Top-Down vs. Bottom-Up: the effects of urchin grazing and nutrient levels on macroalgae in Jamaican coral reefs

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Abstract: There has been some debate over the impact of nutrient concentrations and *Diadema antillarum* herbivory in structuring Caribbean coral reef communities, especially since the post-1983 macroalgal blooms on these reefs. We attempted to evaluate the relative importance of *Diadema* herbivory and nutrient concentrations in structuring benthic macroalgal communities on Jamaican reefs. We hypothesized that both *Diadema* and nutrients would influence macroalgal cover, but *Diadema* would be the more important regulator. We sampled nutrient concentrations, *Diadema* density, and substrate cover for two reefs with different levels of macroalgal cover. On the algae-covered reef, macroalgal cover was negatively correlated with *Diadema* density and not correlated with nutrient concentrations. On the coral-covered reef, macroalgal cover was positively correlated with nutrient concentrations and not correlated with *Diadema* density. Dispersion pattern of *Diadema* may be an important factor in determining the relative importance of nutrients and *Diadema* herbivory on benthic macroalgal cover. Phosphorus and nitrogen concentrations were tightly correlated at both sites, suggesting that the two nutrients come from the same place, possibly freshwater vents, at the two sites.

Key Words: Diadema antillarum, *eutrophication, nitrogen, overfishing, phosphorus,* Tripneustes ventricosus

Introduction

Ecologists have used the concepts of bottom-up and top-down trophic regulation to describe how resource availability and predation can influence the community structure of an ecosystem. A complex interaction of bottom-up and top-down controls may be important on coral reefs, where standing crops of benthic macroalgae are usually inconspicuous on undisturbed coral reefs due to the combined effects of low nutrient availability and grazing by herbivorous fish and invertebrates. During the past two decades, some Caribbean coral reefs have experienced phase shifts away from a system dominated by corals to one dominated by macroalgae or algal turfs (Lapointe 1997). There has been some debate over the cause of these phase shifts. An important grazer on macroalgae, the echinoid species *Diadema antillarum,* suffered mass mortality from a species-specific pathogen throughout the Caribbean from 1982 to 1984. Hughes (1994) attributes the benthic algal bloom on Jamaican reefs that began in 1983 to a reduction of top-down control: the *Diadema* die-off and overfishing of herbivorous fish. Lapointe (1999) advances the idea that nutrients (i.e. phosphorous and nitrogen), under conditions of decreased herbivory, exert a significant and sometimes primary forcing mechanism underpinning macroalgal blooms on reefs in Jamaica.

We attempted to evaluate the relative importance of *Diadema* herbivory and nutrient concentrations in structuring benthic macroalgal communities on Jamaican reefs. We hypothesized that both *Diadema* and nutrients would influence macroalgal cover, but *Diadema* would be the more important regulator. We predicted that macroalgal cover would be negatively correlated with *Diadema* density (Balser and Soucy 1992; Dallison et al. 1999) and, to a lesser extent, positively correlated with nutrient concentrations.

Methods

We sampled nutrients, urchin density, and substrate cover in the first week of March 2001, at two sites with observably different levels of macroalgal cover on the northern shore of Jamaica. Balser and Soucy (1992) provide full site descriptions of both sites. We observed higher macroalgal cover and lower

coral cover at the M1 mooring on the West fore reef of Discovery Bay than at the Pear Tree Bottom fore reef about 2 miles to the east. Pear Tree Bottom also had more conspicuous buttresses and seemed to have larger and more developed stands of coral than Discovery Bay. In general, Pear Tree Bottom seems to have a greater density of *Diadema* and less macroalgal cover than Discovery Bay, which may be indicative of Pear Tree being a less-disturbed reef.

We randomly placed six buoys over buttresses at Pear Tree Bottom and seven buoys at Discovery Bay along a transect parallel to the reef crest at a depth of 4.6 m. At each buoy a water sample was taken at the bottom of the water column on 3 March, after a series of calm days. Water samples were filtered within 2 hours of collection and analyzed for total nitrogen and total phosphorus content in the chemistry laboratory at Discovery Bay Marine Laboratory. We surveyed *Diadema antillarum* and *Tripneustes ventricosus* in a 3 m radius circle around each buoy and haphazardly placed 3 non-overlapping 1 m^2 quadrats within the surveyed circle to estimate the percent cover by macroalgae, live coral, sand, and CTB (coraline algae, turf algae, or bare substrate). We intended to measure macroalgal height at the two sites to roughly assess macroalgal biomass, but were unable to do so due to rough weather. We used Student's t-tests to compare data between the two sites and regressions to compare data within sites.

