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

Ernesto Weil, Juan L. Torres & Mayra Ashton
Department of Marine Sciences, University of Puerto Rico. PO Box 908, Lajas Puerto Rico 00667; eweil@caribe.net; jltorres38@ prtc.com; ashtonmayra@hotmail.com

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 ($r^2 = -0.60$) 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).

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005

219

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

220

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005

TABLE 1

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

CUADRO 1

Coordenadas geográficas y características de los sitios muestreados en La Parguera, Puerto Rico

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

TABLE 2

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

CUADRO 2

Densidades de Diadema antillarum *antes y después del evento de mortalidad masiva en algunas localidades y arrecifes en todo el Caribe*

Locality	Reef	Before (ind/m²)	After (ind/m²)	Source
Barbados	North Bellairs	17.3	1.8	Hunte *et al*. 1986
	SandRidge	14.1	2.9	Hunte *et al*. 1986
	Golden Palms	12.9	3.8	Hunte *et al*. 1986
Jamaica	Montego Bay	6.3	1.8	Hughes *et al*. 1985
	Rio Bueno	7.6	0.5	Hughes *et al*. 1985
Curacao	H. Beach	3.97	0.01	Bak *et al*. 1984
	Buoy I	2.93	0.01	Bak *et al*. 1984
	Buoy III	4.16	0.05	Bak *et al*. 1984
Panama	San Blas	3.63	0.24	Lessios 1988
Puerto Rico	Guayanilla	3.0	0.13	Vicente and Goenaga 1984
Puerto Rico	San Juan	13.8	-	Bauer 1980
	Jobos Bay	2.6	-	Rivera and Vicente 1976
	Turrumote	12.7	-	Craft 1975
Barbados		23	-	Hunter 1977
Virgin Islands		9	-	Ogden 1977
Venezuela	Pescadores	4	-	Weil 1980
	Playuela	3	-	Weil 1980
	Cayman	2.6	-	Weil 1980

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005

221

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

222

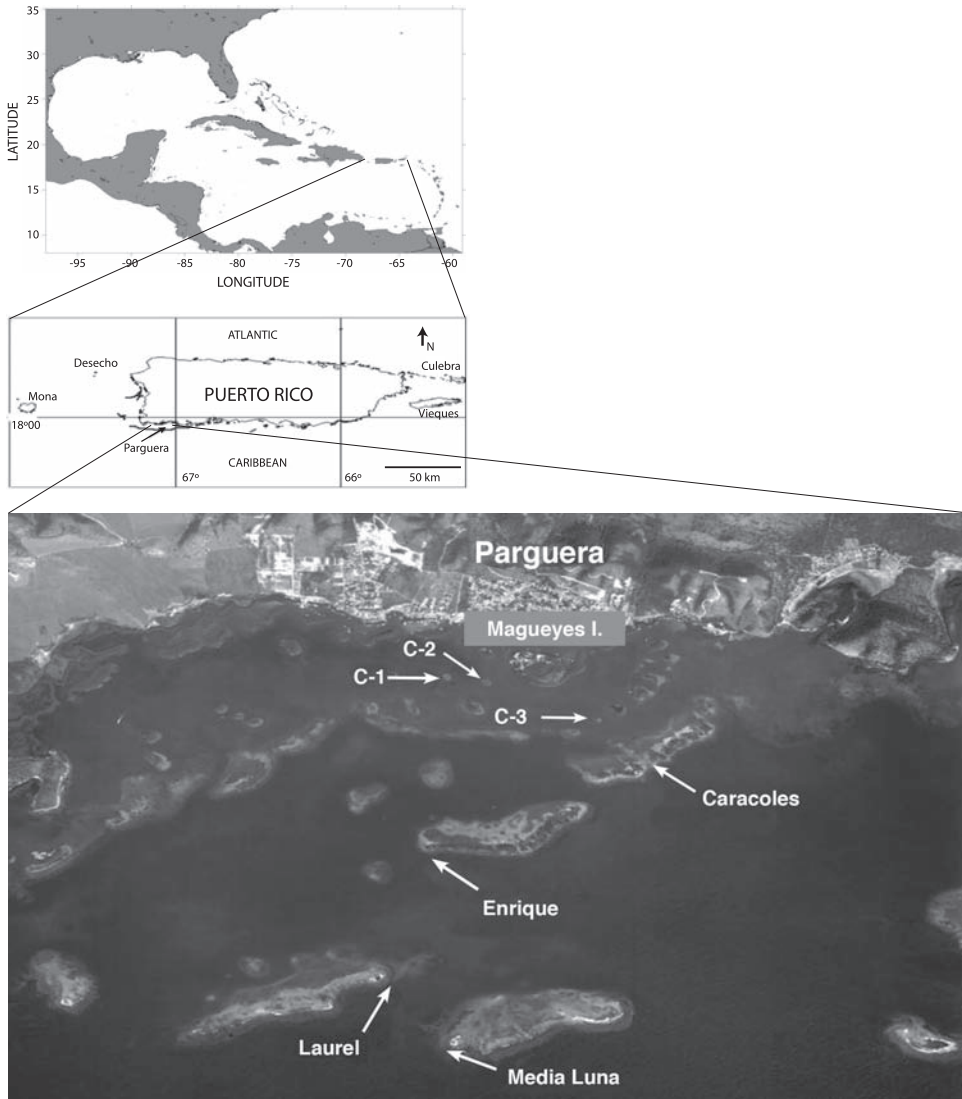Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005

