important determinants of brittlestar community structure.

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Distribution and density of two urchin species and their effects on coral reef community structure

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Abstract: The long-spined urchin, *Diadema antillarum*, is thought to make a substantial impact on coral reef communities through grazing on macroalgae and competition with herbivorous fish. We surveyed the distribution and density of two urchin species (*D. antillarum* and *Tripneustes ventricosus*) in the forereefs of Discovery Bay and Pear Tree Bottom, Jamaica. We examined how macroalgae cover, live coral cover, and herbivorous fish abundances are related to urchin distributions. We predicted that *D. antillarum* would be concentrated in areas of high structural complexity due to its dependence on refuges. We made comparisons between the two sites, as well as within each site; we also compared our findings with a study done in 1992 (Balser and Soucy) to assess the recovery of *D. antillarum* populations and the community response since the 1983 *Diadema* die-off. Urchin densities and live coral cover were significantly higher at Pear Tree Bottom than Discovery Bay, while Discovery Bay had more macroalgae (percent cover and dry weight) and herbivorous fish. At Pear Tree Bottom, we found that as *D. antillarum* densities increased, macroalgae cover decreased and live coral cover increased. At Discovery Bay, herbivorous fish abundances were positively correlated with structural complexity, though there was no corresponding trend at Pear Tree Bottom. Since the 1992 survey, *D. antillarum* and *T. ventricosus* densities have increased at Discovery Bay by 19-fold and 5-fold respectively, while *T. ventricosus* density increased 30-fold at Pear Tree Bottom. Our results indicate that although *D. antillarum* populations have been recovering since the die-off, *T. ventricosus* continues to invade the forereefs, perhaps due to competitive release from *Diadema.* Although our index of structural complexity failed to detect a difference between the sites, Pear Tree Bottom appears to have greater coral development than Discovery Bay. More developed reefs may provide refuges for *D. antillarum*, which may explain the high urchin densities found at Pear Tree Bottom.

Key Words: algal cover, coral cover, Diadema antillarum, Diadema *die-off, herbivorous fish, three-dimensional structure,* Tripneustes ventricosus, *urchin grazing*

INTRODUCTION

As an important herbivore in coral reef ecosystems, the long-spined urchin, *Diadema antillarum*, has a major impact on reef community diversity. Heavy grazing on macroalgae by *D. antillarum* can benefit corals that compete for space with macroalgae (Hughes et al. 1987). Additionally, *D. antillarum* is the main competitor with herbivorous fish, which share macroalgal food resources (Hay and Taylor 1985). An FSP study in 1992 found that algal biomass and species diversity were lower in areas of high *D. antillarum* densities (Balser and Soucy 1992). They also found that the dominant algal forms in these areas were encrusting, toxic, or distasteful algae resistant to urchin grazing.

D. antillarum was the dominant forereef echinoid of Jamaican coral reefs until July 1983, when water borne pathogens caused 91-100% mortality (Lessios 1988). This die-off resulted in dramatic increases in percent cover of fleshy algae and decreases in live coral cover throughout the Caribbean (Carpenter 1990). The decrease in *Diadema* abundance also resulted in a competitive release for *Tripneustes ventricosus* (West Indian Sea Egg), allowing this urchin to invade the forereefs at Discovery Bay and Pear Tree Bottom (Gilmarten and Young 1991).

This study assesses changes in *D. antillarum* and *T. ventricosus* densities since the 1992 report (Balser and Soucy 1992), and the impact these urchin populations have on the community structure in the forereefs of Discovery Bay and Pear Tree Bottom. We surveyed the distribution of *D. antillarum* and *T. ventricosus* in the forereefs of Discovery Bay and Pear Tree Bottom. We predicted that *D. antillarum* would be concentrated in areas of high structural complexity, since they seem more dependent on refuges than *T. ventricosus* (Gilmarten and Young 1991). Furthermore we

examined how these urchin populations may have affected the local community structure, predicting that areas of high *D. antillarum* densities would support less fleshy algae due to urchin grazing and have increased cover of sparse algal turf. We would also expect to find more live coral cover in areas of high urchin density since there would be less competition for space with less fleshy algal cover, aiding coral development and recruitment. Finally, we predicted that there would be less herbivorous fish in areas of high urchin density, since herbivorous fish populations are known to be negatively affected by the presence of *D. antillarum* (Hay and Taylor, 1985).

