Population characteristics of the sea urchin *Diadema antillarum* in La Parguera, Puerto Rico, 17 years after the mass mortality event

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**Abstract:** Recent reports indicate that populations of the black sea urchin *Diadema antillarum* are slowly coming back in several localities in the Caribbean after 15 years of absence. In La Parguera, Puerto Rico, urchins were totally absent from reef localities until 1996, when isolated, medium size individuals were observed in shallow reef habitats. To assess the status (distribution, densities and size structure) of populations of *D. antillarum* 17 years after the die-off, twelve 20 m² (10 x 2 m) band transects in each of four depth interval (0-3, 3-7, 7-11 and >11m) in each of four fringing coral reefs, and six-eight band-transects in each of two depth intervals (0-3 and > 3m) in three lagoonal mounds were surveyed in 2001. All urchins present in the band transects in two depth intervals (0-3 and 3-8 m) were collected and measured (test diameter) *in situ* to determine the average size and size (age) structure of populations. Overall, average densities were low and not significantly different (F=1.29, p= 0.125) across reef sites (0.83-1.39 ind/m²) and the seagrass mounds (1.09 ± 0.6-1.30 ± 0.6 ind/m²). Urchins were only found in the shallow areas (<3 m) on the seagrass mounds where they formed tight aggregations during daytime. Densities decreased significantly with increasing depth (r² = -0.60) in reef sites and were significantly higher (F= 5.97, p<0.001) in shallow reef platforms (0.89 ± 0.69 – 1.98 ± 0.65 ind/m²) (0-3m), and the upper fore-reef (0.56 ± 0.14 – 2.33 ± 1.1 ind/m²) habitats (3-7m), compared to deeper (>7m) habitats (0.01 ± 0.02 – 0.88 ± 1.06 ind/m²). Enrique reef had a significantly higher (K-W, H= 165.19, p<0.001) population average size (Median= 7.7) compared to all other sites. Populations in the sea grass mounds were dominated by midsize to large individuals. Within reefs, the average size did not vary significantly across depth intervals with medium to large size urchins dominating. Higher number of aggregations and higher number of urchins per aggregation were correlated with low complexity (rugosity) habitats (Pearson’s r= -0.772, p<0.001 and r= -0.778, p<0.001 respectively), which supports the idea that this behavior provides protection. Although average densities were well below pre-mass-mortality densities in Puerto Rico, results of this study indicate that *Diadema* seem to be making a slow come back in La Parguera. Rev. Biol. Trop. 53(Suppl. 3): 219-231. Epub 2006 Jan 30.

**Keywords:** *Diadema antillarum*, population recovery, black sea urchin, mass mortality, Caribbean, Puerto Rico.

The black sea urchin *Diadema antillarum* (Philippi, 1845) was a conspicuous and extremely abundant organism in shallow water habitats in the wider Caribbean until the early 1980’s, when a highly specific epizootic event almost eliminated most of the populations along its geographic range (Table 1). Before 1983, this urchin had a wide geographic distribution through the Caribbean, Gulf of Mexico and the West Atlantic, extending from Bermuda to as far south as Surinam (Randall *et al.* 1964) and presumably, the eastern Atlantic from the Azores to the Gulf of Guinea (Mortesen 1940). In the wider Caribbean, this urchin was present in coastal marine habitats including coral reefs, seagrass beds, rocky shores, sandy bottoms and even mangrove roots. They were mostly abundant in shallow areas down to 15 m, but some could be found as deep as 40 m (Randall *et al.* 1964, Sammarco 1972, Weil *et al.* 1984).
Densities were extremely high in many reef areas (Bauer 1980, Hunter 1977, Stern et al. 1977, Scoffin et al. 1980, Weil et al. 1984, Lessios et al. 1984a), a possible consequence of high reproductive success and low predation pressure over several years (Odgen et al. 1973). In some reef habitats in Jamaica for example, densities of up to 71 ind/m² were common (Sammarco 1980).

