

when encounters occur. Additionally, predation intensity may be less severe during the day because brittle stars are more cryptic at this time. When brittle stars were experimentally denied refuge, previous studies found no difference in predation rate or intensity between day and night trials (Eckert and Jones, 1989). However, potential differences may have been obscured due to unnaturally high predation on fully exposed brittle stars, since all brittle stars were eaten regardless of time of day.

An alternative explanation for the predation patterns we observed may be that daytime and nighttime predator populations are composed of entirely different species. Variation in size or foraging strategies across these predator species may account for the differences in predation rate and intensity between day and night trials.

Regardless of time of day, we found very high predation pressure on brittle stars. At such high rates, it is unlikely that the population could sustain itself, indicating that predation may have been artificially enhanced by our experimental design. Although our experimental brittle stars immediately found cover when placed in the rubble zone, it remains possible that the tethering process negatively affected the speed or maneuverability of brittle stars in ways that we could not readily assess. If so, this may have increased predation values above those normally occurring on the reef, thus contributing to the high predation

levels across treatments. It is also possible that injury as a result of the tethering may have attracted predators via odor. However, we believe that the differences between day and night trials remain valid, since our design did not differentially influence day and night trials. Our findings of high predation rate during the day and high predation intensity at night suggest that predation pressure on brittle stars is always high. Thus, brittle stars need to employ cryptic behavior during the day and night in order to cope with such high predation pressure across times.

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Spatial and temporal patterns in *Diadema antillarum* and *Tripneustes ventricosus* densities and macroalgal cover in Discovery Bay, Jamaica

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Abstract: Mass mortality of the sea urchin *Diadema antillarum* and an associated increase in macroalgal cover occurred across the Caribbean in 1983. This die-off opened a niche for another urchin species, *Tripneustes ventricosus*, to extend into the forereef habitat. In recent years, *D. antillarum* populations have begun to recover in the shallow forereef at Discovery Bay and macroalgal cover has decreased. We hypothesized that *D. antillarum* and *T. ventricosus* densities and macroalgal cover would differ between the forereef and backreef habitats, with a change in density from previous levels. Between the forereef and backreef in 2003, we found no difference in urchin densities or macroalgal cover. However, between 1991 and 2003, *D. antillarum* density has remained relatively stable, and *T. ventricosus* density and macroalgal cover have decreased. Therefore, we speculate that the increasing *D. antillarum* population is excluding *T. ventricosus* from the forereef, as well as restricting macroalgal growth.

Key Words: algae, competitive exclusion, coral reef, grazer, herbivory, urchin

INTRODUCTION

Mass mortality of the sea urchin *Diadema antillarum* occurred across the Caribbean in 1983 from a water-borne pathogen (Hunte et al. 1986). Within eight weeks, most of the *D. antillarum* along the Jamaican coastline were infected and local mortality rates were nearly 100% in all habitats (*Thalassia* beds, patch reefs, rocky pavement, coral rubble, and forereef to 45 m; Hughes et al. 1985). The loss of this important grazer precipitated an explosion of algal biomass. At reefs near Discovery Bay, Jamaica, cover by foliose algae increased from 30.7% to 72.3% in four months, and crustose algae and clionid sponges sharply declined (Liddel and Ohlhorst 1986). Another urchin species, *Tripneustes ventricosus*, was observed moving into the forereef, which it had not previously inhabited (Gilmartin and Young 1991, Edmunds and Carpenter 2000). In recent years, *D. antillarum* populations in shallow reefs near Discovery Bay have begun to recover and macroalgal cover has decreased (Edmunds and Carpenter 2000).

We hypothesized that *D. antillarum* and *T. ventricosus* densities and macroalgal cover would differ between the forereef and backreef habitats due to differing habitats

and conditions on either side of the reef crest. Additionally, we hypothesized that urchin densities and macroalgal cover have changed over the past five to ten years due to the recovery of *D. antillarum*. Although we observed several *T. ventricosus* in both the forereef and backreef areas, densities appear to have declined in recent years. Therefore, we predicted that *D. antillarum* density would be higher in the forereef than the backreef, and that *T. ventricosus* would be rare the forereef, similar to their distribution before the 1983 die off. Due to high macroalgal grazing of *D. antillarum*, we predicted that as *D. antillarum* density increased, macroalgal cover would decrease. We also predicted that there would be a higher density of *D. antillarum*, a lower density of *T. ventricosus*, and lower macroalgal cover in both the forereef and backreef than was recorded by studies in 1991 and 1998.

