Phase shift dynamics and intermediate disturbance: *Diadema antillarum* and coral recruitment on a tropical reef

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Abstract: The coral reef community at Discovery Bay, Jamaica experienced a phase shift from coral to macroalgal dominance between 1980 and 1990. Data from the last 10 years indicate that a reversal in phase shift may be occurring in the shallow forereef with a return to coral dominance. This transition is associated with the return of the keystone species, *Diadema antillarum*, after an almost complete die-off in 1983. We surveyed the community structure of the coral reef at Discovery Bay and found that coral and macroalgal distribution and abundance have continued to change since 2000. We also looked at the potentially deleterious effect of very high densities of *D. antillarum* on juvenile coral recruitment. In support of the intermediate disturbance hypothesis, we found evidence that juvenile coral survival was highest at intermediate *D. antillarum* densities. While it appears that *D. antillarum* continues to change the reefscape by decreasing macroalgal cover and increasing juvenile coral survival, higher urchin densities may graze down young corals and lead to reestablishment of a barren zone.

Key Words: juvenile coral, long-spine black urchin, macroalgae, urchin zone

INTRODUCTION

Coral reefs may experience phase shifts to alternative states of structural dominance caused by a variety of anthropogenic and natural disturbances. Discovery Bay, Jamaica experienced a phase shift from coral to macroalgal dominance between 1950 (80% coral cover) and 1990 (5% coral cover). Many factors may have contributed to this change, including two major hurricanes, decades of overfishing, increasing human population pressure, and possibly nutrification (Edmunds and Carpenter 2001). However, this trend was massively accelerated by an almost complete die-off of *Diadema antillarum* in 1983. Grazing by *D. antillarum* decreases macroalgal cover, creating barren areas with distinct boundaries between urchin zones and macroalgal zones. Before the die-off, *D. antillarum* densities were as high as 71 individuals/m^2 (Lessios et al. 1984), and the resulting barren zones were almost entirely clear of macroalgae and corals (Mobley 1983). In the early 1990s, *D. antillarum* populations began to increase in shallow depths along the forereef. In 1996, *D. antillarum* was locally abundant (1.8 individuals/m^2), and by 2000 barren zones with moderate *D. antillarum* abundance were suggestive of a phase shift.

The return of *D. antillarum* and the phase shift from macroalgal to coral dominance was also associated with an increase in juvenile coral abundance (Edmunds and Carpenter 2001). Grazing by *D. antillarum* releases juvenile corals from the negative effects of macroalgae, resulting in an increase in juvenile survivorship (Edmunds and Carpenter 2001). Edmunds and Carpenter (2001) showed that juvenile coral recruitment and survivorship was enhanced at intermediate *D. antillarum* densities (4/m^2). However, a study by Sammarco (1980) showed that at high densities of *D. antillarum*, intense grazing damages juvenile corals, and coral survivorship is reduced.

The goal of this study was to assess the progress of the phase shift from macroalgal to coral dominance presented by Edmunds and Carpenter (2001). We also extended the survey of community structure by looking at the effects of varying densities of *D. antillarum* on juvenile coral recruitment. We predicted that juvenile corals would be most abundant at intermediate *D. antillarum* densities (2 - 10/m^2) and decrease at high *D. antillarum* densities (> 10/m^2), in support of the intermediate disturbance hypothesis.

METHODS

We conducted observations at four sites in Discovery Bay (Dairy Bull, M1, Caricomp and Dancing Lady) along the north shore of Jamaica from March 6 - 10, 2003. At each site we sampled two zones: the urchin zone (*Diadema antillarum* present) and the macroalgal zone (high density of macroalgae; few or no urchins). We randomly placed transects at each site, at depths between 5 and 8 m. Along each transect we measured *D. antillarum* density, percent live coral cover, percent macroalgal cover, juvenile coral density, and size of juvenile corals. We replicated the methods of Edmunds and Carpenter (2001) to compare data between 2000 and 2003.

***Diadema antillarum* density.** We measured sea urchin density in 5 quadrats along a 10 m transect in 2 x 2 m plots, 2 m along the transect tape and 1 m on either side of the transect.

Percent macroalgal and live coral cover. We estimated percent cover along the transect in both urchin and algal zones. We placed 0.5 m^2 quadrats centered at 1, 3, 5, 7, and 9 m along the tape (n = 5 per zone). The quadrats were subdivided into 25 squares, and the number of squares dominated by macroalgae or live coral were counted.

Juvenile coral density and size. We defined juvenile corals as colonies between 2 mm and 4 cm in diameter. We counted the number of juvenile corals in the same (0.5 m^2) quadrat placements used to measure percent cover (meter points 1, 3, 5, 7, 9, along the 10 m transect). We measured their diameters to the nearest 1 mm.