The high density of urchins and their feeding habits played an important role in the structuring dynamics of algal and coral reef communities (Ogden et al. 1973, Ogden and Lobel 1978, Sammarco et al. 1973, Sammarco 1980, Weil 1980, Carpenter 1981, 1984, 1985, 1990, Hay 1984, Lessios et al. 1984a, Jackson and Kaufmann 1987). The presence of this urchin determined the limits of seagrass areas (Vicente and Rivera 1982), maintained the “halos” around lagoonal patch reefs and back reef areas (Ogden et al. 1973, Ogden 1976), and affected the biomass and distribution of macroalgae and corals (Ogden and Lobel 1978, Sammarco 1980, 1982, Solandt and Campbell 2001). *D. antillarum* was regarded as an omnivorous organism with a preference for algae and it was a primary determinant of algal distribution and biomass in many shallow reefs throughout the Caribbean. However, when grazing in high density habitats, they ingested other sessile invertebrates such as zoanthids, sponges and coral tissue (Randall et al. 1964, Weil 1980) affecting recruitment and mortality rates of juvenile corals and other sessile invertebrates (Sammarco 1980, 1982) and in some cases, the growth rates of corals by damaging their tissues (Weil 1980). This urchin was also a major bioeroder and sediment producer in many reef localities (Hunter 1977, Ogden 1977, Stearn et al. 1977, Weil 1980). Because of all these important ecological roles, *D. antillarum* was considered as a keystone species for many Caribbean reef localities (Jackson and Kaufmann 1987).

In the early 1980’s, a massive die off of *D. antillarum* occurred over its geographic range in the western Atlantic (Table 1) produced by an unidentified (but see Bauer and Agerter 1987), water-borne, highly specific and virulent pathogen (Lessios et al. 1984a). Urchins started to die near Punta Galeta in Panamá in the middle of 1983 and then, the epizootic event followed the direction and timing of the ocean currents, dispersing through the northern Caribbean, Gulf of Mexico, and up to Bermuda in less than a year (Lessios et al. 1984b). This event covered an approximate area of 35 million km² killing up to 99% of *D. antillarum* in many locations (Table 1) (Bak et al. 1984, Lessios et al. 1984b, Laydoo 1984, Hughes et al. 1985, Hunte et al. 1986, Lessios 1988, Hunte and Younglao 1988). Only small mortality events were reported before (Glynn 1968).

The biological and physical structure of many Caribbean reefs were greatly affected by the mortality event. Detrimental effects included a significant and fast increase in algal biomass (up to 439%) and a shift in the species composition from algal turf and crustose algae to macroalgae (Vicente and Goenaga 1984, Liddell and Ohlhorst 1986, Carpenter 1985, 1990), a decrease in recruitment of hard corals (Hughes 1989) and a subsequent decline in coral cover due to competition with algae (Liddell and Ohlhorst 1986, Hughes 1989). It was a transition from a community dominated by a grazing-based food web to one where primary production may be exported to adjacent communities (Ogden and Lobel 1978, Carpenter 1990). The greater changes were observed in those areas where overfishing had but eliminated all other important herbivores.

Lack of the herbivorous pressure of *D. antillarum* contributed with the shift from coral dominated- to algal dominated reefs all over the Caribbean (Lessios 1988, Carpenter 1990). In Jamaica, percent cover of algae increased from 30.7% to 72.3% in 4 months (Lidell and Ohlhorst 1986), and there was a significant increase in algae biomass in almost every shallow reef (Carpenter 1984). Increased shading, competition for space and the disappearance
### Table 1

