

DIFFERENTIAL IMPACTS OF ECHINOID GRAZERS ON CORAL RECRUITMENT

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ABSTRACT

It has been argued that recent phase-shifts towards algal dominance in the Caribbean could have a profoundly negative influence on the future survival of settling corals. In the lower Florida Keys, USA, we used field surveys in areas with recovering populations of the formerly abundant herbivorous black urchin *Diadema antillarum* (Philippi, 1845) and comparatively stable populations of the urchin *Echinometra lucunter* (Linnaeus, 1758) to assess differences in the benthic communities associated with these two alternating urchin dominants. Two primary questions were addressed: (1) Are the effects of urchin grazing on benthic community composition differential based on urchin identity? and (2) how are these differences affecting coral recruitment and long-term success? Within the *Diadema* zone, urchin densities approached those of pre die-off levels and were associated with low macroalgal biomass and elevated coral cover. These findings are consistent with those of numerous prior investigations, and suggest that *Diadema* grazing is integral to the maintenance of low-biomass high-turnover algal turfs and prostrate coralline algal crusts that characterize healthy reef systems. Conversely, and despite orders of magnitude greater abundance, *Echinometra* was associated with chemically and morphologically defended macroalgal forms (i.e., *Halimeda* sp. and *Dictyota* sp.) and a benthos dominated by algal canopies with virtually no live coral cover. Overall, our results are concordant with those of other recent studies in the Caribbean and suggest that in the lower Florida Keys *D. antillarum* may be the strongest interactor in a diverse guild of invertebrate and vertebrate grazers.

The direct effects of grazer density on the abundance and growth of marine macroalgae are reasonably well understood. For example, trophic cascades leading to alternating densities of urchins and kelp in the Eastern Pacific are responsible for large-scale fluctuations in kelp biomass and, consequently, both the biodiversity and functioning of these ecosystems (Estes et al., 1998; Halpern et al., 2006). Similarly large impacts on plant biomass have been demonstrated many times for urchins grazing on algae associated with coral reefs (Ogden et al., 1973; Carpenter, 1981; Belliveau and Paul, 2002). Less is known, however, about the indirect effects of grazer-mediated disturbances on alternative space occupiers, such as scleractinian corals. Although removal of algal biomass increases the amount of substrate available for settlement by colonial invertebrates, past investigators have suggested that scouring caused by urchin feeding may also be responsible for appreciable rates of bioerosion (Hughes et al., 1985; Carreiro-Silva and McClanahan, 2001; Griffin et al., 2003) and might contribute to coral death, particularly for juvenile corals (Sammarco, 1980). Understanding the density-dependent relationship between grazing pressure and community composition is particularly important for coral reef systems, where recent declines in both grazing pressure and coral cover have been associated with increases in algal biomass stocks (McCook et al., 2001; Szmant, 2002).

In the Caribbean, declining coral cover and increasing macroalgal biomass have prompted considerable debate regarding the resilience of coral communities that are exposed to anthropogenically-driven disturbance regimes (Hughes et al., 1999; Mc-

Cook, 1999; Nyström et al., 2000; Szmant, 2002; Nedimyer and Moe, 2003; Aronson and Precht, 2006). McCook et al. (2001) have argued that phase-shifts towards algal dominance could have had a profoundly negative influence on the survival of recently settled corals, through shading, overgrowth, and physical disturbance, and may be a factor limiting the diversity and abundance of juveniles beneath algal canopies. Despite recent reports that recovering populations of the herbivorous black urchin, *Diadema antillarum* (Philippi, 1845) can precipitate small-scale reductions in algal cover (Aronson and Precht, 2000; Edmunds and Carpenter, 2001; Moses and Bonem, 2001; Miller et al., 2003; Nedimyer and Moe, 2003; Carpenter and Edmunds, 2006), surprisingly few studies have examined the impacts of: (1) localized increases in grazing intensity, (2) grazer identity or (3) protracted periods of algal dominance on the recruitment dynamics of hermatypic corals.

