The changing North Jamaican reef: The effect of substrate complexity on *Diadema* abundance and percent coral cover

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Abstract: Nineteen years ago, *Diadema antillarum* experienced the greatest mass marine mortality event ever recorded (Lessios, 1988). The loss of this important macroalgal grazer led to a phase shift from predominately coral cover to a substrate dominated by macroalgae. On the north Jamaican reef system, the recent urchin recovery has prompted examinations of potential compositional shifts associated with the loss and recovery of urchin herbivory on a large scale. However, little research has been directed towards understanding factors that drive urchin abundance on a microspatial scale. We investigated the effect of 3-dimensional complexity on urchin abundance, hypothesizing that 1) higher urchin abundance would be associated with increased habitat complexity and 2) substrate cover would vary with urchin abundance. We predicted higher urchin abundance would be associated with reduced macroalgal cover, increased coral and microalgal turf cover, and a greater number of juvenile coral recruits. We found higher urchin abundance in areas with greater substrate complexity. Areas of higher urchin abundance were, as predicted, associated with reduced macroalgal cover and greater coral and microalgal turf cover. Furthermore, a greater number of juvenile corals were found in areas with greater microalgal turf cover and higher abundance of *Diadema*. Compared to data collected ten years ago urchin densities have increased 5.7 fold, while the percent cover of macroalgae has decreased and microalgal turf cover has increased on the reef. Our results are in accordance with well-documented large scale trends, but suggest a dynamic pattern exists at the microspatial scale in which 3-D structure affects the distribution and hence the effects of *Diadema*.

Key Words: herbivory, heterogeneity, juvenile coral, macroalgae, microalgal turf, microspatial, phase shift, recruitment, spatial

Introduction

In 1983, the long-spined sea urchin, *Diadema antillarum*, experienced a Caribbean-wide mass mortality event, with 99% of some local populations dying from a water-borne pathogen that entered the Atlantic via the Panama Canal (Hughes 1994). The loss of this important macroalgal grazer caused a substantial increase in macroalgal cover and subsequent reduction in coral cover on many Caribbean coral reefs (Lessios 1988, Edmunds et al. 2001 and Williams 2001). Macroalgae may outcompete corals for available habitat space and can overgrow existing corals (Williams and Polunin 2000). Overfishing in Jamaica has led to the loss of other important macroalgal grazers as well, and the coral-to-macroalgae phase shift occurring there has been more pronounced than on most other Caribbean reefs (Aronson et al. 2000).

In the past 6 years, however, Caribbean *D. antillarum* populations have begun a significant recovery (Aronson et al. 1999). Current research projects are investigating how urchin grazing might promote coral recruitment and initiate a counter phase shift in the reef community (Williams and Polunin 2001). While many of these studies are examining these trends on a large scale (i.e., across depth gradients, over large distances on a contiguous reef, or between isolated reefs), there has been little work done on the microspatial scale (i.e., at a specific depth within the range of several meters). An increasing body of evidence suggests that spatial heterogeneity is important in modifying processes such as herbivory on the reef community (Andrew 1993).

On a small scale, 3-dimensional complexity may predict the level of herbivory, and hence patterns in substrate cover. Therefore, we investigated *Diadema* abundance on both a macro and microspatial scale at depths of 15 to 20 ft on the fore-reef of Discovery Bay, Jamaica.

We collected background data to assess changes in reef community composition since 1992, and examined the relationship between habitat complexity and urchin abundance. We hypothesized urchins would distribute themselves in a non-random fashion with respect to substrate complexity and predicted that *Diadema* would be more abundant in areas of high 3-dimensional structure. We also hypothesized that substrate cover would vary with urchin abundance. We predicted that areas of high urchin abundance would have less macroalgal cover, more coral and microalgal turf cover and more juvenile coral recruits.

Methods

Research was conducted from 1 – 8 March 2002 on the west fore-reef of Discovery Bay, Jamaica. Using SCUBA, we logged nearly 8.7 h of data-collection time over 10 dives at depths of 15 - 20 ft.

To collect microspatial data on community composition and urchin abundance, we sampled a gradient of 3-dimensionally complex substrates. We randomly selected sites from a distance, without looking for urchins or coral cover, to avoid selection bias for these variables. A square quadrat, haphazardly dropped onto the chosen site, was used to estimate the percent cover of coral, macroalgae, microalgal turf and sand, as well as to count total number of juvenile coral recruits (individuals ≤2 cm). The 0.55 m x 0.55 m quadrat was constructed with PVC piping and divided into 36 smaller squares (0.01 m^2 each). To estimate substrate complexity, we placed a 5.3 m chain along the contours of the substrate (Fig. 1). The midpoint of the chain was located in the center of the quadrat and was stretched out twice, in North-South and East-West directions, respectively. The straight distance between the two ends of the chain was measured and averaged across directions. This average value was then used to calculate an index of plot complexity according to the formula devised by Aronson and Precht (1995):