**Geographic coordinates and characteristics of the sampling sites in La Parguera, Puerto Rico**

<table>
<thead>
<tr>
<th>Site</th>
<th>Type</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Depth (m)</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Corona 1</td>
<td>Seagrass</td>
<td>17º 58.126</td>
<td>67º 03.036</td>
<td>0-3</td>
<td>Lagoonal mound</td>
</tr>
<tr>
<td>Corona 2</td>
<td>Seagrass</td>
<td>17º 58.097</td>
<td>67º 02.868</td>
<td>0-3</td>
<td>Lagoonal mound</td>
</tr>
<tr>
<td>Corona 3</td>
<td>Seagrass</td>
<td>17º 58.159</td>
<td>67º 02.255</td>
<td>0-3</td>
<td>Lagoonal mound</td>
</tr>
<tr>
<td>Caracoles</td>
<td>Reef</td>
<td>17º 57.643</td>
<td>67º 02.165</td>
<td>0-15</td>
<td>Protected fringing</td>
</tr>
<tr>
<td>Enrique</td>
<td>Reef</td>
<td>17º 57.227</td>
<td>67º 03.111</td>
<td>0-18</td>
<td>Protected fringing</td>
</tr>
<tr>
<td>Media Luna</td>
<td>Reef</td>
<td>17º 56.170</td>
<td>67º 03.032</td>
<td>0-18</td>
<td>Exposed fringing</td>
</tr>
<tr>
<td>Laurel</td>
<td>Reef</td>
<td>17º 58.585</td>
<td>67º 03.309</td>
<td>0-12</td>
<td>Exposed fringing</td>
</tr>
</tbody>
</table>

### Table 2

**Diadema antillarum densities before and after the mass mortality event in some localities and reefs in the wider Caribbean**

<table>
<thead>
<tr>
<th>Locality</th>
<th>Reef</th>
<th>Before (ind/m²)</th>
<th>After (ind/m²)</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barbados</td>
<td>North Bellairs</td>
<td>17.3</td>
<td>1.8</td>
<td>Hunte et al. 1986</td>
</tr>
<tr>
<td></td>
<td>SandRidge</td>
<td>14.1</td>
<td>2.9</td>
<td>Hunte et al. 1986</td>
</tr>
<tr>
<td></td>
<td>Golden Palms</td>
<td>12.9</td>
<td>3.8</td>
<td>Hunte et al. 1986</td>
</tr>
<tr>
<td>Jamaica</td>
<td>Montego Bay</td>
<td>6.3</td>
<td>1.8</td>
<td>Hughes et al. 1985</td>
</tr>
<tr>
<td></td>
<td>Rio Bueno</td>
<td>7.6</td>
<td>0.5</td>
<td>Hughes et al. 1985</td>
</tr>
<tr>
<td>Curacao</td>
<td>H. Beach</td>
<td>3.97</td>
<td>0.01</td>
<td>Bak et al. 1984</td>
</tr>
<tr>
<td></td>
<td>Buoy I</td>
<td>2.93</td>
<td>0.01</td>
<td>Bak et al. 1984</td>
</tr>
<tr>
<td></td>
<td>Buoy III</td>
<td>4.16</td>
<td>0.05</td>
<td>Bak et al. 1984</td>
</tr>
<tr>
<td>Panama</td>
<td>San Blas</td>
<td>3.63</td>
<td>0.24</td>
<td>Lessios 1988</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>Guayanilla</td>
<td>3.0</td>
<td>0.13</td>
<td>Vicente and Goenaga 1984</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>San Juan</td>
<td>13.8</td>
<td>-</td>
<td>Bauer 1980</td>
</tr>
<tr>
<td></td>
<td>Jobos Bay</td>
<td>2.6</td>
<td>-</td>
<td>Rivera and Vicente 1976</td>
</tr>
<tr>
<td></td>
<td>Turrumote</td>
<td>12.7</td>
<td>-</td>
<td>Craft 1975</td>
</tr>
<tr>
<td>Barbados</td>
<td></td>
<td></td>
<td></td>
<td>Hunter 1977</td>
</tr>
<tr>
<td>Virgin Islands</td>
<td></td>
<td>9</td>
<td>-</td>
<td>Ogden 1977</td>
</tr>
<tr>
<td>Venezuela</td>
<td>Pescadores</td>
<td>4</td>
<td>-</td>
<td>Weil 1980</td>
</tr>
<tr>
<td></td>
<td>Playuela</td>
<td>3</td>
<td>-</td>
<td>Weil 1980</td>
</tr>
<tr>
<td></td>
<td>Cayman</td>
<td>2.6</td>
<td>-</td>
<td>Weil 1980</td>
</tr>
</tbody>
</table>
of bare areas for coral recruitment by the algae led to a decrease in coral cover and diversity (Carpenter 1984, Lidell and Ohlhorst 1986). Rates of bioerosion and sediment production were also significantly reduced (Hunte et al. 1986), especially in those reefs where densities were very high before the mass mortality (Hunter 1977, Ogden 1976, Scoffin et al. 1980, Sammarco 1982, Weil et al. 1984).

