

# POPULATION STATUS OF THE LONG-SPINED URCHIN *DIADEMA ANTILLARUM* IN PUERTO RICO 20 YEARS AFTER A MASS MORTALITY EVENT

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## ABSTRACT

A mass mortality event of the long-spined sea urchin *Diadema antillarum* (Philippi, 1845) occurred during 1983–1984 across the western Atlantic. Recovery to pre-mortality densities has been slow throughout most of the Caribbean as current stocks remain low, existing at a small fraction of previously recorded levels. To measure population recovery at Puerto Rico, we surveyed 26 localities around the island during 2003–2004. At each reef, we deployed 15 × 2 m belt transects (n = 12) to detect and quantify the presence of *D. antillarum* and obtain data on benthic cover. Density of *D. antillarum* varied significantly among geographic regions and localities, though variability was high. The highest density was documented in the Culebra Island region (0.44 ind m<sup>-2</sup>), followed by the northern region of Puerto Rico (0.23 ind m<sup>-2</sup>). No individuals of *D. antillarum* were found in 11 of the 26 surveyed localities. These densities are still substantially lower than pre- and post-mortality estimates from Puerto Rico. Most of the reefs were characterized by high macroalgal cover and horizontal water transparency < 3 m. Urchin densities were significantly and positively correlated with percentage of coral cover, percentage of coralline algae, and water transparency.

The long-spined sea urchin *Diadema antillarum* (Philippi, 1845) is a large, invertebrate herbivore of Caribbean reefs (Randall et al. 1964, Lessios 1988) and was once considered to be among the most important grazers (Sammarco et al. 1974, Sammarco 1980, Carpenter 1986, 1997), especially after overfishing of large herbivorous reef fishes. The herbivorous activity of *D. antillarum* affects the diversity, abundance, and productivity of algal communities (Sammarco 1982, Lessios 1988). *Diadema antillarum* also influences coral recruitment by consuming algae and opening new reef substrate, which is then available for coral spat settlement (Lessios 1988, Macintyre et al. 2005). It is also a major bioeroder (Carpenter 1986), influencing the benthic community structure of coral reefs (Liddel and Ohlhorst 1986). The spines of *D. antillarum* function as a refuge for their own juveniles (Miller et al. 2007) and for juvenile stages of other species such as lobsters and grunts (Haemulidae). At high densities, however, *D. antillarum* are known to inhibit coral recruitment (Sammarco 1980), as well as prey on living coral tissue of mature colonies (Bak and van Eys 1975). Long-spined urchins also constitute a food source for many crustaceans, gastropods of commercial value (Randall et al. 1964, Vicente and Goenaga 1984), and at least 15 species of fish (e.g., queen triggerfish, grunts; Randall et al. 1964, Ogden 1973). For these reasons, the long-spined sea urchin is considered a key species for maintaining coral reef health in the western Atlantic.

Before 1983, *D. antillarum* was very abundant on coral reefs, *Thalassia* beds, mangroves, and sandy benthic habitats throughout the wider Caribbean region (Ogden et

al. 1973, Lessios et al. 1984, 2001). During the years 1983 and 1984, a mass mortality event occurred, extending from the Caribbean coast of Panama throughout the rest of the basin (Lessios et al. 1984). In most places, this event resulted in 85%–100% population declines (Bak et al. 1984, Moses and Bonem 2001). In the long term, it resulted in a nearly total population collapse throughout the western Atlantic (Lessios 1988), rendering the species functionally extinct and changing the dynamics of Caribbean reefs (Mumby et al. 2006). More than 20 yrs later, *D. antillarum* recovery has yet to occur at a Caribbean-wide scale (Lessios 2005), with the exception of a few localities (Edmunds and Carpenter 2001, Jordán-Garza et al. 2008). The resulting low population densities might have prevented adequate larval production, as predicted by the Allee effect (The Nature Conservancy 2004).

In Puerto Rico, *D. antillarum* populations collapsed at all localities studied after the mass mortality event. Bauer (1980) documented a mean urchin density of 13.8 ind m<sup>-2</sup> at reefs off Condado Beach, San Juan, during 1977. Vicente and Goenaga (1984) documented pre-mortality densities of 18 ind m<sup>-2</sup> and of 1.2 ind m<sup>-2</sup> after the mass mortality event across La Parguera midshelf reefs. Weil et al. (2005) found densities that ranged from 0.83 to 1.55 ind m<sup>-2</sup> across the same reefs. However, recovery patterns have never been adequately documented across other geographic regions in Puerto Rico, outside La Parguera reefs in the southwest.

The objectives of this study were to: (1) document the current status of *D. antillarum* populations in fringing reefs of Puerto Rico, (2) identify which localities had the highest recovery rates, and (3) document any significant correlation between the structure of coral reef benthic communities and urchin densities.