METHODS

We surveyed urchin density and macroalgal cover on 25 and 26 February 2003 in the forereef and backreef of Discovery Bay, Jamaica. We ran 10 x 2 m transects (5 in the forereef, 7 in the backreef) parallel to and on either side of the reef crest. We placed the transects as close as possible to

the locations described in Eaken et al. (1998). The backreef transects were extremely close to the reef crest at 1–2 m depths. The forereef transects were directly adjacent to the reef crest at 3–4 m depths.

In each transect we counted the number of *D. antillarum* and *T. ventricosus* within 1 m on either side of the transect tape. We determined percent macroalgal cover by placing a 0.5 m² grid centered at 3, 6, and 9 m along the transect. The grid was divided into 25 squares, with 5 of the 25 squares labeled with flagging. We determined percent cover using the five flagged squares at each quadrat placement.

We used a Student's t-test and Pearson correlation to analyze normally distributed data (Table 1). We used a Wilcoxon signed-rank test and a Spearman-Rho correlation to analyze data that was not normally distributed. We graphically compared 1991, 1998, and 2003 urchin densities and macroalgal cover (Fig. 3). The data from these three years are not directly com-

parable because censuses were conducted at slightly different depths and locations, but the general trends are still relevant.

RESULTS

2003 results: We found no significant differences between forereef and backreef densities of *D. antillarum* ($t = 1.67$, $df = 10$, $P = 0.13$), *T. ventricosus* ($t = 0.13$, $df = 10$, $P = 0.90$), or percent macroalgal cover (Fig. 1; $t = 1.06$, $df = 10$, $P = 0.32$). *Diadema antillarum* density and percent macroalgae cover were inversely correlated across both sites ($r = -0.58$, $df = 11$, $P = 0.05$). However, *T. ventricosus* density and percent macroalgal cover were not correlated ($r = -0.39$, $df = 11$, $P = 0.21$).

Backreef between years 1998 and 2003: Mean *D. antillarum* backreef densities did not differ significantly between 2003 and 1998 ($S = 26.5$, $df = 10$, $P = 0.34$), although the mean *D. antillarum* density was 2.24 times higher in 2003 than 1998 (Fig. 2). Mean

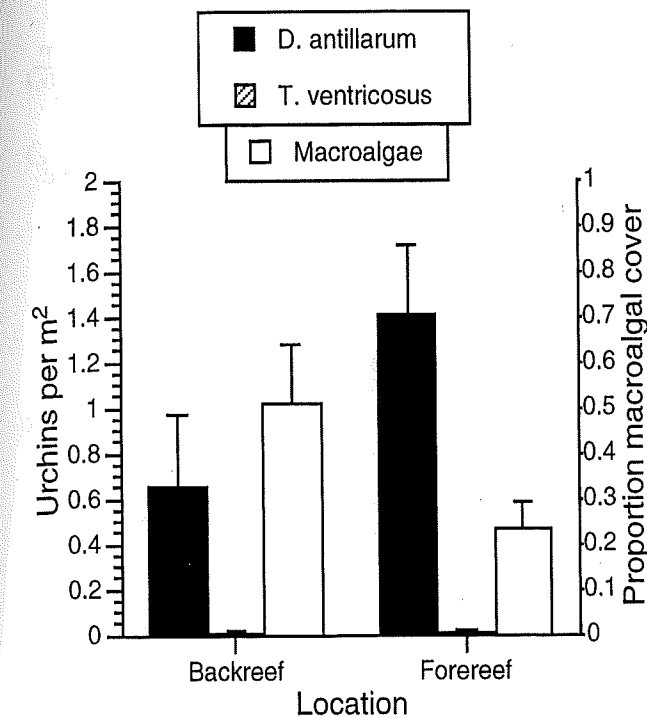


FIG. 1. Density of *D. antillarum* and *T. ventricosus* and proportion macroalgal cover in backreef and forereef sites along the reef crest at Discovery Bay, Jamaica in 2003. *Tripneustes ventricosa* values are 0.01 for both backreef and forereef ($n = 5$ for forereef and $n = 7$ for backreef).

T. ventricosus backreef density was significantly higher in 1998 than 2003 ($S = 46.0$, $df = 10$, $P = 0.02$). We found that mean percent macroalgal cover decreased by ~50% between 1998 and 2003, although this difference was only marginally significant ($t = 2.14$, $df = 10$, $P = 0.06$).

