

In nature the areas of highest flow and greatest light both exist at the tips of the *Thalassia*. This experiment suggests there is a consideration for both: high light would provide greater photosynthetic activity, while high flow would presumably result in greater zooplankton capture. This plus the fact that anemones positioned higher off the substrate have a better chance of avoiding fireworm predation, make the tips of the *Thalassia* leaves the best choice of microhabitat. Further work should attempt to sepa-

rate out the importance of these three variables in microhabitat selection.

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THE EFFECTS OF *DIADEMA ANTILLARUM* ON TWO JAMAICAN REEFS: AN EXAMINATION OF COMMUNITY RESPONSE

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Abstract. It has been suggested that the sea urchin *Diadema antillarum* is an important herbivore in coral reef communities. Until its mass mortality in 1983, it was effective in limiting the cover of upright algae and, subsequently, the number of grazing fish, while allowing coral cover to remain high. The *Diadema* die-off prompted many natural experiments. We looked at two similar reef areas on the north side of Jamaica: Discovery Bay and Pear Tree Bottom. Although the reef at Pear Tree Bottom has only a fraction of its original *Diadema* population, it has significantly more urchins than Discovery Bay. We found that percent cover of upright algae and biomass of upright algae were both lower and the number of herbivorous fish and percent cover of coral were both higher at Pear Tree Bottom than at Discovery Bay. In general, the two reefs have differently structured reef communities and are responding in different ways to the mass mortality of *Diadema*. (SLS)

INTRODUCTION (TCB)

Diadema Antillarum is possibly the most intensely studied coral reef echinoid species (Lessios 1988). It has been shown to have a significant impact on several attributes of a reef community, including algae community structure and diversity, coral cover and recruitment, and herbivorous fish populations (Hay and Taylor 1985, Hughes, et al. 1987, Lawrence and Sammarco 1982).

Prior to 1983 several studies had been done on the effects of removing *Diadema* from an area (Ogden and Lobel 1978, Sammarco 1982a, 1982b, Hay and Taylor 1985). These studies established that *Diadema* keeps algal biomass at a low level, and that algal species diversity decreases with increasing *Diadema* density. The algal community in the presence of *Diadema* is therefore dominated by encrusting forms and a few toxic or distasteful species (Lawrence and Sammarco 1982, Sammarco 1982b, Dart 1972). Removal of *Diadema* results in a dramatic increase in algal cover, a decrease in coral cover, and a shift in

algal species composition from low turf algae to fleshy, upright macroalgae (Ogden and Lobel 1978, Sammarco 1982a, Hay and Taylor 1985, Lessios 1988, Carpenter 1990a). Coral cover is reduced because of overgrowth by macroalgae, and by reduced recruitment (less space for larval settlement; Sammarco 1982a).

Increases in fleshy macroalgae result in increases in herbivorous fish populations (primarily acanthurids and scarids), and in grazing intensity (Hay and Taylor 1985, Lessios 1988), indicating that *Diadema* may limit fish populations via competition for food.

In 1983, *Diadema Antillarum* suffered a mass mortality extending through the Caribbean and along the West Atlantic Coast. Populations were reduced by 95-100% in most areas (Hinte, et al. 1986). The massive die-off provided researchers the chance to conduct large scale natural experiments on the effects of *Diadema* removal on reef communities (Lessios 1988, Carpenter 1990b). The resulting studies indicate the same trends as those seen in pre-mortality studies. However, the magnitude of the

changes was far greater following the die-off (Hughes, et al. 1987, Lessios 1988). It has been suggested that this is due to the larger geographic extent of the die-off relative to the small areas used in removal studies (Hay and Taylor 1985, Hughes, et al. 1987).

Removal experiments focused on patch reefs or on relatively small sections of a reef. Fish migrations from nearby areas were able to temporarily increase the populations of herbivores in the experimental areas, thereby maintaining a lower algal biomass (Hay and Taylor 1985).

