Abundance, distribution and size structure of *Diadema antillarum* (Echinodermata: Diadematidae) in South Eastern Cuban coral reefs

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Abstract: The 1983-1984 mass mortality event of *Diadema antillarum* affected more than 93% of the total Caribbean population. Although there are no records about the status of *Diadema* populations before and after die-off on Cuban reefs, anecdotal information suggests that populations were struck. We analyzed spatial variation in the abundance and size structure of *D. antillarum* in 22 reefs sites in Jardines de la Reina, from June 2004 to September 2005. Counts of *Diadema* were performed in five 30x2m transects at each sampling site and sampling time, and test diameters were measured in September 2005 at the same fore reefs. Abundances were higher at reef crests (mean densities 0.08-2.18 ind./m^2), while reef slope populations reached a maximum site level of 0.13 ind./m^2 at only one site and showed values up to three orders of magnitude lower than those from reef crests. Highest abundance occurred at the west margin of major channels between keys where larval recruitment seems to be favored by local oceanographic features and facilitated by the abundance of *Echinometra lucunter*. The size frequency distribution of *D. antillarum* indicates that recruitment began to be noticeable three years before September 2005, suggesting these populations were depleted in the past and they are recovering now. Rev. Biol. Trop. 58 (2): 663-676. Epub 2010 June 02.

Keywords: *Diadema antillarum*, sea urchin recovery, population density, size structure, Jardines de la Reina, Cuba.

The 1983-1984 mass mortality of *Diadema antillarum* (Philippi 1845) in the Caribbean produced several ill effects on many coral reefs in the region. Beginning in Panama, in January 1983, the mortality spread throughout the area following the course of prevailing surface currents (Lessios *et al.* 1984). Due to an unidentified pathogen, *Diadema* populations were depleted by more than 93% failing to recover in almost the two subsequent decades (Lessios *et al.* 1984, Lessios 1988, 1995, 2005). It was not until the beginning of the 2000´s, with the exception of Barbados where populations recovered up to 57% of pre-mortality levels (Hunte & Younglao 1988), that noticeable increases in population densities were reported for the first time in Jamaica (Aronson & Precht 2000, Edmunds & Carpenter 2001, Moses & Bonem 2001) and St. Croix (Miller *et al.* 2003); events that were followed by a series of subsequent recovery reports in Costa Rica (Alvarado *et al.* 2004, Fonseca *et al.* 2006, Myhre & Acevedo-Gutiérrez 2007), Puerto Rico (Weil *et al.* 2005), Jamaica, St. Croix, Barbados, Grenada, Bonaire, Belize (Carpenter & Edmunds 2006), Curaçao (Debrot & Nagelkerken 2006), Dominica (Steiner & Williams 2006) and Yucatan (Jordán-Garza *et al.* 2008).

In Cuba there are no records about the status of *Diadema* populations before die-off

[only one paper about methodological aspects was published, Herrera-Moreno *et al.* (1981)], nor scientific reports documenting the mortality. However, anecdotal information indicates that *Diadema* abundances decreased considerably around Cuban reefs at the beginning of the 1980´s (Alcolado P.M., pers. comm.). As Lessios (2005) pointed out, pre-mortality density data are essential for determining the degree of subsequent recovery, so any apparent recovery of *Diadema* populations in Cuban reefs should be discussed with caution. In spite of the importance of *Diadema* as a keystone species in structuring coral reefs, available information about its current status in Cuban reefs is scarce. Except for local density data, no other aspects of the species ecology have been reported. The most complete data come from The Atlantic and Gulf Rapid Reef Assessment (AGRRA) surveys carried out at 199 reef sites around the Cuban archipelago from 1999 to 2003. Using that information, Alcolado *et al.* (unpublished data) only reported punctual values of *Diadema* densities showing that there is still little evidence of a country-wide recovery. Williams & Polunin (2001) and Guardia *et al.* (2004a, b, 2006), reported zero or near zero densities in Cuban Western reefs, while the most recent data correspond to surveys in the North coast of Havana where Caballero *et al.* (2006) reported mean densities of *D. antillarum* in collection sites monitored by scientists from the National Aquarium of Cuba.