Fig. 1. Geographic location of Puerto Rico and La Parguera. Aerial photo of La Parguera showing location of reefs and seagrass mounds (C-1 = Corona 1, C2 = Corona 2, C3= Corona 3) sampled.

Fig. 1. Localización geográfica de Puerto Rico y la Parguera. Fotografía aérea de La Parguera mostrando la localización de los arrecifes y pastos marinos (C-1 = Corona 1, C2 = Corona 2, C3= Corona 3) muestreados.

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

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005

223

Locality	Reef	*D. antillarum* (ind/m²)	Source
Florida	Looe Key	0.013	Chiappone *et al*. 2002
Florida	American Shoal	0.01	Chiappone *et al*. 2002
Jamaica	Discovery Bay	0.0	Haley *et al*. 2001
Jamaica	Discovery Bay	0.02	Haley *et al*. 2001
Jamaica	Discovery Bay	0.1	Cho *et al*. 2000
Jamaica	Discovery Bay	0.6	Cho *et al*. 2000
Puerto Rico	Corona 1	1.39 (± 0.62)	This study
Puerto Rico	Corona 2	1.08 (± 0.63)	This study
Puerto Rico	Corona 3	1.31 (± 0.84)	This study
Puerto Rico	Caracoles	1.55 (± 1.19)	This study
Puerto Rico	Enrique	1.19 (± 0.62)	This study
Puerto Rico	Media Luna	0.86 (± 0.62)	This study
Puerto Rico	Laurel	0.83 (± 0.86)	This study

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= [(10 − B)/A] x 100, where R is the rugosity ratio, A is the linear distance between the permanent re-bars (A = 10 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,

224

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005

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).
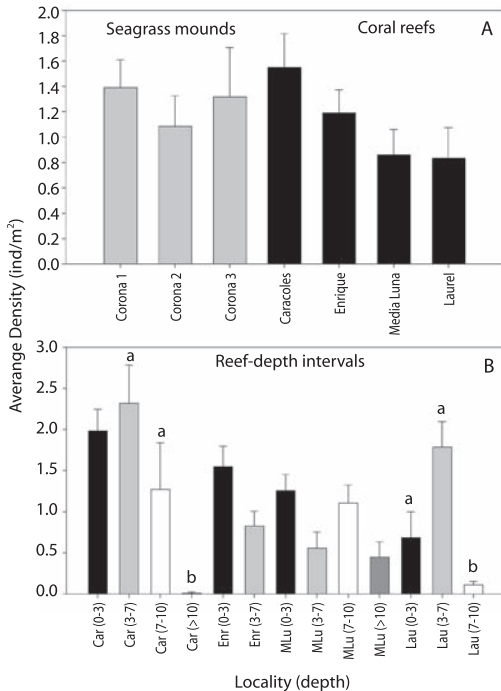

Fig. 2. Average densities (SD) of *D. antillarum* in (A) each one of the reefs and seagrass mounds sampled and (B) at the different depth intervals within each reef. Different letters over the bars indicate significant differences in mean density between those means. Different bar colors indicate different depth intervals (Black= < 3m, gray= 3-7 m, white= 7-10 m and dark gray= >10 m). Car = Caracoles, Enr = Enrique, MLu = Media Luna, Lau = Laurel.