Following the mass mortality, the entire Caribbean became a *Diadema* removal area. Fish from outside such a large area could not migrate in beyond the outer edges and increase the herbivore population artificially; therefore, algae in this area showed a concomitant rise in biomass and abundance (Carpenter 1990a). Herbivorous fish populations in the Caribbean have increased slowly, but because of intense fishing pressure the fish are unable to maintain the algal turfs as the *Diadema* did (Hughes, et al. 1987, Lessios 1988).

Discovery Bay, Jamaica has been well studied in terms of *Diadema* and its effects on the reef community (Sammarco 1982a, 1982b, Liddell and Ohlhorst 1986, Hughes, et al. 1987). Immediately following the mortality, *Diadema* densities were less than 1% of what they had been (Hughes, et al. 1987). Three years later (1986) densities still had not risen significantly (Liddell and Ohlhorst 1988). As a result, the back reef and fore reef of Discovery Bay have become progressively overgrown by algae.

Pear Tree Bottom is a reef ~4 miles east of Discovery Bay. It, too,

lost its *Diadema* population; yet now it seems to show increasing *Diadema* densities on the fore reef. Pear Tree Bottom has a vastly different appearance than Discovery Bay – there seem to be more live corals and less algae on the fore and back reefs.

We hypothesized that there would be a difference in *Diadema* density between the two reefs, and that this density difference would be accompanied by predictable differences in reef community characteristics. We predicted that the area with lower *Diadema* would have higher algal cover and biomass, lower coral cover, and higher herbivorous fish populations.

METHODS (SLS)

Study sites. The study area at Discovery Bay Marine Lab is a fringing reef surrounding a lagoon. The back reef runs from the surface at the reef crest to a depth of about 2m, where it borders a seagrass bed (*Thalassia testudinum*) and a sand flat approximately 10m from the crest. The fore reef extends to a depth of about 20m. Most of the reef is composed of *Acropora palmata* rubble covered by encrusting coralline and fleshy turf algae. Small stands of the corals *Porites astreoides*, *Millepora complanata* and *Montestrea annularis* are also present.

The study area at Pear Tree Bottom, east of Discovery Bay, is also a fringing reef bordering on extensive seagrass beds. The back reef is characterized by coral rubble, encrusting algae and occasional stands of *Millepora* spp. The fore reef is composed of coral buttresses of *Porites* spp., *Montestrea* spp., and *Diploria* spp., divided by sand-channel trenches up to 5m deep.

Densities of the sea urchin *Diadema Antillarum* at both sites are low compared to pre-dieoff densities (early 1983). Herbivorous fish are also present but numbers may be lower than at other reefs in the area due to intense fishing pressure at these sites.

Field methods. We studied four areas: the fore reef and back reef of Discovery Bay and the same at Pear Tree Bottom. We chose to concentrate mostly on the fore reefs of both areas because we felt them to be more similar in terms of substrate complexity and depth. The Pear Tree Bottom back reef was deeper and structurally simpler than that at Discovery Bay.

Counts of *Diadema* and *Tripneustes* were made at all four areas using a 3m transect line weighted at one end. The weight was placed in the substrate while one of us held the free end of the line and swam in a circle of radius 3m. Every urchin within that circle was counted. This procedure was repeated twenty times at each fore reef and ten times at each back reef.

Estimates of algal cover were made using a weighted 1m x 1m square constructed of PVC pipe which was subdivided into 100 10cm x 10cm sections with twine. The square was placed on the substrate and estimates of percent encrusting algae, algae taller than 1cm and coral cover were made by counting the number of subsections that were filled by each of these. Any *Diadema* or *Tripneustes* within the square meter were recorded and these data were added to that obtained using the transect line. Thirty such squares were counted on the fore reefs and fifteen on the back reefs. From within one pre-designated 10cm x 10cm subsection of four squares at each site, we

Table 1. Data summary and student's t-test results.