Edmunds and Carpenter (2001) supplied a first-order approximation of these influences by examining the effect of recently recovered populations of *D. antillarum* on several stretches of forereef in Jamaica. They reported substantial reductions in algal cover and an eleven-fold increase in juvenile coral abundance where *D. antillarum* was abundant and suggested that further recruitment by this urchin could eventually lead to a reversal of algal dominance and a return to scleractinian health (Edmunds and Carpenter, 2001). Recent surveys conducted by this group in 2003 and 2004 supported these findings with nearly identical patterns of echinoid density and algal abundance emerging at sites scattered throughout the Caribbean basin (Carpenter and Edmunds, 2006).

Using a similar approach in the lower Florida Keys, USA, we assessed differences in benthic communities associated with two co-occurring species of urchin: *D. antillarum* and *Echinometra lucunter* (Linnaeus, 1758). By haphazardly choosing adjacent patches with alternating urchin dominance, we were able to indirectly assess the influence of grazer identity on benthic species composition. Past studies have demonstrated that these two species differ markedly in their foraging range and control of benthic production, with *E. lucunter* exhibiting limited potential for grazer control even at densities as high as several hundred per square-meter (Grunbaum et al., 1978; Lawrence and Kafri, 1979; Schneider, 1985). We predicted that these differences would result in benthic assemblages that were differentially affected by the urchin species present, and that coral recruitment success would be negatively associated with algal standing stock.

In this study, two primary research questions were addressed: (1) Are the effects of urchin grazing on benthic community composition differential based on urchin identity? and (2) how are these differences affecting coral recruitment and long-term success?

MATERIALS AND METHODS

STUDY SITE AND DEPTH.—This study was conducted during July 2004 in Bahia Honda State Park on the south side of Little Bahia Honda Island (24°39'47"N, 81°15'50"W, located 0.8 km southwest of Bahia Honda Key). Here, consolidated substrate resembled a small-scale spur and groove arrangement with low-relief platforms separated by basins of accumulated sand and detritus. Platforms varied from 1 to 4 m in depth and were frequently exposed to high rates of flow and surge as tidally driven exchanges with Florida Bay occurred to the west, through Bahia Honda Channel. Benthic community structure was dominated by macroalgae (predominantly, *Halimeda* spp. and *Dictyota* spp.) with sparse cover of hard coral, mostly

Porites astreoides Lamarck, 1816. Within this bathymetric range, and extending some 20 m to the southeast, there existed small, largely monospecific aggregations of *D. antillarum* or *E. lucunter*. These urchin aggregations were readily visible and are hereafter termed “*Diadema*” and “*Echinometra*” zones, respectively. Three such patches per species were selected for study. However, due to inclement weather and strong wave action, only two *Diadema* patches were successfully surveyed. Depth was determined as an average of both transect ends (see below) and varied between 1.5 and 2.3 m, with an average depth (\pm SE) of 1.91 ± 0.38 and 1.73 ± 0.10 m for *Diadema* and *Echinometra* zones, respectively.

ECHINOID SIZE DISTRIBUTIONS.—Urchin abundance was visually estimated along a 5-m transect that was haphazardly positioned within each of the patches ($N = 5$); these transects were used in all subsequent benthic assessments (see below). All urchins within 0.5 m of the transect line were identified and enumerated. The test diameters of 55 *D. antillarum* were measured from the oral hemisphere using a Scienceware Measy 2000 Type 5921 caliper. These 55 individuals were haphazardly collected from the site prior to delineation of the urchin zone and were removed for use in another experiment. Reductions of this nature are not believed to have been significant to the remaining distribution or abundance of *D. antillarum* for two reasons: (1) hand-collections were made over a larger area than the one considered here, and (2) subsequent identification of zones was based on visual assessments made at the time of survey, making any artificially defaunated patches unlikely to have been chosen as representative of our treatment levels.

BENTHIC COVER.—Aerial coverage of macroalgae and live coral were directly assessed with 0.0625-m² photoquadrats positioned on both sides of the transect at 1-m increments ($n = 10$ per transect). Images were taken with an Olympus Stylus 400 digital camera set to its highest resolution and steadied for parallax error with a PVC-constructed tripod. Raw images were adjusted using Auto Levels in Photoshop 7.0 (Mac OS X) and outlined groupings of macroalgae or live coral cover were created using the available selection techniques. Resulting layers were converted to two-tone images (black and white) and exported individually to Carnoy 2.1 (Mac OS X) for area calculation.

