The role of *Diadema antillarum*, macroalgae, and substrate topography in determining *Zoanthus* distribution

Daniel M. Braden and Rafael D. Rosengarten

Abstract: Zoanthus spp. (Cnidaria: Zoanthidea) are abundant, benthic invertebrates that grow as dense colonial mats in coral reef ecosystems. We proposed that the abundance of *Diadema antillarum*, a predator of zoanthids and major macroalgae grazer, may regulate zoanthid distribution by a parabolic relationship. We tested this model by measuring zoanthid colonies, *Diadema* abundance, macroalgal cover, and substrate topographic complexity in two reef habitats at Discovery Bay, Jamaica. The relationships between zoanthid cover and *Diadema* were significant, though the two sites had opposite trends. Our data suggest abiotic disturbance and topographic complexity also may be important factors in determining the distribution of zoanthid colonies.

Key Words: disturbance, grazing, spatial competition

Introduction

Zoanthus spp. (Cnidaria: Zoanthidea) are anemone-like polyps that grow in dense mat colonies (Humann 1992). Zoanthids contain zooxanthellae, and thus utilize both autotrophic and heterotrophic mechanisms of energy acquisition (Sebens 1977). They colonize a variety of reef substrates through larval dispersal, and then propagate asexually (Fadlallah et al. 1984), competing with coral (Lathrop 1980), and presumably macroalgae, for space. Karlson (1983) suggested that zoanthids thrive where substrate is made available by intermediate levels of disturbance such as wave action and grazing by the long-spined urchin, *Diadema antillarum*. In 1983, *Diadema* suffered mass mortality throughout the Caribbean, losing 95 to 99% of its population (Carpenter 1990). Macroalgae responded immediately to the *Diadema* mortality, increasing from sparse substrate coverage to 47% coverage in the first year (Carpenter 1990).

We propose a model for the indirect and direct effects of *Diadema* abundance on zoanthid abundance and growth (Fig. 1). We hypothesize that at low *Diadema* abundance (A), macroalgae grows nearly unchecked and out-competes zoanthids for substrate. At high *Diadema* abundance (C), *Diadema* grazing causes increased mortality of zoanthid polyps. Finally, there is some intermediate *Diadema* abundance (B) at which *Diadema* cause intermediate disturbance (as proposed by Karlson, 1983), clearing some substrate of macroalgae but not grazing so heavily that zoanthids experience increased mortality. In this study we test this theoretical model by quantifying biotic and abiotic characteristics of two reef sites of different zoanthid abundances.

Methods

Sampling was done at two reef sites, Columbus Park (CPK) and East back reef (EBR), in Discovery Bay, Jamaica from 3 March to 10 March 2001. At each site, ten 5 x 1 m transects were haphazardly placed parallel to the reef crest, between the back edge of the reef and the reef crest. We did not sample past the reef crest since Lathrop (1980) found zoanthid abundance drops off dramatically on the fore reef. In each transect we counted zoanthid colonies (i.e. zoanthid patches) and measured their surface area, estimated percent cover of macroalgae, counted the number of *Diadema*, and measured the average depth and topography of the substrate. Topography was measured by the chain length method of Aronson and Precht (1995): we draped a 5.3 m chain onto the reef substrate, and measured the horizontal distance (d) between the ends of the chain. A measure of topographic complexity was calculated as the percent change in chain length: 1 – (d / 5.3 m).

We calculated percent zoanthid cover for each transect. A Student's t-test was used to compare mean zoanthid cover between the CPK and EBR sites. Both percent zoanthid cover and *Diadema* abundance were log (x + 1) transformed in all analyses to achieve normal distribution. Analyses of Covariance (ANCOVAs) were used to compare the regressions of percent zoanthid cover versus *Diadema* abundance, macroalgal cover, and topographic complexity for the two reef sites, as well as the relationship between *Diadema* abundance and topographic complexity at the two sites.

Results

Mean zoanthid cover was higher at CPK than EBR, but not significantly so (t-test = 1.93, df = 18, P = 0.07; Fig. 2). The zoanthid population at CPK is observably much larger, but is highly aggregated so that our sampling effort was likely insufficient to represent the distribution at the two sites accurately.