In Puerto Rico, diseased urchins were first reported in January of 1984 in Laurel reef in La Parguera, southwest coast of Puerto Rico (Fig. 1) (Vicente and Goenaga 1984). Quantitative estimates of D. antillarum densities before the mass mortality were only available for a few localities: (a) the intertidal, high wave action, broken rock zone of Condado Beach at the northeast part of Puerto Rico with average densities of 13.8 ind/m² (Bauer 1980), (b) reef areas in Jobos Bay on the south east coast had high densities. Intense grazing of D. antillarum controlled the depth distribution of T. testudinum in this locality (Vicente and Rivera 1982, Vicente and Goenaga 1984). (c) In La Parguera, on the south-west coast, D. antillarum was more abundant on outer reef localities (12.9 ind/m²) in areas of Acropora palmata and dead coral rubble (Craft 1975). Other less intense mortalities affecting D. antillarum and other sea urchins species (Astropyga magnifica, Eucidaris tribuloides and Tripneustes ventricosus) were reported in following years for different localities in Puerto Rico (Bunkley-Williams et al. 1986, Williams 1991).

Even though populations of D. antillarum have started to come back in a few localities around the Caribbean, no significant recoveries have been reported even after two decades following the die off (Table 2) (Lessios 1988, Karlson and Levitan 1990, Cho et al. 2000, Edmunds et al. 2001, Moses et al. 2001, Chiappone et al. 2002). In La Parguera, urchins were completely absent from coral reef habitats until 1996-97, when we started to observe medium size urchins in shallow water habitats. The main objective of this project was to assess the status of these new populations of D. antillarum 17 years after the mass mortality event by determining their current abundances, distribution and size structure in several localities in La Parguera. Secondary goals included the assessment of potential relationships between the populations characteristics and the spatial heterogeneity (rugosity) of the different sites and habitats.

MATERIALS AND METHODS

**Study area:** The study was conducted at the Natural Reserve of La Parguera, on the southwest coast of Puerto Rico (Fig. 1) during 2001. The area has the most extensive coral reef formations in Puerto Rico and encompasses all major tropical coastal marine communities. Four fringing coral reefs localities and three shallow, lagoonal seagrass-covered mounds were surveyed to assess the distribution, densities and size structure of populations of the black sea urchin D. antillarum (Table 3) in these two habitats. Two of the reefs were located near shore (Caracoles and Enrique) and two were located in the mid-shelf (Media Luna and Laurel), 2-3 km from the shore line. All three seagrass mounds were about the same size (± 900 m²) and shape (round to oval), and all were in the lagoon area (Fig. 1) near isla Magueyes, where the Marine Station of the University of Puerto Rico is located.

**Population densities:** Densities of D. antillarum in each seagrass mound and reef locality were estimated using 20 m² band transects (10 x 2 m). In the seagrass mounds transects were laid across the top of the Thalassia dominated mound in 0-3 m depth interval. Transects were separated by 5 m. No urchins were observed below 3 m in these mounds. Between four and twelve band transects were laid parallel to the reef crest at each of four depth intervals (0-3, 3-7, 7-10 and > 10 m) in each of four reef sites (Fig. 1, Table 3). The number of band transects depended on the area, the reef and the physical conditions. All urchins encountered within 1 m at each side of the plastic tape were counted. A substantial amount of time was expended looking for and counting the juveniles and small
adults that were hiding in the crevices and holes of the reef structure. Qualitative surveys were carried out in several other localities.