METHODS

All sampling was conducted between 6-12 March 1999 at the forereefs of Discovery Bay and Pear Tree Bottom, Jamaica. At each site, we set up nine circular plots (radius = 3 m), at comparable depths (<4 m deep) and locations (within 30 m of the reef crest) as the Balser and Soucy 1992 study. All visible *D. antillarum* and *T. ventricosus* within the plot were counted. All following measurements were recorded for only nine of these plots at each site, since we were unable to locate one plot at each forereef. At each plot, we estimated structural complexity by conforming a demarcated 5.5 m chain as closely as possible to the substrate, along 4 transects radiating in cardinal directions from the center point. We then recorded what distance of chain was required to reach a 3 m horizontal distance from the center point. An index of structural complexity (SCI) was then calculated by dividing the chain distance by 3. An average index for each plot was calculated from the four measurements. Also, the deepest and shallowest points at each plot were recorded with the difference calculated as a measure of vertical relief.

Three estimates of substrate cover were obtained using 0.5 x 1.5 m quadrats placed in three random areas of each plot. The percent cover of fleshy algae (> 1 cm in height); "turf" algae (calcareous encrusting and sparse turf algae < 1 cm in height); live coral; "dead coral" (bare, standing dead coral); bare coral rubble; and bare sand in each quadrat was recorded. All fleshy algae were collected from a 0.5 x 0.5 m area in each of the three quadrats at each plot and combined into one sample per plot. Algae were identified to species, dried for 10 hrs and weighed to obtain dry algal biomass. Also, we counted the number of Acanthuridae (surgeonfish) and Scaridae (parrotfish) seen within each plot over 10 minutes. Each fish was counted only once, regardless of how much time it spent in the plot.

Comparisons between Discovery Bay and Pear Tree Bottom were made by averaging measurements for the 9 plots at each site (10 plots for urchins). We also examined trends within sites by using these plots at each site as independent replicates. Finally, we compared urchin densities, abundances of herbivorous fish, algal and coral percent cover at the two sites with the estimates from the 1992 Balser and Soucy study (Table 1).

RESULTS

Urchin densities

Both *D. antillarum* and *T. ventricosus* densities were significantly higher at Pear Tree Bottom than at Discovery Bay (Table 2). Also, there was a significant increase at Discovery Bay in both *D. antillarum* (19-fold) and *T. ventricosus* densities (> 5-fold) from 1992 (Tables 1 and 2). At Pear Tree Bottom, densities of both urchins increased from the 1992 survey, but only *T. ventricosus* densities (> 30-fold increase) were significantly different (Tables 1 and 2).

Structural complexity

There was no difference in SCI or vertical relief between the two sites (Table 2). Within plots at each of the two sites, there were no significant trends with SCI and urchin densities.

Substrate cover

Percent cover and dry weight of fleshy algae at Discovery Bay was significantly higher than at Pear Tree Bottom (Table 2). We found 25 species of algae at Discovery compared to 21 at Pear Tree Bottom (Appendix A). Discovery Bay had significantly higher percent cover of turf algae and rubble while Pear Tree Bottom had significantly more dead and live coral cover (Table 2).

At Pear Tree Bottom, percent cover of both turf algae and live coral increased with increasing densities of *D. antillarum*. Additionally, biomass of fleshy algae decreased with increasing *D. antillarum* density (Fig. 1). At Discovery Bay, percent cover of both fleshy and turf algae significantly decreased between 1992 and 1999 (Tables 1 and 2). At Pear Tree Bottom, percent

encrusting algae decreased from 1992 (Tables 1 and 2).

Herbivorous fish

Both parrotfish and surgeonfish were significantly more abundant at Discovery Bay than at Pear Tree Bottom (Table 2). Within plots at Discovery Bay, herbivorous fish density increased with increasing structural complexity (Fig. 2) and with increasing rubble cover (regression analysis: $R^2 = 0.6$, df = 1, P = 0.01), though there were no corresponding trends at Peartree Bottom. Also, parrotfish densities at Discovery Bay decreased significantly from 1992 (Tables 1 and 2). Other changes in densities from 1992 at both sites were not significant.

Table 1. 1992 comparison between urchin and herbivorous fish densities and substrate cover at forereefs of Discovery Bay and Pear Tree Bottom, Jamaica (Reprinted from Balser and Soucy, 1992).

