

## INCREASED ALGAL DOMINANCE DESPITE PRESENCE OF *DIADEMA ANTILLARUM* POPULATIONS ON A CARIBBEAN CORAL REEF

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### ABSTRACT

Populations of *Diadema antillarum* (Philippi, 1845) have been slow to recover after their 1983 Caribbean-wide massive mortality. The continued absence of this important coral reef herbivore as well as further impacts on local and regional-scales have severely threatened the health of coral reefs. From 2008 to 2011, the population of *D. antillarum* and structure of the benthic community were monitored within Akumal Bay, Mexico, a heavily impacted ecosystem. Across the 4 yrs of the study, densities of adult *D. antillarum* did not significantly change and were highest on backreef sites (mean 1.30 and 1.44 m<sup>-2</sup>). Coral cover was low at all sites (maximum 14%) and decreased during the 4 yrs of the study. Changes in crustose coralline algae (CCA) cover varied by year but was significantly higher on forereef sites, while cover by turf-algal-sediment (TAS) increased at all four sites. *Diadema antillarum* densities correlated positively with coral and CCA cover in the backreef sites where sea urchin densities were higher but no correlation occurred with TAS and turf. Where *Echinometra lucunter* (Linnaeus, 1758) sea urchins were more prevalent, their densities correlated negatively with coral and positively with CCA. Although densities of adult *D. antillarum* were comparable to other regions of the Caribbean, increases in TAS over the 4 yrs of this study may be evidence that even an important herbivore cannot prevent continued decline of a reef in an impacted ecosystem.

Coral reefs in the Caribbean have experienced major disturbances over the past few decades and continue to be under a combination of stressors including bleaching, overexploitation of herbivores, coral diseases, and declining water quality, which has resulted in an increase in macroalgae cover (Knowlton 1992, Aronson and Precht 2001, Hughes et al. 2003, Bellwood et al. 2004). The importance of long-spined sea urchin, *Diadema antillarum* (Philippi, 1845), in removing macroalgae cover became evident after their massive mortality in 1983, when algal biomass abruptly increased (de Ruyter van Steveninck and Bak 1986, Carpenter 1988, Hughes 1994). As the populations of *D. antillarum* recover after their 1983 Caribbean-wide massive mortality (Lessios et al. 1984b, Lessios 2005), it remains unclear if grazing by this herbivore provides a suitable driver from which to expect a decrease in macroalgal cover on impacted coral reefs. Modeled scenarios indicate that sea urchins impart significant resilience to Caribbean reefs such that continued decline is inevitable when sea urchins are scarce (Mumby et al. 2006). However, abundant literature indicates it is a combination of factors which impacts the benthic dynamics on coral reefs and the propensity for shifts between dominant states [e.g., competition for space (Sandin and McNamara 2012), herbivore diversity (Cheal et al. 2010), biotic histories (Aronson et al. 2004), global climate change and marine diseases (Aronson and Precht 2006)].

Nearly 30 yrs after the mortality event, the *D. antillarum* population recovery dynamics along with concomitant changes in benthic cover have been reported for many sites within the Caribbean basin (summarized in Ruiz-Ramos et al. 2011). Adult *D. antillarum* densities currently reported within the Caribbean (e.g., Jamaica) remain lower than previously recorded densities but are beginning to slowly increase (Carpenter 1988, 2005, Carpenter and Edmunds 2006). The lack of a robust population recovery is attributed to three main causes. First, the loss of cover by corals has decreased habitat complexity necessary for successful recolonization and survival by the echinoids (Lee 2006). Second, *D. antillarum* recovery is constrained through Allee effects since reproduction of sea urchins is density-dependent and requires proximity to conspecifics for successful external fertilization (Levitan 1991). While larvae may recruit into the system (Eckert 1998), settlement typically requires a cue from high adult densities. Lastly, recovery may also be affected through the presence of other populations of echinoids or urchin predators (Lessios 1995). Research suggests an escape size exists where large echinoids are less susceptible to predation, but there are multiple factors which can reduce the probability of successful survival to that size (Hereu et al. 2005, Clemente et al. 2007), including direct predation on sea urchin larvae and subadults. Adult urchin predators [e.g., triggerfish (Randall et al. 1964)] are highly prized commercial species whose densities have declined dramatically throughout the Caribbean. In systems heavily impacted by fishing, predation on adult *D. antillarum* is lower and sea urchin densities subsequently increase (Clemente et al. 2010), which may serve to increase the potential for recovery of these echinoids.

As sea urchin populations slowly recover, it is necessary to reassess their importance and role in driving the relative dominance of macroalgal benthic cover on coral reefs. For ecological studies of macroalgal cover, various strategies have been developed by which to categorize groups of macroalgae based upon their form and function in reference to the experimental questions being posed (Littler and Littler 1980, Steneck and Dethier 1994, Steneck 1997). Form functional groups as developed under the relative dominance model include coral, crustose coralline algae (CCA), and turf algae, and are based upon the relative disturbance (e.g., herbivory) and productivity (e.g., nutrients) experienced on a reef (Littler and Littler 1984). CCA are the "cementers" of the reef and produce an encrusting, calcifying skeleton which can cue coral settlement (Morse et al. 1988). Turf algae are attached to the substratum with rhizoids and have upright microfilamentous branches <2 cm tall. Because many species of macroalgae are phenotypically plastic, the turf functional group may include species that are considered frondose macroalgae during other portions of their life cycle (Hay 1981). Turf can be further divided into turf-algal-sediment (TAS) with identification as such determined by the presence of sediments bound within the turf mat (Airoldi and Virgilio 1998). TAS communities are strong competitors for space on the reef (McCook et al. 2001), and it has been suggested that TAS may also suppress herbivory, at least for alternative herbivores such as fishes (Bellwood and Fulton 2008) due to the presence of sediment bound within the turf.