$$C = 1 - (\text{straight distance} / \text{actual chain length})$$

We then counted *Diadema* within the oval cre-

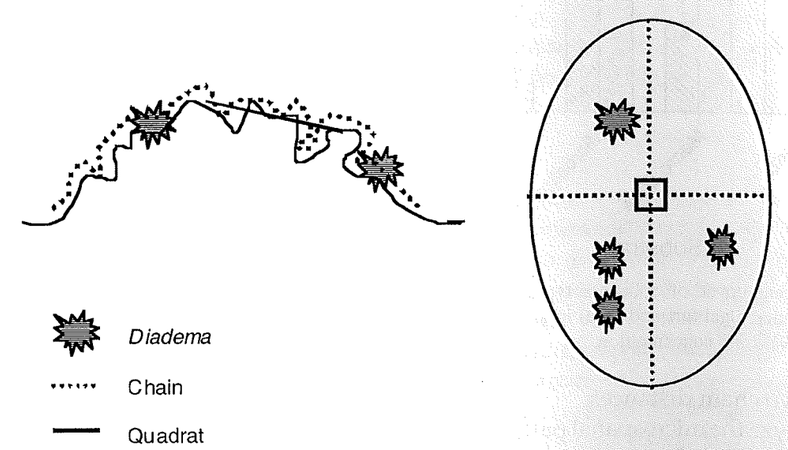

FIG. 1. Diagram of experimental set-up. Cross sectional (left) and bird's eye view (right).

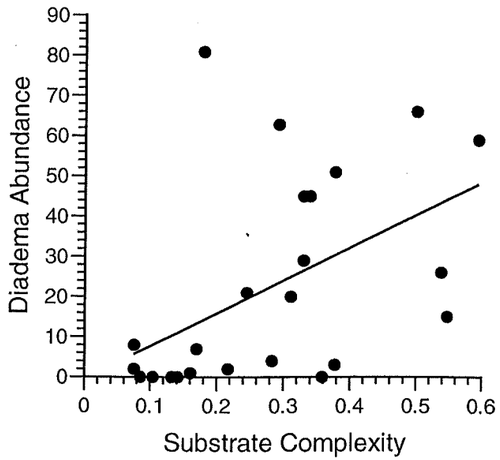

FIG. 2. Comparison of substrate complexity, as defined by Aronson and Precht (1995), with *Diadema* abundance.

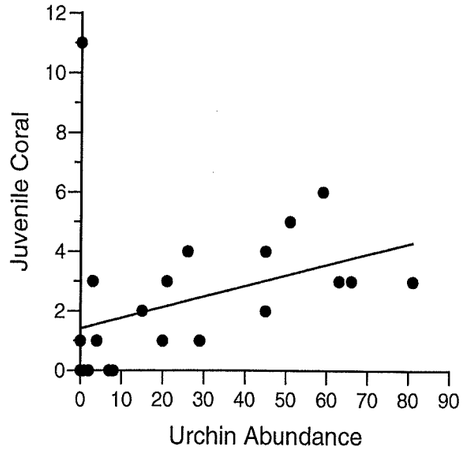

FIG. 4. Number of juvenile corals as a function of urchin abundance.

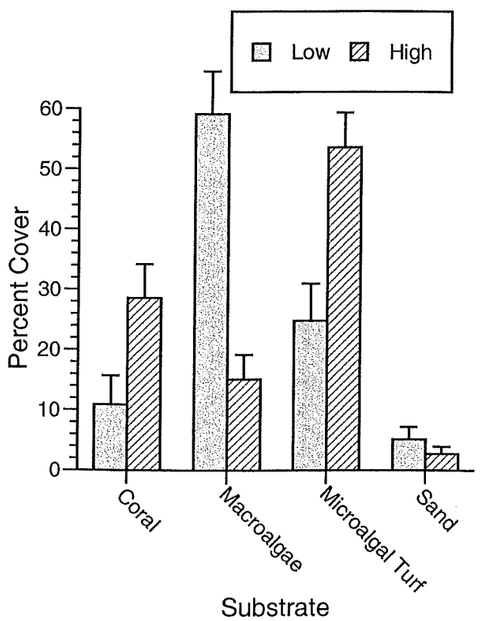

FIG. 3. Percent cover of substrate types (coral, macro-algae, microalgal turf and bare) in areas with low and high *Diadema* concentration.

ated by the two chain distances.

To analyze the microspatial patterns we looked at relationships between urchin abundance, substrate complexity, percent cover and juvenile coral abundance. We used a Spearman Rho rank correlation analysis to determine how urchin abundance varied with substrate complexity. We calculated the urchin dispersion pattern (variance/mean) for both background and microspatial samples. Using a Wilcoxon non-parametric analysis we compared substrate composition (average percent cover of coral, marcoalgae, microalgal turf and sand) among *Diadema* abundance classes. We divided urchin abundance into two classes: high (>10/plot) and low (≤10/plot; Table 1). We used a Spearman Rho rank correlation analysis to test for a possible correlation between juvenile coral abundance and urchin abundance, and between percent cover of macroalgae and microalgal turf.

