DIADEMA ANTILLARUM'S IMPACT ON CORAL COVER AND JUVENILE CORALS ALONG THE WEST FORE REEF, DISCOVERY BAY, JAMAICA: PAST AND PRESENT

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Abstract: The sea urchin *Diadema antillarum* grazes benthic algae, thereby playing a large role in moderating the competitive interaction between corals and algae at Discovery Bay, Jamaica. A massive die-off of *D. antillarum* in 1983 reduced algal herbivory dramatically, leading to an overgrowth of algae on the reef. As *D. antillarum* began to recover in 1996, it's feeding created barren zones on the reef where it grazed macroalgae, allowing coral recruits to establish themselves again. We measured the abundance of *D. antillarum* and the abundance, percent cover, and size-class distribution of corals in both the barren and algal zones to determine whether *D. antillarum* abundances are still benefiting the coral population, or whether they have become so high that they are damaging the coral population. We then compared current patterns to those recorded in past years to determine the trends of each population on a larger scale. We discovered greater *D. antillarum* and coral abundances in the barren zone, which suggests that *D. antillarum* is benefiting coral populations. In fact, when compared with past data, our data are consistent with the coral population's general positive growth trend since *D. antillarum* recovery began. However, differences in the size distributions of corals between the two zones suggest that *D. antillarum* may be approaching an abundance at which it begins to harm small corals by grazing them.

Key Words: Diadema antillarum, *coral, size class, Discovery Bay, Jamaica, macroalgae, grazing*

INTRODUCTION

Corals and macroalgae compete intensively for space in shallow tropical waters. In the absence of herbivores, macroalgae densities will increase dramatically—producing deleterious effects on coral colonies (Lirman 2001). At Discovery Bay, Jamaica, overfishing has caused a dramatic reduction in the abundance of herbivorous fish, and the reef has become highly dependent on other herbivores—such as sea urchins—to keep algal growth in check. One such urchin, *Diadema antillarum*, plays an important role in moderating competition between corals and algae because of its high abundance, especially after disturbances when slow-growing corals are at a disadvantage. In 1980, Hurricane Allen destroyed most of the branching corals at Discovery Bay. Three years later, a large die-off of *D. antillarum* dramatically reduced algal herbivory, dealin a second blow to reef coral by making it more difficult for corals to compete with algae for space. The *D. antillarum* population did not begin to recover until 1996.

Because its distribution is determined by depth and substrate complexity (Copeland, C. 1980; Podolak and Burke 2002), *D. antillarum* only inhabits and grazes macroalgae along certain areas of the shallow fore reef. This creates two distinct zones: (1) a barren zone in which *D. antillarum* abundance is high and macroalga abundance is low, and (2) an algal zone in which *D. antillarum* abundance is low and macroalga abundance is high. The barren zone has more substrate area free of algae

that young corals may colonize, so as *D. antillarum* recovered in the late 1990's and early 2000's, corals also began to recover (Edmunds 2001).

Although both the *D. antillarum* and coral populations in Discovery Bay have been monitored since the 1950's, there have been no surveys in the past several years. Therefore, it is unclear if and how *D. antillarum* abundances continue to influence coral abundance. We investigated the current demographics of *D. antillarum* and coral populations in both the barren zone and the algal zone. We predicted that if *D. antillarum* is still benefiting the corals, live coral abundances would be greater in the barren zone than in the algal zone. We also expected a greater number of medium and large corals in the barren zone than in the algal zone, indicating a history of more coral recruits with higher survival rates. To assess the relationship between *D. antillarum* and corals over time, we also compared our data with data from past studies beginning in 1977. Because there have not been any recent major disturbances, we predicted that the abundance of both *D. antillarum* and all sizes of corals in the barren zone would continue to increase as *D. antillarum* returns to pre-die-off numbers, while algal zone abundances would be largely unchanged.

D. antillarum abundances may also become so high that they harm coral populations. If resources become limiting for *D. antillarum,* it could begin to graze on small corals along with algae (Sammarco 1980). Small corals are more vulnerable to grazing than large corals, so the probability of surviving intense grazing is positively related to size (Mobley, C.T. 1984). If *D. antillarum* populations have become so large that they harm juvenile coral recruitment, we would expect higher proportions of medium and large corals and lower proportions of juveniles in the barren zone compared to the algal zone.