## METHODS

Surveys were conducted between July 2003 and May 2004 at 26 shallow-water (< 4 m) fringing reefs across five geographic regions of Puerto Rico. Fringing reefs are the most common reef type in Puerto Rico and shallower zones are known to sustain higher *D. antillarum* densities than deeper zones at many sites (EA Hernández-Dedgado, pers obs). Seven sites were sampled in the northern region, five in the west, four in the south and east, and six around Culebra Island (Fig. 1, Table 1). Culebra Island was surveyed more intensely because of the presence of the Luis Peña Channel Natural Reserve, the first no-take marine protected area designated in Puerto Rico. The northern region supports low biogenic reef development and is susceptible to the highest wave action resulting from northeast trade winds and North Atlantic winter storms. The southern coast is less exposed to Atlantic wave action and supports extensive reef formations, followed by the eastern and western coast. The width of the shelf at each region varies considerably: 26 km on the west coast, 16 km on the south coast, and 2 km on the north coast (Ballantine et al. 2008).

Populations of *D. antillarum* were sampled using 15 × 2 m belt transects (n = 312). Twelve replicate transects were surveyed at each location following a slight modification of the CARICOMP (2001) method. Transects were placed parallel to the coast or along reef depth contours (< 4 m depth), where *D. antillarum* is generally most abundant. Urchins were classified by size into two categories: individuals with tests < 5 cm diameter and those with tests > 5 cm. Density was expressed as mean number of ind m<sup>-2</sup> ± 95% confidence intervals.

A point-intersect approach was used to characterize benthic communities along the same belt transects. The benthic community under each of 15 points along the transect (i.e., every m) was identified and classified as either: (1) live coral, (2) macroalgae (fleshy algae > 1 cm above ground), (3) filamentous algal turf, (4) crustose coralline algae (CCA; i.e., *Porolithon* spp.), (5) erect calcareous algae (i.e., *Halimeda* spp.), (6) sponges, (7) zoanthids, (8) open sub-

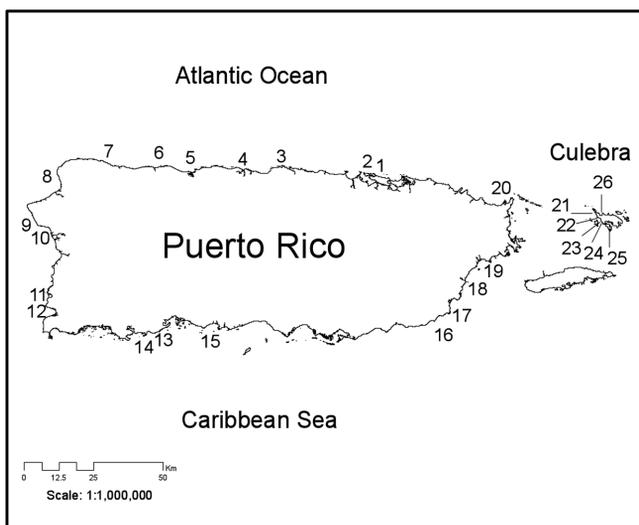


Figure 1. Sampling stations around Puerto Rico where densities of *Diadema antillarum* were surveyed. See Table 1 for locality names.

Table 1. Sampling stations and codes used in this study.

Regions	Accumulative number of each station	Localities	Codes
1 North	1	Condado, San Juan	SJC
	2	Escambrón, San Juan	SJE
	3	Puerto Nuevo, Vega Baja	VBA
	4	Esperanza, Manatí	MAN
	5	La Cueva del Indio, Arecibo	ARE
	6	Sardinera, Hatillo	HAT
	7	Bajura, Isabela	ISA
2 West	8	Peña Blanca, Aguadilla	AGU
	9	Tres Palmas, Rincón-A	RINA
	10	Playa, Rincón-B	RINB
	11	Punta Lamela, Cabo Rojo	PLAM
	12	Playa Buyé, Cabo Rojo	PBUY
3 South	13	Playa Ballena, Guánica	BALL
	14	Cayo Aurora, Guánica	AUR
	15	Punta Cuchara, Ponce	PCN
	16	Los Bajos, Patillas	PAT
4 East	17	Playa Lucía, Yabucoa	YAB
	18	Punta Fraile, Humacao	HUM
	19	Punta Lima, Naguabo	NAG
	20	Cabezas de San Juan, Fajardo	CSJ
5 Culebra	21	Playa Carlos Rosario, Culebra	PCR
	22	Bahía Tamarindo, Culebra	BTAM
	23	Arrecife El Banderote, Culebra	AEB
	24	Bahía Sardinias, Culebra	BSAR
	25	Punta Soldado, Culebra	PSOL
	26	Playa Flamenco, Culebra	PFLA

strate (i.e., rubble, bare pavement), (9) sand, or (10) mixed substrate (i.e., seagrass and algae). Percent cover of each benthic component and mean values were calculated for each parameter per site. Horizontal water transparency was measured at each site in triplicates on a single day using a Secchi disk, between 1000 and 1400 hrs. Sampling was conducted during calm and dry weather conditions to minimize turbid runoff affecting transparency measurements, but historical accounts have shown that some sites are consistently turbid (EA Hernández-Dedgado, pers obs).