Results

Diadema dispersion was uniform at Pear Tree Bottom and aggregated at Discovery Bay (Table 1, Figs. 1, 2). *Diadema* and *Tripneustes* densities, however, were not different between the two sites (Table 1). Densities of *Diadema* have continued to increase since 1992 at both sites but have increased less at Pear Tree Bottom than Discovery Bay (Table 1, Fig. 3). *Tripneustes* densities, on the other hand, have decreased at both sites since 1999 (Table 1). In 2001, there was still more coral and less macroalgal cover at Pear Tree Bottom than Discovery Bay but there was no difference in CTB and sand cover between sites (Table 1).

Coral cover was negatively correlated with macroalgal cover ($r^2 = 0.55$, df = 1, 8, P = 0.008) and has continued to increase as macroalgal cover has decreased at Pear Tree Bottom since 1999 and at Discovery Bay since 1992 (Table 1, Fig. 4). At Discovery Bay, *Diadema* density was negatively correlated with macroalgal cover ($r^2 = 0.63$, df = 1, 5, P = 0.02; Fig. 5) and positively correlated with CTB ($r^2 = 0.56$, df = 1, 5, P = 0.051) and coral cover ($r^2 = 0.66$, df = 1, 4, P = 0.051). At Pear Tree Bottom, *Diadema* density and macroalgal cover were not related ($r^2 = 0.12$, df = 1, 4, P = 0.27; Fig. 6), while *Diadema* density was positively correlated with live coral cover ($r^2 = 0.41$, df = 1, 4, P = 0.17) and negatively correlated with CTB cover ($r^2 = 0.35$, df = 1, 4, P = 0.21).

Mean nitrogen and phosphorus concentrations did not differ between sites (Table 1), and macroalgal cover was not correlated with nitrogen ($r^2 = -0.059$, df = 1, 5, P = 0.45) or phosphorus ($r^2 = -0.11$, df = 1, 5, P = 0.56) within Discovery Bay. Variation in macroalgal cover within Pear Tree Bottom was well-correlated with nutrient concentrations; macroalgal cover increased as either nitrogen ($r^2 = 0.55$, df = 1, 4, P = 0.06) or phosphorus ($r^2 = .57$, df = 1, 4, P = 0.05) concentration increased. Nitrogen and phosphorus concentrations were tightly correlated at both sites (Fig. 9).

Discussion

The continued increase in *Diadema* density at both Pear Tree Bottom and Discovery Bay since 1992 (Fig. 3) indicates that *Diadema* populations are still in the process of recovering from the 1983 *Diadema* die-off. *Diadema* density has increased more rapidly at Discovery Bay than at Pear Tree Bottom, suggesting