	Discovery Bay	Pear Tree Bottom
D. antillarum density (ind/m^2)	0.05	1.07
T. ventricosus density (ind/m^2)	0.013	0.072
Percent upright algae	27.53	6.07
Percent encrusting algae	67.87	67.30
Dry Agal Biomass (g/m^2)	206.30	14.50
Percent coral cover	0.55	22.67
Parrotfish (ind/m^2)	5.03	0.58
Surgeonfish (ind/m^2)	0.65	0.02

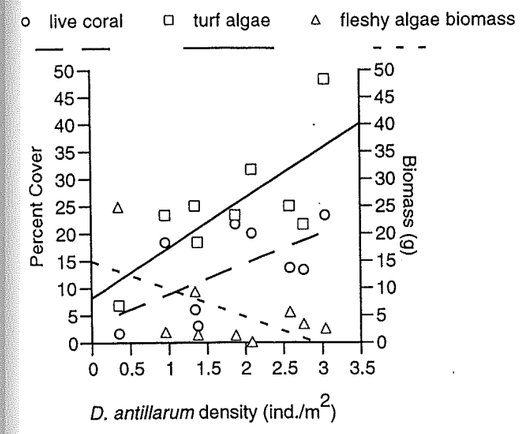

Fig. 1. Relationship between *D. antillarum* densities and percent cover of live coral, turf algae, and fleshy algae biomass at Pear Tree Bottom fore reef, Jamaica (regression analysis; coral: $R^2 = 0.37$, df = 1, P = 0.08; turf: $R^2 = 0.54$, df = 1, P = 0.02; algae biomass: $R^2 = 0.35$, df = 1, P = 0.09).

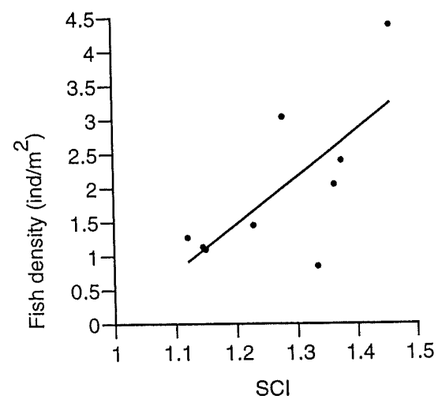

Fig. 2. Relationship between structural complexity index (SCI) and fish density (parrotfish and surgeonfish) at the west forereef at Discovery Bay, Jamaica (regression analysis: $R^2 = 0.51$, df = 1, P = 0.03).

Table 2. 1999 comparison between urchin and herbivorous fish densities, substrate cover, and structural complexity at forereefs of Discovery Bay and Pear Tree Bottom, Jamaica. Values are means ± 1 SE; the 1999 data from the two sites are compared using Kruskal-Wallis test. Df = 1 for all tests. ↓ and ↑ indicates significant decrease and increase (respectively) between 1992 and 1999.

	Discovery Bay	Pear Tree Bottom	χ^2	P
Urchins ind/m^2				
Diadema	1.0 ± 0.17 ↑	1.82 ± 0.30	3.95	0.05
Tripneustes	0.08 ± 0.03 ↑	2.32 ± 0.31 ↑	12.90	0.0003
% Cover				
fleshy algae	12.63 ± 2.56 ↓	4.63 ± 1.29	5.09	0.02
encrusting/turf algae	48.41 ± 2.11 ↓	24.83 ± 3.69 ↓	10.16	0.001
dead coral	26.44 ± 5.7	56.48 ± 6.30	7.25	0.007
live coral	1.29 ± 0.45	13.44 ± 2.72	10.16	0.001
rubble	9.26 ± 3.30	0.74 ± 0.74	4.65	0.03
algae biomass (g/m^2)	16.02 ± 2.38	5.60 ± 2.58	5.07	0.02
vertical relief	1.54 ± 0.18	1.63 ± 0.27	0.07	0.93
SCI	1.27 ± 0.04	1.34 ± 0.05	1.42	0.23
Fish ind/ m^2				
parrotfish	1.77 ± 0.38 ↓	0.79 ± 0.21	4.50	0.03
surgeonfish	0.20 ± 0.06	0.05 ± 0.03	5.13	0.02

DISCUSSION

Urchin densities

Densities of *D. antillarum* were higher at Pear Tree Bottom than at Discovery Bay, possibly because corals at Pear Tree Bottom are more developed, providing more refuges for *D. antillarum*. However, our measure of structural complexity did not differ between the two sites. We believe that this index may not accurately represent the number of refuges available to *D. antillarum*. A direct count of actual refuges would provide a better measure of habitat quality for this urchin. *T. ventricosus* density was also higher at Pear Tree Bottom than at Discovery Bay. The reasons for this are unclear since *T. ventricosus* seems less dependent on refuges than *D. antillarum*.

