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Recovery of the sea urchin *Diadema antillarum* promotes scleractinian coral growth and survivorship on shallow Jamaican reefs

J. A. Idjadi[1,*], R. N. Haring[2], W. F. Precht[3]

[1]Department of Biology, Eastern Connecticut State University, Willimantic, Connecticut 06226, USA
[2]The City of San Diego Marine Biology Laboratory, San Diego, California 92106, USA
[3]Florida Keys National Marine Sanctuary, Key Largo, Florida 33037, USA

ABSTRACT: The decline and potential recovery of Caribbean reefs has been the subject of intense discussion and is of great interest to reef ecologists and managers. The recent return of *Diadema antillarum* sea urchins at some Caribbean locations and the concomitant changes in coral cover and recruitment provide a new perspective on the reversibility of Caribbean coral reef decline. This study examined the influence of recovering populations of *Diadema* and the subsequent formation of dense urchin zones on the growth and density of newly settled juvenile scleractinian corals. In these urchin zones, where *Diadema* graze algae, we documented higher growth rates of juvenile corals, and higher densities of small juvenile recruits (likely to be important precursors to reef recovery). Coral survivorship was higher for juvenile corals living in urchin versus algal zones. Roughly 83% of the juvenile corals in urchin zones survived over the 2 yr period of the study, while ~69% survived in the algal zones. Corals in the urchin zones increased in major diameter by an average of 75 ± 7% from 2001 to 2003 versus 24 ± 4% for corals in the algal zones during the same time period. The relatively abrupt decrease in macroalgal cover and the signs of increasing coral cover along the north coast of Jamaica following the return of *Diadema*, reported here and by other authors, suggest that these reefs have undergone rapid phase shifts, rather than being constrained to alternate stable states. In the Caribbean, it appears that *Diadema* are effective at enhancing scleractinian coral recruitment and growth and thus could be used as an important manipulative tool for returning reefs to a coral dominated state, especially on reefs that are severely overfished.

KEY WORDS: *Diadema antillarum* · Juvenile coral growth · Phase shifts · Coral reef recovery · Caribbean · Scleractinian · Urchin · Macroalgae

INTRODUCTION

The presence or absence of a single herbivore, in this case, the sea urchin *Diadema antillarum*, has been linked to changes in the relative abundance of coral and algae on Caribbean reefs (Knowlton 1992, Hughes 1994, and numerous others). The importance of *Diadema antillarum* (*Diadema* hereafter) in removing macroalgae was underscored when the urchin experienced a sudden, Caribbean-wide die-off in 1983 to 1984 and algal biomass increased abruptly in many locations, including Jamaica (Lessios et al. 1984, Liddell & Ohlhorst 1986, Hughes et al. 1987, Carpenter 1988, 1990).

The reefs off the north coast of Jamaica have served as the archetype of reef decline for the Caribbean (Precht & Aronson 2006, Bruno et al. 2009). The decline in Jamaica was linked to a number of disturbances, including long-term serial overfishing, extensive coral mortality from Hurricanes Allen in 1980 (Woodley et al. 1981) and Gilbert in 1988 (Woodley 1989), and additional coral losses due to predation and coral disease (Knowlton et al. 1990) and coral bleaching (Goreau 1992). Because of the vast amount of sub-

*Email: idjadij@easternct.edu

stratum colonized by macroalgae in the 1980s on these reefs, there appears to have been an interaction between coral cover and lower herbivory in the shift from coral to macroalgal dominance (Knowlton 1992). Chronic overfishing of scarids and acanthurids and the loss of *Diadema* left the reefs without enough grazers to remove macroalgae. The result of these multiple, compounded disturbances along the north coast of Jamaica was a reduction in scleractinian coral cover from ~60 % in the late 1950s to <10 % today, with most reefs at 2 to 3 % coral cover (Goreau 1959, Liddell & Ohlhorst 1992, Hughes 1994, Aronson et al. 1994, Andres & Witman 1995, Aronson & Precht 2000, Edmunds & Carpenter 2001).

A return of *Diadema* along much of the north coast of Jamaica has been documented, resulting in significant top-down changes to the benthic community (Woodley 1999, Aronson & Precht 2000, Cho & Woodley 2002, Bechtel et al. 2006, Carpenter & Edmunds 2006). An important question to emerge from the reduction of macroalgae is 'What is the influence of increased *Diadema* and decreased macroalgae on coral recovery and the return to a coral dominated state?' Answering this is critical to understanding whether these coral-to-macroalgal phase shifts are reversible or whether these reefs are constrained to alternate stable states resistant to change (Knowlton 1992, Petraitis & Dudgeon 2004, Aronson & Precht 2006, Precht & Aronson 2006, Idjadi et al. 2006).