Size structure: Usually, all the urchins found within the band transects in each depth interval, and many outside the transects, were collected with long salad pliers, put into plastic baskets and transported to a nearby sandy area where their oral test diameter was measured with calipers and a measuring tape glued to the UW slate. Between 178 and 484 urchins were collected at each site. Test diameters were
used to calculate urchins average size per depth interval and site. Then, urchins were grouped in size classes of 1.0 cm interval and the proportion of individuals in each size class was determined to assess the size structure of the different populations. Minimum damage was done to the urchins during the process and all were released after measuring.

**Substrate rugosity/heterogeneity:** Substrate rugosity was roughly estimated by carefully draping a 10 m long chain over the substrate along the center of each band transect and characterized as \( R = \left( \frac{10 - B}{A} \right) \times 100 \), where \( R \) is the rugosity ratio, \( A \) is the linear distance between the permanent re-bars (\( A = 10 \text{ m} \)) and \( B \) is the distance covered by the chain draped over the substrate reef profile. The more complex the substrate, the shorter the distance covered by \( B \) and the higher the percent rugosity. As complexity increases, the substrate rugosity ratio \( (R) \) increases and vice versa. Substrate rugosity was correlated with average population densities and sizes to assess differences between sampling areas and depth intervals with respect to the degree of substrate complexity. Those areas with a higher degree of complexity have higher number of hiding places and more microhabitats providing protection to the urchins from predation. In the high rugosity areas therefore, we expected to encounter a lower number of urchin aggregations compared to open, flat areas, where they aggregate for protection.

**RESULTS**

**Population densities and distribution:** Overall, average densities were low across all sites (0.83 - 1.55 ind/m²) when compared to pre-mortality densities (Table 2). In the seagrass mounds, urchins were found only in the shallow areas (<3 m) where they formed tight aggregations during daytime. Densities varied across the three seagrass sites (1.09 ± 0.6 - 1.30 ± 0.6 ind/m²), but no significant differences were found (Fig. 2A). In the reef sites, urchins were found from the shallow,

<table>
<thead>
<tr>
<th>Locality</th>
<th>Reef</th>
<th>( D. \text{ antillarum (ind/m²)} )</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Florida</td>
<td>Looe Key</td>
<td>0.013</td>
<td>Chiappone et al. 2002</td>
</tr>
<tr>
<td>Florida</td>
<td>American Shoal</td>
<td>0.01</td>
<td>Chiappone et al. 2002</td>
</tr>
<tr>
<td>Jamaica</td>
<td>Discovery Bay</td>
<td>0.02</td>
<td>Haley et al. 2001</td>
</tr>
<tr>
<td>Jamaica</td>
<td>Discovery Bay</td>
<td>0.1</td>
<td>Haley et al. 2001</td>
</tr>
<tr>
<td>Jamaica</td>
<td>Discovery Bay</td>
<td>0.6</td>
<td>Cho et al. 2000</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>Corona 1</td>
<td>1.39 (± 0.62)</td>
<td>This study</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>Corona 2</td>
<td>1.08 (± 0.63)</td>
<td>This study</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>Corona 3</td>
<td>1.31 (± 0.84)</td>
<td>This study</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>Caracoles</td>
<td>1.55 (± 1.19)</td>
<td>This study</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>Enrique</td>
<td>1.19 (± 0.62)</td>
<td>This study</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>Media Luna</td>
<td>0.86 (± 0.62)</td>
<td>This study</td>
</tr>
<tr>
<td>Puerto Rico</td>
<td>Laurel</td>
<td>0.83 (± 0.86)</td>
<td>This study</td>
</tr>
</tbody>
</table>
near shore platform to about 5 m deep and few urchins were found below 10 m. Average densities varied from 0.83 ± 0.8 in Laurel to 1.55 ± 1.1 ind/m² in Caracoles reef (Table 3), but no significant differences were found across reef sites. Population densities were higher in the inner, close-to-shore reefs compared to the exposed reefs (Fig. 2A).

