Effects of multiple disturbances on hard coral recruits in Glovers Reef Atoll’s lagoon, Belize

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ABSTRACT

Glovers Reef Atoll, Belize, suffered two large-scale disturbances in the autumn of 1998: a 3-month bleaching event and a hurricane. The authors also participated in a large-scale field study that manually cleared macroalgae from a subset of the atoll’s lagoon patch reefs, creating an additional disturbance. Recruit populations on these patch reefs were sampled two weeks after the algal reduction, which was also during the bleaching event and prior to the hurricane (September 1998). The reefs were then resampled in September 1999. There was a significant reduction both in the density of recruits and in the proportion of bleached recruits between 1998 and 1999. Statistical analysis showed that the reduction in recruit density was not a result of the algal reduction. Benthic transects were conducted to assess coral cover change on these patch reefs. Qualitative observations suggest that the hurricane had little physical impact on these sheltered patch reefs and that declines in coral cover and recruit density were more likely attributable to bleaching. Some coral taxa appear to be especially sensitive (agaricids) or insensitive (*Porites asteroides*) to bleaching in both adult and recruit populations, while other genera exhibited more variation between adult and recruit responses. The variability of response also occurred on small geographic scales between different environmental habitats, illustrating the complexity of reef communities, even at geographically local scales. We conclude by discussing the possible management implications of these findings.

INTRODUCTION

The complex community dynamics of coral reefs includes the influence of disturbances on community structure and population dynamics. Within ecological communities, the abundance of juvenile stages provide insight into the future diversity and abundance of corals in an area (Connell, 1978) and into the community's long-term response to disturbance. Life history strategies, competition, predation and disturbance will all affect the abundance and distribution of recruits. Recruitment patterns, conditions, and the subsequent development of scleractinian coral recruits on coral reefs have been well studied on coral reefs (Bak and Engel, 1979; Rylaarsdam, 1983; Meesters and Bak, 1993; Bak and Meesters, 1998; Edmunds et al., 1998). This paper focuses on the effects of multiple disturbances on coral recruit populations in the lagoon of Glovers Reef Atoll, Belize.

Disturbance plays an important part in structuring coral reefs with low disturbance leading to dominance by a few species, and high disturbance leading to physical degradation (Connell, 1978). Most reefs undergo multiple disturbances, which may have synergistic or unforeseen effects. Most natural disturbances on reefs are “pulse events” such as hurricanes, bleaching events, freshwater inputs due to storms and *Acanthaster* outbreaks. These disturbances vary in intensity and spatial extent but tend to be of low frequency. When pulse events occur at scales (intensity, frequency, spatial) that do not allow the reef to recover they can become chronic disturbance (Connell, 1978). Chronic stress may not directly cause mortality, however it can reduce resilience in ecological communities (Holling, 1996). The impacts of these disturbances will depend on the type, scale and frequency of the disturbance (Meesters and Bak, 1993; Hughes, 1994; Bak and Nieuwland, 1995; Connell et al., 1997; Porter et al., 1999).

Similar to other reefs in the Caribbean, the patch reefs in Glovers Reef Atoll’s lagoon have undergone a shift from coral-domination to algae-domination over the last 25 years (Hughes, 1994; Shulman and Robertson, 1996; McClanahan and Muthiga, 1998). The cause of this shift remains unclear (McClanahan et al., 2000; 2001), but could result from several disturbances and their interactions such as white-band disease that wiped out the *Acropora spp.* (Koltes et al., 1998), reduced herbivory by over-fishing and/or because of the *Diadema* die-out in the 80s (Hughes, 1994), nutrient enrichment from terrestrial runoff or upwelling (Mumby, 1998) increased water temperatures (Hoegh-Guldberg, 1999) and deposition of sediments from the Sahara in the Caribbean (Shinn, 2000).