Prior studies have described negative effects of macroalgae on corals (see review by McCook et al. 2001). When macroalgae grazers are excluded, abundant algae can result in reduced growth and increased tissue damage to corals because of abrasion, shading, and direct competitive interactions (River & Edmunds 2001). Potential coral settlement and growth space can be preempted by macroalgae reducing hard substratum available for settlement and lateral growth by corals (Hughes & Tanner 2000, McCook et al. 2001). Further, there is evidence that water soluble chemicals (exudates) released by macroalgae can inhibit settlement of coral larvae (Miller et al. 2009). Small corals are particularly susceptible to the negative effects of macroalgae, which may have community-level implications for coral on reefs where macroalgal cover is high or increasing (Tanner 1995, Lirman 2001, River & Edmunds 2001, McCook et al. 2001).

There is wide interest in the return of *Diadema* to the Caribbean and whether the reduction in macroalgae due to grazing will facilitate a region-wide trend toward coral recovery by increasing recruitment and reducing direct and indirect negative effects of algae on corals (Knowlton 2001). In the last decade, *Diadema* densities in Discovery Bay, Jamaica, have increased, and the urchins are forming highly grazed 'urchin zones' (as shown in Fig. 1; Edmunds & Carpenter 2001). In areas where *Diadema* are grazing, there is high turnover of algal turfs as well as the dislodging of erect macroalgae resulting in a substratum with high cover of crustose coralline algae (CCA) (Sammarco 1980). Previous research has indicated that cues pre-

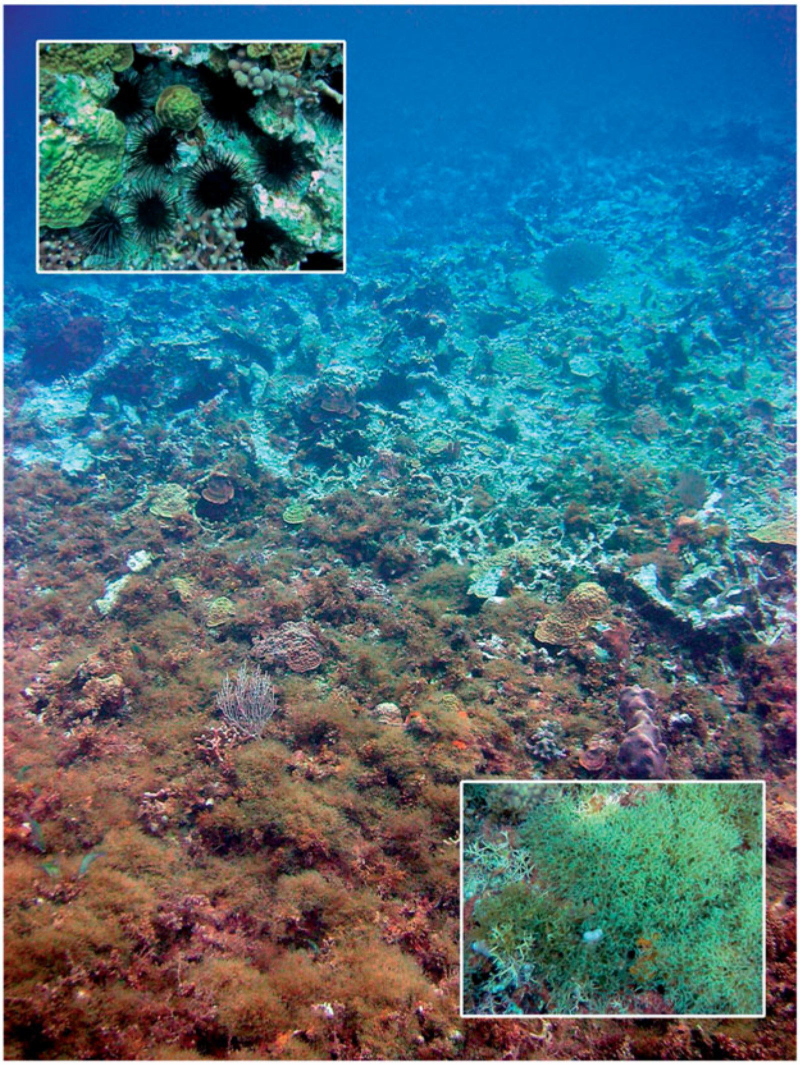

Fig. 1. Photograph showing the boundary between algal and urchin zones in shallow water off Discovery Bay, Jamaica. Insets depict typical urchin zone (top) and algal zone (bottom) composition

sent in CCA appear to encourage coral settlement and metamorphosis (Heyward & Negri 1999, Raimondi & Morse 2000, Harrington et al. 2004). Indeed, juvenile coral densities were found to be 11-fold higher in urchin zones when compared to algae-covered zones (algal zones hereafter) at the same depth (Edmunds & Carpenter 2001). CCA may also increase the settlement of herbivorous sea urchins (Rodríguez et al. 1993).