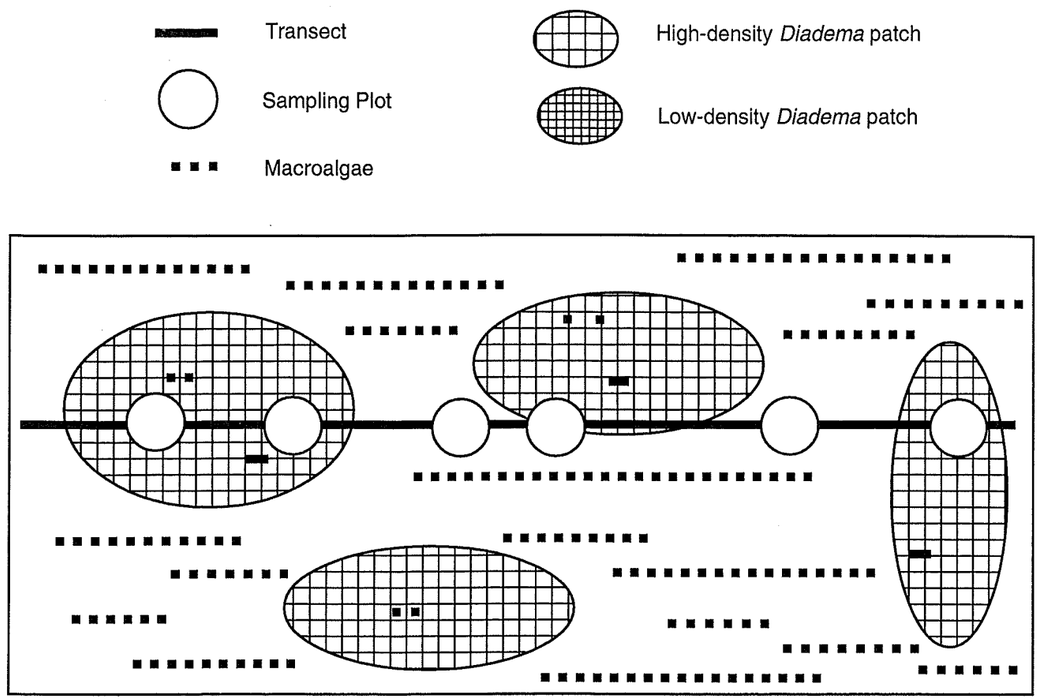

Fig. 1. Model of *Diadema* and macroalgal distribution as well as sampling technique at Discovery Bay, Jamaica. Sampling shows *Diadema* to be aggregated and macroalgal cover to be depleted in *Diadema* patches.

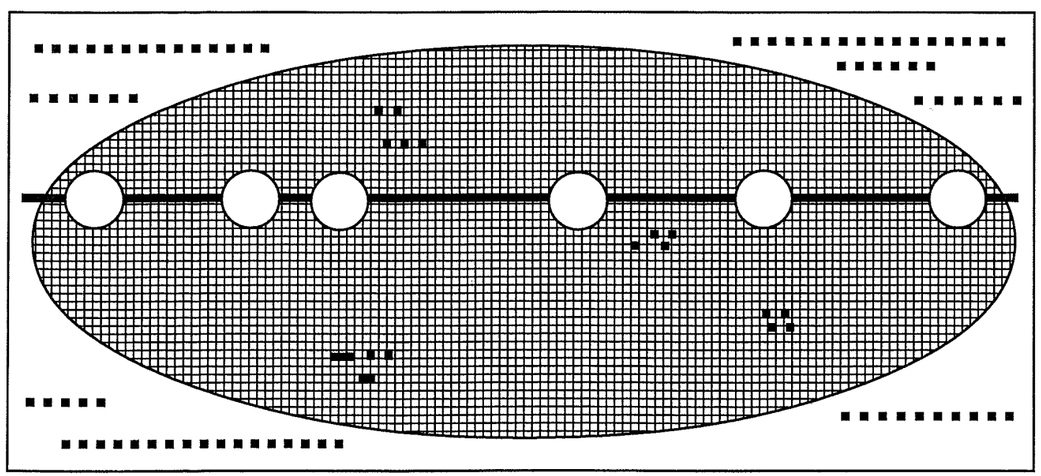

Fig. 2. Model of *Diadema* and macroalgal distribution as well as sampling technique at Pear Tree Bottom, Jamaica. Sampling shows *Diadema* to be uniformly distributed and variation in macroalgal cover can be attributed to factors other than *Diadema* density.

that the *Diadema* population has begun to stabilize at Pear Tree Bottom and may be closer to full recovery than at Discovery Bay (Fig. 3, Table 1).

Coral density has been greater at Pear Tree Bottom since at least 1992 (Balser and Soucy 1992), implying that Hurricane Allen damaged less coral at Pear Tree Bottom than at Discovery Bay in 1980, or that coral growth is more rapid at the former than at the latter site. Macroalgal cover was negatively correlated with coral cover at both sites, perhaps because macroalgae are less able to establish where more space is occupied by coral. Space

Table 1. Data summary of 1992, 1999, and 2001 and comparison of 2001 data between Discovery Bay and Pear Tree Bottom, Jamaica, using student's t-tests. Values are means ± 1 SE. * = a significant difference between Discovery Bay and Pear Tree in 2001. CTB = coralline algae, turf algae, or bare substrate. Dashes indicate lack of data from 1992 (Balser and Soucy) or 1999 (Dallison et al.) studies.