In the autumn of 1998, Belize's reefs were disturbed by two important large-scale events, a mass bleaching event, defined as when more than 25% of coral colonies are bleached, with some individual colonies more than 90% bleached, over large geographic areas (Hoegh-Guldberg, 1999; McField, 1999). Late in October 1998, Hurricane Mitch passed within approximately 100km of Glovers Reef Atoll. While mainland Belize reported relatively minor structural damage (mainly to piers and minor flooding of outer cayes), reefs experienced battering waves for several days, resulting in structural damage (Mumby, 1999). Finally, a large-scale experiment, consisting of manual removal of macroalgae from patch reefs in the atoll's lagoon in September 1998 (McClanahan et al., 2000), can be considered a third, albeit artificial, disturbance. A similar algal reduction experiment performed in Australia found that removal of the algal canopy increased bleaching in the corals previously shaded by the algae (Jompa and McCook, 1998).

The goal of this study was to determine the effects of these three disturbances on coral recruits, and whether these effects varied from adult populations. Our hypotheses were:

1. Algal reduction would increase bleaching of recruits by increasing exposure to solar radiation, and possibly decrease recruit density due to bleaching related-mortality. Alternative hypotheses: Algal reduction would increase recruitment on experimental patch reefs by opening suitable surfaces.
2. Mass bleaching of the adult coral population in 1998 should result in decreased density of the smallest size classes due to failed reproduction in 1999 and a skewing of the population distribution of affected species towards larger sized recruits.
3. Overall, recruitment density would be lower in 1999 vs. 1998 due to the combination of natural disturbances (bleaching and hurricane).

Site Description:

Glovers Reef Atoll is one of four atoll structures within the MesoAmerican Barrier Reef System and lies about 40 kilometres east of Belize mainland, measuring 25 kilometres north to south and 10 kilometres east to west. It is surrounded by a nearcomplete sea-level reef crest with three cuts (Figure 1), and the inner lagoon contains approximately 700 patch reefs that range in size from about 25 to 10,000 m^2 (Stoddart, 1962).

This study was conducted in the Wilderness Zone of the Glovers Reef Marine Reserve where fishing is prohibited. Six patch reefs were studied, consisting of three experimental patch reefs where macroalgae was manually removed and three uncleared control reefs (McClanahan et al., 2000).

Bleaching occurred from late August to November 1998 and began to improve following the passage of hurricane Mitch when water temperatures began to drop. During the bleaching event, 70-90% of adult colonies appeared to be fully bleached on the atoll (McField, personal observation) and subsequent decreases in live coral in the lagoon were around 50% (McClanahan et al., 2000). The event was associated with a global ENSO episode that affected many coral reefs in the world (Wilkinson, 1998). Hurricane Mitch was a category 5 storm that passed about 100 kms south-east of the atoll and caused several days of high seas along the coast of Belize and subsequent structural damage on reefs (Mumby 1999).

FIGURE 1: Map of Glovers Reef Atoll, Belize, Central America.

METHODS

Recruit sampling

Six patch reefs were sampled in the Wilderness Zone of the atoll. These were a subset of the eight patch reefs sampled in this zone by McClanahan et al. (2000; 2001). There were two sample periods for recruitment, the first in September 1998 about two weeks after the algal reduction, and again in September 1999, about 8 months after the hurricane. We consider the 1998 recruit sample to represent the pre-disturbance population, although the bleaching event was already underway at the time of our first sample. Weighted 10m transect lines marked at one metre intervals were laid along two locations on each patch reef: on the shallowest part or "shoulder", and one in the centre of the patch reef. Transects were laid perpendicular to the growing edge of patch reefs that face the predominant winds from the north-east. Twelve 50 x 50 cm quadrats (PVC pipe) were laid along each transect at 0.5 m intervals giving a total sample area of 6 m^2 per patch reef (the sample unit) and a total of 36 m^2 surveyed in each sampling period (see Edmunds et al., 1998). As recruits require hard substratum on which to settle, loose sediment surfaces were avoided (Bak and Engel, 1979). We define “recruits” as recently settled juvenile scleractinian corals and *Millepora sp.* that are ≤ 5 cm in maximum axis, approximately corresponding to Edmunds et al. (1998) definition of recruits that have settled in the last 50 months.