All ANCOVA statistics for the interactions between the biotic or abiotic factors and reef sites are reported in Table 1. *Diadema* abundance varied significantly between reef sites (site effect), with a mean (± 1 SE) of 1.8 ± 0.7 per 5 m^2 at CPK and 10.4 ± 3.1 per 5 m^2 at EBR. With all data points (from both sites) taken together, the effect of *Diadema* abundance alone on zoanthid cover was not significant (*Diadema* effect). Percent zoanthid cover did vary significantly with *Diadema* abundance at each reef site, and the slopes of the two regressions reflected opposite relationships (interaction, Fig. 3).

Percent macroalgal cover was significantly different between sites (site effect), with a mean (± SE) of 44.3 ± 8.2. % at CPK and 33.0 ± 8.6 % at EBR. With all data points taken together, percent zoanthid cover decreased as percent macroalgal cover increased (% macroalgal cover effect). The regression slopes were similar for both sites (interaction, Fig. 4).

The topographic complexity was significantly different between sites (site effect). CPK had a mean (± 1 SE) relative topographic complexity of 0.14 ± 0.034, compared to 0.19 ± 0.34 for EBR. With all data points taken together, the effect of topographic complexity alone on zoanthid cover was not significant (topographic complexity effect). The slope of the regression of % zoanthid cover and topographic complexity was significantly different at each reef site (interaction; Fig. 5).

Diadema abundance was directly pro

Table 1. ANCOVA statistics for four models relating % zoanthid cover, *Diadema* abundance, % macroalgal cover, and topographic complexity across two reef sites. ** indicates significant effect.

Model	R^2	Effect	F	df	P
Log % zoanthid cover x log *Diadema* abundance	0.50	Site	21.32	1, 16	0.0003**
		Log *Diadema* abundance	0.00	1, 16	1.00
		Interaction	13.69	1, 16	0.0019**
Log % zoanthid cover x % macroalgal cover	0.71	Site	6.22	1, 15	0.025**
		% macroalgal cover	27.64	1, 15	0.0001**
		Interaction	0.080	1, 15	0.78
Log % zoanthid cover x topographic complexity	0.46	Site	17.87	1, 16	0.0006**
		Topographic complexity	0.26	1, 16	0.62
		Interaction	12.83	1, 16	0.0025**
Log *Diadema* abundance x topographic complexity	0.52	Site	2.55	1, 16	0.13
		Topographic complexity	11.29	1, 16	0.0040**
		Interaction	0.077	1, 16	0.79

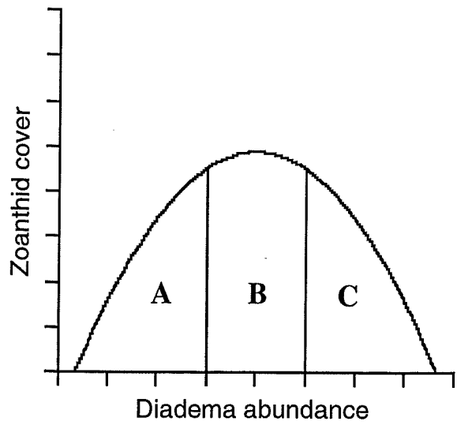

Fig. 1. Hypothesized model relating zoanthid cover to *Diadema* abundance. (A) represents high macroalgae growth and competition for space as an indirect effect of low *Diadema* abundance. (B) represents an intermediate *Diadema* abundance that reduces macroalgae but does not heavily graze zoanthid colonies. (C) represents the direct effect, zoanthid mortality due to grazing, of high *Diadema* abundance.