	Discovery Bay			Pear Tree Bottom					
Year	1992	1999	2001	1992	1999	2001	t	P	df
Urchins (m^{-2})									
Diadema	0.05 ± 0.01	1.0 ± 0.17	1.92 ± 0.55	1.07 ± 0.17	1.82 ± 0.30	2.01 ± 0.13	0.17	0.87	11
Tripneustes	0.014 ± 0.005	0.08 ± 0.03	0.01 ± 0.01	0.072 ± 0.02	2.32 ± 0.31	0.05 ± 0.03	1.36	0.22	11
Nutrients (μM)									
Total N	-	-	2.53 ± 1.0	-	-	2.28 ± 0.72	0.40	0.69	11
Total P	-	-	0.16 ± 0.06	-	-	0.15 ± 0.04	0.38	0.71	11
Dispersion									
Diadema	0.054	0.26	1.10	0.55	0.49	0.05			
Total N			2.78			1.35			
Total P	-	-	0.15	-	-	0.057			
% Cover									
macroalgae	27.53 ± 2.57	12.6 ± 2.6	22.2 ± 1.1	6.1 ± 1.6	4.63 ± 1.29	2.2 ± 1.1	2.57	* 0.041	11
live coral	-	1.3 ± 0.5	7.6 ± 2.6	-	13.44 ± 2.72	35.0 ± 4.8	5.05	* 0.0005	10
CTB	67.87 ± 2.72	84.1 ± 11.1	46.0 ± 11.1	67.3 ± 3.1	82.1 ± 10.7	62.2 ± 4.2	1.28	0.22	11
sand	-	-	13.9 ± 8.8	-	-	0.55 ± 0.55	1.51	0.19	10

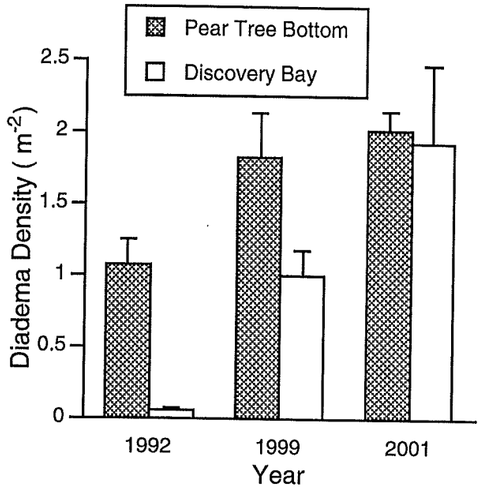

Fig. 3. Mean *Diadema* density (± 1SE) on the Pear Tree Bottom fore reef and the Discovery Bay west fore reef, Jamaica in 1992, 1999, ans 2001. 1992 data from Balser and Soucy and 1999 data from Dallison et al.

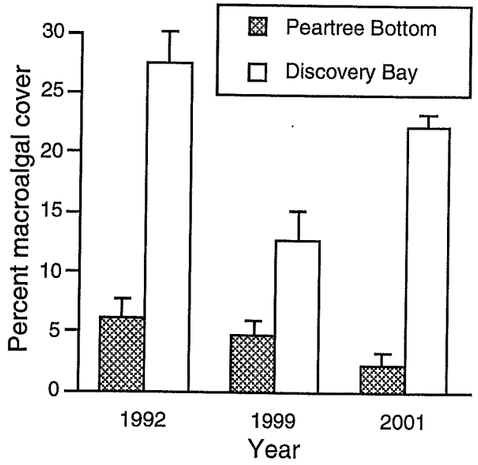

Fig. 4. Percent macroalgal cover (± 1 SE) at the Pear Tree Bottom fore reef and the Discovery Bay West fore reef, Jamaica, in 1992, 1999, and 2001. 1992 data from Balser and Soucy and 1999 data from Dallison et al.

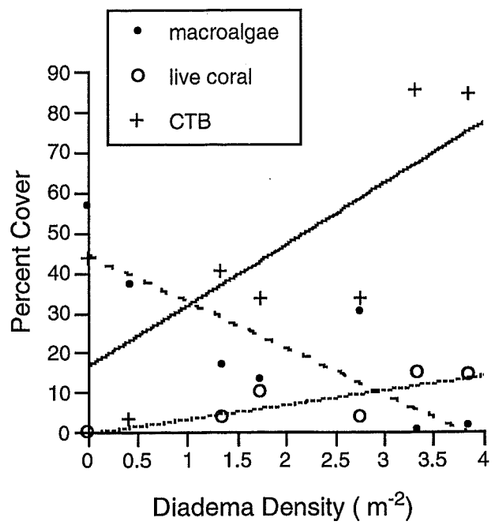

Fig. 5. Relationships between *Diadema antillarum* densities and percent cover of macroalgae, live coral, and coraline algae/turf algae/bare rock at Discovery Bay West fore reef, Jamaica.