Recruits were recorded to the species level where possible, and were measured *in situ* along their longest axis and placed into one of five size classes: 0-1.4 cm, 1.5-2.4 cm, 2.5-3.4 cm, 3.5-4.4 cm and 4.5-5.0 cm. We found that recruits on cryptic surfaces became reliably visible once they have reached 0.5 cms. The number of recruits per species per quadrat that were bleached was also recorded. No recruits were seen with overgrowth of filamentous algae, which are characteristic of corals considered "recently dead" from bleaching.

Benthic coral cover

The percent coral cover data presented in this paper is a subset of the data collected by McClanahan et al. (2000; and 2001). These papers studied two zones on the atoll and consisted of 16 patch reefs and five time periods (see McClanahan et al., 2001). The present study was limited to the Wilderness Zone of the atoll and therefore uses the eight patch reefs sampled for benthic cover and the December 1998 time period from McClanahan et al. (2001). The patch reefs surveyed for recruits were a subset of these patch reefs (N = 6). Ten metres transect lines were laid along three locations on each patch reef: edge (deepest), shoulder (shallowest) and centre of reef, using the line intercept method. All canopy cover greater than three centimetres was recorded into functional groups and hard corals were recorded at the species level.

RESULTS

Recruit density

Recruit abundance data were converted to density (recruits per m^2) for each transect. There was a 53% reduction in recruit density between September 1998 (35.8 per m^2) and 1999 (17.4 per m^2) (Table 1). T-tests confirmed that there was no significant difference between the shoulder and centre transects so these were pooled for each patch reef (the sample unit). The data were normally distributed (Cochran's test on homogeneity of variances) and untransformed. A two-way ANOVA for time and treatment revealed a significant difference ($p = 0.005$) in recruit density between 1998 and 1999. However the algal reduction treatment had no effect, and there were no significant interactions (Table 1). Ordination of samples by Multi-dimensional scaling plots (MDS) were created using PRIMER ecological statistics (Clarke, 1993) illustrating the separation of samples by time period (Fig. 2). In 1999, the patch reefs had greater variability, shown by less tight clustering, compared to the pre-disturbance 1998 cluster.

TABLE 1: Recruit density (number of recruits/ m2) in Oct. 98 and Sept. 99 and statistical analysis (2-way ANOVA).
FIGURE 2: MDS of recruit abundance (Stress = 0.06)

Recruit species composition and size class frequency

A reduction in recruit abundance occurred in all species, with the exception of *P. asteroides*, which increased slightly (Table 2). The total number of taxa identified in 1998 was 15, compared to 11 in 1999. *Agaricia agaricites, Favia fragum, Porites asteroides* and *P. porites* accounted for 95 and 96% of all recruits in 1998 and 1999 respectively. The species whose recruits decreased the most (not including those with < 10 individuals) were *Agaricia tenuifolia, A. agaricites*, *Mycetophyllia sp.* and *Porites porites* (Table 2).

The size frequency distributions for recruits as a whole, as well as for the four main species of recruits (> 50 recruits/ time period) are shown in Figure 3. The most common size class for all species was 2 cms (1.5 – 2.4 cm; Figure 3), this was also largely true for the size class distributions of the four main species (> 50 recruits per time period; Figure 3). The 1998 distribution was more skewed toward the smaller size classes than in 1999. In particular, the pre-disturbance size-frequency pattern changed in three of the dominant species, *P. porites, Favia fragum* and *P. asteroides*.

TABLE 2: Total recruit abundance and percent of bleached recruits for 1998 and 1999 respectively. (The four most abundant species are highlighted)

FIGURE 3: Size frequency distributions of all recruits and of the recruits of the main species.

Benthic hard coral cover species composition

The three transects were pooled to give a hard coral cover value per patch reef (N = 8). No significant differences between control and experimental patch reefs were found prior to the algal reduction (1-way ANOVA; Table 3). Thus, data from all eight patch reefs were pooled for the remaining inter-specific analysis (Table 4). Overall, coral cover on the eight patch reefs studied within the Wilderness Zone experienced a significant decline of 48% between 1998 and 1999 ($p = 0.0002$) (Table 4). The main hard coral species (> 2% cover) were *Montastrea annularis, Porites porites, Agaricia agaricites* and *Siderastrea siderea* (Table 4). The species that decreased the most (>0.3% initial cover and decreased by >50%) between September and December 1998, were *Agaricia agaricites, Porites porites, Agaricia tenuifolia, Millepora alcicornis*, and *A. palmata* (Table 4). Species that decreased over the whole year were *Montastrea annularis* and *Millepora complenata* (Table 4).