The present report analyzes spatial variation in densities and size structure (for the first time) of *D. antillarum* within and adjacent to a marine reserve in Jardines de la Reina Archipelago, Cuba, compares density data from local and country wide assessments and discusses the possible factors that influence sea urchin abundance and distribution in the study area. Surveys were part of a broader research to evaluate the effectiveness of the marine reserve on reef fish assemblages.

MATERIALS AND METHODS

Study area: The Archipelago of Jardines de la Reina is one of the four main groups of islands around Cuba and the best conserved of all. Stretching approximately 360km, it is formed by 661 keys, which are located in the south-central part of the Cuban shelf between the Gulf of Ana María and the Gulf of Guacanayabo (Fig. 1). The archipelago has three groups of keys, the most important one is that of "Las Doce Leguas" (The Twelve Leagues) located in its westernmost end. In 1996 two thirds of the archipelago (about 950km^2) were declared as Zone Under Special Regime of Use and Protection (equivalent to the internationally known Marine Reserves, and so termed in this paper) by the Ministry of Fisheries and currently pending approval as a National Park by the Cuban Government. This is the largest of the Caribbean Marine Reserves and its coral reefs are among the best preserved in the region (Appeldoorn & Lindeman 2003). Several patch reefs exist to the north of the keys while the most important and well developed fringing reefs are found in the southern side, where the most conspicuous are reefs crests (1-3m depth) and reefs slopes (12-15m the shallow reef slope and 20-30m the deep reef slope).

Survey methodology: Surveys were conducted in the southern fore reefs of Jardines de la Reina, in the group of keys of "Las Doce Leguas", in June 2004, April 2005 and September 2005. Counts of *D. antillarum* were performed at each sampling time in five 30x2m transects located parallel to 12 reefs crests (specifically in the front part) and 22 shallow reefs slopes, all distributed along 22 sampling sites (Table 1, Fig. 1). *Diadema* test diameters were measured in September 2005 at the same fore reefs; maximum test diameter of individuals encountered in transects was measured to the nearest millimeter with long-jawed calipers.
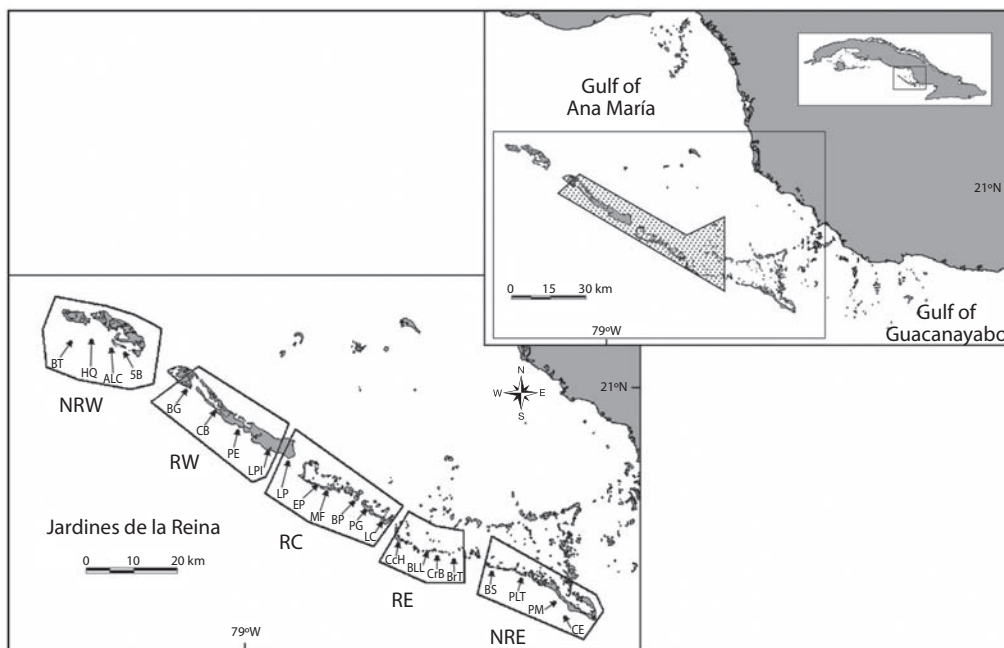
Fig. 1. Study zones and sampling sites in Jardines de la Reina, Cuba. Doted area represents the Zone Under Special Regime of Use and Protection. NRW=Non-reserve Western Zone, RW=Reserve Western Zone, RC=Reserve Central Zone, RE=Reserve Eastern Zone, NRE=Non-reserve Eastern Zone, BT=Bretón, HQ=Horqueta, ALC=Alcatraz, 5B=Cinco Balas, BG=Boca de Guano, CB=Caseta Blanca, PE=Punta Escondida, LPI=Los Pinos, LP=La Puntica, EP=El Partido, MF=Mari Flores, BP=Boca de Piedra, PG=Piedra Grande, LC=Las Cruces, CcH=Cachiboca, BLL=Ballena, CrB=Carabinero, BrT=Bártolo, BS=Boca Seca, PLT=Peralta, PM=Punta Macao, CE=Cabeza del Este.