Recovery of *Diadema* and the formation of these urchin zones may encourage settlement, growth, and survival of corals. However, there is a possibility that at high densities *Diadema* may graze upon coral spats and could negatively affect both coral cover and recruitment (Bak & van Eys 1975, Sammarco 1980, 1982). No work or multi-year monitoring has tracked the influence of these zones on growth of individual corals. Furthermore, patterns in abundance for recently settled corals (≤1 cm) have not yet been quantified in these zones.

The present study represents a dual approach to examining the influence of increasing urchin numbers on juvenile coral growth, recruitment, and survivorship. First, we tested, by tracking individual corals over 2 yr, whether the presence of *Diadema* improves growth and/or survivorship of juvenile corals (<4 cm). Secondly, we compared the density of the smallest corals (≤1 cm, small juveniles hereafter) in urchin and algal zones to determine whether the benefit of urchin grazing is manifest in the most recently settled coral size class. The goal of the study was to examine the effects, positive or negative, of the ongoing *Diadema* recovery on small size classes of scleractinian corals in recently formed urchin zones.

MATERIALS AND METHODS

Site description. This study was conducted at 3 sites near the Discovery Bay Marine Laboratory, Jamaica, West Indies (18° 28′ N, 77° 25′ W) between January 2001 and January 2003. Two of the study sites, Mooring 1 (M1) and Long-Term Study site (LTS), were located on the west forereef of Discovery Bay; the third, East Dairy Bull (EDB), was located approximately 2 km east of the Discovery Bay Marine Laboratory (Fig. 2). Prior studies have described the reef structure near Discovery Bay (Morrison 1988, Hughes 1994, Edmunds & Carpenter 2001). The study took place on shallow reefs at depths between 4 and 7 m within distinct areas designated as algal and urchin zones on each of the 3 reefs. Urchin zones within a reef were characterized as having *Diadema* present, with little or no macroalgal cover (see Aronson & Precht 2000 for a description). In contrast, the substratum within algal zones was nearly

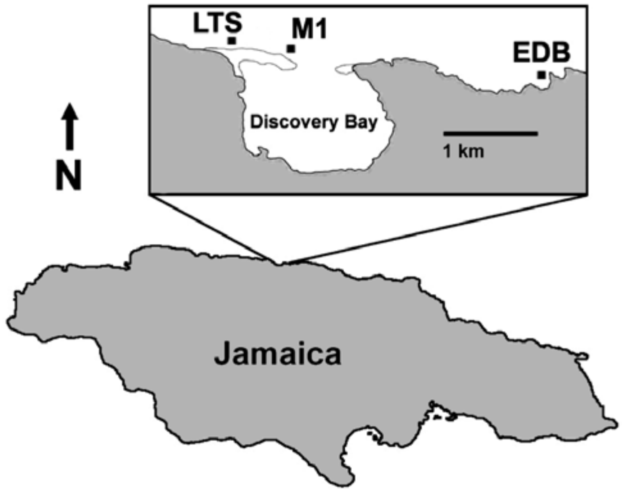

Fig. 2. Discovery Bay, Jamaica, (18° 28.21′ N, 77° 24.47′ W) with study sites Long-Term Survey (LTS), M1, and East Dairy Bull (EDB)

devoid of *Diadema,* with a relatively high percent cover of macroalgae similar to the conditions described by Andres & Whitman (1995) and Aronson et al. (1994). Subsequent to the regional mass mortality of *Diadema* in 1983 to 1984 and prior to the recent documented recovery of *Diadema* on these reefs, both zones contained abundant macroalgae and essentially no *Diadema* (Aronson et al. 1994, Aronson & Precht 2000, Cho & Woodley 2002).