TABLE 3: Total hard coral cover (%) in September 98 on control and experimental patch reefs and statistical analysis (1-way ANOVA).

TABLE 4: Change in benthic hard coral cover (%cover) by species between Sep 98 and Dec 98 and Sep 98 and Sep 99, and statistical analysis (t-test).

Effects of Bleaching

Bleached recruit abundance data were converted into percentage of bleached recruits per species per patch reef for analysis, and subsequently arcsin transformed to obtain normality for statistical analysis. The data presented in the tables are the original data. In 1998, 63% of the recruits were bleached compared to 7% in 1999 (Table 5). A two-way ANOVA (independent variables time and algal removal treatment), on the percent bleached recruits data revealed that the proportion of bleached recruits decreased significantly between 1998 and 1999 ($p < 0.001$) but that treatment and the interaction of the two factors were not significant (Table 5). Of the species with 10 or more recruits, *Agaricia tenuifolia, A. agaricites, Mycetophyllia sp.* and *P. porites* were most affected by bleaching (Table 2).

TABLE 5: Change in proportion (%) of bleached recruits from Sept. 98 to Sept. 99 and statistical analysis (2-way ANOVA with time and treatment as independent variables).

Effects of Hurricane Mitch

There was no observed structural damage to the patch reefs following the hurricane with the exception of patch reef eight that was partially buried by sand and must have undergone substantial scouring (personal observation, Huitric and McField). However, the MDS analysis of recruit density indicates that this scoured patch reef did not differ from the other patch reefs in its time period (Figure 2), suggesting that sand scouring did not have a major impact on recruit density. Furthermore, the benthic cover of massive species like *Montastrea annularis,* which are more resistant to hurricane damage (Stoddart, 1974; Hughes, 1994), also decreased, suggesting that hurricane damage was not the major cause of the decline in coral cover on the patch reefs.

DISCUSSION

Between September 1998 and September 1999, the patch reefs in this study experienced a 50% decline in scleractinian recruit abundance and percent benthic coral cover, indicating that recruits may respond similarly to the adult colonies to the given combination of disturbances. Whereas a smaller proportion of recruits bleached (60%) than did adult colonies (75-80%), both suffered similar levels of decline (50%). This suggests that recruits may initially be more resistant to bleaching but are less resilient and suffer greater mortality. However, reduced recruitment could also be attributed to reduced fecundity of the adult population subsequent to the bleaching event, as has been demonstrated in other studies and this is discussed further below (Harrison and Wallace, 1990; Szmant and Gassman, 1990; Wilkinson et al., 1999).

Our analysis found that the algal reduction experiment did not cause significant change to recruit density. A similar algal removal experiment in Australia found that the removal of the algal canopy increased bleaching in the newly exposed corals, probably as a result of increased exposure to solar radiation (Jompa and McCook, 1998). Corals react quickly to increased radiation (Gleason and Wellington, 1993) therefore the two weeks between the reduction and the surveying should have been enough time to observe increased bleaching as a results of increased exposure. That there was no significant difference in bleaching between the experimental and control patch reefs suggests that water temperature may have been more important than increased exposure to solar radiation in this particular bleaching event. Recruits in the Glovers lagoon tended to settle on protected surfaces, like crevices and underhangs, which are plentiful on these highly bioeroded patch reefs. Thus, the preferred shaded microhabitat for recruits on these patch reefs may have offered them additional protection from bleaching.