Non-parametric, one-way ANOVA (Zar 1984) was used to test the null hypothesis of no differences in the density of the urchins among regions and localities. This was conducted using separate urchin size categories, as well as the entire pool of individual urchins. Dunn's test for median comparison (Zar 1984) was used to identify significant differences among sites and regions.

Multivariate statistical analysis was carried out to identify spatial variation in the structure of the benthic communities. The mean proportion of percent cover averages of each benthic category at both region and location level were square-root-transformed to standardize variances and normalize the data (Zar 1984). Localities were classified by hierarchic ordination using the Bray-Curtis cluster analysis of community dissimilarity. Results of this analysis were graphically organized in a multidimensional scaling plot (MDS, Clarke and Warwick 2001). The relationship between benthic components and location clustering patterns, as a function of sea urchin density, was examined through a principal component ordination (Anderson et al. 2008). Correlations were computed to evaluate relationships between *D. antillarum*, benthic cover, and water clarity (Zar 1984).

## RESULTS

**STATUS OF *DIADEMA ANTILLARUM* POPULATIONS.**—ANOVA of the density of *D. antillarum* at the regional level revealed significant differences ( $P < 0.001$ , Fig. 2, Table 2) among regions. The highest densities of *D. antillarum* occurred at Culebra and the north region, which were significantly higher than densities of the west, south, and east regions (Dunn's test:  $P < 0.001$ , Fig. 2, Table 2). No individuals of *D. antillarum* were found in eleven of the 26 localities surveyed (none in the eastern region), while densities  $< 0.33$  ind  $m^{-2}$  were documented at ten localities. Densities between 0.33 and 0.67 ind  $m^{-2}$  were observed at only three localities, and  $> 0.67$  ind  $m^{-2}$  at only two localities. Arrecife El Banderote, in Culebra, had the highest density of *D. antillarum* (0.91 ind  $m^{-2}$ ,  $P < 0.0001$ ), followed by two other Culebra localities: Bahía Tamarindo and Bahía Sardinas, with 0.70 and 0.51 ind  $m^{-2}$ , respectively (Fig. 3, see Table 1 for abbreviations). Outside of Culebra, the two northern localities, Isabela and Arcibo, had the highest densities of urchins (0.45 and 0.44 ind  $m^{-2}$ , respectively).

ANOVA of the density of *D. antillarum*  $> 5$  cm for the localities within the individual regions showed significant differences ( $P < 0.0001$ ) among the localities within the north, west, and Culebra regions. A significantly higher density of urchins  $> 5$  cm

Table 2. Analysis of variance of *Diadema antillarum* densities among regions of Puerto Rico by urchin size (those  $< 5$  cm test diameter, and those  $> 5$  cm test diameter).

Factors	df <sup>a</sup>	F	P	Dunn's Test <sup>b</sup>	
Total density	4, 21	6.15	$< 0.0001$	<u>5, 1</u>	<u>2, 3, 4</u>
Density $< 5$ cm	4, 21	1.22	$< 0.0001$	<u>1, 5</u>	<u>5, 2</u> <u>2, 3, 4</u>
Density $> 5$ cm	4, 21	8.03	0.0004	1	5 <u>2, 3, 4</u>

<sup>a</sup>df = Degrees of freedom (between, within).

<sup>b</sup>Test of median comparison. Numbers denote regions described in Table 1. Underlined numbers indicate regions with similar urchin densities.

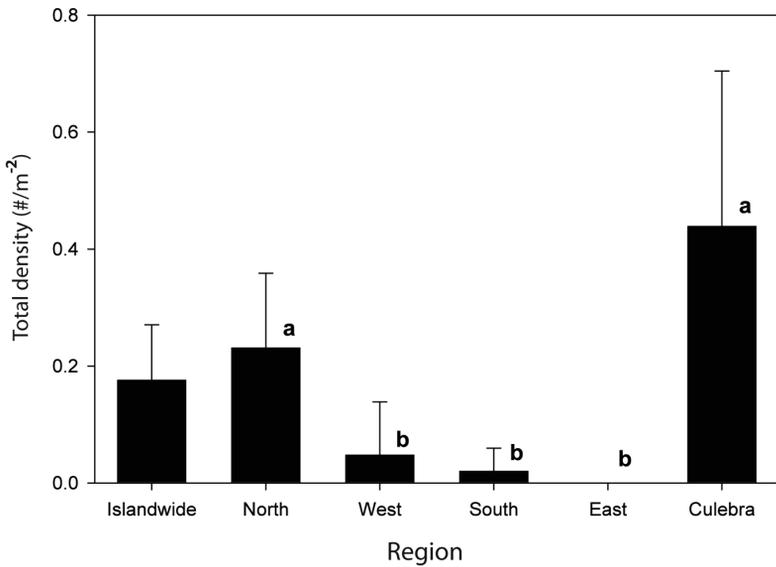


Figure 2. Total density of *Diadema antillarum* of Puerto Rico by region. Error bars represent 95% confidence intervals. Letters above bars indicate significantly different densities of urchins ( $P < 0.05$ ).