JUVENILE AND SMALL CORAL COMMUNITIES.—We operationally defined juvenile corals to be colonies < 4.0 cm in diameter (Bak and Engel, 1979; Carpenter and Edmunds, 2006) and of taxa not known to sexually reproduce at that size (Edmunds and Carpenter, 2001; Carpenter and Edmunds, 2006). Colonies in violation of the latter property were termed ‘small’ species and considered separately during analysis. All colonies meeting the size criterion were visually located within 0.0625-m² quadrats (discussed above), identified to the lowest possible taxonomic level, enumerated, and measured (in situ). Size was estimated as the average of the two longest colony diameters (± 0.01 cm).

STATISTICAL ANALYSES.—Multivariate analyses of benthic cover, juvenile coral abundance, small coral abundance, and total colony abundance (i.e., “small” and “juvenile” taxa) were performed independently using the PRIMER 5 (Windows 98) software for ANOSIM (analysis of similarities) and SIMPER (similarity percentages). Multidimensional scaling (MDS) of species-level abundance data was based on resemblance matrices of square-root transformed, Bray-Curtis similarities. Global R statistics were assessed for significance at $P = 0.05$.

Parametric (univariate) statistical analyses were not performed due to the uneven sample sizes. However, factor plots (mean \pm SE) of individual metrics were used to assess relative effect size and general trends. Wherever possible, one-way comparisons were conducted using nonparametric Mann-Whitney U tests.

RESULTS

ECHINOID DISTRIBUTION.—Urchin diversity in the surveyed patches was largely comprised of *D. antillarum* and *E. lucunter*. Only a single individual of one other species, the pencil urchin *Eucidaris tribuloides* (Lamarck, 1816), was observed. Ur-

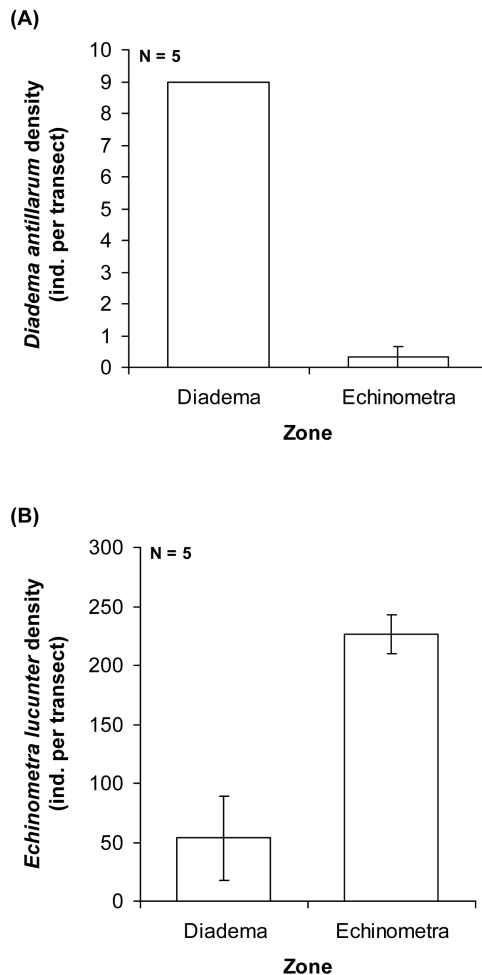


Figure 1. Mean urchin density as determined by 5-m² visual transects for (A) *Diadema antillarum* and (B) *Echinometra lucunter* in Florida Keys patches dominated by *Diadema* and *Echinometra* (zone).

urchin distributions were consistent with zone assignments, as the representative species averaged an order of magnitude greater abundance when compared by zone (Fig. 1). However, within both zones *E. lucunter* remained the numerical dominant, reaching densities of 226 ± 16.56 (hereafter, mean \pm SE) per transect for the *Echinometra* zone and 53.5 ± 35.50 for *Diadema* transects (Fig. 1). *Diadema antillarum* ranged from 9 ± 0.00 individuals per transect within its zone to only 0.33 ± 0.33 in the *Echinometra* zone (Fig.1). These densities translated to a zone-wide average of 45.2 ind m⁻² for *E. lucunter* and 1.8 ind m⁻² for *D. antillarum*. The latter was consistent with the Jamaican forereef abundance reported by Edmunds and Carpenter (2001), where *D. antillarum* was assumed to have been the dominant grazer. We made a similar working assumption in this study, despite the numerical dominance of *E. lucunter*.