In sites where *D. antillarum* populations are recovering, cover of turf and TAS algae are expected to decrease and cover by CCA and coral to increase (Littler and Littler 1984, Edmunds and Carpenter 2001, Carpenter and Edmunds 2006, Jordan-Garza et al. 2008). Where TAS and turf cover has decreased, coral cover is often higher. For systems with high nutrient levels and high benthic grazing rates, a

benthos dominated by CCA is to be expected, as CCA is adapted to resist grazing pressures (Steneck 1983). The echionid-benthos relationship would be reflected in a positive correlation of *D. antillarum* with coral and CCA and a negative relationship with TAS and turf. Studies tracking the relationship between these different benthic covers in relatively nutrient replete sites over longer time scales are lacking but can provide interesting insight into this dynamic.

The goals of the present study were to determine: (1) whether the population of *D. antillarum* on a reef with high nutrient availability was recovering and producing larvae, and if they were susceptible to predation by any sea urchin predator; (2) if significant correlations occurred between sea urchin densities and coral reef benthic communities; (3) whether cover by these benthic communities changed with time; and (4) the role of any other fish herbivores, if any, within the study system on these same benthic covers. We hypothesized that while *D. antillarum* populations may be recovering at this nutrient-replete study site and driving shifts towards increased CCA cover, turf and TAS biomass removal by the herbivore population in such a resource-rich environment will fail to control or decrease cover by these algal functional groups.

## MATERIALS AND METHODS

**STUDY SITE.**—The coast of Quintana Roo, Mexico, on the Yucatán Peninsula consists of multiple bays and lagoons along the periphery of the Meso-American barrier reef, the second largest coral reef system in the world. The area is experiencing a dramatic increase in tourism pressure as development projects increase land use (Murray 2007). Stream flow of pollutants directly into the water is uncommon because of the highly porous, karstic geology characteristic of this region. Instead, terrestrially-derived nutrients enter the coastal zone via submarine groundwater discharge and influence coastal coral, seagrass, and macroalgae ecosystems. The nitrogen and phosphorus concentrations and isotopic ratios of macrophytes indicate the land-based sources of nutrients (Carruthers et al. 2005, Mutchler et al. 2007) and coral diseases have become increasingly common from eutrophication of coastal waters (Harvell et al. 2007). Studies of nitrogen isotopic content of gorgonians from Akumal established significant enrichment when compared to other sites along the Meso-American reef (Baker et al. 2007).

Akumal Bay reef is located approximately 300 m from shore and is characterized by a semi-enclosed lagoon sloping toward the 3–4 m deep backreef, a shallow northern and southern reef crest, and a 3–4 m deep forereef (Fig. 1). The reef has low coral cover (13.8%; E Jordán-Dahlgren, Universidad Autónoma de México, unpubl) with 50% loss of coral cover over the last 20 yrs (Harvell et al. 2007) and high fishing pressure (Garcia-Salgado et al. 2008). For the present study, Akumal's barrier reef was divided into the northern and southern portions, separated by approximately 400 m of patchy rather than continuous reef structure, with backreef and forereef areas for a total of four sites (Fig. 1). In 1998, these reefs suffered massive El Niño bleaching and outbreaks of disease, after which coral cover dramatically declined (Steneck and Lang 2003). The North Forereef (NF) is characterized by dead stands of *Acropora palmata* (Lamarck, 1816) and occasional live *Porites asteroides* (Lamarck, 1816) and *Montastraea* sp. colonies, while the South Forereef (SF) is predominantly dead stands of *A. palmata*. Both NF and SF are exposed to more wave action than the back reef areas, as is typical of barrier reefs. The North Backreef (NB) and South Backreef (SB) sites are characterized by live *Agaricia tenuifolia* (Dana, 1848), *Montastraea* sp., and occasional *P. asteroides* colonies. Backreef sites are intermixed with octocorals, *Gorgonia ventalina* (Linnaeus, 1848) (NB and SB) and *Plexaurella nutans* (Duchassaing, 1860) (NB). Recently, the SB and SF sites have been increasingly colonized by the zooxanthid, *Palythoa caribaeorum* (Duchassaing and

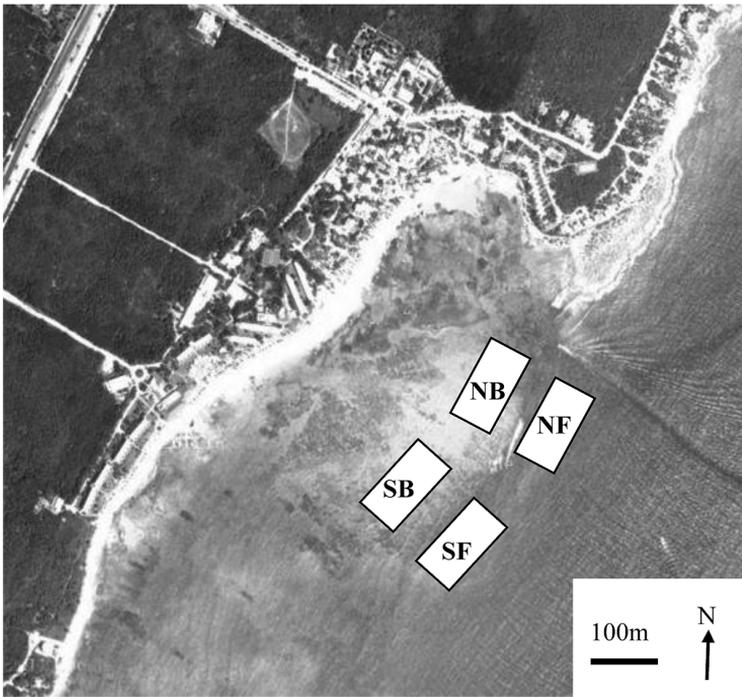


Figure 1. Map of Akumal Bay, Quintana Roo, Mexico ( $20^{\circ}23'45''\text{N}$ ,  $87^{\circ}18'52''\text{W}$ ). Study sites indicated by boxes (SF = South Forereef, NF = North Forereef, SB = South Backreef, NB = North Backreef).