	Discov- ery Bay (mean ± s. d.)	P. Tree Bottom (mean ± s. d.)	t	p
FORE REEF				
Urchins (inds/m ²)				
<i>Diadema</i>	0.0504 ±0.052	1.069 ±0.7718	6.034	* <.001
<i>Tripneust.</i>	0.0135 ±0.0237	0.0720 ±0.0780	3.288	* <.01
Algae (% cover)				
encrust	67.87 ±12.18	67.30 ±13.96	0.1385	>0.5
upright	27.53 ±11.50	6.070 ±7.070	8.707	* <.001
biomass (mg/cm ²)	1.530 ±1.110	0	2.757	>0.05
Fish (#inds/24m ²)				
Scarids	120.83 ±24.58	13.83 ±7.414	10.21	* <.001
Acanthids	15.67 ±10.56	0.5000 ±0.550	3.514	* <.01
Herbivory (#bites blade ⁻¹ hr ⁻¹)	0.8333 ±2.522	0.5625 ±1.888	0.9210	>0.2
BACK REEF				
Urchins (inds/m ²)				
<i>Diadema</i>	0.0257 ±0.0421	0.0286 ±0.0304	0.1850	>0.5
<i>Tripneust.</i>	1.033 ±0.7230	0.0997 ±0.0819	4.254	* <.01
Algae (% cover)				
encrust	1.467 ±1.850	0	3.071	* <.01
upright	90.87 ±5.170	17.43 ±8.570	28.42	* <.001
biomass (mg/cm ²)	20.63 ±15.4	1.45 ±0.597	2.489	* <.05
Fish (#inds/24m ²)				
Scarids	52.67 ±41.77	6.667 ±3.011	15.804	* <.001
Acanthids	13.83 ±12.38	6.667 ±8.017	1.190	>0.2
Herbivory (#bites blade ⁻¹ hr ⁻¹)	0.2833 ±1.32	5.500 ±3.820	9.939	* <.001

*indicates a significant result

collected all of the upright algae and brought it to the lab for analysis. We

first identified the algae in these samples and then obtained a dry biomass for each by drying the samples at 80°C for 8 hours and weighing them with a Mettler balance. We compiled species lists for each site using species present in our samples, as well as any prominent species that were within the total area of our squares.

Direct counts of parrotfish and surgeonfish were made by slowly swimming 12m along transects through each of the four sites. The sampling area was standardized by staying in areas 1-3m deep and looking down and slightly forward resulting in a transect width of about 2m (see Hay & Taylor 1985). This procedure was replicated six times at each location. All parrotfish and surgeonfish were counted regardless of size.

Finally, grazing activity of herbivorous fish was monitored using transplanted blades of the seagrass *Thalassia testudinum* as a bioassay. Twenty bundles of six blades each were used at the fore reefs while ten bundles were used on each back reef. The samples were left alone at the sites for an hour at a time (except for the Pear

Table 2. Fore reef algal species richness. The number in parentheses is total # species.

Discovery Bay (14)	Pear Tree Bottom (10)
<i>A. fragilissima</i>	<i>A. fragilissima</i>
<i>D. cervicornis</i>	<i>A. taxiformis</i>
<i>D. ciliolata</i>	<i>C. racemosa</i>
<i>D. divaricata</i>	<i>D. cervicornis</i>
<i>G. oblongata</i>	<i>D. divaricata</i>
<i>H. cervicornis</i>	<i>G. oblongata</i>
<i>L. intricata</i>	<i>P. sanctae-crucis</i>
<i>L. farinosa</i>	<i>S. fluitans</i>
<i>L. pinnata</i>	<i>S. polyceratium</i>
<i>L. variegata</i>	<i>T. turbinata</i>
<i>P. sanctae-crucis</i>	
<i>S. fluitans</i>	
<i>S. polyceratium</i>	
<i>T. turbinata</i>	

Tree Bottom back reef samples which were left for 30min) and then collected. We counted the number of blades bitten by urchins or fish and the average number of bites taken per blade by the fish.