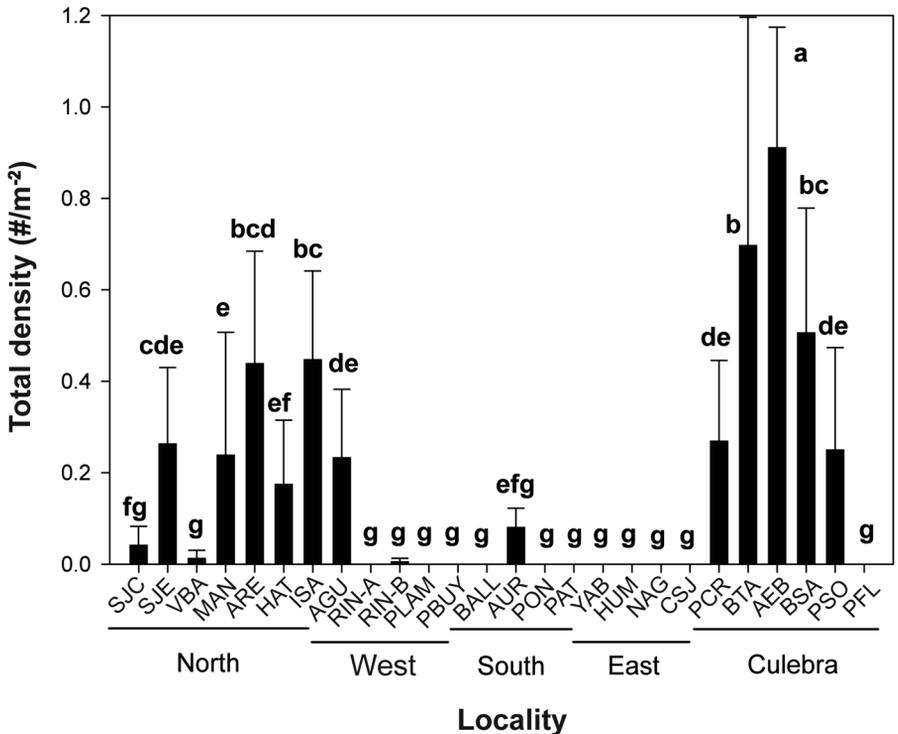


Figure 3. Total density of *Diadema antillarum* by locality. Error bars represent 95% confidence intervals. Letters above bars indicate significantly different densities of urchins ( $P < 0.05$ ).

was observed in Culebra and the North region ( $P = 0.001$ ). The large individuals from the northern region populations were also significantly larger ( $P < 0.05$ ) in comparison to the western, southern, and eastern populations. Arrecife El Banderote had the highest density of individuals  $> 5$  cm ( $0.81$  ind  $m^{-2}$ ), followed by Bahía Tamarindo and Bahía Sardinias ( $0.67$  and  $0.50$  ind  $m^{-2}$ , respectively). In the north region, Isabela and Vega Baja were the most disparate localities, due to the high density of urchins in Isabela, compared to the extremely low density of urchins in Vega Baja. In the west region, Aguadilla was the only location where urchins were found. In the region of Culebra, Flamenco was the only locality where *D. antillarum* was absent.

The distribution of urchins  $< 5$  cm exhibited significant differences ( $P < 0.0001$ ) among the localities within each region, except in the east. Urchins with test diameters  $< 5$  cm were more abundant in the north region (Dunn's test:  $P < 0.05$ , Table 2), followed in order by the west, Culebra, and south regions. The highest density of *D. antillarum*  $< 5$  cm was observed in Peña Blanca in Aguadilla and El Escambrón in San Juan, followed by Arrecife El Banderote ( $P < 0.0001$ , Fig. 3). In the north region, up to 4–5 times more sea urchins were measured in Escambrón (San Juan) than Condado or Vega Baja.

**WATER TRANSPARENCY.**—Horizontal water transparency had a mean island-wide value of 6.2 m, with significantly higher values ( $P = 0.0397$ ) in the north region. The lowest values were recorded in the east (Table 3). At the locality level, water transparency ranged from 14.8 m at Isabela to 1.2 m at Punta Lamela (Online Appendix 1). Sea urchin density was positively correlated to water transparency ( $r = 0.5753$ ,  $P = 0.0021$ ).

**STRUCTURE OF THE BENTHIC COMMUNITIES.**—Benthic community structure differed significantly among regions ( $P = 0.004$ ) and among localities ( $P < 0.0001$ ; Tables 3, 4, Online Appendix 1). There was also a significant region by location interaction ( $P = 0.017$ ). The benthic community structure of the north region differed significantly from that of south, east, and Culebra; Culebra also differed significantly from east and south (Table 4). A large group of 15 localities clustered together as a result of significantly higher macroalgal cover (Fig. 4). Sea urchins were absent in eight of the 15 localities and density of sea urchins was  $< 0.33$  ind  $m^{-2}$  in four of them (Fig.