Forereef across years 1991, 1998 and 2003: In forereef measurements, both average *T. ventricosus* density and percent macroalgal cover increased after 1991, reaching maximum values in 1998, and then decreasing to minimum values in 2003 (Fig. 3). Average *D. antillarum* density was relatively constant between 1991, 1998 and 2003.

DISCUSSION

We found no significant differences in urchin densities or macroalgal cover between forereef and backreef sites in 2003. *Diadema antillarum* density was more than two times greater on the forereef than the

backreef, but the difference between sites was not significant due to high variability in the backreef. Some of our backreef transects were characterized by high *D. antillarum* density and low macroalgal cover while others had low *D. antillarum* densities and high macroalgal cover. These inconsistencies between transects suggest that *D. antillarum* may still be recovering in this zone.

Further data should be collected in future years to determine if *D. antillarum* variability decreases as its range expands in the backreef. *Tripneustes ventricosus* densities were low on both the forereef and backreef, which may be due to paucity of their preferred habitat (turtle grass and perhaps macroalgae; Gilbert, pers. comm.). We found that macroalgal cover decreased as *D. antillarum* density increased, supporting our prediction. *Diadema antillarum* feeds preferentially on microalgal turf and may reduce macroalgal growth by grazing to

TABLE 1. Statistical methods used to analyze data from 1998 and 2003 censuses of *D. antillarum* and *T. ventricosus* densities and percent macroalgal cover. The statistical test column refers to the method used to compare paired rows.

Year	Habitat	Variable	Statistical Test
2003	forereef	<i>D. antillarum</i> density	Student's t-test
2003	backreef	<i>D. antillarum</i> density	
2003	forereef	<i>T. ventricosus</i> density	Wilcoxon signed-rank test *
2003	backreef	<i>T. ventricosus</i> density	
2003	forereef	% macroalgal cover	Student's t-test
2003	backreef	% macroalgal cover	
1998	backreef	<i>D. antillarum</i> density	Wilcoxon signed-rank test *
2003	backreef	<i>D. antillarum</i> density	
1998	backreef	<i>T. ventricosus</i> density	Wilcoxon signed-rank test *
2003	backreef	<i>T. ventricosus</i> density	
1998	backreef	% macroalgal cover	Student's t-test
2003	backreef	% macroalgal cover	
2003	backreef / forereef	<i>D. antillarum</i> density	Pearson correlation
2003	backreef / forereef	% macroalgal cover	
2003	backreef / forereef	<i>T. ventricosus</i> density	Spearman's Rho correlation *
2003	backreef / forereef	% macroalgal cover	

* Non-parametric test used because data were not normally distributed.

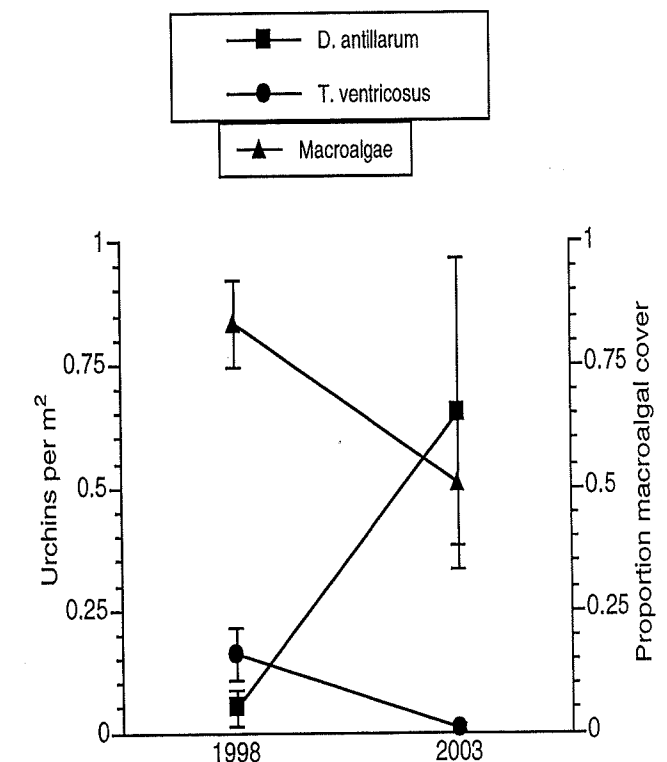


FIG. 2. Density of *D. antillarum* and *T. ventricosus* and proportion macroalgal cover across two years in the back reef at Discovery Bay, Jamaica ($n = 7$ for 2003). Data for 1998 from Eaken et al. (1998).