METHODS

We collected data on 2-6 March 2006 on the west fore reef at Discovery Bay near two separate dive sites: Dancing Lady and M1. At each site, we haphazardly chose 5 x 4 m transects in two distinct zones: the barren zone (< 20% algal cover; n = 8) and the algal zone (> 70% algal cover; n = 7). All transects were between 3 and 7 m deep. We counted the total number of *D. antillarum* and corals in each transect, and divided corals into eight taxonomic categories: *Diploria* spp., *Siderastrea* spp., *Agaricia* spp., *Porites porites, Porites astreoides, Acropora palmata, Erythropodium caribaeorum*, and other less common corals. We further divided corals into size classes: small corals (< 3 cm diameter), medium corals (3-6 cm), and large corals (> 6 cm). We also estimated total percent coral cover in each zone by haphazardly measuring corals in each size class and then multiplying the mean surface area of each size class by the number of colonies of that size class in a given transect.

To look at current *D. antillarum* and coral abundances in the context of historical trends, we compiled data presented in past studies starting in 1977 on *D. antillarum* abundance, coral cover, and juvenile coral density at depths between 3 and 7 meters on the west fore reef. We added current abundances to the historical data to

determine long-term patterns in *D. antillarum* and coral populations. We present the studies used in Table 1.

We examined differences in *D. antillarum* and coral densities between barren and algal zones using ANOVA. We examined differences in size class frequencies between zones for all corals and for each coral species individually with G-tests. We looked at the relationship between *D. antillarum* density and juvenile coral density within zones using linear regression. We used JMP 5.0.1 for all analysis.

Table 1: Source, year, and method for obtaining historical data on *D. antillarum* abundance, percent coral cover, and juvenile coral density between 3 and 7 meters depth on the west fore reef, Discovery Bay, Jamaica.

D. antillarum		
Source	Years	Method for getting data
Carpenter 1981	1977	Estimated from figure
Hughes et al. 1985	1982-84	Value given in paper
Liddel and Ohlhorst 1986	1982	Value given in paper
Hughes 1994	1985-96	Estimated from figure
Hughes et al. 1987	1986	Value given in paper
Balser and Soucy 1992	1993	Value given in paper
Aronson and Precht 2000	1993-96, 98-99	Estimated from figure
Edmunds and Carpenter 2001	2000	Estimated from figure
Erickson et al. 2001	2001	Value given in paper
Podolak and Burke 2002	2002	Value given in paper
Chamberlin and Wickre 2003	2003	Value given in paper
Current study	2006	See methods
Coral cover		
Source	Years	Method for getting data
Huston 1985	1977	Estimated from figure
Hughes 1994	1977, 81-93	Estimated from figure
Liddel and Ohlhorst 1986	1982-84	Value given in paper
Hughes et al. 1987	1986	Value given in paper
Aronson and Precht 2000	1993-96, 98-99	Estimated from figure
Edmunds and Carpenter 2001	2000	Estimated from figure
Chamberlin and Wickre 2003	2003	Value given in paper
Current study	2006	See methods
Juvenile corals		
Source	Years	Method for getting data
Edmunds and Carpenter 2001	1994, 96, 2000	Estimated from figure
Edmunds and Bruno 1996	1995	Estimated from figure
Erickson et al. 2001	2001	Estimated from figure
Current study	2006	See methods

RESULTS

We found more *D. antillarum* in the barren zone (mean ± SE; 4.4 ± 5.28 individuals/m^2) than in the algal zone (0.1 ± 5.64 individuals/m^2; $F_{1,13}$ = 122.55 $p < 0.0001$). We found 2144 coral colonies across all barren zone transects, covering a mean of 18% of total area, and 938 coral colonies in the algal zone, covering a mean of 6% of total area. Coral colony density was significantly greater in the barren zone (1340 ± 166 individuals/100 m^2) than the algal zone (670 ± 177 individuals / 100 m^2; $F_{1,13}$ = 7.61, $p < 0.02$; Fig. 1). This relationship was driven largely by

differences in densities of *Agaricia* spp. and *Porites asteroids* (Fig. 2).