Fig. 1. Zonas de estudio y sitios de muestreo en Jardines de la Reina, Cuba. El área punteada representa la Zona Bajo Régimen Especial de Uso y Protección. NRW=Zona No Reserva Oeste, RW=Zona Reserva Oeste, RC=Zona Reserva Centro, RE=Zona Reserva Este, NRE=Zona No Reserva Este, BT=Bretón, HQ=Horqueta, ALC=Alcatraz, 5B=Cinco Balas, BG=Boca de Guano, CB=Caseta Blanca, PE=Punta Escondida, LPI=Los Pinos, LP=La Puntica, EP=El Partido, MF=Mari Flores, BP=Boca de Piedra, PG=Piedra Grande, LC=Las Cruces, CcH=Cachiboca, BLL=Ballena, CrB=Carabinero, BrT=Bártolo, BS=Boca Seca, PLT=Peralta, PM=Punta Macao, CE=Cabeza del Este.

Bottom rugosity was estimated at sites surveyed in June 2004 by means of the tape contour method. Measures (n=5) were made by laying a 10m long PVC tape over the substrate, positioned to follow the contours of the reef as closely as possible and then measuring the distance between the start and end of the "contour". Rugosity was calculated as the ratio of "contour" length to tape length. Complementary information, based on the results of Pina-Amargós *et al.* (2008) who analyzed habitat complexity at the same sites in April 2005, September, 2005 and December 2005 by means of a semi-quantitative scale, were used for discussion.

Data collected from sites were grouped in pre-determined zones, three within the marine reserve and two (westward and eastward) adjacent to the marine reserve (Fig. 1). The zone classifying criteria was based on the existing different degrees of protection in the Marine Reserve regarding that protection decreases from Reserve Central Zone (RC), Reserve Western Zone (RW), Reserve Eastern Zone (RE) to Non-reserve Western Zone (NRW) and Non-reserve Eastern Zone (NRE) which

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TABLE 1
Sampling sites in Jardines de la Reina, Cuba