Fig. 2. Densidades promedio (DS) de *D. antillarum* en (A) cada uno de los arrecifes y pastos marinos muestreados y (B) a los diferentes intervalos de profundidad entre cada arrecife. Las diferentes letras sobre las barras indican diferencias significativas en la densidad promedio entre esos promedios. Las diferentes barras de color indican los diferentes intervalos de profundidad (negro =< 3 m, gris = 3-7 m, blanco = 7-10 m y gris oscuro => 10 m). Car = Caracoles, Enr = Enrique, MLu = Media Luna, Lau = Laurel.

Within each site, urchin densities decreased significantly with increasing depth ($r^2 = -0.60$) and densities were significantly higher ($0.56 \pm 0.14 - 2.33 \pm 1.1$ 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 ($0.01 \pm 0.02 - 0.88 \pm 1.06$ 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 ($6.32 \pm 1.4 - 6.92 \pm 1.5$ 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

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005
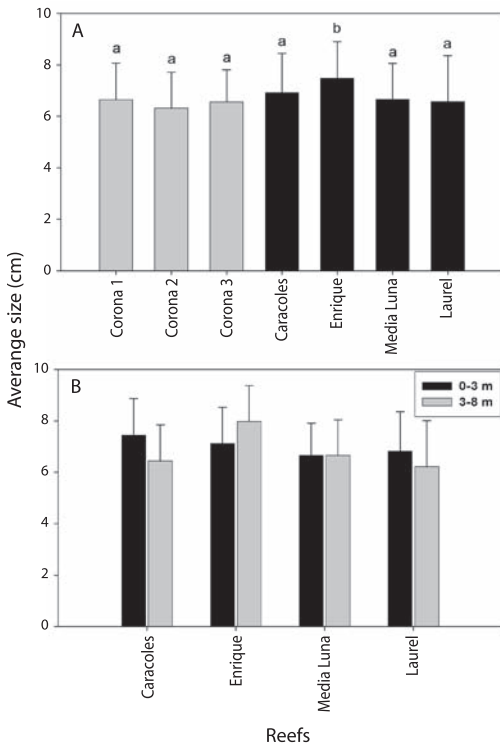
225

Fig. 3. Average size (test diameter in cm) in (A) each one of the reefs and seagrass sites sampled and (B) at the different depth intervals within each reef. Different letters over the bars indicate significant differences in mean density between those means.

Fig. 3. Talla promedio (diámetro de la test en cm) en (A) cada uno de los arrecifes y pastos marinos muestreados y (B) a los diferentes intervalos de profundidad entre cada arrecife. Las letras diferentes sobre las barras indican las diferencias significativas en la densidad promedio entre los promedios.

Fig. 4. Size (age) frequency structure for the different sub-populations of the sea urchin *D. antillarum* in the different sampled sites.

Fig. 4. Estructura (frecuencia) de tallas (edad) de las diferentes subpoblaciones del erizo negro *D. antillarum* en los sitios muestreados.

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 tests diameters at the two depths, and there was no relationship between mean sea urchin test diameter and population density ($r^2 = 0.11$).

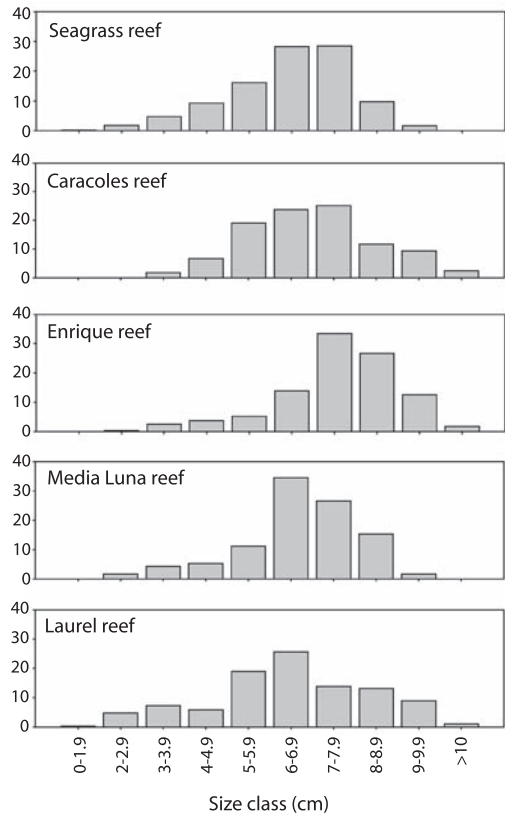Higher numbers of aggregations with higher number of urchins/aggregation were found in low complexity habitats (reef platforms and seagrass mounds) (Fig. 5). The number of urchin aggregations and the number of urchins per aggregation were negatively ($r= -0.772$, $p<0.001$ and $r= -0.778$, $p<0.001$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