Within each site, urchin densities decreased significantly with increasing depth ($r^2 = -0.60$) and densities were significantly higher ($0.56 ± 0.14 – 2.33 ± 1.1$ ind/m²) ($F=5.97$, $p<0.05$) in shallow platform (0-3 m) and upper fore-reef (3-7 m) habitats compared to deeper (>7 m) habitats ($0.01 ± 0.02 – 0.88 ± 1.06$ ind/m²) (Fig. 2B, Table 2). The highest urchin density ($2.33 ± 1.14$ ind/m²) was found in the upper fore reef habitat at Caracoles reef, comparable to some pre-mass mortality densities in Caribbean reefs.

**Size and size structure:** In general, populations were dominated by medium to large individuals (6-9 cm in test diameter) (Fig. 3). In the seagrass mounds, urchin aggregations were formed mainly by medium sized urchins with high abundances of individuals between 5 and 8 cm in diameter and very few juveniles (Fig. 4). One of the inner reefs (Caracoles) showed a similar size class structure to that of the seagrass mounds, Enrique and Media Luna however, had higher abundances of medium-large and large individuals (6 to 9 cm in test diameter) with few small juveniles (<4 cm in test diameter). Laurel showed an almost normal distribution with a higher abundance of small sizes and lower abundances of medium-large and large individuals compared to the other sites (Fig. 4). High abundances of juveniles however, were observed when snorkeling in protected, back reef and lagoonal reef habitats, as well as some semi-exposed and spatially complex shallow platforms and short slopes, indicating that higher recruitment/survival is occurring in these habitats compared to the generally more exposed reef habitats studied here. The overall average urchin size (diameter) for the reefs and *Thalassia* mounds was $6.75 ± 1.6$ cm. Urchins in Enrique reef were significantly larger ($7.48 ± 1.42$ cm) with higher abundances of larger individuals (Fig. 3), compared to all the other sites ($6.32 ± 1.4 – 6.92 ± 1.5$ cm). Average sizes varied across depth intervals within reefs, but no significant differences were found (Fig. 3). Medium to large size urchins dominated at all depths with few small urchins in the shallow, complex habitats. No pattern was found
between average test diameter and the different depths sampled. Some reefs had smaller urchin sizes in shallow habitats (more juveniles like in Laurel), while smaller urchins were found at intermediate depths in other reefs (Enrique and Caracoles). Media Luna presented similar average test diameters at the two depths, and there was no relationship between mean sea urchin test diameter and population density ($r^2 = 0.11$).

Higher numbers of aggregations with higher number of urchins/aggregation were found in low complexity habitats (reef platforms and seagrass mounds) (Fig. 5). The number of urchin aggregations and the number of urchins per aggregation were negatively ($r = -0.772$, $p<0.001$ and $r = -0.778$, $p<0.001$ respectively) correlated (Pearson’s) with reef rugosity (spatial heterogeneity).

**DISCUSSION**

It has taken at least 17 years for new population of *D. antillarum* to start showing some clear signs of recovery in many localities around the Caribbean. The most recent
studies of recovery in Jamaica and Florida found mean urchin densities ranging from 0.013 to 0.6 ind/m² (Forcucci 1994, Haley and Solandt 2001, Chiappone et al. 2002), well below the mean densities found in this study. This research showed variable mean urchin densities ranging from 0.56-1.88 ind/m², with some habitats already supporting similar densities (2.33 ind/m²) to those reported for many Caribbean reef localities before the mass mortality (Rivera et al. 1976, Bak et al. 1984, Weil et al. 1984, Lessios 1988). Even at these low densities however, shallow and intermediate reef habitats showed a remarkable reduction in algal cover (substrate appears “clean” of the green-brownish algal cover) compared to similar habitats (same depths) with no urchins or lower densities.

Overall, populations of *D. antillarum* in the reefs studied were unevenly distributed, with a patchy pattern in many localities with higher urchin densities in shallow, well lit areas, probably a result of the stochastic recruitment of planktonic larvae, the differential mortality of juveniles, the higher spatial heterogeneity, presence of refuges and the preference for algae (highly abundant) as a food source of this species in these habitats. This pattern was common before the mass mortality event in many localities (Stearn et al. 1977, Ogden and Lobel 1978, Scoffin et al. 1980, Weil 1980, Weil et al. 1984, Carpenter 1990). Deep distributions in some reef sites and other coastal habitats before the mass mortality were probably the result of intra-specific competition in the crowded shallow habitats.