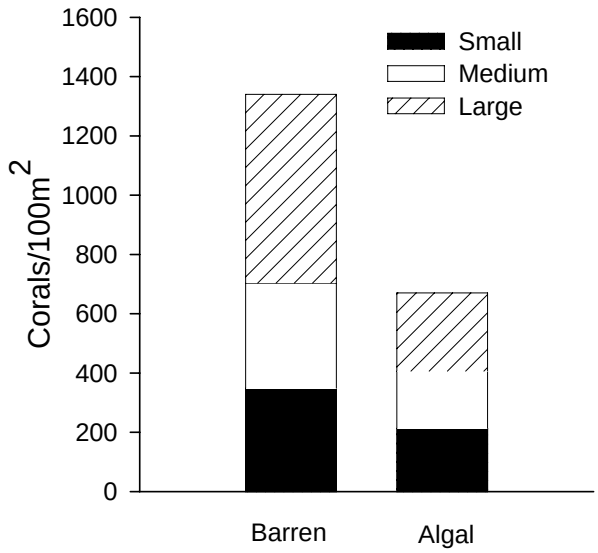

Figure 1: Coral densities and percent composition of total corals by size class pooled across transects at two dives sites in barren (n=4 at M1, n=4 at Dancing Lady) and algal (n=4 at M1, n=3 at Dancing Lady) zones along the west fore reef, Discovery Bay, Jamaica. There was significant difference in density and percent composition between zones ($p < 0.05$).

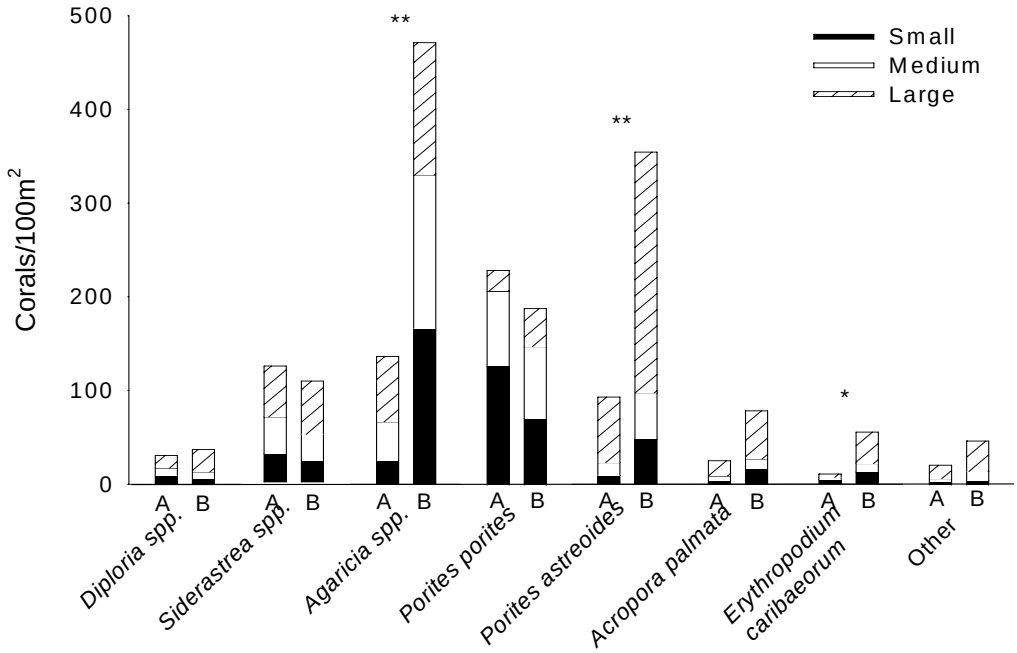

Figure 2: Density of different coral species by size class pooled across transects at two dive sites in algal (A) (n=4 at M1, n=3 at dancing Lady) and barren (B) (n=4 at M1, n=3 at Dancing Lady) zones along the west fore reef, Discovery Bay, Jamaica. * denotes significant difference in total counts of a coral species between zones ($p<0.05$), ** denotes significant difference ($P<0.01$). Refer to table 2 for differences in size class composition for each coral species between zones.

Table 2. Differences in abundances of three size classes of seven corals between algal and barren zones in the west fore reef, Discovery Bay, Jamaica. Data are pooled across transects at two sites (Dancing Lady: n=4 in barren, n=3 in algae; M1: n=4 in barren, n=4 in algae).

Coral taxa	Zone	No. small	No. medium	No. large	G	P
Diploria spp.	barren	9	12	38	4.71	0.09
	algal	13	11	19		
Siderastrea spp.	barren	36	45	91	2.81	0.25
	algal	42	55	76		
Agaricia spp.	barren	266	262	226	34.81	< 0.0001
	algal	35	58	98		
Porites porites	barren	114	123	65	26.38	< 0.0001
	algal	178	112	31		
Porites asteroides	barren	77	79	411	1.27	0.53
	algal	13	19	98		
Acropora palmata	barren	26	17	82	1.34	0.51
	algal	5	7	23		
Erythropodium	barren	21	14	54	4.24	0.12
caribaeorum	algal	7	3	5		
Total	barren	557	568	1019	18.64	< 0.0001
	algal	298	270	370		

Distribution of corals across size classes was significantly different between barren and algal zones ($G = 18.64$, $p < 0.001$; Table 2; Fig. 1). Density of large and medium corals, but not small corals was significantly greater in the barren zone than the algal zone (Table 3; Fig. 1). Size class differences were driven primarily by distribution of *Agaricia* spp. and *Porites porites* (Table 2). However, we found no relationship between *D. antillarum* densities and juvenile coral densities within each zone (linear regression, barren zone: $r^2 < 0.11$, $p > 0.42$; algal zone: $r2 < 0.0003$, $p > 0.97$).