226

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005
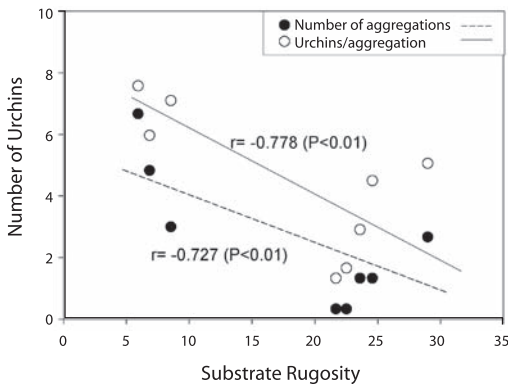
Fig. 5. Relationship between the number of urchins per aggregation and the number of aggregations with the spatial heterogeneity (= rugosity) in reef localities sampled in La Parguera.

Fig. 5. Relaciones entre el número de erizos de mar por agregación y el número de agregaciones con la heterogeneidad espacial (= rugosidad) en las localidades arrecifales muestreadas en La Parguera.

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

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005

227

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.

The average size of urchins in La Parguera was comparable with those reported for other localities prior to the mass mortality event (Ogden *et al*. 1973, Bauer 1980, Weil *et al*. 1984). In Barbados, Hunte and Younglao (1988) found that mean urchin size increased with distance from the reef front. This was not the case in our study area where no significant trend in mean population size across the reef structure was found. Overall, a dominance of bigger individuals (more than 6.0 cm) at all depths was typical for Parguera. Nevertheless, a more normal distribution was found at inter-mediate depths than in shallow-waters. Small sized individuals were more common in shallow reef waters than in the *Thalassia* mounds, where aggregations of up to 20 individu-als were frequently found. 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 possibly indicating that higher recruit-ment/survival is occurring in these habitats compared to the generally more exposed reef habitats studied here.

Population size structure provides an indi-cation of the dynamics of past recruitment/survival events in the different populations. Populations with high proportions of urchins of similar size might indicate a successful recruit-ment of a particular reproductive event/season. By documenting the population size structure and characterizing the minimum reproductive size and the growth rate, it is possible to predict the reproductive contribution of that population to the genetic pool. Our results showed that most populations were unimodal, dominated by medium size urchins with low proportions of very large and very small individuals.

In La Parguera, recovering populations of *D. antillarum* were mostly found in shal-lower, spatially complex reef habitats and large numbers of aggregations with many individu-als were found in less complex, open habitats (shallow reef flats and seagrass mounds, sup-porting the idea that this behavior provides pro-tection to these organisms), and small urchins were usually hidden during the day. All of these support the hypothesis that the distribu-tion, densities and size structure of *D. antil-larum* populations are ultimately the result of the source of larvae, successful recruitment, morphological complexity of the habitat, food availability, and differential mortality of juve-niles (predation pressure) (Weil *et al.* 1984).

The higher densities of urchins (compared to other localities in the Caribbean), the pres-ence 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 over 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.