Table 3. Horizontal water transparency and benthic community parameters among regions of Puerto Rico (mean  $\pm$  95% confidence intervals). CCA = crustose coralline algae, ECA = encrusting coralline algae.

Parameter	North	West	South	East	Culebra
Transparency (m)	8.3 $\pm$ 2.5	5.5 $\pm$ 3.0	3.8 $\pm$ 1.4	3.5 $\pm$ 2.9	7.7 $\pm$ 3.1
% Coral	4.3 $\pm$ 4.8	8.4 $\pm$ 5.7	0.8 $\pm$ 1.6	0.1 $\pm$ 0.3	12.6 $\pm$ 8.4
% Macroalgae	4.2 $\pm$ 4.4	10.1 $\pm$ 13.8	28.3 $\pm$ 32.5	20.3 $\pm$ 17.2	14.4 $\pm$ 10.5
% Turf	12.5 $\pm$ 19.9	3.7 $\pm$ 5.3	3.2 $\pm$ 5.5	16.4 $\pm$ 23.8	16.8 $\pm$ 10.7
% CCA	0	0.2 $\pm$ 0.4	0.1 $\pm$ 0.3	0.3 $\pm$ 0.5	1.8 $\pm$ 2.0
% ECA	0.1 $\pm$ 0.2	0.6 $\pm$ 0.7	0.1 $\pm$ 0.3	2.1 $\pm$ 1.8	3.9 $\pm$ 6.4
% Sponge	0	0.6 $\pm$ 1.1	1.4 $\pm$ 2.7	0	0
% Zoanthid	0	7.3 $\pm$ 9.9	2.9 $\pm$ 5.4	8.9 $\pm$ 17.4	0.6 $\pm$ 0.9
% Bare substrate	33.0 $\pm$ 20.3	30.1 $\pm$ 27.0	2.1 $\pm$ 3.4	10.0 $\pm$ 10.7	20.7 $\pm$ 14.2
% Sand	42.7 $\pm$ 19.2	27.2 $\pm$ 28.1	12.6 $\pm$ 17.8	12.5 $\pm$ 23.1	21.2 $\pm$ 15.3
% Seagrass + algae	3.4 $\pm$ 3.5	11.9 $\pm$ 14.8	48.3 $\pm$ 53.9	29.3 $\pm$ 29.6	8.0 $\pm$ 4.2

Table 4. Results of ANOSIM test for the structure of the benthic community.

Factors <sup>a</sup>	Global statistic r	Significance
Global test		
Region	0.249	0.0040
Location	0.643	< 0.0001
Region × locality		0.0170
Paired tests per regions		
North vs west	-0.021	0.4810 <sup>b</sup>
North vs south	0.534	0.0060
North vs east	0.508	0.0150
North vs Culebra	0.280	0.0310
West vs south	0.056	0.3250 <sup>b</sup>
West vs east	0.094	0.2300 <sup>b</sup>
West vs Culebra	0.227	0.7600 <sup>b</sup>
South vs east	-0.073	0.5430 <sup>b</sup>
South vs Culebra	0.552	0.0100
East vs Culebra	0.413	0.0100

<sup>a</sup>Data are square-root-transformed. Based on 5000 permutations.

<sup>b</sup>Not significant.

5). Coincidentally, six of these localities had a horizontal water transparency < 3 m and urchins were absent. Water transparency ranged between 3 and 6 m at five of the localities within this cluster, and urchins were absent in six of them, with very low densities in the remaining localities. The remaining four localities had water transparency > 6 m and higher urchin densities. Percent coral and CCA coverage were significantly lower at most of the localities within this cluster, particularly at

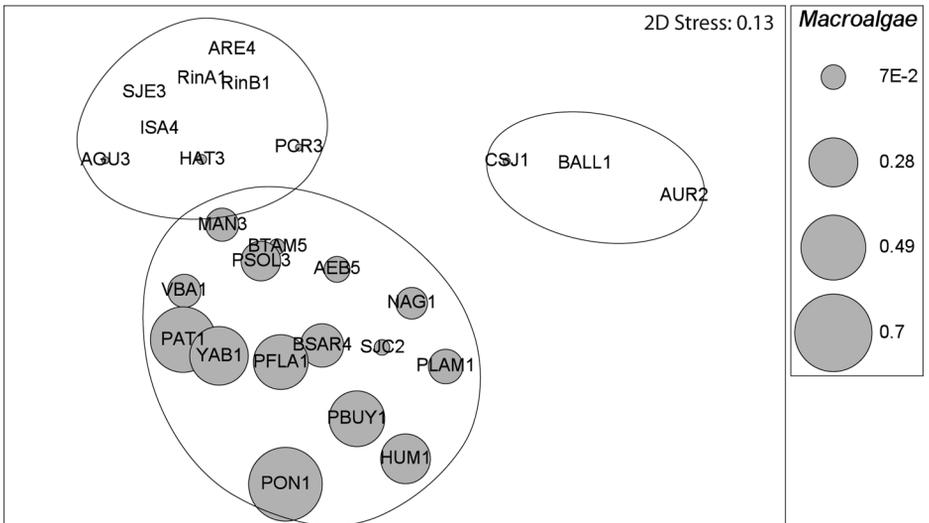


Figure 4. Spatial patterns of benthic communities: Multidimensional scaling bubble plot as a function of macroalgal cover. Numbers (1–5) after the location codes identify the categories of the density of urchins (ind m<sup>-2</sup>): 1 = < 0.03; 2 = 0.03–0.17; 3 = 0.17–0.33; 4 = 0.33–0.67; and 5 = > 0.67. Large bubbles in MDS plot represent the 50% community similarity cutoff level.