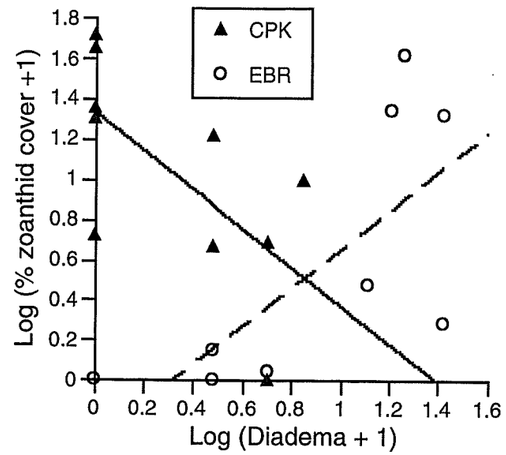

Fig. 3. Zoanthid cover varied differentially with *Diadema* abundance in the two reef sites (n = 10).

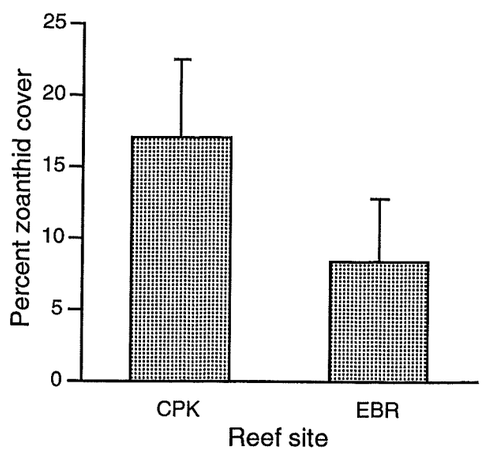

Fig. 2. Mean percent zoanthid cover (± 1 SE) in two reef sites, Columbus Park (CPK) and East back reef (EBR), at Discovery Bay, Jamaica (n = 10).

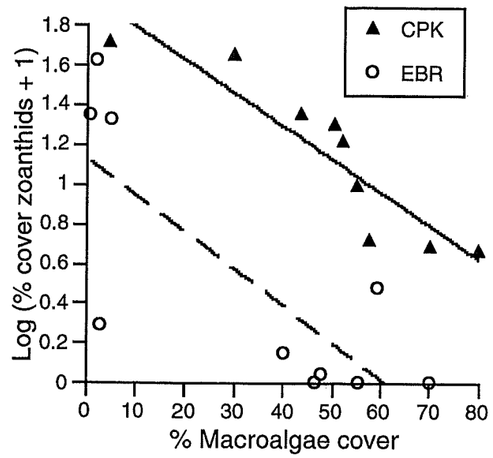

Fig. 4. Zoanthid cover varied inversely with macroalgal cover in both reef sites (CPK n = 9, EBR n = 10).

portional to topographic complexity (topographic complexity effect), though there was no significant difference in mean at each reef site (site effect). The slopes of the regressions were statistically similar (interaction; Fig. 6).

Discussion

Our results suggest that *Diadema* abundance, macroalgal cover, and reef topography may all play a role in determining zoanthid cover. At Columbus Park, there is more

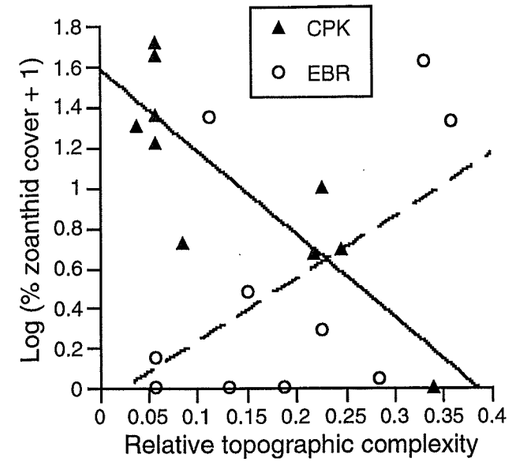

Fig. 5. Zoanthid cover varied differentially with topographic complexity in the two reef sites (n = 10).