CUADRO 1
Sitios de muestreo en Jardines de la Reina, Cuba

| Site | Reef crests | | |
	Latitude	Longitude	Depth (m)
Bretón (BT)	21º 04' 03"	79º 25' 29"	2-3
Horqueta (HQ)	21º 04' 16"	79º 23' 57"	2-3
Alcatraz (ALC)	21º 02' 83"	79º 20' 28"	2-3
Cinco Balas (5B)	21º 01' 51"	79º 17' 44"	2-3
Boca de Guano(BG)	20º 58' 00"	79º 10' 47"	2-3
Caseta Blanca (CB)	20º 55' 48"	79º 08' 06"	2-3
Punta Escondida (PE)	20º 51' 26"	79º 02' 53"	2-3
Los Pinos (LPI)	20º 50' 76"	79º 00' 78"	2-3
La Puntica (LP)	20º 49' 55"	78º 58' 52"	2-3
El Partido (EP)	78º 55' 01"	20º 46' 47"	2-3
Mari Flores (MF)	20º 46' 30"	78º 53' 61"	2-3
Boca de Piedra (BP)	20º 45' 72"	78º 50' 65"	2-3
	Reef slopes		
Bretón (BT)	21º 03' 52"	79º 26' 12"	12-15
Horqueta (HQ)	21º 04' 02"	79º 23' 36"	12-15
Alcatraz (ALC)	21º 02' 54"	79º 20' 24"	12-15
Cinco Balas (5B)	21º 01' 45"	79º 17' 34"	12-15
Boca de Guano(BG)	20º 57' 49"	79º 10' 45"	12-15
Caseta Blanca (CB)	20º 55' 38"	79º 07' 58"	12-15
Punta Escondida (PE)	20º 51' 44"	79º 03' 30"	12-15
Los Pinos (LPI)	20º 50' 61"	79º 00' 71"	12-15
La Puntica (LP)	78º 59' 05"	20º 49' 50"	12-15
El Partido (EP)	78º 55' 11"	20º 46' 35"	12-15
Mari Flores (MF)	20º 46' 14"	78º 53' 48"	12-15
Boca de Piedra (BP)	20º 45' 70"	78º 50' 62"	12-15
Piedra Grande (PG)	20º 44' 08"	78º 48' 59"	12-15
Las Cruces (LC)	20º 42' 33"	78º 46' 59"	12-15
Cachiboca (CcH)	20º 40' 08"	78º 44' 45"	12-15
Ballena (BLL)	20º 38' 56"	78º 41' 09"	12-15
Carabinero (CrB)	20º 38' 39"	78º 39' 51"	12-15
Bártolo (BrT)	20º 38' 08"	78º 37' 41"	12-15
Boca Seca (BS)	20º 36' 46"	78º 32' 57"	12-15
Peralta (PLT)	20º 35' 56"	78º 29' 10"	12-15
Punta Macao (PM)	20º 33' 11"	78º 24' 57"	12-15
Cabeza del Este (CE)	20º 31' 30"	78º 23' 38"	12-15

show a higher human activity. That informa-
tion was obtained previously to the design of
this study which is part of a broader research
(Pina-Amargós 2008) carried out to evaluate the
effectiveness of the Marine Reserve. Densities
and test diameters of *D. antillarum* recorded
from reef crests were compared among zones
at each sampling time using a one way ANOVA
and the Student-Newman-Keuls test for post-
hoc comparisons. Density data were transformed
using the fourth root transformation as sugges-
ted by the log-mean vs log-variance relationship
(Taylor's Law) for conformity to the assump-
tions of normality and variance homogeneity.
No statistical analyses were performed with
densities recorded from reef slopes to prevent
erroneous results caused by a high proportion of
zero values. Because of obvious differences in
Diadema densities between habitats, statistical
comparison was unnecessary.

The size frequency distributions of *Dia-
dema* pooled across all sites and pooled across
sites of different zones at reef crests were deter-
mined and the latter were compared among
zones with chi-square tests. Pearson's correla-
tion coefficient was used to determine whether
mean test diameters were correlated with mean
densities of *Diadema* at reefs crests and wheth-
er there was a relationship between the mean
densities of *Diadema* and the mean densities of
Echinometra lucunter (Linnaeus) recorded at
the same sites in June 2004, prior to the begin-
ning of *Diadema* counts.

A one way ANOVA was also used to test
for significant differences among zones in
habitat structural complexity and the Student-
Newman-Keuls test for post-hoc comparisons.
Pearson's correlation coefficient was also used
to test for the influence of substrate rugosity
on *Diadema* population densities across sites
at both the reef crest and reef slope habi-
tats (Power calculations were performed using
GPOWER 2.0). All statistical analyses were
performed using STATISTICA 6.0.