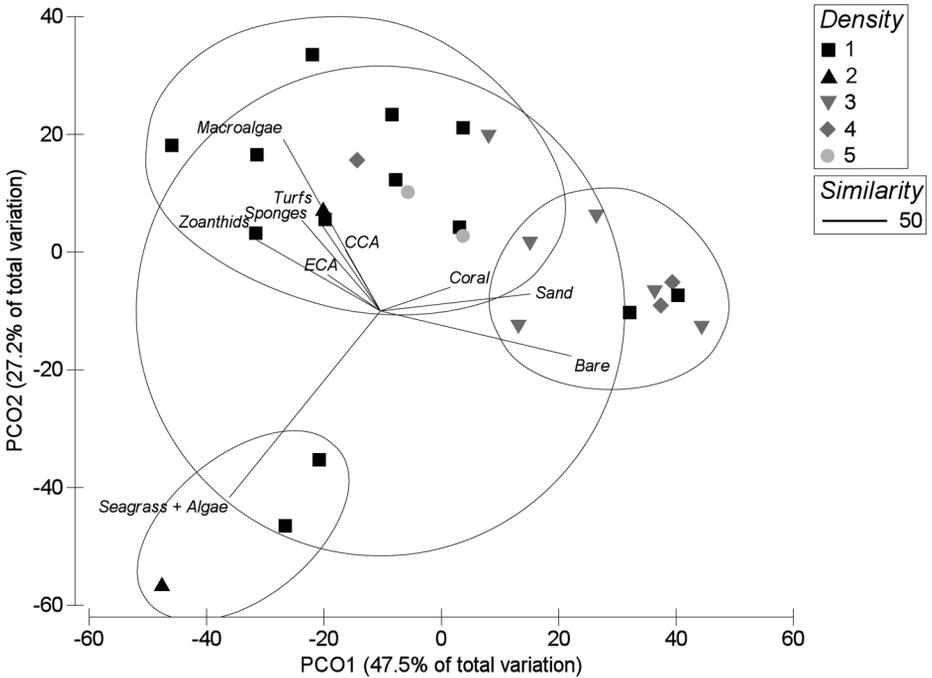


Figure 5. Principal component ordination of benthic community structure as a function of sea urchin density. Numbers (1–5) identify the categories of the density of urchins (ind  $m^{-2}$ ): 1 = 0–0.03; 2 = 0.03–0.17; 3 = 0.17–0.33; 4 = 0.33–0.67; and 5 = > 0.67.

those with no urchins or with low urchin densities, low water transparency, and high macroalgae.

A second small cluster consisted of Cabezas de San Juan, Ballena, and Cayo Aurora, and was dominated by mixed seagrass-macroalgal habitats, where urchins were present only at Cayo Aurora (0.17 ind  $m^{-2}$ ). The third cluster was composed of eight localities characterized by moderate to low percent macroalgal cover, but significantly higher CCA and coral cover. Mean urchin density was higher (0.17–0.67 ind  $m^{-2}$ ) at these sites (Fig 4). Principal component ordination explained 74.7% of the observed clustering patterns for benthic community structure (Fig. 5).

Multiple regressions of *D. antillarum* density, water transparency, and the different components of the benthic community revealed positive relationships for *D. antillarum* density and water transparency ( $r = 0.5753$ ,  $P = 0.0021$ ), percent coral cover ( $r = 0.4685$ ,  $P = 0.0158$ ), and percent CCA cover ( $r = 0.4098$ ,  $P = 0.0376$ ). However, there was no significant relationship between the density of *D. antillarum* and macroalgae, filamentous algae, encrusting coralline algae, sponges, zoanthids, open substrate, sand, and mixed seagrass-algal substrates. There was a significant, non-linear increase in percent macroalgal cover with reduced water transparency ( $r = 0.6417$ ,  $P = 0.0004$ ).