ACKNOWLEDGMENTS

RESUMEN

Trabajos recientes indican que las poblaciones del erizo negro *Diadema antillarum* parecen estar recuperándose lentamente en varias localidades del Caribe, luego de 15 años de ausencia. En La Parguera, Puerto Rico, estos erizos estuvieron ausentes hasta 1996, cuando individuos aislados de tallas medianas y pequeñas agregaciones comenzaron a ser observadas en zonas arrecifales someras. Para evaluar el estado (distribución, densidad y estructura de la talla) de las poblaciones de *D. antillarum*, 17 años después de la mortalidad, 12 transectos de banda de 20 m² (10 x 2m) en cada uno de cuatro intervalos de profundidad (0-3, 3-7, 7-11 y >11m) en cuatro arrecifes y seis-ocho transectos de banda en cada uno de dos intervalos de profundidad (0-3 y > 3 m) en montículos de pastos marinos en la laguna fueron muestreados en el 2001. Todos los erizos en los transectos de banda en dos intervalos de profundidad (0-3 y 3-8 m) fueron recolectados y medidos (diámetro de la test) *in situ* para determinar la talla promedio y talla (edad) de la estructura de la población. En general, las densidades promedio fueron bajas (0.83 - 1.39 ind/m²) y no mostraron diferencias significativas (F=1.29, p= 0.125) entre sitios arrecifales (0.83-1.39 ind/m²) y montículos de pastos marinos (1.09 ± 0.6-1.30 ± 0.6 ind/m²). Los erizos solo fueron encontrados en áreas someras (<3 m) en los montículos de pastos marinos donde forman agregaciones durante el día. Las densidades disminuyeron con la profundidad (r² = -0.60) y fueron significativamente más altas (F= 5.97, p<0.001) en las plataformas someras (0.89 ± 0.69–1.98 ± 0.65 ind/m²) (0-3m), y el frente arrecifal (0.56 ± 0.14 – 2.33 ± 1.1 ind/m²) (3-7m) que en hábitats más profundos (>7m) (0.01 ± 0.02 – 0.88 ± 1.06 ind/m²). El tamaño promedio de los erizos fue significativamente mayor (K-W, H= 165.19, p<0.001) en Enrique (Mediana = 7.7cm) comparado con las otras localidades. Las poblaciones en los pastos marinos estuvieron dominadas por tallas medianas a grandes. Entre los arrecifes, las tallas no variaron significativamente con respecto a los intervalos de profundidad con la predominancia de erizos de mar de tallas medianas a grandes. Un número mayor de agregaciones y un número mayor de erizos por agregación se encontraron en hábitats menos complejos (rugosidad) (Pearson, r= -0.772, p<0.001 y r= -0.778, p<0.001 respectivamente) apoyando la hipótesis de que este comportamiento provee protección. Las densidades promedio estuvieron bastante por debajo de las densidades pre-mortalidad en Puerto Rico. Los resultados de este estudio indican que las poblaciones del erizo negro *D. antillaron* en la Parguera muestran una recuperación significativa pero lenta luego de 17 años de la mortalidad masiva.

Palabras claves: *Diadema antillarum*, recuperación de la población, erizo negro de mar, mortalidad masiva, Caribe, Puerto Rico.

REFERENCES

Bak R.P.M., M.J.E. Carpay and E.D. de Ruyter van Steveninck. 1984. Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curacao. Mar. Ecol. Prog. Ser. 177: 105-108.

Bauer J.C. 1980. Observations on geographical variations in population density of the echinoid *Diadema antillarum* within the western North Atlantic. Bull. Mar. Sci. 30: 509-515.

Bauer J.C. and A.C. Agerter. 1987. Isolation of bacteria pathogenic for the sea urchin *Diadema antillarum* (Echinodermata: Echinoidea). Bull. Mar. Sci. 40: 161-165.

Bellwood D.R., T.P. Hughes, C. Folke and M.Nyström. 2004. Confronting the coral reef crisis. Nature 149: 827-833.

Bunkley-Williams L., E.H. Williams Jr., and A.G.Bunkley Jr. 1986. Isolated mortalities of the sea urchins *Astropyga magnifica* and *Eucidaris tribuloides* in Puerto Rico. Bull. Mar. Sci. 38: 391-393.

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005

229

Carpenter R.C. 1981. Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. J. Mar. Res. 39: 749-765.

Carpenter R.C. 1984. Predator and population density control of homing behavior in the Caribbean echinoid *Diadema antillarum*. Mar. Biol. 82: 101-108.

Carpenter R.C. 1985. Sea urchin mass mortality: effects on reef algal abundance, species composition, and metabolism and other coral reef herbivores. Proc. 5th Int. Coral Reef Congress. 4: 53-60.

Carpenter R.C. 1990. Mass mortality of *Diadema antillarum*. I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. Mar. Biol. 104: 67-77.

Chiappone M., Swanson, D.W., Miller, S.L. & S.G. Smith. 2002. Large scale surveys on the Florida Reef Tract indicate poor recovery of the long-spined sea urchin *Diadema antillarum*. Coral Reefs 21: 155-159.