RESULTS

**Urchin abundance and habitat struc-
tural complexity:** Abundances of *D. antil-
larum* were lowest at reef slopes during the
study. In June 2004, urchins were found at
six of nine sites surveyed (67%), while in the
next year *Diadema* was present at only 58 %
(of 19 sites) and 55% (of 20 sites) in April
and September respectively. Mean population
densities recorded at this habitat ranged from
0.010-0.070 ind./m^2 in June 2004, while the
lowest local value in April 2005 was 0.003
ind./m^2 (Table 2). The maximum site level
density (0.133 ind./m^2) occurred in April 2005,
but there was only one site showing this value.
Abundances remained low in September 2005
ranging from 0.003-0.083 ind./m^2 with only
three sites showing densities higher than 0.020
ind./m^2 (Table 2).

In contrast to reef slopes, mean densities of
Diadema at reef crests were up to three orders
of magnitude higher, showing local values from
0.013 ind./m^2 at **BT** to 1.016 ind./m^2 at **LP** in
June 2004 while in April 2005 densities ranged
from 0.013-1.553 ind./m^2 with extreme values
at same sites. The maximum site level density
was recorded in September 2005, at **PE**, popu-
lation densities were higher than 1 ind./m^2 at 42
% of the reef crests surveyed (Table 2).

Mean population densities of *D. antil-
larum* varied significantly among zones at reef
crests at each sampling time ($F_{(1, 28)}$=36.434,
p<0.01, in June 2004; $F_{(2, 46)}$=36.522, p<0.01,
in April 2005; $F_{(2, 57)}$=45.409, p<0.01, in Sep-
tember 2005; Fig. 2) and followed the same
spatial pattern of variation as mean densities
across sites ($F_{(5,24)}$=12.426, p<0.01, in June
2004, $F_{(9,39)}$=10.155, p<0.01, in April 2005 and
$F_{(11,48)}$=17.596, p<0.01, in September 2005;
data not shown). Mean abundances were higher
at zones **RC** (0.741 ind./m^2) and **RW** (1.465
ind./m^2) in June 2004 and September 2005
respectively while in April 2005 there were

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Site	June 2004		April 2005		September 2005	
	R. Slope	R. Crest	R. Slope	R. Crest	R. Slope	R. Crest
BT	0	0.013±0.009	0	0.013±0.013	0	0
HQ	0	0.087±0.037	0	0.197±0.078	0	0.077±0.049
ALC	N/A	N/A	0.003±0.003	0.020±0.010	0.020±0.012	0.043±0.012
5B	0.010±0.007	0.117±0.022	0	0.053±0.033	0.003±0.003	0.077±0.016
BG	N/A	N/A	N/A	0.870±0.208	0	1.327±0.441
CB	N/A	N/A	0.020±0.013	0.757±0.230	0	1.220±0.543
PE	N/A	N/A	0	1.297±0.430	0	2.183±0.240*
LPI	N/A	N/A	0.020±0.012	N/A	0	1.130±0.218
LP	0.070±0.037	1.013 ± 0.440	N/A	1.553±0.478	N/A	1.137±0.189
EP	N/A	N/A	0	N/A	0	0.103±0.033
MF	0.017±0.013	0.410±0.052	0	0.713±0.240	0	0.597±0.155
BP	0	0.797±0.195	N/A	1.010±0.301	N/A	0.740±0.273
PG	N/A	N/E	0.003±0.003	N/E	0.003±0.003	N/E
LC	N/A	N/E	0.017±0.007	N/E	0.003±0.003	N/E
CCH	N/A	N/E	0.057±0.016	N/E	0.083±0.029	N/E
BLL	N/A	N/E	0.003±0.003	N/E	0.067±0.033	N/E
CRB	N/A	N/E	0.133±0.059*	N/E	0.003±0.003	N/E
BRT	N/A	N/E	0.020±0.013	N/E	0.003±0.003	N/E
BS	0.013±0.006	N/E	0	N/E	0.003±0.003	N/E
PLT	0.013±0.008	N/E	0.003±0.003	N/E	0	N/E
PM	0.050±0.021	N/E	0.007±0.007	N/E	0.027±0.015	N/E
CE	N/A	N/E	0	N/E	0.020±0.013	N/E

SE=Standard error; R. Slope=Reef Slope; R. Crest=Reef Crest; N/A=Data not available; N/E=Habitat does not exist; *=Maximum site level density during the study at corresponding habitat.

no significant differences in densities recorded from these zones which were indeed significantly higher than density recorded from **NRW** zone, where lowest values occurred during the study (Fig. 2).