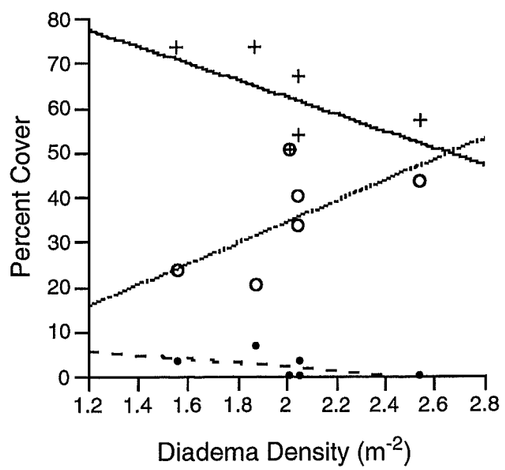

Fig. 6. Relationships between *Diadema antillarum* densities and percent cover of macroalgae, live coral, and coraline algae/turf algae/bare rock at Pear Tree Bottom fore reef, Jamaica. Refer to Figure 5 for key to symbols.

limitation caused by coral presence may explain why macroalgal cover is greater at Pear Tree Bottom than Discovery Bay, even though we found no difference in mean *Diadema* density at the two sites.

We found *Diadema* dispersion to be highly uniform at Pear Tree Bottom and aggregated at Discovery Bay (Table 1). Previous research has shown that *Diadema* seeks shelter during the day, and in the absence of suitable cover will aggregate, possibly to deter predation or protect against wave surge (Randall et al. 1964, Woodley 1982). The different structural complexity of our two sites (higher at Pear Tree Bottom than at Discovery Bay, personal observation) may therefore explain the observed differences in *Diadema* dispersion.

Diadema density was negatively correlated with percent macroalgal cover at Discovery Bay (Fig. 5), but the two were not correlated at Pear Tree Bottom (Fig. 6). This is probably due to the differing *Diadema* dispersion patterns at the two sites. The uniform dispersion of *Diadema* at Pear Tree Bottom means that very little resolution was available to assess the effect of *Diadema* density

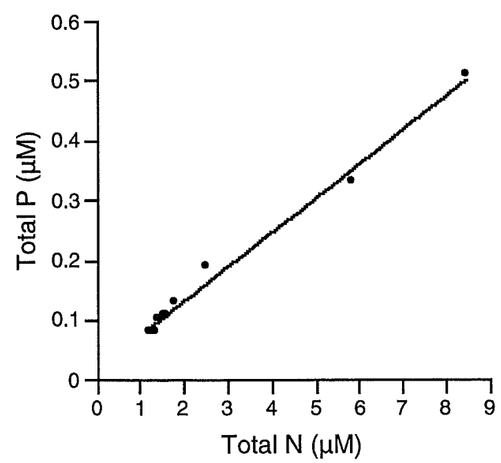

Fig. 7. Relationship between nitrogen and phosphorus levels in the waters of Pear Tree Bottom and the West fore reef of Discovery Bay, Jamaica ($r^2 = 0.99$, df = 1, 11, $P < 0.001$).

onmacroalgal cover, while the aggregated dispersion of *Diadema* at Discovery Bay allows a comparison of macroalgal cover across a wide range of *Diadema* densities.

Despite the possible existence of better measures of the macroalgal community dynamics (such as growth rate, biomass, or height, which we were unable to gauge in this study), we were surprised to find a significant positive correlation between percent macroalgal cover and nutrient concentrations at Pear Tree Bottom. This suggests that bottom-up influences may play a part in the structure of the macroalgae on the reef. The lack of a relationship between nutrients and macroalgal cover at Discovery Bay, where *Diadema* densities were variable, indicates that top-down influences have a stronger effect on the macroalgae; nutrients were patchily distributed at both sites (Table 1), but the influence of varying nutrient levels was only measurable in the absence of variation in *Diadema* density.

Dispersion patterns of *Diadema* may explain some of the variation in the importance of nutrients and herbivory on macroalgal communities. Future study could examine the patchy distribution of nutrients in the water over both fore reefs. The extremely tight correlation of total N and total P concentrations (Fig. 7) suggests that the two are entering the water from the same places, possibly freshwater vents.

Acknowledgements

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