Characterization of benthic community. In order to quantify the benthic cover in areas of dense urchin cover and in the absence of urchins, six 25-m surveyor's tapes were laid haphazardly in the LTS study area at depths of 5 m and 10 m. Using the linear point intercept (LPI) sampling strategy, a diver swam along each transect and recorded the sessile organism or substratum type beneath each 10 cm mark on the tape. This yielded 6 estimates of each category of substratum cover (one from each transect), with each estimate based on 250 point counts. On low-diversity reefs where only a few functional categories are compared, the LPI method is sufficiently accurate for comparative purposes (Ohlhorst et al. 1988). Point counts for each transect were tallied for the following functional categories of substratum cover to yield percentages of fleshy and filamentous macroalgae; hard corals (Scleractinia plus Milleporina); and a category called CTB which combined CCA, algal microturfs (algal filaments, 2 cm tall and so sparse that the substratum was visible), and bare space.

Abundance of *Diadema*. To characterize urchin and algal zones, abundances of *Diadema* were estimated within each zone during the day. All visible *Diadema* within a belt transect 2 m wide and 40 m long were counted. Three transects were placed haphazardly within each zone at each site in winter 2001 and 5 transects in winter 2003.

Juvenile coral survivorship and growth. To test the hypothesis that juvenile coral survivorship and growth differed between urchin and algal zones, juvenile coral survivorship and growth were monitored in each zone at each site along permanent 10 m transects from winter 2001 to winter 2003. We defined juvenile corals as colonies ≤4 cm in diameter (see Bak & Engel 1979, Edmunds & Carpenter 2001). Transect locations were selected haphazardly in each zone and ran parallel to the reef crest or shoreline at depths of approximately 4 to 7 m (see Aronson et al. 1994 for description on use and selection of haphazard surveys on coral reefs). In January 2001, juvenile corals were selected haphazardly along the transects, their genus identified, and their major diameter measured with calipers (±0.1 mm). After coral measurement, a numbered aluminum forestry tag was epoxied nearby using Koppers Splash Zone compound, and its location relative to the coral and distance along the transect were recorded. In many cases, 1 tag served to mark the location of more than 1 juvenile coral, and a total of 424 juvenile corals were measured and marked using 204 tags throughout all the sites and zones with 228 corals marked in the urchin zones and 196 in the algal zones. Effort was made to tag an equivalent number of corals at each site; approximately 70 corals zone^{-1} in each site were monitored for 2 yr. In January 2002 and 2003, 197 of the 204 aluminum tags were re-located using an underwater metal detector (Tesoro Electronics); the juvenile corals were scored for survivorship, and the diameters of living corals were re-measured. The change in major diameter over 2 yr was calculated and used as a proxy for growth.

The juveniles we encountered were similar in composition to those reported before Hurricane Allen by Rylaarsdam (1983) for the forereef at Discovery Bay when coral cover was high and the number of macroalgae was low. Eight genera were represented among the 424 tagged corals. Corals of the genera *Agaricia, Porites*, *Siderastrea*, *Dichocoenia, Diploria, Montastraea, Acropora,* and *Stephanocoenia* were found and tagged in this study. Growth rates of scleractinian corals can vary considerably among genera (Hubbard & Scaturo 1985). To allow genera with different growth rates to be considered together, data were standardized (z-transformed) by genus, which expresses magnitude of growth in standard deviations. In order to compare 2-yr growth rates between zones and among sites, data were analyzed using a 2-way mixed model ANOVA with site and zone as factors. Coral survivorship was compared between zones using a chi-squared test and a 2 × 2 contingency table, with zone (urchin or algal) and survivorship (alive or dead) as categories. Genera for which too few individuals were tagged and recovered including *Acropora* spp. were excluded from the analysis.

Small juvenile coral densities (≤1 cm). Neither settlement rates nor differential rates of early post-settlement mortality were experimentally addressed in this study. However, this study identified differences in juvenile coral abundances at a very early life history stage to estimate the importance of urchins on recently settled corals. Small juvenile corals (<1 cm) having major diameters between 2 and 10 mm were censused in each zone at each site in winter 2001 and 2003. Densities were estimated by counting all juvenile corals within 0.25 m^2 quadrats that were randomly placed (n = 10 zone^{-1}). Time and care were taken to ensure that all the smallest corals within a quadrat were accounted for and high magnification (10 to 12× in air) hand lenses were used *in situ* to aid location of the smallest corals. When required, some macroalgae and sediment were removed from the substratum within the quadrats to prevent any hidden corals from being overlooked. We were confident that we could find and measure corals as small as 1 mm using this method. Small juvenile corals were identified to genus and measured to the nearest 0.1 mm using calipers. We compared small juvenile coral densities in urchin and algal zones in replicate sites using a 2-way mixed-model ANOVA with site and zone as random and fixed factors, respectively.