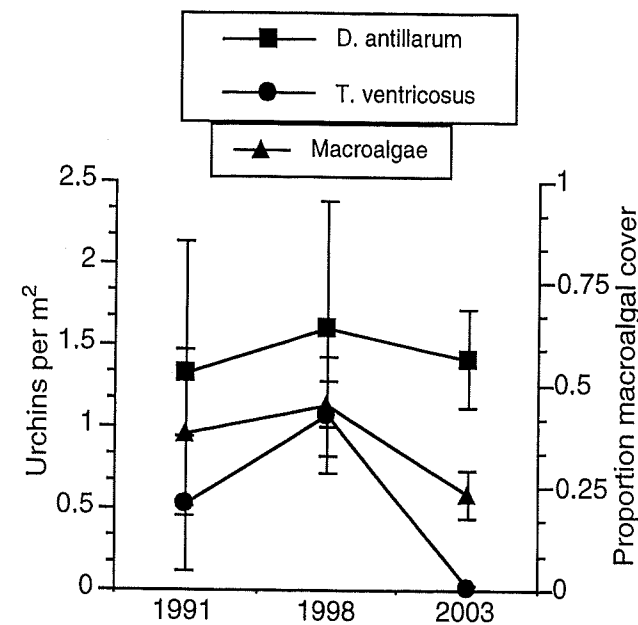


FIG. 3. Density of *D. antillarum* and *T. ventricosus* and proportion macroalgal cover across three years in the forereef at Discovery Bay, Jamaica ($n = 5$ for 2003). Data from 1991 and 1998 from Gilmartin et al. (1991) and Eaken et al. (1998).

maintain this food source (Carpenter 1981). This finding provides support for the role of *D. antillarum* as an important ecosystem engineer in this reef system.

Comparing backreef sites between 1998 and 2003, we found that mean *D. antillarum* density was 13 times greater in 2003 than 1998, although this change was not significant. Macroalgal cover decreased from 80% to 40% between 1998 and 2003 (marginally significant), suggesting that major changes have occurred in the backreef habitat and are most likely due to *D. antillarum* grazing. The backreef substrate composition was highly variable in both years, resulting in large variance in the data. *Tripneustes ventricosus* density was significantly lower in 2003 than 1998, which may be explained by the increase in *D. antillarum* and the change in habitat from macroalgae to microalgal turf.

Our study suggests that *T. ventricosus* density at the forereef site (near the reef crest) has returned to levels occurring before the *D. antillarum* die off. Ogden et al. (1973) and Sammarco et al. (1974) found that when

D. antillarum were removed from an area, *T. ventricosus* advanced into the opened habitat, but were displaced from their new habitat when *D. antillarum* returned. These previous studies support our findings and suggest that the decrease in *T. ventricosus* density in the forereef may be explained by the return of *D. antillarum*. High *D. antillarum* populations alter the forereef habitat, making it less preferable for *T. ventricosus*, which then retreat to their former habitats in the backreef and *Thalassia* beds (Edmunds and Carpenter 2000). However, our study found that *D. antillarum* density in the forereef has remained relatively stable since 1991, suggesting that there may be a time lag between *D. antillarum* return and *T. ventricosus* retreat. Macroalgal cover in the forereef declined very slightly from 1991 to 2003, which may reflect the lingering affects of the *D. antillarum* recovery (pre-1991; Fig. 3). Future monitoring of urchin density and macroalgal cover could reveal if the trends we observed continue in future years.

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Appendix A: Summary of 2003 data for urchin densities and macroalgal cover in the backreef and forereef at Discovery Bay, Jamaica.

Site	Depth (m)	Transect #	<i>Tripneustes</i> (# per m²)	<i>Diadema</i> (# per m²)	% Algal cover
Backreef	1-2	1	0	0	0.57
		2	0	0	0.91
		3	0	2	0.87
		4	0	0	0.50
		5	0	23	0.57
		6	1	42	0.02
		7	0	24	0.12
Forereef	3-4	1	0	37	0.03
		2	0	33	0.31
		3	1	43	0.19
		4	0	16	0.37
		5	0	12	0.28