To gauge background (unbiased selection of 3-D substrate) patterns of urchin abundance and substrate cover, ten 10 m transects parallel to the reef crest were randomly laid out at a 20 ft depth. Along the transect lines, the aforementioned quadrat technique was used again to estimate percent cover of coral, macroalgae, microalgal turf and sand every 4 m. We also counted urchins within 1 m of the transect and compared this urchin and cover data with previous studies.

TABLE 1. Percent cover by substrate type for low and high urchin abundance. Low abundance is ≤ 10 urchins/plot (mean = 2.08 ± 0.76). High abundance is >10 urchins/plot (mean = 43.4 ± 6.14).

Urchin abundance	Cover type	% Cover	Stdev	Sterr
Low	Coral	10.9	17.4	4.8
	Macroalgae	59.2	25.8	7.1
	Turf	24.8	22.4	6.2
	Sand	5.1	7.8	2.1
High	Coral	28.6	19.3	5.6
	Macroalgae	15.1	14.2	4.1
	Turf	53.6	20.1	5.8
	Sand	2.7	4.2	1.2

TABLE 2. Percent cover of substrate at 20 ft. and urchin density in 1992 and 2002. "Other" represents microalgal turf and sand.

Year	Percent Cover			
	Coral	Macroalgae	Other	Urchins/m^2
1992	13.4	63.6	21.4	0.21
2002	8.0	41.0	51.0	1.19

Results

Our results supported the prediction that greater habitat complexity was associated with *Diadema* abundance ($r_s = 0.59$, $p = 0.002$; Fig. 2). We found a bimodal distribution of urchins in our micro-spatial data that closely approximated the bimodal distribution found in our background data. The dispersion of *Diadema* was clumped in both the background and microspatial samples (variance/mean = 24.9 and 29.9, respectively).

Between the two urchin abundance classes, there were significant differences in percent substrate cover (Table 1). High urchin abundance was associated with greater percent coral and microalgal turf cover and lower percent macroalgal cover ($P = 0.004$, $P = 0.003$, $P = 0.001$, respectively; Fig. 3). There was no relationship between the urchin abundance classes and percent cover of sand ($P = 0.568$).

The number of juvenile coral recruits was positively correlated with *Diadema* abundance ($r_s = 0.558$, $P = 0.004$) and the percent cover of microalgal turf, ($r_s = 0.479$, $P = 0.015$; Fig. 4). However, the number of juvenile corals decreased with increasing macroalgal cover ($r_s = 0.640$, $P = 0.001$).

Compared to data collected ten years ago at a nearby site also at 20 ft (Isaacs et al. 1992), we found a 5.7-fold increase in urchin abundance. During this period, macroalgal cover decreased while coral cover remained relatively constant (Table 2).

Discussion

Diadema were clumped in areas with high 3-dimensional complexity. The similarity in urchin distribution between these two samples indicates that a clumped distribution is an accurate representation of the *Diadema* population. *Diadema* abundance is probably greater in areas with greater complexity because more complex habitats provide refuge from predators and surge. McClanahan (1988) showed that predator avoidance is the major factor driving urchin distribution and that

predation pressure causes *Diadema* to aggregate in canyons or crevasses on the ocean floor. Although we did find a positive relationship between urchin abundance and substrate complexity, our measure of complexity may not have provided the best estimate of potential refuge. For example, a relatively flat substrate with many crevices may have the same calculated complexity value as a mounded substrate, but may offer a different level of protection to *Diadema*.

Urchin abundance was probably a major factor determining the community composition. As predicted, areas with high urchin abundance had less macroalgal cover and more coral and microalgal turf cover. Although this is a well-documented large-scale trend (Aronson et al. 2000, Edmunds et al. 2001), our results suggest this trend is also evident on a microspatial scale even within areas of high urchin abundance. We found a positive correlation between urchin abundance and juvenile coral abundance, which suggests urchin grazing may promote coral recruitment by opening up suitable settlement space for larval corals (Howarth 1979). If herbivory by *Diadema* is opening up suitable settlement space for juvenile corals, a clumped urchin distribution may result in a clumped distribution of successful coral recruits at a microspatial scale.

Community composition on the reef has changed considerably in the past 10 years. Our background data reflect the macroalgae-to-coral phase shift that is being documented on Caribbean reefs. However, a more rapid phase shift may be occurring on the microspatial scale in more complex areas that experience greater grazing pressure. Our results suggest *Diadema* density and substrate complexity may drive microspatial patterns in substrate cover and coral recruitment. As urchin populations continue to recover from the die-off, they may distribute themselves differentially with regard to microspatial habitat complexity, and thus alter community composition differentially on a localized scale. Future research should attempt to examine how this phase shift may affect the distribution and composition of coral and alga species on a local scale.

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