Size frequency distributions of test diameters for *D. antillarum* were unimodal and consistent among collection dates (12–13 June and 19 August) with a cumulative average of 68 ± 1.09 mm (mean \pm SE).

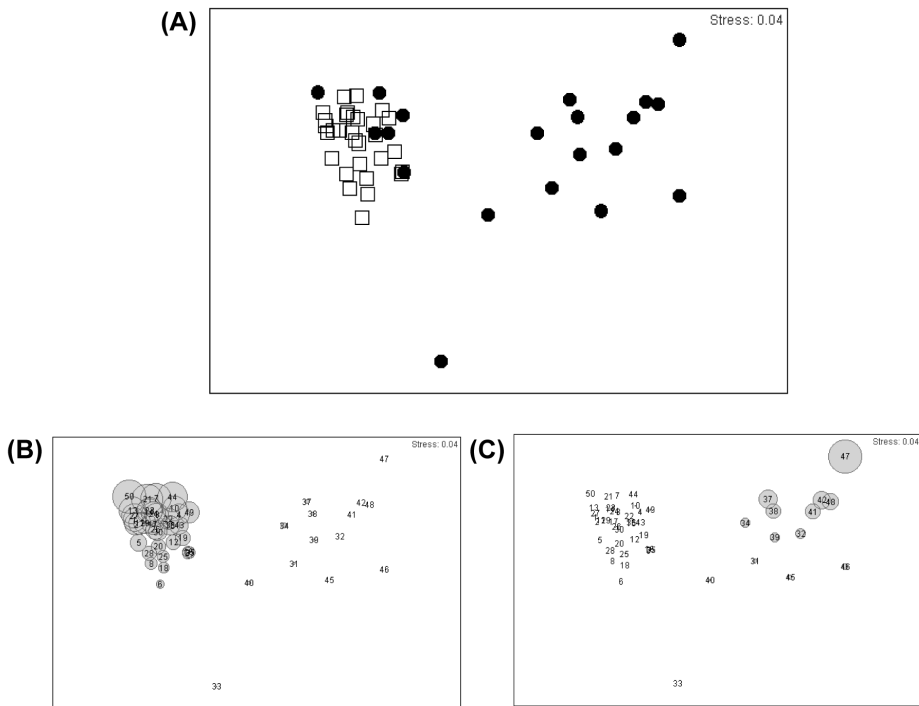


Figure 2. MDS ordination of benthic cover at Bahia Honda in the Florida Keys. Two-dimensional ordinations produced from square-root transformed, Bray-Curtis similarity matrices are presented with samples delineated by (A) urchin zone (*Diadema* depicted as black circles and *Echinometra* depicted as hollow squares) and superimposed with (B) macroalgal and (C) live coral cover. The diameter of the bubble plot overlay indicates relative magnitude of cover.

BENTHIC COVER.—A two-dimensional configuration of samples from MDS ordination of square-root transformed data for benthic cover (i.e., live coral cover and macroalgae) revealed a strong pattern by urchin zone (Fig. 2A). A one-way ANOSIM test confirmed that these differences were significant (ANOSIM, Bray-Curtis similarity, square-root transformed, “global” $R = 0.568$, $P = 0.001$). Macroalgal cover alone (94.21%), explained group similarity within the *Echinometra* zone (Fig. 2B), whereas high coral cover (57.19%) drove group cohesion among *Diadema* samples (Fig. 2C; hereafter, SIMPER, square-root transformed, 90.00% cut-off). Overall, zone similarities were 87.48% and 56.59% respectively. Diametrically opposed distributions of algal and coral dominance lead to 50.46% dissimilarity among zones, with macroalgae (53.98%) explaining the bulk of the differences. This small-scale spatial correlation between urchin abundance and benthic cover indicates the possible influence of urchin grazing on the development of benthic communities, as *Diadema* zones were consistently characterized by higher coral cover ($19.8 \pm 4.65\%$; Fig. 3A) and *Echinometra* zones by higher macroalgal cover ($39.68 \pm 4.65\%$; Fig. 3B).