Craft L.L. 1975. Aspects of the biology of the crab *Percnon gibbesi* (Milne Edwards) and its commensal association with the sea urchin *Diadema antillarum* Phillipi. M.S. Thesis, University of Puerto Rico. Mayagüez, Puerto Rico, USA.

Edmunds P.J. & R.C., Carpenter.2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. www.pnas.org/cgi/doi/10.1073/pnas.071524598. April 24, 2001.

Forcucci D. 1994. Population density, recruitment and 1991 mortality event of *Diadema antillarum* in the Florida keys. Bull. Mar. Sci. 54: 917-928.

Glynn P.W. 1968. Mass mortalities of echinoids and other reef flat organisms coincident with mid-day, low water exposures in Puerto Rico. Mar. Biol. 1: 226-243.

Haley M.P. & J.L. Solandt, 2001. Population fluctuations of the Sea Urchins *Diadema antillarum* and *Tripneustes ventricosus* at Discovery Bay, Jamaica: a case of biological succession? Caribbean Journal of Science 37: 239-245.

Hay M.E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology 65: 446-454.

Hughes T.P. 1994. Catastrophes, phase shifts and large scale degradation of a Caribbean coral reef. Science 265: 1547-1551.

Hughes T.P. 1989. Community structure and diversity of coral reefs: the role of history. Ecology 70: 275-279.

Hughes T.P., B.D. Keller, J.B.C. Jackson & M.J. Boyle. 1985. Mass mortality of the Echinoid *Diadema antillarum* Philippi in Jamaica. Bull. Mar. Sci. 36: 377-84.

Hughes T.P., D.C. Reed & M.J. Boyle. 1987. Herbivory on coral reefs: community structure following mass mortalities of sea urchins. J. Exp. Mar. Biol. Ecol. 113: 39-59.

Hunte W. & D.Younglao. 1988. Recruitment and population recovery of *Diadema antillarum* (Echinodermata; Echinoidea) in Barbados. Mar. Ecol. Prog. Ser. 45: 109-119.

Hunte W., I. Côté & T. Tomascik. 1986. On the dynamics of the mass mortality of *Diadema antillarum* in Barbados. Coral Reefs 4: 135-139.

Hunter I.G. 1977. Sediment production by *Diadema antillarum* on a Barbados fringing reef. Proc. 3rd Int. Coral Reef Symp. 1: 105 –109.

Jackson J.B.C. & K.W. Kaufmann. 1987. *Diadema antillarum* was not a keystone predator in cryptic reef environments. Science 235: 687-689.

Karlson R.H. & D.R. Levitan.1990. Recruitment-limitation in open population of *Diadema antillarum*: an evaluation. Oecologia 84:40-44

Laydoo R. 1984. Recent Mass Mortality of the Sea Urchin *Diadema antillarum* populations in Tobago, West Indies. Pres. Ann. Meet. Assoc. Island. Mar. Lab. Caribb., 18th Trinidad.

Lessios H.A., J.D.Cubit, R.D. Robertson, M.J. Shulman,, M.R.Parker, S.D. Garrity & S.C. Levings. 1984a. Mass mortality of *Diadema antillarum* on the Caribbean coast of Panama. Coral Reefs 3: 173-182.

Lessios H.A., D.R. Robertson & J.D. Cubit. 1984b. Spread of *Diadema* mass mortality through the Caribbean. Science 226: 335-337

Lessios H.A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: What have we learned? Ann. Rev. Ecol. Syst. 19: 371-393.

Levitan D.R. 1988. Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Philippi. Oecologia 76: 627-629.

Lewis S.M. & P.C. Wainwright. PC.1985. Herbivore Abundance and Grazing Intensity on a Caribbean Coral Reef. J. Mar. Biol. Ecol. 7: 215-288.

Liddell W.D. & S.L. Ohlhorst. 1986. Changes in benthic community composition following the mass mortality of *Diadema* at Jamaica. J. Exp. Mar. Biol. Ecol. 95: 271-278.

Miller R.J., A.J. Adams, N.B. Ogden, J.C. Ogden & J.P. Ebersole 2003. *Diadema antillarum* 17 years after

230

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005

mass mortality: is recovery beginning on St. Croix? Coral Reefs 22: 181-187.

