although there was some evidence that mortality rates were elevated during the two years post-hurricane (Fig. 6), there was no dramatic population collapse comparable with that seen in *Acropora cervicornis* populations in Jamaica following Hurricane Allen (Knowlton et al. 1990). Consequently, tissue turnover rates found for *M. annularis* of 15 y are comparable with previous estimates for the species from deeper water (36 y calculated from colony mortality data; Bak and Luckhurst 1980, and 26 y reported by Hughes and Jackson 1985), while rates of 179 y for *D. strigosa* were well outside these ranges. No existing data were available for comparison for *D. strigosa*.

Significant variation was seen in mortality rates between sampling sites which were within a few hundred meters of each other (Table 1). This indicates that disturbance levels, or the responses of each species to these disturbances are very patchy, and may vary in response to relatively small differences in environmental conditions.

The large differences in chronic mortality rates between species (Fig. 2) reinforces the need to account for coral population dynamics when establishing monitoring programs or assessing environmental impacts on reefs (Brown and Howard 1985; Brown 1988; Rogers 1988). Only slight changes in coral cover may involve highly significant whole colony losses in terms of the routine population turnover of normally resistant species such as *Diploria strigosa*. This species showed hurricane-related reductions in planar surface area of 0.4% and 0.1% at two sites on the north side of Buck Island; changes undetectable by standard methods of reef community assessment (Hubbard et al. 1991; Gladfelter et al. 1991). This apparently tiny loss represented 86% and 100% of the whole colony mortality rates due to chronic factors over 26 months, however. Size-frequency distributions for both the massive species *M. annularis* and *D. strigosa* suggest that they have not recruited successfully in large numbers at Buck Island in recent years. It therefore seems unlikely that *D. strigosa* populations will recover rapidly, particularly in the shallow areas of the south reef, which were severely damaged during the hurricane. To regain the pre-hurricane population structure will take decades at least. *Montastrea annularis*, while apparently not recruiting in abundance, routinely undergoes a high degree of chronic mortality which is apparently compensated for by colony fission and growth. The population size (colony numbers) of this species thereby remained stable over the period of the study, despite the hurricane. Since no whole genet loss was recorded for *M. annularis* in our study, the pre-hurricane population structure could be regained in just a few years, without any further interruptions in the recovery process.

Porites astreoides shows the life-history characteristics and population dynamics of a more opportunistic or "mobile" species (Loya 1976; Hughes and Jackson 1985). Its size-frequency distributions suggest an actively recruiting population. Mortality rates were substantial, both on a chronic basis and due to the hurricane, and mortality did not drop as sharply as *M. annularis* in relation to colony size (Fig. 5). These attributes may explain why *P. astreoides* dominates the shallow forereef, a zone where *M. annularis* is virtually absent and *D. strigosa* is a relatively small component of the community (Rylaarsdam 1983; Rogers et al. 1984; Chornesky and Peters 1987). Hughes and Jackson (1985) observed that more mobile species such as *P. astreoides* are favoured in shallow, more disturbed habitats whilst more robust, massive species are often favoured in deeper, less disturbed ones, despite the fact that the latter may be more resistant to physical perturbation from wave-action.

Bak and Luckhurst (1980) suggested that predation pressure, in addition to physical disturbance, may be higher in shallow water. Results of their seven year study also showed that "catastrophic" events (loss of the entire colony, including dead skeleton, between monitoring periods) were the main cause of mortality, presumably due to physical disturbance during storms. Physical disturbance was not a major cause of coral mortality in the present study, except that due to the hurricane. Therefore even in shallow-water environments it is possible for the major causes of chronic mortality to be biological, not physical in origin, with predation by grazing parrotfishes being of major importance at the site described (Simpson 1979).