Michelottie, 1861). The NB and NF sites are adjacent to the navigation channel, where water exchange from inside the bay occurs.

**SAMPLING METHODOLOGY.**—At each site in July from 2008 to 2011, 30-m long transects were sampled parallel to the reef crest ( $n = 6\text{--}10$ ) and 10  $1\text{-m}^2$  quadrats were placed randomly along each transect to quantify percent benthic cover and adult *D. antillarum* density. Depths among all sites ranged 2–3 m. Benthic cover was classified as: turf (mix of filamentous algae <2 cm high), turf-algal-sediment (TAS) matrix, crustose coralline algae (CCA), macroalgae, live coral, open substrate (e.g., dead coral, bare rock), and sand. As habitat structural complexity can be a driver of *D. antillarum* distribution (Lee 2006), rugosity measurements were made every 5 m using the Atlantic and Gulf Rapid Reef Assessment (AGGRA) line intercept transect methodology ([www.aggra.org](http://www.aggra.org)). The difference between the highest and lowest relief portions of the reef within a 1-m sweep of the 5-m interval were recorded, providing a spatial index of the reef and a ratio of reef surface contour distance. Within the same  $1\text{-m}^2$  quadrat where percent cover was recorded, density of *D. antillarum* with test diameter >4 cm was determined. These surveys were completed during the daylight relying on the assumption that daytime locations were an adequate representation of individual sea urchin foraging areas (Carpenter 1986).

*Diadema antillarum* larval recruitment into the system was measured using the methods described in Miller et al. (2009), modified from (Bak 1985). In total, 25 plates were deployed, five per buoyed line, along the backreef (North and South), where larval retention is highest (Hernandez et al. 2008) and at a distance 0.5–2 m above the substrate. Following results from *D. antillarum* recruitment studies conducted in Puerto Rico (Miller et al. 2009, Williams et al. 2010), settlement plates were moved to the North Backreef site during the winter after

rugosity was found to be significantly higher than both forereef sites (Table 1). The plates were visually surveyed in situ for recruits monthly in April and May 2010, biweekly in June and July 2010, and biweekly in January and February 2011, seasonal periods when sea urchin settlers have been reported in other parts of the Caribbean (Miller et al. 2009, Williams et al. 2010). After each visual survey, the larval settlement plates were replaced with clean plates to avoid settlement-inhibition by fouling. Retrieved larval plates were placed in plastic bags and transported to the laboratory where they were further examined under magnification to count any settled larvae that may have been missed during the in situ surveys.

In 2011, each of the four sites was surveyed using a modified AGGRA method ([www.aggra.org](http://www.aggra.org)) to identify and quantify all fishes present. Six 25-m long  $\times$  2-m wide belt transects were completed in each of the study sites where data on fish length, density, and identity were quantified. Following the survey, fishes were placed in groups based on whether they were considered to be an herbivore or sea urchin predator (e.g., triggerfishes, hogfishes, grunts, snappers). After determining that the majority of fishes surveyed could be placed in three main herbivore groups (parrotfishes, damselfishes, and surgeonfishes) and insufficient predators precluded forming a predator group, mean counts in the three herbivore groups were normalized to a density of 100-m<sup>2</sup> census area per size class [0–5, 6–10, 11–20, 21–30 total length (TL) cm]. Mean lengths per each size class (e.g., 2.5 cm for size class 0–5 cm) were converted to estimated biomass using length-weight relationships (Bohnsack and Harper 1988, Paddock et al. 2006). After the first year of the study, when it was determined that there was a small, rock-boring echinoid *Echinometra lucunter* (Linnaeus, 1758) at the sites, density measurements of these sea urchins were made in the same quadrat and with the same methodology as was used for *D. antillarum*.

**STATISTICAL ANALYSIS.**—To test for significant differences in *D. antillarum* and *E. lucunter* densities and benthic covers between the four sites each year, one-way Kruskal-Wallis tests were performed in SPSS (PASW). Mann-Whitney U tests were used for post-hoc pairwise comparisons between sites with Bonferroni corrections for experiment-wide Type I error rates. To test for significant differences in *D. antillarum* densities and benthic covers at each site over the 4 yrs of the survey, one-way Kruskal-Wallis tests were performed in SPSS (PASW). Mann-Whitney U tests were used for post-hoc pairwise comparisons between years with Bonferroni corrections for experiment-wide Type I error rates. Spearman  $\rho$  correlations were calculated to determine the relationship between the areas of high density *D. antillarum* (SB and NB) and *E. lucunter* (SF and NF) with the benthic cover categories (TAS, turf, CCA, coral). Because sea urchin populations did not significantly change at any of the sites for the 4 yrs of the study, data were not segregated by year but were pooled for a single correlation. Quadrat-level comparisons were utilized rather than transect or site averages as the *D. antillarum* exhibited aggregative behavior on the meter-scale, as found in other studies (Macia et al. 2007). ANOVA was used to test for significant differences among sites in total fish density and biomass (both determined to be homoscedastic prior to analysis).