RESULTS

Urchin densities and benthic characterization

The distribution and density of *Diadema* were patchy on the forereef of Discovery Bay between 2001 and 2003. In algal zones, *Diadema* were almost completely absent, averaging 0.01 ± 0.004 SE urchins m^{-2} in 2002 and 0.02 ± 0.002 SE urchins m^{-2} in 2003. In contrast, *Diadema* densities were ~200-fold higher in urchin zones compared to algal zones, averaging 2.7 ± 0.2 SE urchins m^{-2} and 4.1 ± 0.5 SE urchins m^{-2} in 2002 and 2003, respectively. Benthic cover varied greatly between urchin zones and algal zones. Benthic surveys taken in urchin zones with 3.6 ± 1.8 urchins m^{-2} showed far less algal cover and more coral cover than surveys in the algal zones which yielded no urchins, abundant macroalgae, and low coral cover (Table 1), confirming the designation of algal and urchin zones.

Juvenile coral survivorship and growth

Survivorship over 2 yr was significantly higher for juvenile corals living in urchin zones versus algal

Table 1. Table of percent benthic cover of hard corals, macroalgae, and CTB (crustose coralline algae, turf algae, and bare space) in urchin and algal zones at the Long-Term Study site in 2003

Benthic component	Percent cover: Urchin zone	Percent cover: Algal zone
Hard corals	10.6 ± 2.91	4.2 ± 2.22
Macroalgae	6.2 ± 3.34	67.6 ± 9.63
CTB	73.5 ± 8.70	16.4 ± 5.32

zones (χ^2 = 11.078, n = 410, df = 1, p < 0.001, Table 2). Of the 424 juvenile corals measured in 2001, 410 were found and scored for survivorship in 2003. Of these, 314 (77%) were still alive after 2 yr. Survivorship (pooled among sites) for corals in the urchin zones was 82.9% versus 68.9% in the algal zones.

Corals living in the presence of *Diadema* grew larger and at a faster rate than their counterparts in the algal zones (Fig. 3). Corals in the urchin zones increased in major diameter by an average of 75% ± 7% from 2001 to 2003 versus 24% ± 4% for corals in the algal zones during the same time period. Standardized growth rates were significantly higher for corals living in the urchin zones than for those living in the algal zones (Table 3), with the pattern of growth rates consistent within each zone across all 3 sites and with no interaction between site and zone. Coral growth was both positive and negative, with some corals experiencing tissue necrosis and coral/algal competitive interactions resulting in receding margins. Some of the differences in growth rates between urchin and algal zones were attributable to this negative growth. For example, 10.8% of urchin zone corals decreased in major diameter from 2001 to 2003 compared to 27.9% of algal zone corals (Fig. 4).

Table 2. Living and dead juvenile corals in algal and urchin zones from January 2001 to January 2003

Zone	Survivorship: Alive	Survivorship: Dead	Survivorship: Total
Algal zone	129	58	187
Urchin zone	185	38	223
Total	314	96	410

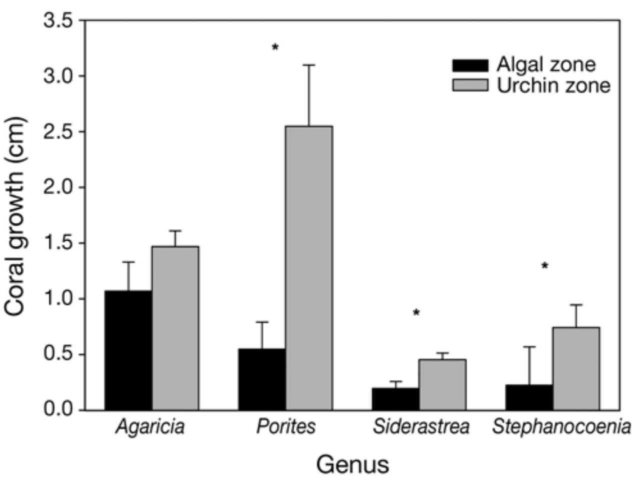

Fig. 3. Mean (±SEM) changes in coral diameters from 2001 to 2003 (for the 4 coral genera which we recovered in sufficient numbers) across experimental sites in algal (black) and urchin (gray) zones. Asterisks indicate significant differences between urchin and algal zone coral growth in that genus

Densities of small juvenile corals (≤1 cm)

Densities of small juvenile corals were greater in the urchin zones compared to algal zones. Corals ≤1 cm were ~5 times more abundant in the urchin zones than in the algal zones in both 2001 and 2003 (Table 4). The density of small juvenile corals differed significantly between zones for both years censused (2001 census: df = 1, F = 29.03, p = 0.03; 2003 census: df = 1, F = 467.34, p = 0.002). Neither the site factor nor interaction between site and zone was significant for 2001 or 2003 data (p > 0.2).