All experiments and surveys were done from 24 February to 2 March 1992 between 0800 and 1100 except for the Discovery Bay back reef which was surveyed from 1400 to 1600 for all parts of our study. Two of the six fish counts for Discovery Bay fore reef were also done between 1400 and 1600.

RESULTS (SLS)

Urchin Densities. *Diadema* densities at the fore reefs of Discovery Bay and Pear Tree Bottom were 0.05/m² and 1.07/m², respectively. *Tripneustes* densities of these sites were 0.013/m² and 0.072/m². Both sets of values were significantly different using a student's t-test ($p < 0.001$ and $p < 0.01$). *Diadema* densities on the back reefs of these sites were 0.026/m² at Discovery Bay and 0.029/m² at Pear Tree Bottom. These values were not significantly different ($p > 0.5$). The difference in *Tripneustes* densities on the backreefs (1.033/m² at Discovery Bay and 0.0997/m² at Pear Tree Bottom) were different ($p < 0.01$; Table 1).

Algal cover. The percent cover of upright algae in the fore reefs of the two sites was significantly different ($p < 0.001$), with Discovery Bay having an average of 27.53% cover and Pear Tree Bottom having 6.07% cover. Similarly, the back reef of Discovery Bay had a larger percent cover (90.87%) of upright algae than did the back reef

Table 3. Back reef species richness.

Discovery Bay (23)	Pear Tree Bottom (18)
<i>A. spicifera</i>	<i>A. spicifera</i>
<i>A. fragilissima</i>	<i>A. fragilissima</i>
<i>C. racemosa</i>	<i>A. rigida</i>
<i>C. nitens</i>	<i>C. sertularioides</i>
<i>Ceramium</i> sp. 1	<i>Ceramium</i> sp. 1
<i>C. irregularis</i>	<i>Ceramium</i> sp. 2
<i>D. cervicornis</i>	<i>C. linum</i>
<i>D. simplex</i>	<i>D. cervicornis</i>
<i>Er. verticillata</i>	<i>D. simplex</i>
<i>G. subverticillata</i>	<i>G. oblongata</i>
<i>G. acerosa</i>	<i>G. intricata</i>
<i>G. pusillum</i>	<i>G. pusillum</i>
<i>H. incrassata</i>	<i>L. intricata</i>
<i>H. opuntia</i>	<i>L. farinosa</i>
<i>H. tuna</i>	<i>P. capitatus</i>
<i>H. cervicornis</i>	<i>S. polyceratium</i>
<i>L. intricata</i>	<i>T. herveyi</i>
<i>L. papillosa</i>	<i>V. ventricosa</i>
<i>P. sanctae-crucis</i>	
<i>P. capitatus</i>	
<i>P. polyphysoides</i>	
<i>V. utricularis</i>	
<i>V. ventricosa</i>	

of Pear Tree Bottom (17.43%, $p < 0.001$). The encrusting algae cover was not significantly different at the fore reefs ($p > 0.5$); however, it was different at the back reefs (Discovery Bay 1.5%, Pear Tree Bottom 0%; $p < 0.01$; Table 1).

The dry biomass of samples taken from the four areas indicate no difference between the fore reefs ($p > 0.05$) but the values of 20.63 mg/cm² at Discovery Bay back reef and 1.45 mg/cm² at Pear Tree Bottom back reef were different ($p < 0.05$; Table 1).

The algae species present on the fore reef of Pear Tree Bottom were similar to but not as extensive as those found at Discovery Bay. These included *Dictyota* spp., *Sargassum* spp. and *Turbinaria turbinata* (Table 2). The number of species of algae found at either back reef were still more than those found at the Discovery Bay fore reef. Eighteen species were identified

in the samples from Pear Tree Bottom while 23 were found in Discovery Bay. Species at both back reefs included *Amphiroa* spp., *Ceramium* spp., *Halimeda* spp., and *Lourenzia* spp. (Table 3).