## RESULTS

**DIADEMA ANTILLARUM DENSITY.**—Akumal Bay reef sites were characterized by isolated, high-density aggregations of *D. antillarum* with maximum 16 adults m<sup>-2</sup> in plots containing sea urchins, but 77% of surveyed quadrats had no sea urchins (Table 1). Across all sites there was no significant difference in sea urchin density through time (Table 2), while a significant difference in density occurred each year across sites (Fig. 2). NF and SF sites had significantly lower sea urchin densities (mean: 0.24, 0.20 sea urchins m<sup>-2</sup>, respectively) than NB and SB (mean: 1.07, 1.31 sea urchins m<sup>-2</sup>, respectively; Fig. 2). An average of 85% of quadrats in the forereef sites had no *D. antillarum* and, when present, their mean abundance was 1.52 sea urchins m<sup>-2</sup>. An

Table 1. Maximum density of *Diadema antillarum* per m<sup>2</sup>, frequency of plots without *Diadema antillarum*, and rugosity index by site at four sites on a Caribbean coral reef.

Site	Metric	Year			
		2008	2009	2010	2011
South Foreereef	Max density (per m <sup>2</sup> )	4	4	1	1
	Frequency of plots without <i>D. antillarum</i>	74%	84%	98%	92%
	Rugosity	Index: 60 (SE 4)			
North Foreereef	Max density (per m <sup>2</sup> )	3	5	0	1
	Frequency of plots without <i>D. antillarum</i>	72%	66%	100%	95%
	Rugosity	Index: 61 (SE 4)			
South Backreef	Max density (per m <sup>2</sup> )	7	8	8	9
	Frequency of plots without <i>D. antillarum</i>	87%	63%	58%	73%
	Rugosity	Index: 82 (SE 5)			
North Backreef	Max density (per m <sup>2</sup> )	16	11	12	8
	Frequency of plots without <i>D. antillarum</i>	67%	68%	64%	67%
	Rugosity	Index: 111 (SE 11)			

average 68% of quadrats in the backreef sites had no *D. antillarum* and, when present, their mean abundance was 3.53 sea urchins m<sup>-2</sup>.

**BENTHIC HABITAT AND CORRELATIONS WITH *DIADEMA ANTILLARUM* DENSITY.**— Across all sites the dominant benthic cover was TAS, which over time significantly increased while coral and turf cover significantly decreased, regardless of *D. antillarum* presence. Positive correlations of *D. antillarum* with CCA cover occurred in the backreef, while CCA cover increased significantly at SF, despite lower densities of *D. antillarum*.

Coral cover decreased significantly over time across all sites (Table 2) with the largest reduction occurring at the SB and NB sites, where cover decreased 8% and 13%, respectively (Fig. 3A). Coral cover differed significantly among all sites in 2008 ( $\chi^2 = 5.093$ ,  $P = 0.024$ ) and 2009 ( $\chi^2 = 5.217$ ,  $P = 0.022$ ), when backreef sites had significantly higher cover than foreereef sites. By 2011, all sites were not significantly different from each other ( $\chi^2 = 1.026$ ,  $P = 0.311$ ) and mean coral cover was 2% (SE 0.3). At these backreef sites where *D. antillarum* densities were highest, there were positive correlations of *D. antillarum* with coral and CCA cover (Table 3). Significant differences in CCA cover occurred among sites in time ( $\chi^2 \geq 3.760$ ,  $P \leq 0.042$ ), which was caused by the 2–6 times more CCA cover on foreereef sites compared to backreef sites in 2010 and 2011. By 2011, at the foreereef sites, >20% of the benthos was covered by CCA and SF CCA cover more than doubled (11%–26%) over the period 2008–2011 (Table 2, Fig. 3B). *Diadema antillarum* densities were positively correlated with CCA cover on the backreef sites (Table 3). By 2011, TAS cover became the dominant benthic cover at all four sites, having increased significantly over the course of the study (Table 2, Fig. 3C). Backreef sites had significantly less TAS than foreereef sites ( $\chi^2 \geq 14.486$ ,  $P < 0.001$ ; Fig. 3C) yet correlations between *D. antillarum* density and TAS were not significant (Table 3). Across all sites, there was a significant effect of time on turf cover as sites NB, SF, and NF experienced a significant decrease in turf while turf cover at SB did not vary significantly over time (Table 2, Fig. 3D).

Table 2. Results of Chi-square comparison of *Diadema antillarum* density, and percent cover of coral, crustose coralline algae (CCA), turf-algal-sediment (TAS), and turf. Values of the Kruskal-Wallis Chi-square ( $\chi^2$ ) test statistic and *P*-values across all years for each site (df 3; independent variable: year). Years not significantly different indicated with a “-” between years (2008 = 1, 2009 = 2, 2010 = 3; 2011 = 4).

Site	<i>Diadema antillarum</i>			Coral			CCA			TAS			Turf		
	$\chi^2$	<i>P</i> -value	Significance	$\chi^2$	<i>P</i> -value	Significance	$\chi^2$	<i>P</i> -value	Significance	$\chi^2$	<i>P</i> -value	Significance	$\chi^2$	<i>P</i> -value	Significance
South Foreereef	22.31	<0.001	1-2-3-4	80.22	<0.001	2-3-4	46.78	<0.001	1-2 2-3 3-4	121.09	<0.001	2-3-4	276.22	<0.001	2-3-4
	34.97	<0.001	1-2-4 2-3	28.05	0.011	2-3-4	11.18	0.011	1-2 1-3-4	148.43	<0.001	1-2 3-4	193.68	<0.001	3-4
South Backreef	20.36	<0.001	1-4 2-3-4	60.62	<0.001	1-2-3	33.99	<0.001	1-2 2-3 3-4	54.09	<0.001	1-2-3	10.51	0.015	1-3 3-4
	21.66	<0.001	1-2-3-4	21.66	0.186	2-3	4.81	0.186	1-2 2-3-4	8.45	0.038	1-2-3 3-4	42.06	<0.001	1-2 2-3 3-4