Mortesen T. 1940. A monograph on the Echinoidea. 3 (1-2) Aulodonta (with additions to vol. 2): 1-370, 1-22. CA Reitzel, Copenhagen.

Moses C.S. & R.M. Bonem. 2001. Recent population dynamics of *Diadema antillarum* and *Tripneustes ventricosus* along the north coast of Jamaica, W.I. Bull. Mar. Sci. 68: 327-336.

Ogden J.C. 1976. Some aspects of herbivore-plant relationships on Caribbean reefs and seagrass beds. Aq. Bot. 2: 103-116.

Ogden J.C. 1977. Carbonate-sediment production by parrot fish and sea urchins on Caribbean reefs. Studies in Geology 4: 281-288.

Ogden J.C., R.A. Brown & N. Salesky. 1973. Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. Science 182: 715-71.

Ogden J.C. and P.S. Lobel. 1978. The role of herbivorous fishes and urchins in coral reef communities. Env. Bio. Fish 3: 49-63.

Pearse J.S. 1974. Reproductive patterns of tropical reef animals: three species of sea urchins. Proc. 2nd Int. Coral Reef Symp. 1: 235-240.

Randall J.E., R.E. Schroeder & W.A. Starck II. 1964. Notes on the biology of the echinoid *Diadema antillarum*. Carib. J. Sci. 4: 421-433.

Rivera J.A. & V.P. Vicente. 1976. *Diadema antillarum* (Philippi): Enhancement of coral species in *Thalassia* beds. Proc. Assoc. Is. Mar. Lab. Carib. 12:18.

Robertson D.R. 1991. Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panama indicates food limitation. Mar. Biol. 111: 437-444.

Sammarco P.W. 1972. Some aspects of the ecology of Diadema antillarum Philippi: food preferences and effect of grazing. Special problems report to the West Indies Lab. of Fairlaigh Dickinson University, St. Croix: 1 - 47.

Sammarco P.W. 1980. *Diadema* and its relationship to coral spat mortality: grazing competition and biological disturbance. J. Mar. Res. 32: 254-272.

Sammarco P.W. 1982. Effects of grazing by *Diadema antillarum* Philippi on algal diversity and community structure. J. Exp. Mar. Biol. Ecol. 65: 83-105.

Sammarco P.W., J.S Levinton & J.C. Ogden. 1974. Grazing and control of coral reef community structure by *Diadema antillarum* Philippi (Echinodermata: Echinoidea):A preliminary study. J. Mar. Res 32: 47-53.

Scoffin T.P., G.W. Stearn, D. Boucher, P. Fridl, G.W. Mocokins, J.G. Hunter & J.K. McGeachy. 1980. Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part II. Erosion, sediment and internal structure. Bull.Mar.Sci. 30: 475-508.

Solandt J.L. & A.C. Campbell 2001. Macroalgal feeding characteristics of the sea urchin *Diadema antillarum* Phillipi at Discovery Bay, Jamaica. Carib. J. Sci. 37: 227-238.

Stearn G.W., T.P. Scoffin & P.W. Martindale. 1977. Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part I. Zonation and productivity. Bull. Mar.Sci. 27: 473-510.

Vicente V.P. & J.A. Rivera. 1982. Depth limits of the seagrass *Thalassia testudinum* (Konig) in Jobos and Guayanilla bays, Puerto Rico. Carib. J. Sci. 17: 73-79.

Vicente V.P. & C. Goenaga. 1984. Mortandades masivas del erizo de mar *Diadema antillarum* (Philippi) en Puerto Rico. Centro para Estudios Energéticos y Ambientales, Div. Ecología Marina, Univ. Puerto Rico. Reporte CEER-M-195. 30 p.

Weil E. 1980. Papel del erizo negro *Diadema antillarum* (Philippi) en la regulación de la estructura comunitaria de algunos arrecifes del Parque Nacional Morrocoy, Venezuela. Tésis, Universidad Central de Venezuela, 180 p.

Weil E., F. Losada & D. Bone.1984. Spatial variations in density and size of the echinoid *Diadema antillarum* Phillipi on some Venezuelan coral reefs. Bijdragen tot de Dierkunde. 54: 73-82.

Williams E.H. Jr. 1991. Threat to black sea urchins. Nature 352: 385.

Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 53 (Suppl. 3): 219-231, December 2005

231