## DISCUSSION

Our results indicate that more than two decades after the mass mortality event of 1983–1984, the presence of *D. antillarum* in Puerto Rico is highly variable. Although densities in Puerto Rico have not rebounded to pre-1983 levels based upon the limited historical data (13.8–18 ind m<sup>-2</sup>; Bauer 1980, Vicente and Goenaga 1984), current levels are generally higher than many other wider Caribbean reef systems (Table 5). This might have been influenced by a combination of factors such as fishing of urchin predators (i.e., Balistidae, Sparidae), diminished larval supply, recruitment failure, localized post-recruitment mortality, oceanography, or lack of appropriate habitat due to long-term decline of coral reefs. The recovery patterns of *D. antillarum* in intensively fished systems are likely to be different from reefs that are lightly fished or completely protected, as a result of different algal assemblages. This might be the case of localities such as AEB, BTA, and PCR at Culebra Island, which are located within the Canal Luis Peña No-Take Natural Reserve and supported the highest densities of sea urchins. Differences in density among localities and regions may also be related to the degree of reef topographic complexity and/or simply due to the urchins' patchy distribution, even within topographically similar areas. Areas with more corals generally provide greater topographic complexity and hence more refuges for urchins, but they typically have fewer algae for urchin foraging. However, the fact that urchin densities have not recovered in most surveyed reefs after more than 20 yrs suggests that some other factors beyond reef topography are necessary to support greater urchin recruitment and survivorship.

Surveys in La Parguera, southwestern Puerto Rico, during 2001 by Weil et al. (2005) estimated the density of *D. antillarum* across reef sites (0.83–1.39 ind m<sup>-2</sup>) and seagrass mounds (1.09–1.30 ind m<sup>-2</sup>). In comparison to these reported densities, our values are lower and more variable (Table 5). All reported values are well below the *Diadema* density estimate of up to 18 ind m<sup>-2</sup> in Puerto Rico (Vicente and Goenaga 1984), 14.4 ind m<sup>-2</sup> in St. Thomas, and 25.8 ind m<sup>-2</sup> in Cozumel, Mexico (Bauer 1980), before the 1983–1984 mortality event. The question remains whether these pre-mortality event high densities are attainable or whether sites are too environmentally stressed to support such densities again. Given that *D. antillarum* were absent until 1996 in La Parguera (Weil et al. 2005), their relatively high densities in 2001 (Weil et al. 2005), and recent presence in almost all reefs (NV Schizas, pers obs) indicates that a slow recovery of urchin populations is probably underway. Similar slow recoveries of *Diadema* populations have been reported to islands of the Lesser Antilles (Hunte and Younglao 1988, Levitan 1988, Steiner and Williams 1996a,b, Miller et al. 2003, Debrot and Nagelkerken 2006) and other Caribbean localities (Moses and Bonem 2001, Alvarado et al. 2004, Jordán-Garza et al. 2008), including Dry Tortugas (Chiappone et al. 2001). The apparent increased presence of *Diadema* at some islands is still a fraction of historical pre-mortality estimates and recovery has yet to be detected at a region-wide scale. Extensive surveys of urchins in Panama (Lessios 2005) and Florida Keys (Chiappone et al. 2002) have reported no significant increases of populations.

*Diadema antillarum* is a moderator of algal abundance (Sammarco 1980, Lessios 1988, Carpenter 1990, Knowlton 2001) and reef structural heterogeneity (Alvarez-Filip et al. 2009), influencing the settling and survival of coral larvae (Sammarco 1980, Edmunds and Carpenter 2001) and benefiting the growth of other commu-

Table 5. Mean densities of *Diadema antillarum* at localities in the Caribbean before and after the mass mortality event of 1984. All densities are reported as #ind m<sup>-2</sup>.

Location	Before 1984	After 1984	1990 to present	Source
Barbados	12.9–17.3	3.1–7.4		Hunte and Younglao (1998)
Barbados	9.26	0.72		Lessios (1988)
Bahamas, Rose Island	2.9			Bauer (1980)
Belize	1.06	< 0.01		Lessios (1988)
Belize			< 0.001	McClanahan and Muthiga (1998)
Belize, Carrie Bow Cay		< 1.0–4.3		Lewis and Wainwright (1985)
Bermuda	0.6			Bauer (1980)
Costa Rica, Cahuita Natl Park	4.33		0.3	Alvarado et al. (2004)
Costa Rica			0.2	Myhre and Acevedo-Gutiérrez (2007)
Curaçao	~0.003–0.023	~0.0–0.0002		Bak et al. (1984)
Curaçao	2.58	0.02		Lessios (1988)
Curaçao			0.00–0.32	Debrot and Nagelkerken (2006)
Dominica			0.50	Hunte and Younglao (1998)
Dominica			2.00	Steiner and Williams (2006)
Florida, Dry Tortugas			0.33	Chiappone et al. (2001)
Florida, Florida Keys			0.006–0.25	Chiappone et al. (2002)
Grand Cayman	1.7–12.7			Bauer (1980)
Grand Cayman			< 0.01	Williams and Polunin (2001)
Jamaica	3.9–12.2	0.00–0.80		Hughes et al. (1987)
Jamaica	7.32	0.03		Lessios (1988)
Jamaica, Discovery Bay	19			Williams (1984)
Jamaica, Discovery Bay	2.5–13.9	0.00		Liddell and Ohlhorst (1986)
Jamaica, Discovery Bay			0.1–3.4	Cho and Woodley (2000)
Jamaica, Discovery Bay	0.16–0.5		2.95	Haley and Solandt (2001)
Jamaica, Discovery Bay			~5	Edmunds and Carpenter (2001)
Jamaica, Negril			< 0.01	Williams and Polunin (2001)
Mexico			7.29	Jordán-Garza et al. (2008)
Mexico, Cozumel	9.1–25.8			Bauer (1980)
Panama	0.05–0.98	0.00–0.43		Lessios et al. (1984)
Panama	1.38–3.63	0.00–2.1		Lessios (1988)
Puerto Rico, San Juan	13.8			Bauer (1980)
Puerto Rico	~18	1.2		Vicente and Goenaga (1984)
Puerto Rico, La Parguera			0.83–1.55	Weil et al. (2005)
Puerto Rico			0–0.9	Present study
St. Croix, USVI	5.9	0.10		Lessios (1988)
St. Croix, USVI	5.8–13.4	0.00–2.1		Carpenter (1990)
St. Croix, USVI			0.02–2.86	Miller et al. (2003)
St. John, USVI	14.38	0.08		Lessios (1988)
St. John, USVI	14.38	~0.312		Levitan (1988)
St. Lucia			0.80	Hunte and Younglao (1998)
St. Thomas, USVI	14.3			Bauer (1980)
Tobago	5.0	< 0.01		Lessios (1988)
Venezuela, Bahia Mochima	0.28–4.0		0.15–0.47	Noriega et al. (2006)