DISCUSSION

The recent appearance of dense zones of *Diadema* in shallow depths (i.e. 4 to 7 m) along the north coast of Jamaica appears to facilitate growth, survivorship, and recruitment of scleractinian corals. Previous studies also have suggested that *Diadema* facilitate coral colonization (see Woodley 1999, Edmunds & Carpenter 2001, Carpenter & Edmunds 2006, Precht & Aronson 2006).

In this study, juvenile scleractinian corals experienced higher growth rates in urchin zones when compared with algal zones. The relationship between the presence of sea urchins and reduced macroalgal cover has been substantiated by this and other studies that have examined removal of sea urchins. This includes pre– and post–*Diadema*-die-off comparisons, and com-

Table 3. Results of ANOVA comparing standardized (z-transformed) coral growth between urchin and algal zones at each site

Source	df	MS	F	p
Zone	1	14.003	14.82	<0.001
Site	2	0.255	0.27	0.764
Zone × Site	2	0.369	0.39	0.677
Error	305	0.945		

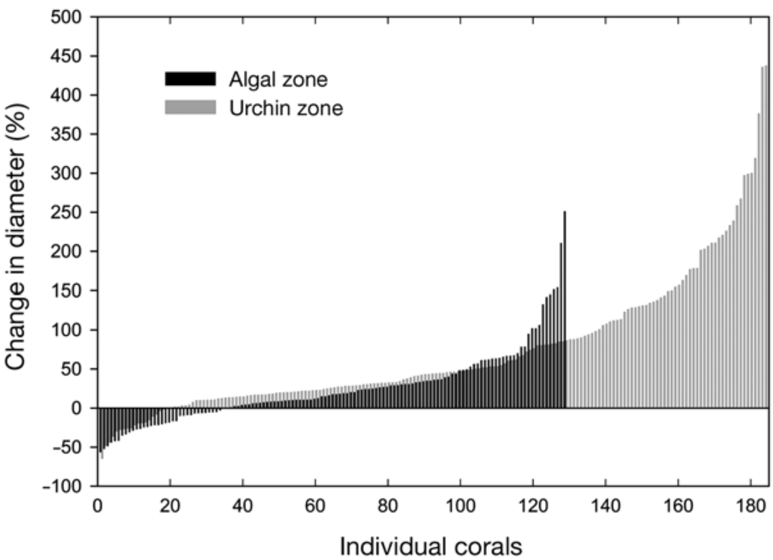

Fig. 4. Percent growth (change in diameter) for all surviving individual corals from 2001 to 2003 in algal and urchin zones. Data sorted by ascending growth without respect to genus or experimental site. Surviving corals in algal zones (black): n = 129; surviving corals in urchin zones (gray): n = 185

Table 4. Density (number m^{-2}) of small juvenile corals in urchin and algal zones in 2001 and 2003

Year	Density of small juveniles	
	Urchin zone	Algal zone
2001	9.1 ± 1.3	1.9 ± 0.5
2003	11.1 ± 1.4	2.3 ± 0.6

parisons between urchin and non-urchin zones of comparable depth (Sammarco 1982, Hughes et al. 1987, Morrison 1988, Aronson & Precht 2000, Edmunds & Carpenter 2001). Increased coral growth probably is due to a reduction in direct and indirect competition with macroalgae for light and space (River & Edmunds 2001, McCook et al. 2001). For corals living in urchin zones, the metabolic costs of competition with macroalgae might instead be allocated to growth (McCook et al. 2001). Increased growth allows corals more quickly to enter a size refuge where they are less likely to encounter algae-induced shading, abrasion, and overgrowth, reducing overall mortality of juvenile corals (McCook et al. 2001, River & Edmunds 2001). Greater growth rates may also be a key to allowing corals to grow large enough to prevent direct damage by urchins through incidental grazing (Sammarco 1980). Growth rate increases, in part, may explain differences found in survivorship between zones.