SMALL CORAL DISTRIBUTION.—Coral colonies (< 4.0 cm) represented seven species from four genera, of which only two, *Siderastrea radians* (Pallas, 1766) and *Favia fragum* (Esper, 1795) were large enough to be capable of sexual reproduction (Edmunds and Carpenter, 2001). The remaining juvenile taxa were *Siderastrea siderea* (Ellis and Solander, 1786), *Porites porites* (Pallas, 1766), *Porites astreoides* Lamarck, 1816 the hydrocoral *Millepora alcicornis* Linnaeus, 1758 and one unidentified spe-

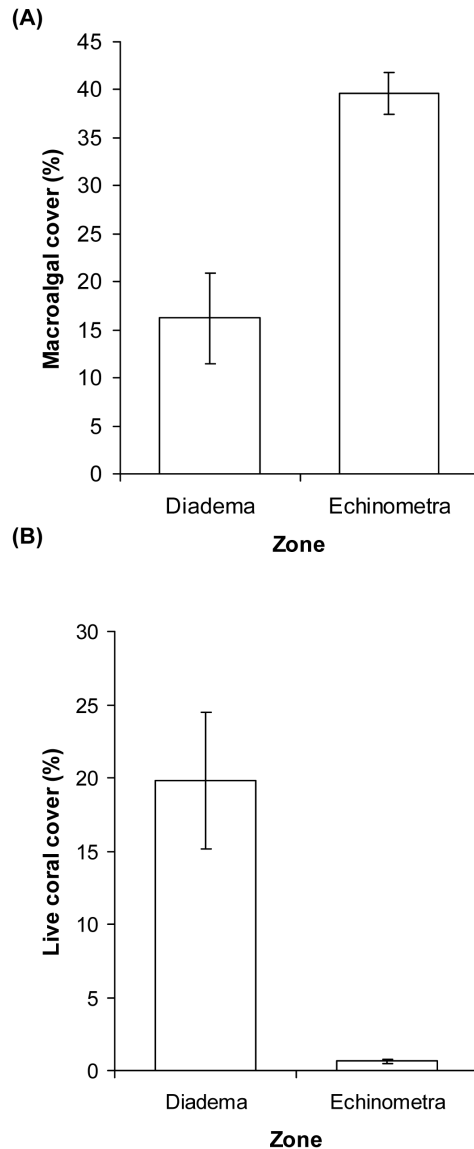


Figure 3. Mean percent cover and standard errors of (A) macroalgal and (B) live coral in zones dominated by *Diadema* and *Echinometra* (Bahia Honda, Florida Keys). All values were quantified with area calculating software.

cies of *Porites*. In total, 80 colonies (34 juvenile and 46 small colonies) were surveyed across the 5 transects and 50 quadrats.

MDS ordination of total colony abundance revealed two distinct clusters based on urchin zone (Fig. 4). These differences were significant in a one-way ANOSIM (Bray-Curtis similarity, square-root transformed, $R = 0.318$, $P = 0.001$) with 84.08% dissimilarity explained by the differential abundance of *F. fragum* (30.74%), *S. siderea* (26.45%), and *S. radians* (25.70%). Despite clear separation by urchin zone, variation among samples within zones produced low group similarities that ranged from a

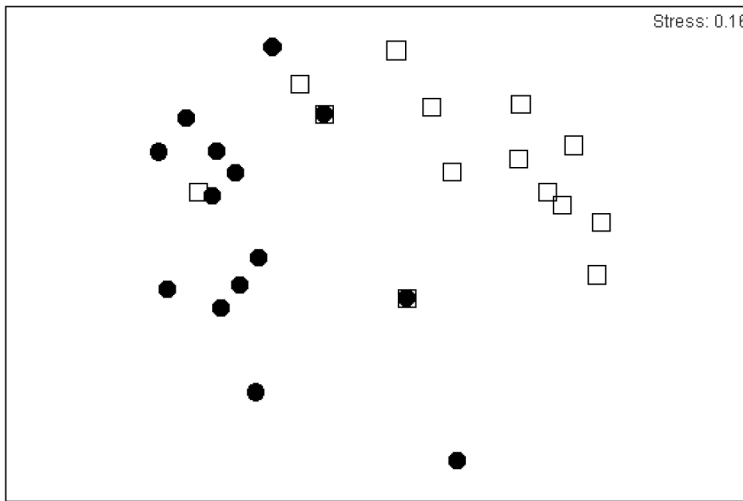


Figure 4. MDS of total coral colony abundance (“small” and “juvenile” taxa) in urchin-dominated zones at Bahia Honda, Florida Keys. Two-dimensional ordination was produced from square-root transformed, Bray-Curtis similarity matrices. Samples delineated by urchin zone with *Diadema* depicted as black circles and *Echinometra* as hollow squares.