D. antillarum has generally increased in the barren zone and stayed relatively constant in the algal zone since 1996 (Fig. 3a). Coral cover has been increasing in both zones, but was higher in the algal zone until our study in 2006, where it increased substantially in the barren zone (Fig. 3b). Juvenile corals increased between 1994 and 2000, with greater increases in the barren zone, but have decreased since then in both zones (Fig. 3c).

Discussion

Because coral abundances are greater in the barren zone where *D. antillarum* abundances are highest, and lower in the algal zone where there are few *D. antillarum*, it seems that the *D. antillarum*

Table 3: Differences in small, medium, and large coral density (mean number ± SE/ 100m^2) between barren and algal zones along the west fore reef, Discovery Bay, Jamaica.

Size class	Barren zone	Algal zone	ANOVA $F_{1,13}$	P
Small	348 ± 54.0	213 ± 50.5	3.35	0.09
Medium	355 ± 48.3	193 ± 51.6	5.27	0.04
Large	637 ± 80.3	264 ± 85.8	10.05	0.007

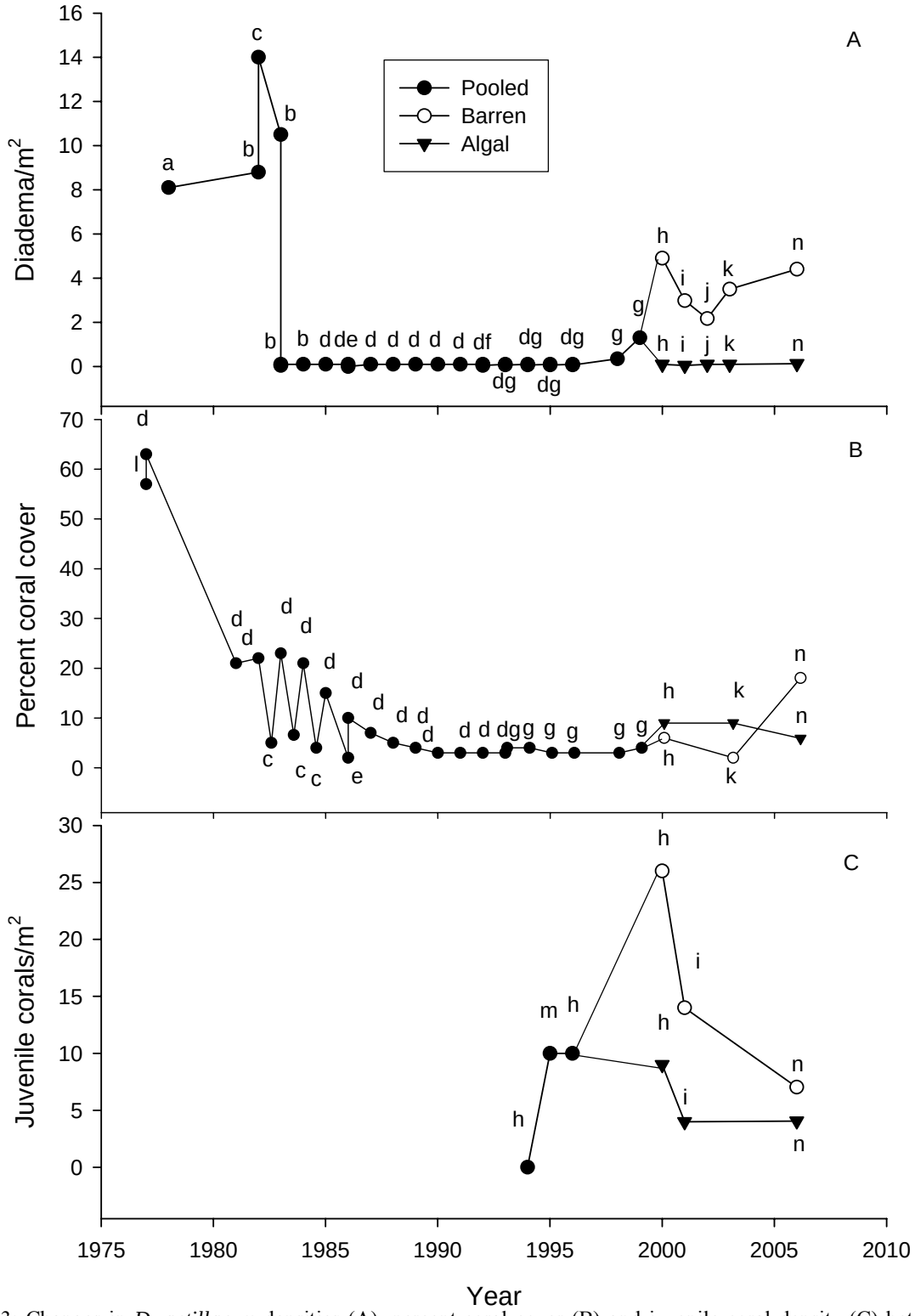

Figure 3: Changes in *D. antillarum* densities (A), percent coral cover (B) and juvenile coral density (C) between 3 and 7 meters depth on the west fore reef, Discovery Bay, Jamaica. Letter above each data point corresponds with its source: (a) Carpenter 1981, (b) Hughes et al. 1985, (c) Liddell and Ohlhorst 1986, (d) Hughes 1994, (e) Hughes et al. 1987, (f) Balser and Soucy 1992, (g) Aronson and Precht 2000, (h) Edmunds and Carpenter 2001, (i) Erickson et al 2001, (j) Podolak and Burke 2002, (k) Chamberlin and Wickre 2003, (l) Huston 1985, (m) Edmunds and Bruno 1996, (n) current study.

population still benefits the coral population. The past several years' general trend of increasing coral cover in the barren zone and relatively constant coral cover in the algal zone also supports this conclusion. Furthermore, the presence of more large corals in the barren zone reflects the greater number of coral recruits to the zone in the late 90's/early 2000's (Fig. 3) and suggests higher coral recruitment and survivorship coincided with *D. antillarum* recovery.

However, we found evidence that *D. antillarum* may not continue benefiting corals in the barren zone. Small coral abundance in the barren zone has decreased over the past 6 years. We found a greater proportion of large and medium corals to small corals in the barren zone compared to the algal zone (Table 2; Table 3), suggesting that the barren zone's small corals are diminishing. This may indicate that the *D. antillarum* population is reaching a critical size at which it becomes detrimental to the coral population by grazing juvenile corals. Although we found no relationship between *D. antillarum* density and juvenile coral density within zones, it is possible that the high mobility of *D. antillarum* obscured evidence for this relationship at the scale we chose for our sampling. It is also possible that the fluctuations in juvenile coral density indicate a convergence towards a stable age distribution.