The lagoon was sheltered from Hurricane Mitch’s storm surges by the shallow eastern reef crest and Middle Caye, which should have dissipated much of the wave energy produced by the hurricane. Although Bak and Engel (1979) found that recruit mortality as a result of sedimentation and that sediment scouring might be a more important factor in mortality in recruits than in adult colonies, the one visibly scoured patch reef does not differ from the other patch reefs in our MDS analysis. The preferred settlement of recruits onto protected surfaces could have further protected them from wave damage and sand scouring. The hurricane could have produced secondary effects such as disturbing the settlement of coral larvae through wave activity, increased terrestrial run-off and nutrient pulses (Andrefouet et al., in review), favouring the subsequent algal blooms recorded in McClanahan et al. (2001). The hurricane also deposited coral rubble on the eastern crest, which reduced water flow into the lagoon (Huitric and McField, personal observation). However, based on our analysis and observations, we suggest that the bleaching event was the primary disturbance affecting both recruits and adult colonies in the Glovers lagoon.

Our conclusion that the bleaching event was the primary cause of the decreased recruitment appears to conflict with those of Mumby (1999), that determined that the hurricane, and not the bleaching event, had a significant effect on recruit densities on shallow forereefs on the atoll. However, Mumby's conclusion was based on the difference in reduction of recruit densities on windward (eastern) forereefs compared to leeward (western) forereefs. We suggest that the physical and environmental differences between the windward forereefs and patch reefs could reasonably account for these differences. The eastern forereef sustained massive structural damage from the hurricane, which was not evident on the protected patch reefs or leeward forereefs. The question remains as to why the leeward forereef did not experience a reduction in recruitment due to the bleaching event. This latter disparity with our results may again be attributable to physical and environmental differences between the forereef and the lagoon patch reefs. Greater temperature fluctuations have been recorded on the shallow enclosed patch reefs versus the exposed forereefs of both the eastern and western sides of the atoll (McField unpublished temperature logger data). Only 25% of the forereef recruits were bleached (Mumby, 1999), versus 60% on the patch reefs (this study), thus the recruits on the patch reefs most likely experienced greater environmental stress and more severe bleaching than recruits on the forereefs.

Like other studies in the Caribbean we found that brooding species, agaracids in particular, dominated the recruit population (Bak and Engel 1979; Rylaarsdam, 1983; Sammarco, 1985; Smith, 1992; McField, 1999). Although some of the dominant species in the recruit and adult benthic communities overlapped, the dominant broadcasting species on these patch reefs, *M. annularis* and S. *siderea*, are under-represented in the recruit population. Recruit populations are known to have patchy distributions, due to the variability in recruitment rates and localised clustering of some brooding species such as *Favia fragum* (Harrison and Wallace, 1990; Miller et al., 2000). However, as discussed by Mumby (1999), we also have used a larger sampling design than that used in previous studies (Bak and Engel, 1979; Edmunds et al., 1998) in order to account for these patchy distributions.

All observed size classes were similarly affected by the disturbance except for two species. *Porites porites* and *Favia fragum* decreased in their smallest size classes. In contrast, *Porites asteroides* was the only species with increased recruit abundance in 1999. This was evidenced by an increase in its two smallest size classes, while the larger ones declined. McField (1999) found this species to be less affected by bleaching in 1995 and Smith (1992) found it was the primary colonising species after a ship-grounding disturbance in Bermuda. This is consistent with our findings for *Porites asteroides* that experienced a relatively small decrease in coral cover, low bleaching frequency of recruits (34% vs. the average of 64%), and an increase in young recruits following the disturbance. Studies have found that disturbances such as bleaching can suppress fecundity in adult colonies (Szmant and Gassman, 1990). We suggest that fecundity in surviving adults might have been reduced in late 1998 to early 1999, which would lead to a decline in the smallest size class of recruits measured in September 1999, assuming that this size class represents recruits that have settled since the disturbance. Such a pattern appears in *Porites porites*, and to a smaller extent in *Favia fragum*.

Analysis of our data on bleached recruits together with studies in the literature allowed us to consider specific responses to bleaching. Agaracids are susceptible to bleaching and bleaching-related mortality in both recruit populations (suffering an 80% decrease in this study) and adult colonies (nearly 100% mortality in Aronson et al. 2000). *Montastrea annularis*, a broadcasting massive coral, is less prone to direct mortality from bleaching but becomes susceptible to disease and longer-term mortality (this study; McField, 1999). Disturbance may even benefit some species such as *P. asteroides* which does not appear to be as susceptible to bleaching (McField, 1999). *P. asteroides* recruit density increased by 9% over the year, and its benthic cover was one of those least affected. However, distinguishing hurricane from bleaching effects based on changes in species composition is difficult, as most species are susceptible to damage from both disturbances. Branching corals (~1/3 of the species for both benthic coral and recruits) are susceptible to hurricane damage and many of these species, such as *Agaricia tenuifolia, Millepora alcicornis* and *M. complenata*, are also susceptible to bleaching (Bak and Engel, 1979; McField, 1999; Aronson et al., 2000).