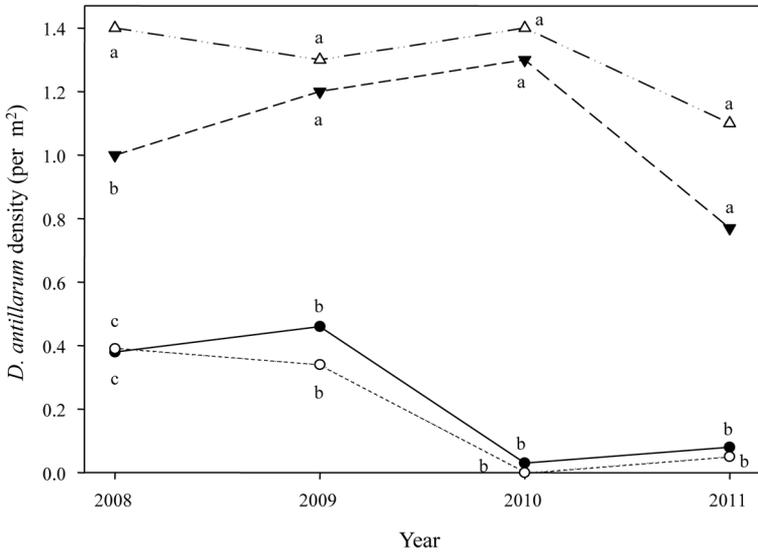


Figure 2. Density of adult *Diadema antillarum* (letters indicate significant differences in the same year between sites). Solid circle = South Foreereef, open circle = North Foreereef, solid triangle = South Backreef, open triangle = North Backreef.

**DIADEMA ANTILLARUM LARVAL RECRUITMENT.**—No *D. antillarum* larval recruits were found on the settlement plates during summer during both in situ or magnified examinations in the laboratory. There were also no *E. lucunter* larvae found on settlement plates over the course of the study. After relocation of the plates within the backreef based on more recent literature recommendations, settlement plates still did not yield any recruits.

**OTHER FAUNAL DENSITIES AND CORRELATIONS.**—Population densities of *E. lucunter* did not change with time ( $\chi^2 \geq 3.846$ ,  $P \geq 0.061$ ), but each year NF and SF sites (7.5 sea urchins m<sup>-2</sup>) had significantly more *E. lucunter* than NB and SB sites (0.4 m<sup>-2</sup>;  $\chi^2 \geq 13.331$ ,  $P < 0.001$ ; Fig. 4). Densities of *E. lucunter* populations on the SF and NF were negatively correlated with coral and turf cover, and positively correlated with CCA (Table 3). *Diadema antillarum* predators were scarce throughout the duration of the study and there was no significant variation among sites for the three fish herbivore taxa: damselfishes, surgeonfishes, and parrotfishes (ANOVA:  $P = 0.873, 0.799, 0.521$ , respectively; Table 4). Throughout the entire reef, no lobsters and no more than three triggerfish were seen over the 4 yrs of the study. No triggerfish were recorded during the 2011 surveys and other potential sea urchin predators (e.g., grunts, snappers, and hogfishes) were absent or occurred at densities  $< 1$  100 m<sup>-2</sup> at all sites. Fish herbivores such as blue tang, *Acanthurus coeruleus* (Bloch and Schneider, 1801), doctorfish, *Acanthurus chirurgus* (Bloch, 1787), and dusky damselfish, *Stegastes adustus* (Troschel, 1865), were present at densities averaging 19.5 100 m<sup>-2</sup> across all four sites and the majority were  $< 10$  cm TL with mean biomass of 14.2 g m<sup>-2</sup> (Table 4). Princess parrotfish, *Scarus taeniopterus* (Desmarest, 1831), stoplight parrotfish, *Sparisoma viride* (Bonnaterre, 1788), striped parrotfish, *Scarus iserti* (Bloch, 1789), and yellowtail parrotfish, *Sparisoma rubripinne* (Valenciennes, 1840), across all four sites were present at lower densities (13.9 100 m<sup>-2</sup>) with 14%  $> 20$  cm in TL and a mean biomass of 9.7 g m<sup>-2</sup> (for all parrotfishes).