The interaction between *D. antillarum* and coral differs depending on coral species: not all coral species were more abundant in the barren zone or showed the same patterns in size class distribution across zones. The difference in abundance (more corals in the barren zone) was driven largely by *Agaricia* spp. and *Porites astreoides*, while differences in size distribution (more large corals in the barren zone) were driven largely by *Agaricia* spp. and *Porites porites.* Because these species survive equally well across a large depth range (Liddell and Ohlhorst 1987), and because we limited our study to a fairly small depth range, these distribution differences are not likely a result of depth. This suggests that these coral species may be less competitive against algae than other coral species and thus benefit more from the presence of *D. antillarum* (Sammarco 1980).

D. antillarum densities have increased steadily since 1996, and there is little reason to think they might stop soon as they continue to recover. If urchins have indeed reached a density at which they start to graze young corals, coral cover could be further diminished as a result. When we compare present *D. antillarum* density-coral population dynamics to those recorded before the hurricane and *D. antillarum* die-off (by Copeland 1980), we see that a negative effect of urchins on coral juveniles is occurring at much lower urchin densities.

It is possible that large-scale environmental conditions (substrate, water temperature, nutrient input, etc.) are making small corals more susceptible to grazing, and lowering the density at which *D. antillarum* becomes detrimental to corals. In fact, it seems that one of these conditions, the substrate topography, is having more local effects in the barren zone. Copeland (1980) found many pieces of loose substrate under which numerous juvenile corals grew, sheltered from *D. antillarum* grazing.

We found no loose substrate. Without this refuge from grazing for juvenile corals, the density at which *D. antillarum* becomes detrimental may be lower. Thus, although *D. antillarum* densities seem to be the primary factor driving coral success on the reef, we must also consider how environmental factors are contributing to coral recovery.

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