Between 1982 and 1984, *D. antillarum* density at Pear Tree Bottom dropped from 8.9 to 0 individuals/m^2 (Hughes et al. 1985). The current density of 1.82 individuals/m^2 at this site indicates continued population recovery following this die-off, although it appears that more time is needed for full recovery of this population. *T. ventricosus* density increased significantly at both sites since 1992, possibly due to continued competitive release following the *Diadema* die-off. Although *D. antillarum* densities appear to be increasing, current densities may not be high enough to cause a decline in abundance of *T. ventricosus*. Relative increases in *D. antillarum* densities were higher at Discovery Bay while increases in *T. ventricosus* densities were higher at Pear Tree Bottom. The reasons for this pattern are unclear.

Substrate cover

Our prediction that fleshy algae cover and algal biomass would decrease with increasing urchin densities was supported. Urchin density was higher at Pear Tree Bottom, and percent cover and dry weight of fleshy algae were lower. Also, percent cover of both live and dead coral were higher at Pear Tree Bottom, possibly due to greater urchin grazing and lower algae abundance. Our results further suggest that *D. antillarum* plays an important role in determining the relative abundances of algae and coral since fleshy algae abundance decreased while coral cover and turf algae cover increased with increasing *D. antillarum* densities at Pear Tree Bottom (Fig. 1). Increases in *D. antillarum* densities may result in increased herbivory on fleshy macroalgae, while low lying turf and calcareous encrusting algae may be more resistant to this herbivory. It has been suggested that *D. antillarum* preferentially feed on macroalgae species (Carpenter 1986). Also, intense herbivory by urchins has been shown to limit algal growth forms to fast growing species (turf algae) or those with morphological defenses, such as calcareous encrusting algae (Foster 1987).

Percent cover of algae decreased at both sites since 1992, which may be due to higher urchin densities. Finally, percent cover of rubble was higher at Discovery Bay, possibly indicating a higher amount of damage by Hurricane Allen (1980) experienced at this site.

Herbivorous fish

Densities of both parrotfish and surgeonfish were higher at Discovery Bay than at Pear Tree Bottom (both in 1992 and in our study), which may be due to higher algal abundance and decreased levels of competition with urchins (due do lower urchin densities) at Discovery Bay. Within plots at Discovery Bay, fish densities increased with increasing SCI and percent cover of rubble. Areas of higher structural complexity provide more refuge for fish, as well as recruitment sites for resources such as algae and invertebrates (Bizarro et al. 1992).

Herbivorous fish densities decreased at both sites since 1992. Increases in urchin densities during the past seven years may have increased competition experienced by these fish, resulting in fish population declines at both sites.

Conclusions

Densities of *T. ventricosus* have continued to increase since 1992 in the forereefs of both Pear Tree Bottom and Discovery Bay. This may be due to competitive release in these areas following the drastic reduction in *D. antillarum* populations in 1983. Although populations of *D. antillarum* appear to be recovering, densities are still well below those seen before the 1983 die-off. Thus, the densities of *D. antillarum* still appear to be low enough to allow *T. ventricosus* populations to increase in these areas.

Increases in total urchin densities at these sites appear to be accompanied by decreases in abundances of algae, presumably due to increased herbivory by urchins. The increases in urchin abundance may also account for decreases in densities of herbivorous fish through competition in these areas over the past seven years.

These patterns can also be seen in comparisons between current communities at the two sites. Pear Tree bottom had higher urchin densities, and lower algae and herbivorous fish densities than Discovery Bay, further suggesting that urchins play an important role in determining community structure at these two areas.

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Appendix A. Forereef algal species richness. The number in parentheses is the total number of species for each site. Species listed above the bold line were found at both sites.

Discovery Bay (25)	Pear Tree Bottom (21)
Amphiroa fragilissima	*Amphiroa fragilissima*
Dictyota ciliolata	*Dictyota ciliolata*
D. dichotoma	*D. dichotoma*
Galaxaura oblongata	*Galaxaura oblongata*
Halimeda goreaui	*Halimeda goreaui*
H. opuntia	*H. opuntia*
H. tuna	*H. tuna*
Padina gymnospora	*Padina gymnospora*
Sargassum fluitans	*Sargassum fluitans*
S. hystrix	*S. hystrix*
S. polyceratium	*S. polyceratium*
Spyridia sp.	*Spyridia sp.*
Turbinaria tricostata	*Turbinaria tricostata*
Ventricaria ventricosa	*Ventricaria ventricosa*
Caulerpa racemosa	*Acanthophora spicifera*
Dasya harveyi	*Centroceras clavulatum*
D. mertensii	*Ernodesmis verticillata*
Gracilaria damaecornis	*G. subverticillata*
Laurencia intricata	*Hypnea cervicornis*
Lobophora variegata	*Laurencia poitei*
Rosenvingea intricata	*P. sanctae-crucis*
S. hystrix var. buxifolium	
S. platycarpum	
T. turbinata	
Valonia spp.	