Coral species were most abundant at the fore reef of Pear Tree Bottom. Representative species include *Montastrea annularis*, *Diploria* spp. and three species of *Porites*. No more than three species were found at any of the other sites. *Millepora complanata* was the only species found at all sites (Tables 4 & 5). Coral cover was highest at Pear Tree Bottom fore reef (22.67% cover) with values of 0.55%, 0.3%, and 0.2% cover at Discovery Bay fore reef, Pear Tree Bottom back reef and Discovery Bay back reef, respectively (Tables 4 & 5).

Fish Communities. There were significantly more parrotfish in the Discovery Bay fore reef than in the fore reef of Pear Tree Bottom (120.83/24m² and 13.83/24m² respectively; $p < 0.001$).

Table 4. Fore reef coral species richness and percent cover. Total number of species are in parentheses.

Discovery Bay (3)	Pear Tree Bottom (9)
<i>Millepora complanata</i>	<i>Dendrogyra cylindrus</i>
<i>Montastrea annularis</i>	<i>Diploria labyrinthiformes</i>
<i>Porites astreoides</i>	<i>strigosa</i>
%cover: 0.55 ± 1.61	<i>Millepora complanata</i>
	<i>Montastrea annularis</i>
	<i>Porites astreoides</i>
	<i>P. furcata</i>
	<i>P. porites</i>
	<i>Stephanocoenia michelini</i>
	% cover: 22.67 ± 18.17

Table 5. Back reef coral species richness and percent cover.

Discovery Bay (1)	Pear Tree Bottom (3)
<i>Millepora complanata</i>	<i>Gorgonia ventalina</i>
%cover: 0.2 + 0.53	<i>Millepora complanata</i>
	<i>Stephanocoenia michelini</i>
	%cover: 0.3 + 0.92

Similarly, parrotfish were more abundant in the Discovery Bay back reef (52.67/24m²) than in the Pear Tree Bottom back reef (6.67/24m²; $p < 0.001$). As with the parrotfish on the fore reefs, the number of surgeonfish at Discovery Bay were higher than those at the Pear Tree Bottom fore reef (15.67/24m² and 0.500/24m², respectively; $p < 0.01$). However, the numbers of surgeonfish in the back reefs of the two areas were not significantly different ($p > 0.2$; Table 1).

Our herbivory index using *Thalassia* blades as a bioassay indicate no difference in herbivory pressures in the two fore reefs ($p > 0.2$), yet there was a much greater incidence of herbivory on blades at the back reef of Pear Tree Bottom (5.5 bites blade⁻¹ hour⁻¹) than at the back reef Discovery Bay (0.28 bites blade⁻¹ hour⁻¹; $p < 0.001$; Table 1).

DISCUSSION (TCB, SLS)

Algal response. It has been shown that algal communities in the absence of *Diadema* will show increased biomass and percent cover, and will show a shift in species composition from turf forming algae to fleshy macroalgae (Sammarco 1982b, Lessios 1988).

At both Discovery Bay and Pear Tree Bottom we saw patterns similar

to those predicted above, with the magnitude of the difference being greater where *Diadema* abundance was lower (Figure 1). This is most likely because *Diadema* at both reefs are still at very low density relative to pre-mortality densities (Hughes, et al. 1987). The difference in *Diadema* abundance is accompanied by quantifiable differences in the communities at the two study reefs.

Algal biomass. Algal biomass was generally higher at Discovery Bay. However, two things lead us to discount the accuracy of our results: (i) since the two back reef areas have similar *Diadema* densities, they should have similar biomass values, and (ii) our sampling method may have been inadequate to accurately sample biomass on the two fore reefs.