nity components (Liddell and Ohlhorst 1986, Edmunds and Carpenter 2001). The rapid increase in macroalgal cover observed across the wider Caribbean following the mass mortality event provided additional evidence of the influence *D. antillarum* has on the composition of the benthic community (Bak et al. 1984, Hughes et al. 1987, Aronson and Precht 2000, Edmunds and Carpenter 2001, Carpenter and Edmunds 2006, Debrot and Nagelkerken 2006, Myhre and Acevedo-Gutiérrez 2007). Our results suggest a significant, positive relationship between the density of *D. antillarum* and the percent of coral cover, consistent with previous reports (Edmunds and Carpenter 2001, Myhre and Acevedo-Gutiérrez 2007), in which the herbivorous activity of *D. antillarum* indirectly favored an increased abundance of coral recruits, probably by the removal of algae. Our findings are not consistent with studies reporting a reduction in percent macroalgal cover when densities of *D. antillarum* are high (Edmunds and Carpenter 2001). Macroalgal cover was significantly higher on coral reefs under highly turbid conditions, due to recurrent, highly-sediment, nutrient-rich runoff pulses. Likewise, no *Diadema* urchins were detected at highly turbid sites. Additionally, the significantly positive relationship between density of *D. antillarum* and percent CCA cover is consistent with the hypothesis that *D. antillarum* foraging favors the growth of CCA, which may favor the settlement of coral larvae (Edmunds and Carpenter 2001). However, in Costa Rica, the *D. antillarum* density was independent of the coverage of calcareous macroalgae (Myhre and Acevedo-Gutiérrez 2007). Discrepancies among studies may be related to contrasting algal species compositions or variation in local densities of *D. antillarum*.

In Puerto Rico, regions with the largest abundance of mixed seagrass–algal dominated substrata contained the lowest density of urchins, which is in contrast with observations that *D. antillarum* is readily present in seagrasses, particularly in < 2 m depth (Randall et al. 1964, Ogden et al. 1973, P Yoshioka, University of Puerto Rico, Mayagüez, pers comm). These shallow water habitats were composed of transitional zones between old *Porites porites* (Pallas, 1766) biotopes and seagrass habitats dominated by a mixture of sparse *Thalassia testudinum* Banks & Soland. ex Koenig, green calcareous algae (e.g., *Halimeda* spp., *Penicillus* spp.), and brown algae (e.g., *Dyctiota* spp.). In contrast, Culebra Island and the north region, the areas with the highest density of *D. antillarum*, were characterized by CCA, sand, open substrate, filamentous algae, and coral; yet a relationship between *D. antillarum* density and most of those benthic components was not apparent.

The present study suggests several testable hypotheses regarding sea urchin distribution. Do higher urchin densities reflect higher recruitment? Is algal grazing rate higher where urchin densities are higher? Is poor water quality across large spatial scales a significant barrier to effective population connectivity and sea urchin recruitment? Are local oceanographic patterns (i.e., localized gyres) a significant factor promoting self-recruitment at the reef scale?

Under an imminent scenario of increasing atmospheric CO<sub>2</sub> concentration and ocean acidification (Veron et al. 2009), population recovery of *D. antillarum* seems remote. Further, even though the genetic signature of a population bottleneck has not been recovered from *D. antillarum* (Lessios et al. 2001), a sustained bottleneck will eventually impact the standing genetic variation as bottleneck duration is negatively correlated with allelic diversity (Allendorf 1986). Continuous surveys of *D. antillarum* are warranted as the evolutionary fate of one of the largest invertebrate herbivores of Caribbean coral reefs is likely linked to that of the declining coral reefs.

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