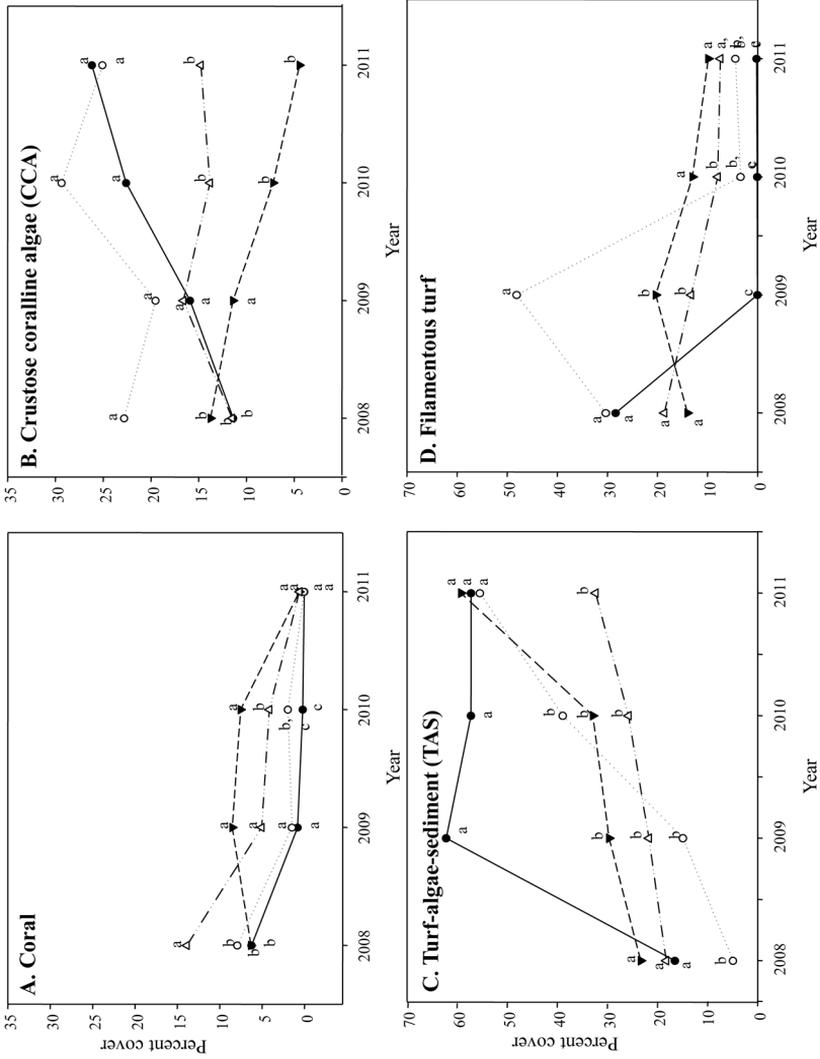


Figure 3. Percent cover of (A) coral, (B) crustose coralline algae, (C) turf-algae-sediment, and (D) filamentous turf for each of the four sites over 4 yrs (letters indicate significant differences in the same year among sites). Note the difference in y-axis scales between A–B and C–D. Solid circle = South Foreereef, open circle = North Foreereef, solid triangle = South Backreef, open triangle = North Backreef.

Table 3. Spearman  $\rho$  correlations between *Diadema antillarum* densities on the North and South Backreef sites and for benthic cover categories [coral, crustose coralline algae (CCA), turf-algal-sediment (TAS), and turf] and *Echinometra lucunter* densities on the North and South Forereef sites for the same benthic cover categories (*ns* = no significant correlation).

Species		Coral	CCA	TAS	Turf
<i>Diadema antillarum</i>	Spearman $\rho$	0.322	0.484	<i>ns</i>	<i>ns</i>
	<i>P</i> -value	< 0.001	< 0.001	<i>ns</i>	<i>ns</i>
<i>Echinometra lucunter</i>	Spearman $\rho$	-0.116	0.247	<i>ns</i>	-0.200
	<i>P</i> -value	0.011	< 0.001	<i>ns</i>	< 0.001

## DISCUSSION

Population densities of *D. antillarum* in Akumal Bay, Mexico, at the beginning of the present study were low but comparable to current densities found at other sites within the Caribbean. Expected correlations (positive relationships between *D. antillarum* and CCA and coral cover) were found at backreef sites where *D. antillarum* densities were highest although coral cover decreased significantly over time at all sites. Despite the presence of sea urchins, temporal trends indicate a significant increase in the TAS dominated state at all sites. Herbivore populations of both sea urchins and fishes remained low throughout the study and the prevalence of this epilithic TAS cover within the bay may deter feeding by these herbivores and prevent adequate control of algal biomass on the reefs of Akumal Bay.

**DIADEMA ANTILLARUM ABUNDANCE.**—*Diadema antillarum* populations in Akumal Bay did not significantly increase from 2008 to 2011, which is consistent with results reported from elsewhere (Panama: Lessios 2005, Florida Keys: Chiappone et

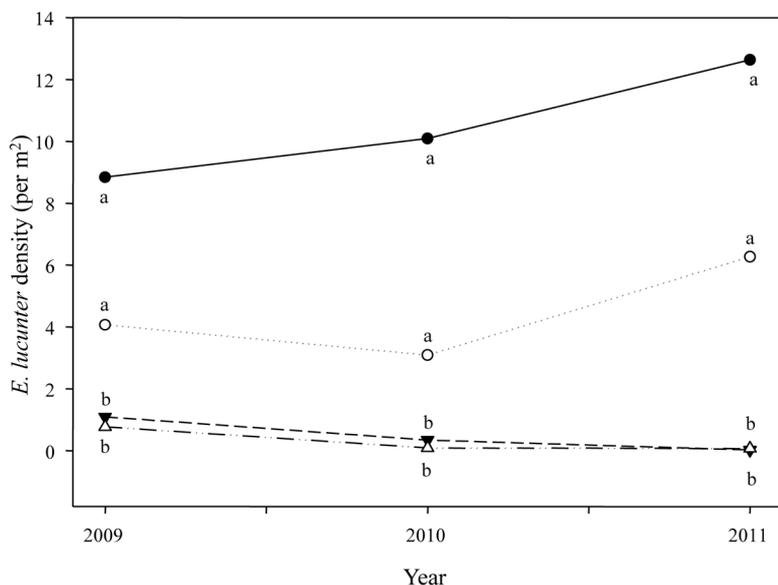


Figure 4. Density of *Echinometra lucunter* (letters indicate significant difference in the same year between sites). Solid circle = South Forereef, open circle = North Forereef, solid triangle = South Backreef, open triangle = North Backreef.

Table 4. Herbivorous fish densities [per 100 m<sup>2</sup> (SE)] overall and by size category (total length), and overall biomass (g m<sup>-2</sup>) at all four sites in Akumal Bay, Mexico, in 2011.