The back reef at Pear Tree Bottom is very dissimilar to that at Discovery Bay. It is deeper and far less structurally complex, consisting primarily of bare substrate (sand), with very low algal cover. This seems to have nothing to do with daytime echinoid density, and therefore an estimate of algal biomass at Pear Tree does not reflect the effect of *Diadema*.

The fore reefs of both sites had patchily distributed macroalgae. When we sampled algae we had a pre-designated subquadrat from which we removed all algae >1cm weight. This subquadrat never fell on these large patches of *Sargassum* spp. or *Turbinaria* spp., yet these genera were abundant at both sites. We feel that a line transect with samples taken every meter would have enabled us to better represent the biomass of macroalgae on the fore reefs.

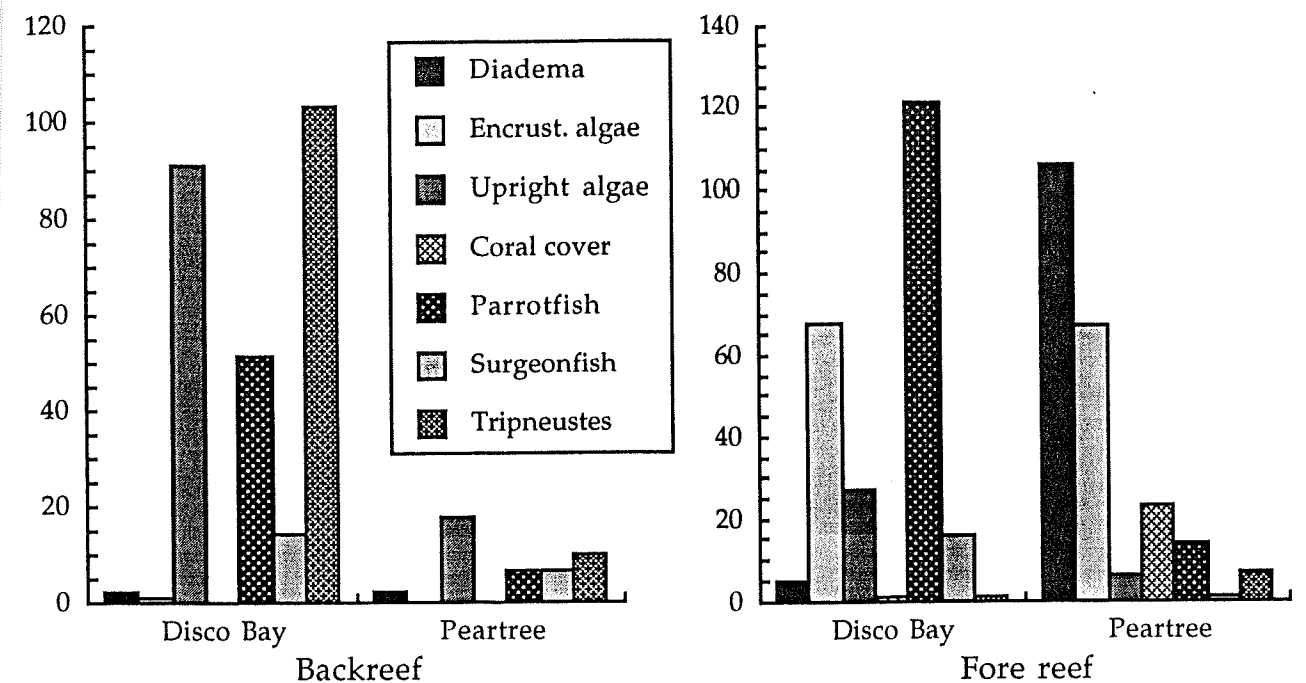


Figure 1. Relative abundances of urchins (#/100m²), algae (% cover), coral (% cover), and herbivorous fish (#/100m²) at Discovery Bay and Pear Tree Bottom in the fore and back reefs.

Algal and coral percent cover. As predicted, overall percent algal cover was higher at Discovery Bay. The values for percent cover by encrusting algae at the two fore reef sites are the same, yet the un-encrusted space is utilized differently at the two sites. Discovery Bay has almost no coral cover, and much upright algae, whereas Pear Tree Bottom has little upright algae and higher coral cover.