29.11% (*E. lucunter*) to 28.57% (*Diadema*). Here, cohesion was driven by *S. siderea* (53.84%) for *Echinometra* patches and *F. fragum* (53.27%) for *Diadema* patches.

Separate ANOSIM analyses using “juvenile” ($R = 0.127$, $P = 0.018$) and “small” ($R = 0.278$, $P = 0.002$) species showed a slight divergence. Although total colony densities were greater in the *Diadema* zone, juvenile taxa tended to predominate in *Echinometra* patches (13.87 ± 3.49 ind m^{-2} compared to 5.6 ± 2.40 ind m^{-2} ; Fig. 5). Most corals within patches grazed by *Diadema* were small colonies, with a mean density of 26.40 ± 5.48 ind m^{-2} , while *Echinometra*-dominated patches supported only 6.93 ± 2.73 ind m^{-2} . Despite these clear differences in community composition, there were no distinctions in the mean colony sizes of juvenile corals: of the 34 measured individuals, a mean diameter of 1.05 ± 0.25 cm was found for *Diadema* and 1.50 ± 0.13 cm for *Echinometra* zones ($U = 59.5$, $P = 0.136$). When examined by species that occurred in both zones, the similarities were even more pronounced. The four co-occurring species (*S. radians*, *F. fragum*, *P. porites*, and *Porites* sp.) showed no difference in mean colony diameter based on urchin zone ($U = 1-76$; $P = 0.242-0.786$), although species-specific sizes varied from 0.87 ± 0.33 cm (*P. porites*) to 2.30 ± 0.29 cm (*S. radians*).

DISCUSSION

Past studies have demonstrated or inferred synergistic relationships between herbivorous fishes and echinoid grazing in the suppression of reef-associated seaweeds (Lewis, 1985; Carpenter, 1986, 1990b). However, following the Caribbean-wide loss of *D. antillarum* in the early 1980s and nearly two decades of localized extinction (Lessios, 1988), there have been surprisingly few reports documenting the niche expansions of any of several other echinoid grazers [isolated exceptions include *Triploneustes ventricosus* (Lamarck, 1816) (Moses and Bonem, 2001) and *Echinometra viridis* Agassiz, 1863 (R. Aronson, University of South Alabama, pers. comm.)]. This

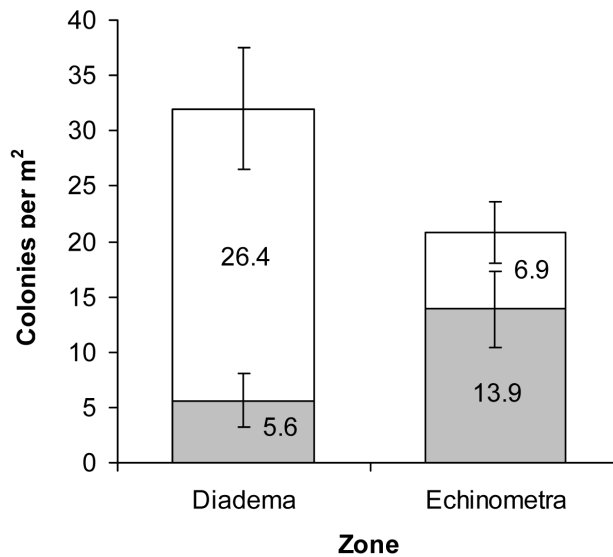


Figure 5. Mean densities and standard errors of juvenile (gray) and small (white) coral colonies (m^2) in zones dominated by *Diadema* and *Echinometra* (Bahia Honda, Florida Keys).

absence of functional redundancy was supported by our results, as markedly different benthic assemblages developed in the presence of the two urchin species.