Diploria strigosa, which was not seriously damaged by chronic impacts, was also moderately abundant on the south shallow forereef at Buck Island prior to Hurricane Hugo (whereas *M. annularis* was virtually absent but became dominant below approximately 6-m depth). The severe damage to *D. strigosa* populations in this area during the hurricane was perhaps a part of the ongoing process which limits population development in this zone. *Diploria strigosa* populations may therefore be controlled principally by sporadic catastrophic events, whereas *M. annularis* and *P. astreoides* are controlled largely by chronic disturbances. However, historical effects (Hughes 1989) may have been equally important. Specifically, competition from the overtopping coral *Acropora palmata* has been gradually removed over the past 18 y as its populations at Buck Island have been decimated by White Band Disease (Gladfelter 1982; Bythell et al. 1989; Gladfelter et al. 1991). *Diploria strigosa* populations on the south shallow forereef may thereby have been favoured, accounting for the severe destruction during the hurricane. Populations of the once dominant *Acropora palmata* would perhaps have been more suited to cope with the hurricane disturbance, being able to re-establish by fragmentation and cementation (Highsmith et al. 1980; Highsmith 1982). *Montastrea annularis* generally escaped hurricane damage, which supports previous studies which have shown it to be a relatively hurricane-resistant species (Woodley et al. 1981; Porter et al. 1981). The near absence of this species in the south shallow forereef prior to the hurricane may have resulted from any of a number of possible factors, but certainly contributed to its avoidance of major mortality during the hurricane.

Acknowledgements. This study was carried out as part of the regional coral reef assessment program of the US Department of Interior, National Park Service. We thank Caroline Rogers for her hard work and inspiration in instigating and managing the program. We were aided by many people and would particularly like to acknowledge the help of Zandy Hillis, Kathi French, Sarah Lewis, Michelle Woodbury, Shanti Archer, Dennis and Karla Hubbard and Jeff Miller. The Buck Island program was administered by Island Resources Foundation after the untimely closure of the West Indies Laboratory in 1990. An earlier version of the manuscript was much improved by Terry Hughes and two anonymous reviewers.

References

Antonius A (1981a) The "band" diseases in coral reefs. Proc 4th Int Coral Reef Symp 2:6–14

Antonius A (1981b) Coral reef pathology: a review. Proc 4th Int Coral Reef Symp 2:3–6

Bak RPM, Steward-van Es Y (1980) Regeneration of superficial damage in the scleractinian corals *Agaricia agaricites* and *Porites astreoides*. Bull Mar Sci 30:883–887

Bak RPM, Luckhurst BE (1980) Constancy and change in coral reef habitats along depth gradients at Curaçao. Oecologia 47:145–155

Brown BE (1988) Assessing environmental impacts on coral reefs. Proc 6th Int Coral Reef Symp 1:71–80

Brown BE, Howard LS (1985) Assessing the effects of "stress" on reef corals. Adv Mar Biol 22:1–63

Brown BE, Suharsono (1990) Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. Coral Reefs 8:163–170

Bythell JC, Gladfelter EH, Gladfelter WB, French KE, Hills Z (1989) Buck Island Reef National Monument – changes in modern reef-community structure since 1976. In: Hubbard DK (ed) Terrestrial and marine geology of St. Croix, US Virgin Islands. 12th Caribbean Geological Conference, West Indies Laboratory Spec Pub 8, pp 145–154

Case RA, Mayfield M (1990) Annual summaries: Atlantic hurricane season of 1989. Mon Weather Rev 118:1165–1177

Chornesky EA, Peters EC (1987) Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. Biol Bull 172:161–177

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111:1119–1144

Edmunds PJ, Witman JD (1991) Effect of Hurricane Hugo on the primary framework of a reef along the south shore of St. John, US Virgin Island. Mar Ecol Prog Ser 78:201–204

Gates RD (1990) Seawater temperature and sublethal coral bleaching in Jamaica. Coral Reefs 8:193–197

Gladfelter EH, Bythell JC, Gladfelter WB, Lewis SK, Woodbury M (1991) Ecological studies of Buck Island Reef National Monument St. Croix, US Virgin Islands: a quantitative assessment of selected components of the coral reef ecosystems and establishment of long-term monitoring sites. Part 1. US Dept. Interior, National Park Service, Spec Rep 177 pp