Fish	Site	0–5 cm	6–10 cm	11–20 cm	21–30 cm	Overall density	Overall biomass
Damsel <span>fishes</span>	South Forereef	3.0 (0.5)	5.4 (0.6)	7.4 (0.4)	0.0 (0.0)	15.8	11.8
	North Forereef	0.4 (0.2)	5.0 (0.5)	9.4 (0.8)	0.0 (0.0)	14.8	13.6
	South Backreef	3.0 (0.5)	4.0 (0.5)	9.4 (0.4)	0.0 (0.0)	16.4	13.5
	North Backreef	0.4 (0.2)	5.0 (0.5)	8.6 (0.7)	0.0 (0.0)	14.0	12.9
Surgeon <span>fishes</span>	South Forereef	3.0 (0.3)	10.0 (0.7)	10.6 (1.1)	0.0 (0.0)	23.6	15.7
	North Forereef	3.0 (0.3)	12.4 (0.9)	9.4 (0.6)	0.0 (0.0)	24.8	14.9
	South Backreef	3.0 (0.3)	9.0 (0.7)	10.0 (0.8)	0.0 (0.0)	22.0	14.9
	North Backreef	3.0 (0.3)	10.4 (0.5)	11.4 (0.8)	0.0 (0.0)	24.8	16.5
Parrot <span>fishes</span>	South Forereef	0.0 (0.0)	6.4 (1.1)	4.6 (0.6)	1.6 (0.4)	12.6	8.1
	North Forereef	0.0 (0.0)	5.0 (1.2)	7.6 (0.6)	3.0 (0.6)	15.6	10.5
	South Backreef	0.0 (0.0)	4.4 (1.0)	6.0 (0.6)	2.4 (0.4)	12.8	9.1
	North Backreef	0.0 (0.0)	4.6 (0.8)	8.2(0.7)	1.6 (0.4)	14.4	10.9

al. 2002). Although historic sea urchin density data are not available for Akumal Bay, the highest average densities recorded during this survey (1.44 m<sup>-2</sup> NB 2008) are within range of those currently reported for many other areas within the Caribbean region, where *D. antillarum* populations have not yet recovered (Ruiz-Ramos 2011). Significantly higher populations of *D. antillarum* at NB may be associated with significantly higher rugosity at this site. Previous research has shown that *D. antillarum* use physical structures as refuge (Ogden 1976, Levitan and Genovese 1989). In field manipulations, alterations in structural complexity significantly reduced macroalgal cover and increased *D. antillarum* densities (Lee 2006). Habitat-complexity therefore facilitates the removal of macroalgae and has important consequences for both the recovery of this important herbivore and the efficacy at which macroalgal cover is reduced. The lower topographic complexity of some of our sites may act as a positive feedback to the resilience of the algal dominated state at these sites.

Successful sexual reproduction is required if local populations of sea urchins are to increase in the absence of immigration. Maximum densities of adult *D. antillarum* (16 sea urchins m<sup>-2</sup>) were more than twice mean densities reported for another Meso-American Reef site in Mahahual Bay (7 sea urchins m<sup>-2</sup>; Jordan-Garza et al. 2008), yet in Akumal there was an absence of *D. antillarum* larvae on settlement plates. Even if a proportion of larvae produced in Akumal Bay is lost due to planktonic predators or other factors, it is reasonable to expect that some local larvae would settle on the substrate made available on the settlement plates. In addition, larvae from successfully reproducing upstream adults could also arrive during the 3–5 wk planktonic stage (Eckert 1998). The lack of urchin settlement in Akumal Bay may be due to fewer reproducing adults in Akumal Bay as well as at upstream locations resulting in inadequate larval supply. As quantified in other studies, sperm limitation often leads to extremely low larval production and associated Allee effects [reviewed in Levitan (1995)], which would lead to an absence of settlers. Deployment of larval settlement plates was similar to other studies that detected available larvae (e.g., Puerto Rico and the Florida Keys; Miller et al. 2009), but the scale of our study may have impacted results. Additional studies into the demographics of *D. antillarum* in this area may yield important information on the mechanisms preventing successful

larval production and retention into the system as well as inferences for other impacted systems within the Caribbean.

Another factor contributing to reduced recruitment is the existence on the fore-reef sites of a population of *E. lucunter* sea urchins, which may aggressively attack *D. antillarum* as a burrow defense strategy (Grunbaum et al. 1978), increasing juvenile mortality and preventing successful *D. antillarum* larvae recruitment on the fore-reef. *Echinometra lucunter* densities are significantly higher on the fore-reef than on the backreef as they prefer microhabitats with greater exposure to wave action and currents (McGehee 1992), thus limiting habitat overlap with *D. antillarum*. Perhaps because of this, studies on the competitive outcomes of *D. antillarum* as an intruder as well as defender with *E. lucunter* are limited (Shulman 1990). Despite the perceived minimal interactions between these two echinoids, Akumal Bay *E. lucunter* populations on the fore-reef are on average higher than those found on other Caribbean reefs ( $1.24 \text{ m}^{-2}$ ; Lessios et al. 1984a), thus potentially increasing their relative importance in structuring the benthos at this study site. Establishment of populations of *E. lucunter* on the fore-reef may exclude other echinoids similar to original hypotheses on interactions between *Echinometra viridis* (A. Agassiz, 1863) and *D. antillarum* (Williams 1981), rather than through later theorized mechanisms of settlement facilitation (McClanahan 1999, Lessios 2005).