Within the *Diadema* zone, *D. antillarum* densities approached those of pre die-off levels (Kier and Grant, 1966; Bauer, 1980; Chiappone et al., 2002) and were associated with low macroalgal cover and elevated coral cover. These findings are consistent with those of numerous field manipulations (Ogden et al., 1973; Sammarco, 1982; Nedimyer and Moe, 2003) and correlative work (de Ruyter van Steveninck and Bak, 1986; Liddell and Ohlhorst, 1986; Carpenter, 1990a; Myhre and Acevedo-Gutiérrez, 2007), suggesting that *D. antillarum* grazing is integral to the maintenance of low-biomass high-turnover algal turfs and prostrate coralline algal crusts that characterize healthy reef systems.

Conversely, and despite orders of magnitude greater abundance, *E. lucunter* was associated with chemically and morphologically defended macroalgal forms (i.e., *Halimeda* sp. and *Dictyota* sp.) and a benthos dominated by algal canopies with virtually no live coral cover. This suggests that on shallow consolidated substrates in the lower Florida Keys, *D. antillarum* is the strongest interactor (sensu Paine, 1992) in a diverse guild of invertebrate grazers.

A much less investigated effect of differential grazing by *D. antillarum* and *E. lucunter* has been on the recruitment and post-settlement survival of juvenile corals. Here, we demonstrated that although dense algal canopies and high numbers of *E. lucunter* are not altogether restrictive to coral settlement and short-term survival, they may impose levels of lethal and sublethal stress (e.g., shading, overgrowth, physical abrasion, and incidental ingestion) that through slow attrition can prevent reef development (River and Edmunds, 2001). This was evidenced by substantially higher densities of juvenile taxa in the algal dominated *Echinometra* patches despite the paucity of larger coral colonies. Interestingly, the abundances of juveniles were greater than in nearby *Diadema* patches, suggesting that either overgrazing led to spat mortality (Sammarco, 1980) or that larval retention was simply greater in the

structurally more complex and less physically-disturbed algal matrix. Regardless, our findings are consistent with those of Edmunds and Carpenter (2001) and Carpenter and Edmunds (2006), as total colony abundances were greater in *Diadema* zones, although we failed to observe the agariciid recruitment that drove their inter-zone trends.

Reconstructions based on the inferred ages of the interacting species (i.e., *D. antillarum* and juvenile coral taxa) support a functional relationship between *D. antillarum* grazing and coral spat survival and reef development. Under the assumption of resource-replete *D. antillarum*, and using the published growth rates of Ogden and Carpenter (1987), we estimated the ages of individuals with an average test diameter of 68 mm to have been roughly 2 yrs old. For juvenile corals, the relationship between colony diameter and age is not strong (see Van Moorsel, 1988; Edmunds and Carpenter, 2001); however, using the conservative growth rate of 12 mm yr⁻¹ we estimated the mean ages of juvenile taxa present in both urchin zones to have been approximately 1–1.5 yrs. This suggests that the benthic conditions (i.e., grazing pressure and algal cover) at the time of coral settlement were likely to have been similar to those currently observed, with low algal cover and higher rates of disturbance predominating in *Diadema* zones. Therefore, the impacts of echinoid grazing on benthic community development and coral recruitment success appear to have been based on urchin identity and are consistent with their inferred histories.

It has been proposed that a return of *Diadema* could precipitate a reversal in algal/coral dominance (Edmunds and Carpenter, 2001; Carpenter and Edmunds, 2006), and while this is consistent with our findings, the comparative lack of diversity in coral recruitment suggests that, at our study site, settlement of larvae may limit recovery over short time-scales. As source populations in the region continue to suffer substantial losses due to coral disease and bleaching events (Aronson et al., 2002), their regeneration may not only be limited by slow growth rates, but also by frequent recruitment failures (Aronson and Precht, 2006). Therefore, for *D. antillarum* to positively affect the long-term viability of reef ecosystems, relatively high densities must be maintained for longer periods than have been currently observed along the Florida reef tract. However, should their numbers persist long enough to encompass the infrequent recruitment of reef-building corals, a reversal of nearly two decades of algal growth and a return to scleractinian dominance could be expected to follow *D. antillarum* as its population expands.

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