Extreme urchin density. To extend the survey done by Edmunds and Carpenter (2001), we investigated the influence of varying urchin densities on juvenile coral abundance in the absence of high macroalgal cover. We selectively chose sample locations within the urchin zone at the Caricomp site representing extreme *D. antillarum* densities. We categorized urchin density based on personal observations and data from Edmunds and Carpenter (2001), as low (< 2/m^2), medium (2 - 10/m^2), or high (> 10/m^2). At each location we counted the number of *D. antillarum* in a 1 m^2 quadrat. We measured percent live coral cover, percent macroalgal cover, juvenile coral density and juvenile coral size using the same methods as described above with 0.5 m^2 quadrats, centered at the middle of the 1 m^2 quadrat used for urchin density. We pooled these data with urchin zone data from the previous transects in order to analyze a wide range of urchin densities.

RESULTS

For the randomly placed transects in the urchin zone, we found a positive relationship between density of juvenile corals and *D. antillarum* density (Fig. 1; $r^2 = 0.22$, df = 1, 19, P = 0.038). No such trend was observed in the macroalgal zone, where no urchins are present. Juvenile coral density decreased with increasing percent macroalgal cover in the urchin zone (Fig. 2; $r^2 = 0.25$, df = 1, 19, P = 0.023). In the macroalgal zone we did not find a signifi-

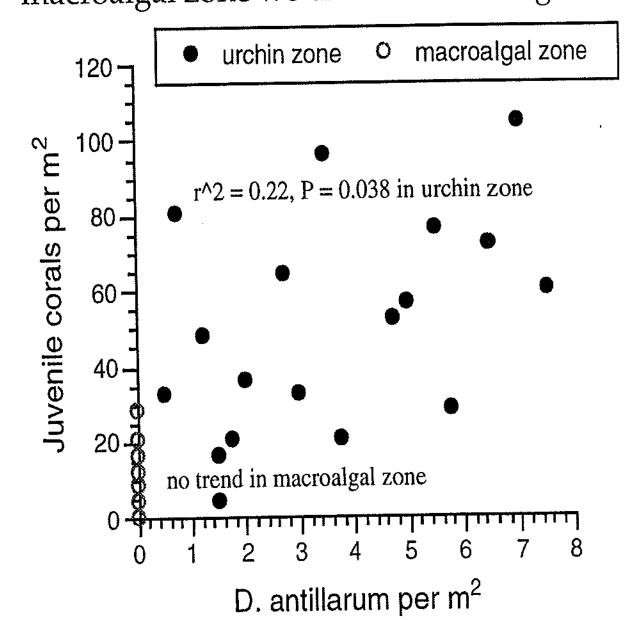

FIG. 1. Relationship between juvenile coral density and *D. antillarum* density at Discovery Bay, Jamaica. Data collected from the urchin zone and the macroalgal zone along the forereef. n = 40.

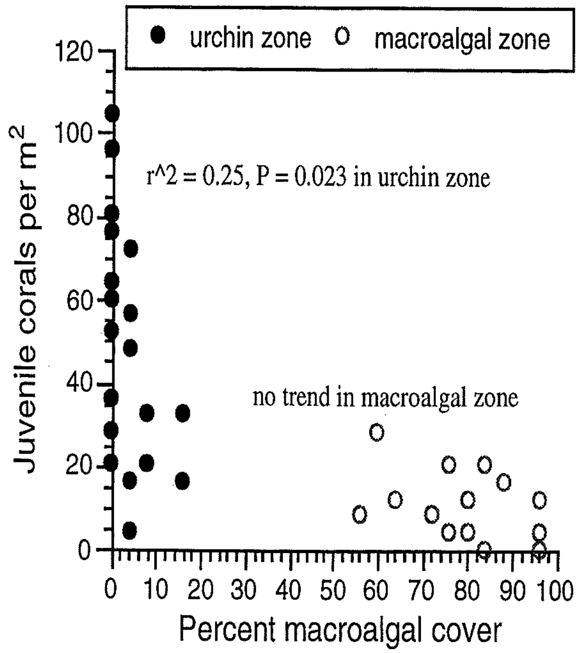

FIG. 2. Relationship between juvenile coral density and *D. antillarum* density at Discovery Bay, Jamaica. Data collected from the urchin zone and the algal zone along the forereef. n = 40.

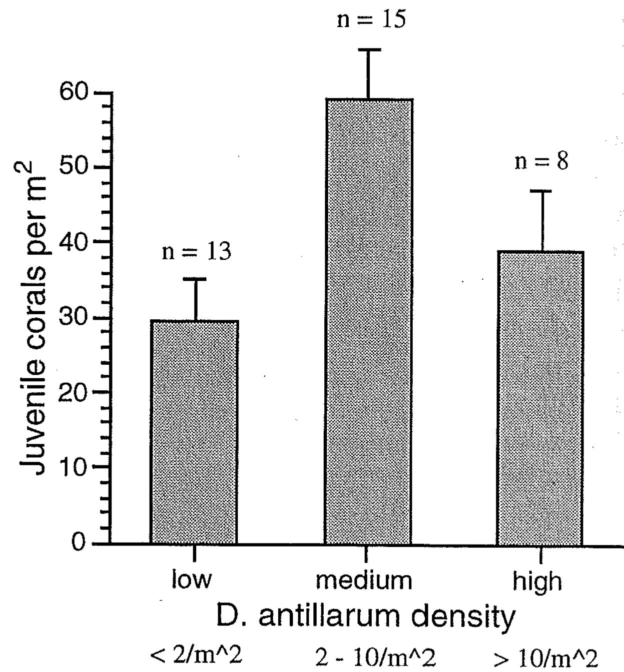

FIG. 3. Juvenile coral density as a function of *D. antillarum* density at Discovery Bay, Jamaica. Data collected from four sites on the forereef.