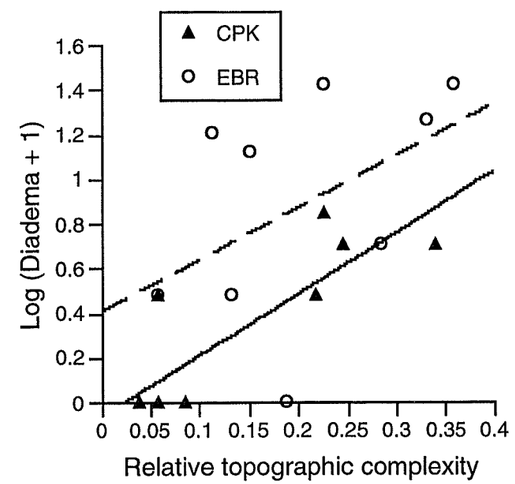

Fig. 6. *Diadema* abundance increased with increasing topographic complexity in both reef sites (n = 10).

zoanthid cover, lower *Diadema* abundance, more macroalgal cover, and a less complex topography than at the East back reef. From the lower urchin abundance at CPK, it follows there is a greater amount of macroalgae. Zoanthids at CPK are found where the topography is least complex, while *Diadema* seek refuge in the more complex areas. At EBR, less macroalgae correlates with the higher *Diadema* abundance. Zoanthids are found in the same topographically complex, often inclined or sheltered places as *Diadema* at EBR.

Our data do not support the hypothesized model (Fig. 1). Zoanthid cover increased with *Diadema* abundance at the site with more *Diadema* (EBR), and decreased with *Diadema* abundance at the site with fewer *Diadema* (CPK). Zoanthids are negatively correlated with macroalgae cover in both reef sites, strongly suggesting that competition for substrate affects zoanthid distribution. Topographic complexity seems to drive both zoanthid distribution and *Diadema* abundance, although each site is different. We suggest that higher wave action (Karlson 1983, pers. obs.) and sedimentation (Karlson 1983) at EBR requires zoanthids to seek refuge in the more structurally complex, sheltered reef edge at this site. *Diadema* also prefers refuge in more complex reef structures at both sites to avoid disturbance and possibly predation. At the sheltered CPK, however, zoanthids prefer sun-oriented flats, with more exposure to light and less exposure to *Diadema*. The cohabitation of zoanthids with *Diadema* at EBR suggests that wave disturbance, storm exposure, and sedimentation may currently be more important than *Diadema* grazing in determining zoanthid distribution.

Further research should quantify zoanthid predation by *Diadema*, and that by other potential predators such as fireworms (*Hermodice carunculata*) and damselfish (*Stegastes* spp.) (Karlson 1983), as well as competition between zoanthids and macroalgae. Characterizing the biotic and abiotic factors that affect zoanthid survival is central to understanding the way in which these colonial organisms distribute themselves and propagate along reefs.

Literature Cited

Aronson, R. B., and W. F. Precht. 1995. Landscape patterns of reef coral diversity: A test of the intermediate disturbance

hypothesis. Journal of Experimental Marine Biology and Ecology 192: 1-14.

Carpenter, R. C. 1990. Mass mortality of *Diadema antillarum*: I. Long term effects on sea urchin population-dynamics and coral reef algal communities. Marine Biology 104: 67-77.

Fadlallah, Y. H., R. H. Karlson, and K. P. Sebens. 1984. A comparative study of sexual reproduction in three species of Panamanian zoanthids (Coelenterata: Anthozoa). Bulletin of Marine Science 35: 80-89.

Humann, P. 1992. Reef creature identification: Florida, Caribbean, Bahamas. Pp. 100-101 *in* N. Deloach, editor. New World Publications, Inc., Jacksonville, Fl, USA.

Karlson, R. H. 1983. Disturbance and monopolization of a spatial resource by *Zoanthus sociatus* (Coelenterata: Anthozoa). Bulletin of Marine Science 33: 118-131.

Lathrop, R. 1980. Differential importance of biotic and abiotic factors in governing zoanthid distributions, according to zone on the East reef at Discovery Bay, Jamaica. (unpublished, Dartmouth Foreign Study)

Sebens, K. P. 1977. Autotrophic and heterotrophic nutrition of coral reef zoanthids. Proceedings, Third International Coral Reef Symposium.