One hypothesis for the increased cover of macroalgae (and decrease in coral cover) on the Glovers Reef's patch reefs is reduced grazing as a result of over-fishing (McClanahan and Muthiga, 1998; McClanahan et al., 2000; 2001). Sammarco (1985) found that the dominant juvenile corals on Jamaican reefs were *Agaricia, Porites,* and where there was reduced grazing, *Favia*. These three genera correspond to the dominant recruit species recorded in this study, potentially indicating low grazing on these patch reefs. It would be interesting to evaluate the possibility of using the species dominance patterns of the recruit population as an indicator of which processes are most affecting reef health and function.

If global predictions of increased bleaching events are correct, we may see permanent alteration of the species composition of these reefs. The ability of a reef to recover following a disturbance will depend on the disturbance's intensity, which affects the areal extent of surviving colonies as well as subsequent recruitment (Roberts, 1997), and frequency of disturbances, which affects recovery time (Connell, 1978). Recovery from bleaching varies according to the conditions of the bleaching event and according to species composition on the reef (Meesters and Bak, 1993; McField, 1999; Mumby, 1999).

CONCLUSION

The Glovers reef lagoon patch reefs have experienced major ecological changes cover over the last 25 years, including a 75% decline in coral cover and a 315% increase in macroalgae (McClanahan and Muthiga, 1998). They have also experienced numerous disturbances during this time period, including other hurricanes, bleaching, coral disease (acroporid loss), and the *Diadema* die-off.

The impact of the 1998 disturbance events on recruitment and recruit populations will have an important impact on the future structure of the hard coral community in this area. Overall, the 53% reduction in density of recruits in this study corresponds closely to the 48% reduction in live coral cover on these patch reefs during the same time period (1998 – 1999). In addition, it corresponds to the 48% reduction in live coral cover recorded from 12 forereef sites throughout Belize from 1997 to 1999 (McField, in review). While such similarities may only be a curiosity, the given combination of hurricane and bleaching disturbances which affected Belize's reefs in 1998 seem to have halved the viable coral population.

In conclusion, we report contrasting results in the response of coral recruits to bleaching on what would often be considered a local scale (forereef versus patch reefs within 1- 8km of each other). This reinforces the danger of extrapolating results within even small geographic ranges (Levin 1992; McField, 1999). This variation in responses has important implications for management. Although both reefs lie within the wilderness zone of the Glovers Reef Marine Reserve, local management efforts were unable to affect any change in the response to these two natural disturbances. Gaining a better understanding of the physical oceanographic differences between reef zones, and the predicted response implications of these differences in relation to future disturbances, should be a priority research area for adaptive scientific reef management. Our findings also highlight the need for expanding the normal scale of reef conservation efforts, as healthy coral larval sources may lie beyond a reserve's boundaries (Ogden, 1997; Roberts, 1997). In other words, this work emphasises the need to incorporate scale and the concept of spatial resilience into reef management planning efforts in order to increase management effectiveness (Meesters and Bak, 1993; Nyström et al., 2000).

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TABLE 1: Recruit density (number of recruits/ m2) in Oct. 98 and Sept. 99 and statistical analysis (2-way ANOVA).