cant relationship between juvenile coral density and percent algal cover (Fig. 2; r^2 = 0.13, df = 1, 19, P = 0.13). As suggested by the phase shift from algal dominance to *D. antillarum* dominance in the urchin zone, percent macroalgal cover was lower in areas of higher *D. antillarum* density across zones (r^2 = 0.57, df = 1, 39, P < 0.001).

Along these transects, percent coral cover was negatively correlated with percent macroalgal cover (r = 0.4, df = 1, 39, P = 0.012) and showed a trend toward positive correlation with *D. antillarum* density (r = 0.28, df = 1, 39, P = 0.076). Size of juvenile corals was not correlated with *D. antillarum* density, percent macroalgal cover, or percent coral cover (r = 0.12, df = 1, 39, P = 0.45; r = 0.042, df = 1, 39, P = 0.79; r = 0.13, df = 1, 39, P = 0.44, respectively).

We investigated the same factors across a broader range of *D. antillarum* densities in the barren zone alone, including points with extremely high and low *D. antillarum* density. We found maximum juvenile coral density at intermediate *D. antillarum* density (Fig. 3; F = 5.67, df = 2, 35, P = 0.008). Pair-wise comparisons (Tukey Kramer HSD) showed that points with low *D. antillarum* density (< 2/m^2) had significantly lower juvenile coral density than points with medium *D. antillarum* density (2 – 10/m^2). Neither points of medium and high *D. antillarum* density (> 10/m^2), nor points of high and low *D. antillarum* density were significantly different from one another.

The overall density of juvenile corals in the urchin and algal zones was 50.4 ± 7.19/m^2 (mean ± SE), more than double Edmunds and Carpenter's result of 24/m^2 from 2000. We found the highest density of juvenile corals in the urchin zone at Dairy Bull (68/m^2). Edmunds and Carpenter (2001) found the highest density in the urchin zone at LTS (43/m^2), close to our survey at Caricomp.

D. antillarum density did not change from the values reported by Edmunds and Carpenter (2001). We found mean *D. antillarum* density in the urchin zone of 3.5 ± 0.86/m^2. Edmunds and Carpenter recorded an average *D. antillarum* density in the

urchin zone of 5/m^2 in 2000 and 4 ± 0.9/m^2 in 2000.

Macroalgal cover was slightly higher than Edmunds and Carpenter found in 2000. We found an average percent macroalgal cover of 3 ± 1.8% in the urchin zone and 82 ± 3.9% in the macroalgal zone. Edmunds and Carpenter reported values ranging from 5 – 7% macroalgal cover in the urchin zone and 55 – 75% in the algal zone (2001).

Unlike Edmunds and Carpenter (2001), we found a significant difference between coral cover in the macroalgal and urchin zones (2.0 ± 0.52% and 9 ± 4.8%, respectively; F = 5.15, df = 1, 39, P = 0.029).

Discussion

At intermediate densities, *D. antillarum* grazing may release juvenile corals from the negative effects of macroalgal cover. However, at high densities *D. antillarum* grazing may have a direct deleterious effect on juvenile coral recruitment and survival. This suggests that coral recruitment or survival may be highest at intermediate *D. antillarum* densities, in support of the intermediate disturbance hypothesis.

It appears that the phase shift from macroalgae to urchins, coral and microalgal turf has continued to progress since 2000. We observed similar average juvenile coral diameters and similar densities of *D. antillarum* to those reported by Edmunds and Carpenter (2001). However, we did find a higher density of juvenile corals overall, suggesting that the *D. antillarum* has continued to change distribution and abundance of corals on the reef since 2000.

The exacerbation of differences in percent coral cover and percent algal cover between urchin and macroalgal zones since 2000 further supports this trend. Coral cover appears to be increasing in the urchin zone and decreasing in the macroalgal zone, where percent macroalgal cover has increased since 2000. These differences suggest that while the displacement of macroalgae by *D. antillarum* persists, *D. antillarum* continues to change the reefscape by increasing juvenile coral recruitment or survival. If *D. antillarum* density remains at current levels, reef coral communities may continue to recover toward levels recorded before the *D. antillarum* die-off in 1983 (Edmunds and Carpenter 2001). However, if *D. antillarum* density increases, we would expect to see a detrimental effect on coral recruitment and survival, which might lead to denuded barren zones similar to those described by Mobley (1983).

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