Even though predation pressure is highly reduced due to low population densities (or absence) of the urchin’s main predators, *D. antillarum* still showed the typical diel behavior, being more active during night time and hiding during the day. All of our surveys were conducted during the day, in complex habitats we probably missed a few urchins even though extra effort was put to check crevices and holes. More recent qualitative surveys during night time indicated that our estimates might be conservative in some localities. Also, higher abundances of juveniles were observed during the night, indicating that they hide deep in the reef structure during the day and could be easily missed in day light counts in complex habitats. One particular reef, El Atravesado, had significant higher densities with higher number of urchins inhabiting deeper (8-10 m) habitats and higher abundances of juveniles (pers. observations). This reef is formed by living and dead stands of the staghorn coral *A. palmata* extending down to 5 m in some areas, leveling off at about 7-8 m, and continuing on a wide platform with living stands of *A. cervicornis* and small stands of large *A. palmata* colonies intermingled with massive *Montastraea* spp. and other massive species. The high complexity of this area might provide more/better refuge and food for the urchins. Furthermore, because this reef runs perpendicularly to the coast (N to S), it basically blocks the currents flowing from east-to-west and might receive a higher number of larvae after each reproductive event.

Before the mass mortality, population densities for *D. antillarum* were characteristically higher in areas with high structural complexity and significantly lower in areas with low
structural complexity (Weil et al. 1984). It was surprising to find relatively large numbers of urchins in the open Thalassia mounds. This might indicate that recruitment is not limited to highly complex, calcium carbonate habitats, or that there is low predation pressure and urchins can move long distances in the open (Weil 1980), or any combination of these. D. antillarum feeds on Thalassia leaves (Ogden et al. 1973), however, it hardly digest these as they come out almost complete in their feces (Weil 1980), rather, they digest the epiphyte community living on the blades. Furthermore, Diadema tends to be gregarious in open areas (Levitan 1988). More and larger aggregation were found in less complex habitats and in the Thalassia mounds, juveniles were always inside the aggregates rather than exposed at the edges, further supporting the hypothesis that this behavior provides mutual protection between closely spaced urchins in open areas (Hunte and Younglao 1988). A higher density of spines is a powerful predator deterrent when refuges are not available (Randall et al. 1964). This behavior seems to be conserved and even in the absence of predators, urchins tend to aggregate during the day in open spaces.

In La Parguera, recovering populations of D. antillarum were mostly found in shallower, spatially complex reef habitats and large numbers of aggregations with many individuals were found in less complex, open habitats (shallow reef flats and seagrass mounds, supporting the idea that this behavior provides protection to these organisms), and small urchins were usually hidden during the day. All of these support the hypothesis that the distribution, densities and size structure of D. antillarum populations are ultimately the result of the source of larvae, successful recruitment, morphological complexity of the habitat, food availability, and differential mortality of juveniles (predation pressure) (Weil et al. 1984).

The higher densities of urchins (compared to other localities in the Caribbean), the presence of large numbers of reproductive adults with abundant juveniles in many localities, no signs of disease or unhealthy individuals, and the fact that up to 1996, there were hardly any urchins in the area, indicate that even though the distribution of populations is still patchy on large spatial scales, local populations of the sea urchin D. antillarum were healthy and seem to be slowly recovering in La Parguera. Similar results were recently reported for St. Croix (Miller et al. 2003). The low densities and/or
absence of the main predators of Diadema (15 fish species, Cassis helmet gastropods and the spiny lobster Panulirus argus), (Randall et al. 1964, Ogden et al. 1973), might favor a faster build up in the numbers of urchins. When densities increase enough to support a higher reproductive output, rate of recovery might increase due to the abundance of food, the general lack of competition and low predation pressure in most reef habitats in this area.

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