Coral survival was higher for juvenile corals living in urchin versus algal zones. Roughly 83 % of the juvenile corals monitored in urchin zones survived over the 2 yr study period, whereas ~69 % survived in the algal zones. It is noteworthy that the surviving algal-zone corals experienced more negative growth due to partial mortality from algal competition (Fig. 4) (Bak & Engel 1979). Bak & Engel (1979) found survivorship rates among juvenile corals on the pre–die-off reefs of the mid 1970s to be 68 % yr^{-1} and found survival rates of 63 % yr^{-1}. Compared to these rates, the juvenile corals we tracked over 2 yr experienced higher survival particularly in urchin zones. In algal zones, small corals living in the macroalgal understory may not receive enough incident light and may not have access to favorable flow regimes for heterotrophy or gas exchange (River & Edmunds 2001, Box & Mumby 2007). The ~14 % increase in juvenile coral survival in the urchin zones is likely to influence the number of reproductive individuals and thus may have population level consequences for the scleractinian coral community. It is also worth noting that we did not find sufficient juvenile colonies of many species of coral, including the primary frame-builders such as the *Acropora* spp. or the *Montastraea annularis* species complex. Thus, it could be hypothesized that this indicates that urchin-driven coral recovery favors weedier species rather than foundation species. However, the juveniles we encountered were similar in both composition and number to those reported on the forereef at Discovery Bay before Hurricane Allen (Rylaarsdam 1983) and before the die-off of *Diadema* (Hughes 1989). Because of their life history strategies and poor sexual recruitment, these foundation species are likely to experience low recruitment and are particularly vulnerable to major perturbations (Kojis & Quinn 1994).

The increased number of small juvenile corals observed in urchin zones in this study (i.e. corals <1 cm) and by Edmunds & Carpenter (2001; i.e. corals <4 cm) could be explained by increased settlement and/or post-settlement survival of corals. Changes in the substratum by sea urchins are well documented (Sammarco 1982), and echinoids are more effective than fish at reducing algae and enhancing coral recruitment.

Diadema is among the most important substratum modifiers in the Caribbean, changing algal abundance and composition on reefs (Carpenter 1981) as well as contributing substantially to bioerosion (Hunter 1977, Ogden 1977, Sammarco 1982). Grazing by sea urchins decreases abundance of both fleshy and turf algae and thus reduces space preemption of coral settlement by the physical presence of algae (McCook et al. 2001). Further, since some macroalgae can inhibit coral settlement by chemical influences, a reduction in macroalgae presumably would reduce those influences. This reduction in macroalgae is followed by increases in CCA cover (Belliveau & Paul 2002), which in turn, may attract coral larvae and induce metamorphosis (Morse et al. 1994, Heyward & Negri 1999, Raimondi & Morse 2000, Rahmani & Ueharai 2001).

Substratum modifications by *Diadema* grazing appear to facilitate increases in settlement which explain the greater abundance of small juveniles in our study. Secondarily, post-settlement processes are another potential contributor to the overall trends in coral densities observed in this study. These factors include reduced direct competition with macroalgae, reduction in algal exudates shown to enhance detrimental microbes, as well as reduced shading and abrasion (River & Edmunds 2001, Smith et al. 2006); all of these factors aid coral survival and growth.

The patterns we have observed in urchin zones and algal zones will be relevant only if urchin numbers continue to increase throughout the region. Increasing urchin numbers have been observed at a number of locations throughout the Caribbean (Macintyre et al. 2005, Weil et al. 2005, Carpenter & Edmunds 2006, Debrot & Nagelkerken 2006, Steiner & Williams 2006, Jordán-Garza & Rodríguez-Martínez 2008), with many reefs experiencing an abrupt increase in *Diadema* populations since the mid-1990s (Chiappone et al. 2001, Miller et al. 2003, Myhre & Acevedo-Gutiérrez 2007). Because overfishing of the predators of *Diadema* (triggerfish and larger wrasses such as the hogfish *Lachnolaimus maximus*) is widespread on many of the Caribbean island reef systems, including Jamaica, this could increase survivorship and recruitment of *Diadema,* aiding in its recovery (Aronson & Precht 2006). In Jamaica, pre–die-off urchin densities were higher than current densities (Sammarco 1982). Whereas increased densities may indicate recovery of the urchin population, the facilitative effect of urchin grazing on coral growth and settlement could decline if urchin densities increase enough to cause tissue and skeletal damage due to incidental grazing (Bak & van Eys 1975, Sammarco 1980). In Sammarco's study, the highest coral spat density was observed at *Diadema* densities of 4 m^{-2}, which is slightly lower than the density of *Diadema* on the shallow forereef of Discovery Bay, Jamaica, prior to the demise of this species in the 1980s and is similar to the densities recorded at the time of this study. If this density is maintained, increases in urchin numbers manifest as increases in the area of urchin zones, and urchins expand into deeper regions of the forereef, then these reefs might come to resemble pre-phase shift Jamaican reefs of the 1970s when average coral cover was ~55% (Rylaarsdam 1983) and macroalgal cover was generally less than 10% (Liddell & Ohlhorst 1992).