Gladfelter WB (1982) White band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. Bull Mar Sci 32:639–643

Gleason MG (1993) Effects of disturbance on coral communities: bleaching in Moorea, French Polynesia. Coral Reefs 12:193–201

Highsmith RC (1982) Reproduction by fragmentation in corals. Mar Ecol Prog Ser 7:207–226

Highsmith RC, Riggs AC, D'Antonio CM (1980) Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. Oecologia 46:322–329

Hubbard DK, Parsons KM, Bythell JC, Walker ND (1991) The effects of Hurricane Hugo on the reefs and associated environments of St. Croix, US Virgin Islands – a preliminary assessment. J Coastal Res Spec Iss 8:33–48

Hughes TP (1989) Community structure and diversity of coral reefs: the role of history. Ecology 70:275–279

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55:141–166

Karlson R, Hurd L (1993) Disturbance, coral reef communities, and changing ecological paradigms. Coral Reefs 12:117–125

Knowlton N, Lang JC, Keller BD (1990) Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. Smithsonian Contrib Mar Sci 31:25

Knowlton N, Weil E, Weight LA, Guzman HM (1992) Sibling species in *Montastrea annularis*, coral bleaching, and the coral climate record. Science 255:330–333

Lang JC, Chornesky EA (1990) Competition between scleractinian reef corals – a review of mechanisms and effects. In: Dubinsky Z (ed) Coral reefs. Elsevier, Amsterdam (Ecosystems of the World, vol 25, pp 209–252)

Loya Y (1976) The Red Sea coral *Stylophora pistillata* is an r strategist. Nature 259:478–480

Porter JW, Battey JF, Smith GJ (1982) Perturbation and change in coral reef communities. Proc Natl Acad Sci USA 79:1678–1681

Porter JW, Woodley JD, Smith GJ, Neigel JE, Battey JF, Dallmeyer DG (1981) Population trends among Jamaican reef corals. Nature (Lond) 294:249–250

Rogers CS (1988) Recommendations for long-term assessment of coral reefs: US National Park Service initiates regional program. Proc 6th Int Coral Reef Symp

Rogers CS, Fitz III HC, Gilnack M, Beets J, Hardin J (1984) Scleractinian coral recruitment patterns at Salt River submarine canyon, St. Croix, US Virgin Islands. Coral Reefs 3:69–76

Rogers CS, McClain LN, Tobias CR (1991) Effects of Hurricane Hugo (1989) on a coral reef in St. John, USVI. Mar Ecol Prog Ser 78:189–199

Rogers CS, Suchanek TH, Pecora FA (1982) Effects of hurricanes David and Frederick (1979) on shallow *Acropora palmata* reef communities: St. Croix, US Virgin Islands. Bull Mar Sci 32:532–548

Rylaarsdam KW (1983) Life histories and abundance patterns of colonial corals on Jamaican reefs. Mar Ecol Prog Ser 13:249–260

Sammarco PW (1982) Echinoid grazing as a structuring force in coral communities: whole reef manipulations. J Exp Mar Biol Ecol 61:31–55

Simpson G (1979) Predation on live coral by the parrotfishes *Scarus vetula* and *Sparisoma viride*. In: Ecological studies of Buck Island Reef National Monument, US National Park Service, Spec Rep., pp 7.1–7.11

Slobodkin LB, Sanders HL (1969) On the contribution of environmental predictability to species diversity. Brookhaven Symposia in Biology 22:82–93

Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. Science 214:749–755

Note added in proof

Surveys in February 1993 revealed a major recent recruitment event on the south reef at Buck Island, the only such occurrence since regular monitoring began in 1988. Up to 16 recruits per m^2 were recorded with colony diameters of 5–20 mm dominated by *Diplora* and *Porites* sp. This supports evidence from size-frequency distributions (Fig. 4B) that coral recruitment events occur sporadically. If survivorship is high, then rehabitation of the south shallow forereef will be faster than we anticipated. However, there will have been a complete community shift from dominance by *Acropora palmata* over a period of approximately 30 y, mediated by disease and hurricane disturbance.