**BENTHOS RELATIONSHIPS.**—Although *D. antillarum* densities were within ranges found at other sites and suggest a positive relationship between sea urchin density and CCA/coral cover in the backreef environment, the system is still experiencing an overall increase in TAS cover. Sea urchins may be removing some turf and TAS algal cover, providing space for CCA to settle and cue coral settlement, yet sea urchins are not decreasing TAS cover. Prior to the massive mortality event, *D. antillarum* densities of  $16 \text{ m}^{-2}$  were shown to completely clear algae from the reef while coral spat densities were highest at sea urchin densities of  $4 \text{ m}^{-2}$  (Sammarco 1980). More recent research suggests densities as low as  $1 \text{ m}^{-2}$  can maintain a cropped algae patch [C Dahlgren, pers comm in Mumby et al. (2006)]. Our densities along the backreef were  $>1 \text{ m}^{-2}$  yet the population of *D. antillarum* was unable to maintain a cropped algal substrate and an increase in coral cover did not occur. Decline in coral cover may be caused by a multitude of factors including stresses the coral experiences in competition with the increased epilithic TAS cover (McCook et al. 2001), reproductive restrictions within the coral population itself, historic disturbances from diseases throughout the MesoAmerican region (Aronson and Precht 2001) and many other factors impacting coral reef health (Mumby and Steneck 2008). Like sea urchins, corals are impacted by the Allee effect and the highest coral cover found at the end of the study (1% at NB) is very low compared to other regions of the MesoAmerican Reef (approximately 22%; Schutte et al. 2010). Small scale disturbances from the low level of herbivory or from wave action may be providing substrate for coral larvae settlement, but coral populations within Akumal may have decreased to the extent that they are unable to successfully produce enough planulae to counter their mortality. There are a multitude of unknown factors in addition to herbivory which should be considered when addressing causes of coral reef decline. While there is some research to suggest a more direct correlation between sea urchins and coral growth (Myhre and Acevedo-Gutierrez 2007, Idjadi et al. 2010), in Akumal this relationship does not seem to be as direct.

Considering the characteristics of macroalgal functional groups, potentially higher rates of herbivory from sea urchin populations should be reflected in a benthos dominated by CCA. In areas with fewer sea urchins and less herbivory, macroalgae should dominate the benthos. A positive correlation between *D. antillarum* and coral and CCA was evident on the backreef, where these sea urchin populations were highest, yet CCA was not the dominant cover at these sites. In fact, overall cover by CCA on the total reef area surveyed during all 4 yrs of the study was low (<17%). Despite low densities of *D. antillarum* on the forereef, CCA cover was higher than backreef sites, contrary to our hypothesized outcomes. This may be a response to *E. lucunter* populations present there or may be representative of recently explored negative effects of *D. antillarum* on CCA (O'Leary and McClanahan 2010). In addition to herbivory as a source of disturbance, forereefs are typically highly influenced by wave action (Roberts and Suhayda 1983), which can influence epilithic cover. Cover by CCA is highly resistant to mechanical stress and research on TAS mats suggest they may be characteristic of high-energy environments (Bellwood and Fulton 2008), despite reduced sedimentation rates in these areas (Airoldi and Virgilio 1998). This consideration of wave action as a disturbance in addition to herbivory is not often considered when predicting dominate benthic cover on coral reefs.

The population of *E. lucunter* may add to the overall level of herbivory at the forereef sites, increasing the amount of substrate available for CCA colonization and growth. For *E. lucunter*, intra- and interspecific aggression increases the dispersion of this species relative to resources (Shulman 1990). This dispersion can control the spatial distribution not only of the echinoids, but also of the benthic cover resistant to their herbivory, as may be evident in the significant increase in CCA cover on the south forereef. As *E. lucunter* dominate the forereef environment, their presence was positively correlated with CCA cover similar to the correlation between *D. antillarum* and CCA cover in the backreef. Of note is the significant negative correlation of *E. lucunter* densities with coral cover on the forereef, the mechanisms behind which are unknown. *Echinometra lucunter*, similar to *D. antillarum*, did not have a significant correlation with TAS cover and therefore cannot be categorized as an adequate controller of this algal cover. Further study of this relationship may reveal a new ecological role in these echinoid/benthos dynamics.

Densities of Akumal Bay herbivorous fish populations did not differ significantly among the four sites and therefore cannot explain differences in benthic cover. Their low biomass (22%–72% less than other Caribbean reefs; Paddack et al. 2009), may explain the increase in algal cover, particularly as the high-sediment content in TAS mats has been shown to suppress herbivory by fishes (Bellwood and Fulton 2008). Caribbean-wide reef fish population densities are decreasing (Paddack et al. 2009) and modeled scenarios on the resilience of Caribbean coral reefs indicate that while herbivorous fishes may be able to compensate for the loss of sea urchins, reefs with low coral cover have less resistance to grazer loss and reef decline may be inevitable (Mumby et al. 2006). Low herbivore biomass may be caused by a dominance of smaller-sized fishes within the herbivore guild and results in decreased algal consumption (Paddack et al. 2006). With 86% of parrotfish <20 cm TL, the reduced herbivore biomass may decrease the ability of this guild of herbivores to control macroalgal cover. These factors, in addition to variable densities of *D. antillarum*, have an important role in the interpretation of changes to benthic cover on Akumal reefs.

In summary, Akumal reefs experienced a decline in coral cover and an increase in TAS cover despite *D. antillarum* densities comparable to other sites reported within the Caribbean. While coral and CCA covers were highest where densities of *D. antillarum* were highest along the backreef, this relationship did not hold universally across Akumal Bay. This suggests that grazing by *D. antillarum* has not decreased the dominance of an algal-dominated state and supports those modeled scenarios which indicate a disproportionate decrease in resilience as coral reefs with low coral cover continue to decline (Mumby et al. 2006). It is worth noting that a snapshot in 2008 rather than over the 4 yrs of this survey may have resulted in a substantially different conclusion regarding the fate of this reef, illustrating the importance of tracking temporal trends during studies of herbivores in coral-algal dynamics. In Akumal Bay, declines in coral cover may be evidence that the presence of *D. antillarum* cannot prevent the decline of the reef as it has been impacted by high TAS cover and a paucity of suitable herbivores.

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