An important question resulting from this study in Jamaica is whether the coral- and algae-dominated states are stable alternatives, each of which resists conversion to the other (Knowlton 1992), or whether instead the coral–macroalgal transition is an easily reversible phase shift (see Precht & Aronson 2006 for discussion). Answering this question is critical in determining the resilience of reef communities not just along the north coast of Jamaica but throughout the entire Caribbean Sea (Scheffer & Carpenter 2003, Bellwood et al. 2004, Mumby et al. 2007a). The rapid diminution of macroalgae and increased recruitment and survivorship of corals are directly related to the ongoing recovery of shallow reef communities around Jamaica (Woodley 1999, Aronson & Precht 2000, Edmunds & Carpenter 2001, Cho & Woodley 2002, Bechtel et al. 2006) and appear to be inexorably linked to the recovery of *Diadema* populations.

Degraded reefs in the Caribbean have shown little or no evidence of recovery from a macroalgae-dominated state (e.g. Rogers & Miller 2006). However, this view is now changing as increased recruitment of juvenile corals and reduced macroalgal cover have occurred in some places with the local reappearance of *Diadema* populations. The results from this study are consistent with the idea of Petraitis & Dudgeon (2004) that the alternative stable-states view is not supported on Caribbean coral reefs and that switches between coral- and macroalgae-dominated communities are relatively simple, non-hysteretic, phase-shift responses to changes in environmental or ecological conditions, in this case, recovery of the keystone herbivore *Diadema*. For instance, the rapid phase-shift reversal noted at Dairy Bull Reef (Idjadi et al. 2006, Precht & Aronson 2006, Crabbe 2009) occurred on reefs that were characterized as so polluted and overfished that they could not recover under current levels of protection and management (Lapointe et al. 1997, Bellwood et al. 2004, Mumby et al. 2006, 2007a). However, fishing pressure continues to be severe on reefs along the north coast of Jamaica (Woodley & Sary 2002). Fish and other vertebrate consumers are scarce, and water quality (sediment loads, dissolved nutrient concentrations, etc.) have not improved in the last few decades (Cho & Woodley 2002, Greenaway & Gordon-Smith 2006). Considering this, the rapid reversal of the coral to macroalgal phase shift suggests that algal dominance is not the inevitable and irreversible consequence of overfishing or localized pollution. Whereas restoring herbivorous fish populations is a worthy goal of reef management (Mumby 2006), it is clear from this study that in Jamaica where these fish are largely absent, *Diadema* can singlehandedly drive rapid and effective reductions in macroalgae, facilitating coral recovery.

CONCLUSIONS

On Jamaican reefs, *Diadema* appears to be a disproportionately large player by removing macroalgae and indirectly promoting growth, recruitment, and survival of corals. Evidence from this study supports the conclusions of other work that correlates *Diadema* recovery with increased coral cover and abundance (Macintyre et al. 2005, Carpenter & Edmunds 2006, Myhre & Acevedo-Gutiérrez 2007).

Because of the strong relative influence of *Diadema* on limiting macroalgae and enhancing coral recruitment (Sammarco 1980, 1982, Carpenter 1988, Carpenter & Edmunds 2006, Precht & Aronson 2006), restoration of this keystone herbivore could serve as a tool for local reef conservation and management, especially on overfished reefs (Halpern et al. 2007). This conservation tool is in its infancy, and early demonstration projects have met with mixed results (Chiappone et al. 2003, Miller & Szmant 2006, Macia et al. 2007). However, this tool could be among our best options for implementing a rapid and effective increase in herbivory that facilitates coral recruitment, survival, and growth, especially when employed with other conservation measures (Aronson & Precht 2006, Mumby et al. 2007b).

Further monitoring is required to determine whether the urchin recovery will continue, whether the urchin zone will expand to deeper water, or whether urchin densities will increase throughout the Caribbean. In addition, our understanding of facilitation by *Diadema* will be helped by investigation into which coral life history stages the benefit of urchin grazing is imparted. If *Diadema* populations continue to increase, this may herald significant promise for one component of the recovery of Jamaican coral reefs.

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