	1998	1999	2-Way ANOVA (p =)		
	mean (st dev)	mean (st dev)	Time	Treatment	Interaction
Control	31.1 (8.6)	18.5 (5.0)	0.005	ns	ns
Experimental	41.4 (13.7)	15.8 (4.3)			
Total	36.3 (11.7)	17.1 (4.4)			

TABLE 2: Total recruit abundance and percent of bleached recruits for 1998 and 1999 respectively (The 4 most abundant species are highlighted)

	1998		1999		% change in abundance*
	Total N	% blch	Total N	% blch	
Agaricia agaricites	754	84	281	10	-63
A. humilis	5	60	0		
A. tenuifolia	13	100	0		
Collophyllia natans	0		1		
Dichocoenia stokesii	0		1		
Diploria strigosa	3	33	1	0	
Favia fragum	294	29	200	7	-32
Manicina areolata	3	100	0		
Millepora alcicornis	1	100	2	0	
Montastrea annularis	12		10		
Mycetophyllia sp.	15	87	0		
Porites asteroides	56	34	61	0	9
P. branneri	2		0		
P. porites	135	47	49	0	-64
Scolymia sp.	3	67	2	0	
Siderastrea siderea	5		1		
Stephanocoenia michilini	2	40	0	0	
Unidentified coral	3		8		
TOTAL	1306	63	617	7	-53

* calculated only for species with >50 individuals sampled

TABLE 3: Total hard coral cover (%) in September 98 on control and experimental patch reefs and statistical analysis (1-way ANOVA).

	September 1998 mean (st dev)	t – Test (p =)
Control (N = 3)	19.2 (4.6)	ns
Experimental (N = 3)	20.2 (4.1)	
Total	19.7 (4.1)	

TABLE 4: Change in benthic hard coral cover (%cover) by species between Sep. 98 and Dec. 98, and Sep. 98 and Sep. 99, and statistical analysis (t-test).

	Sep-98		Dec-98		Sep-99		%change	
	mean	st dev	mean	st dev	mean	st dev	Sep98:Dec99	Sep98:Sep99
Hard coral total	19.7	4.1	15.7	6.3	10.4	3.2	-20.4	-47.5
Acropora palmata	0.3	0.7	0.0	0.1	0.0	0.0	-93.0	-100.0
Agaricia agaricites	2.8	1.4	1.3	0.7	0.6	0.4	-52.4	-79.7
A. tenuifolia	0.3	0.5	0.0	0.0	0.0	0.0	-100.0	-100.0
Colpophyllia natans	0.1	0.2	0.0	0.0	0.1	0.2	-100.0	41.3
Diploria clivosa	0.1	0.2	0.4	1.2	0.0	0.0	376.2	-100.0
D. labyrinthiformis	0.1	0.2	0.5	0.8	0.0	0.0	894.5	-100.0
D. strigosa	0.7	0.5	0.3	0.4	0.4	0.5	-54.7	-50.6
Eusmilia fastigiata	0.0	0.1	0.0	0.0	0.1	0.1	-100.0	105.0
Favia fragum	0.1	0.1	0.0	0.1	0.1	0.1	-42.0	28.1
Manicina areolata	0.0	0.1	0.1	0.1	0.0	0.0	9.3	-100.0
Millepora alcicornis	0.5	0.4	0.2	0.2	0.2	0.3	-70.4	-54.7
M. complanata	0.3	0.6	0.1	0.2	0.1	0.2	-47.7	-72.3
Montastrea annularis	9.4	2.3	9.4	5.2	6.2	2.2	-0.5	-34.2
M. carvernosa	0.0	0.0	0.1	0.4	0.1	0.2		
Porites asteroides	0.9	0.9	0.6	0.6	0.8	0.5	-34.2	-12.4
P. porites	2.9	2.1	1.4	1.3	0.8	0.5	-52.4	-73.3
Siderastrea siderea	1.2	0.9	1.2	1.6	1.1	1.0	-0.1	-13.8
t-test p-value							n.s	0.0002

TABLE 5: Change in proportion (%) of bleached recruits from Sept. 98 to Sept. 99 and statistical analysis (2-way ANOVA).

	1998		1999		2-way ANOVA (p =)		
	mean	(st dev)	mean	(st dev)	Time	Treatment	Interaction
Control	56.7	(5.1)	7.1	(2.8)	0.000	ns	ns
Experimental	68.3	(11.5)	6.3	(3.9)			
Total	62.5	(10.2)	6.7	(3.1)			

FIGURE 3: Size frequency distributions of recruits (total) and of the main species