The two back reef sites had similar values for coral cover (~0.25%), yet beyond that, the similarity between the two sites ends. Discovery Bay has over 90% cover by upright algae forms, and Pear Tree Bottom is primarily bare substrate.

Low coral cover at Discovery Bay may be due to overgrowth by upright forms of algae, and lowered recruitment of larval corals in an area where bare substrate is limited (Sammarco 1982a).

Community species composition. Both Pear Tree Bottom's and Discovery Bay's algal communities are dominated by fleshy macroalgae species from genera such as *Dictyota*, *Sargassum*, *Turbinaria*, *Acanthophora* and *Halimeda*. This is probably because *Diadema* densities are still relatively low at both sites, and grazing is not intense enough to remove all fleshy algae. Despite this, the fore reef and back reef communities at Discovery Bay are richer in species than at Pear Tree, most likely as a result of lower *Diadema* grazing pressure (Lawrence and Sammarco 1982).

Herbivorous fish communities. An important consequence of the higher algae biomass, percent cover and incidence of fleshy species can be seen in the herbivorous fish populations. In the Discovery Bay fore reef we found

more herbivorous fish coinciding with the higher algae cover. The same was true in the Discovery Bay back reef. Compared to the minimal upright algae cover at Pear Tree Bottom, the algal community at Discovery Bay supports a larger population of juvenile and adult parrotfish.

The surgeonfish population at the Discovery Bay fore reef is greater than that at Pear Tree Bottom. However, this trend is not seen in the back reef. We believe that before the 1983 *Diadema* dieoff, the surgeonfish in this reef were not in competition with *Diadema* for algal resources because they utilized different food niches (Robertson, 1991). For this reason, the population would not show a response to an increase in food resources.

The results of our *Thalassia* bioassay show that grazing is most intense at the back reef of Pear Tree Bottom. This conflicts with our fish censuses of herbivorous fish. We believe that other factors were influencing the activity of the grazing fish. For instance, damselfish territoriality may have excluded parrotfish from feeding on the blades at Discovery Bay. At the fore reef of Pear Tree Bottom, nearby *Diadema* could have discouraged fish from approaching the *Thalassia*. These would both result in far fewer bites per blade and number of blades bitten in these reefs. A more careful study of the fish populations at our sites would help in interpreting our results.

Conclusions. Hughes, et al. (1987) describe the state of post-mortality Jamaican reefs as being one where algae continues to overgrow the reef, especially in shallow water. This seems to

be happening at Discovery Bay, whereas at Pear Tree Bottom, *Diadema* seems to be recruiting well enough to limit algal cover, allowing for more coral growth and recruitment.

It may be possible to reverse the trend of overgrowth by upright algae at Discovery Bay. Three things could effect this change: (i) an increase in *Diadema* recruitment, (ii) an increase in other echinoid densities, and (iii) a decrease in fishing pressure off the fore reef.

Diadema is unlikely to begin recruiting rapidly, as it has not to date; it has been suggested that it cannot recruit well where there is high cover by filamentous algae (Ogden and Lobel 1978). However, Ogden and Lobel (1978) also describe the movement of *Tripneustes ventricosus*, a common back reef echinoid, from the turtlegrass beds bordering the reef onto the algal covered back reef where *Diadema* once dominated. A similar phenomenon may be occurring at Discovery Bay. We noted very high densities of *Tripneustes* at our back reef site. It may be that they are moving into the niche *Diadema* once occupied.

A final hope for the reef is the reduction of fishing pressure. An increase in herbivorous fish populations would most likely maintain algae at a lower level of cover and biomass (Carpenter 1990b, Robertson 1991). However, there is generally local opposition to fisheries reform and a substantial reduction in fishing pressure may be unlikely to happen soon.

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