Mean densities of *Diadema* at reef crests were correlated with mean densities of *E. lucunter* showing a significant positive relationship in June 2004 (Pearson's correlation, r=0.85, p=0.03, n=6).

Bottom rugosity in June 2004 did not vary significantly among zones neither at reef slopes nor at reef crests ($F_{(1, 43)}$=0.20, p>0.05, Power=1; $F_{(1, 28)}$=0.34, p>0.05 Power=1 respectively). Correlation between mean values of substrate rugosity and mean population densities of *D. antillarum* were not significant at reef crest (r=0.74, p=0.09, n=6, Power=0.81).

Size structure: Mean test diameter of *D. antillarum* in September 2005 was 57.04±3.56mm at reef slope and 56.85±0.68 at reef crest (Table 3). Due to the low number of measurements at reef slopes (n=24) no statistical analyzes were performed. On the other hand, mean sizes at reef crests were significantly different among zones ($F_{(2, 566)}$=33.914, p<0.01; Fig. 3) and showed a significant positive relationship with mean population density (Pearson's correlation, r=0.94, p<0.05; Fig. 4).

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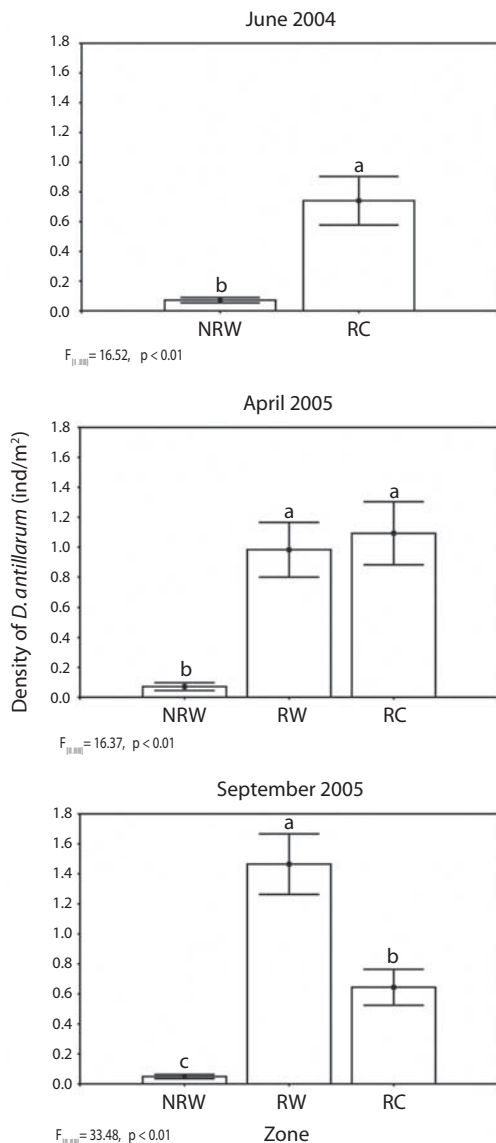
Fig. 2. Mean population densities (SE) of *Diadema antillarum* at reef crests across zones in Jardines de la Reina at each sampling time. Different letters indicate significant differences.

Fig. 2. Densidades promedio (EE) de *Diadema antillarum* por zona en las crestas arrecifales muestreadas en Jardines de la Reina en cada mes de muestreo. Las letras diferentes indican diferencias significativas.

TABLE 3
Mean sizes of Diadema antillarum *at fore reef sites in Jardines de la Reina (September 2005)*

CUADRO 3
Tallas promedio de Diadema antillarum *en los arrecifes de Jardines de la Reina (Septiembre 2005)*

Site	Mean size (mm)±SE	N
	Reef Crest	
HQ	41.22±2.84	32
5B	39.20±3.53	20
BG	62.91±1.77	64
CB	57.78±2.16	86
PE	58.82±1.59	74
LPI	58.81±1.65	57
LP	60.53±2.06	76
EP	47.75±2.54	16
MF	56.58±1.14	94
BP	57.28±2.07	50
All sites	56.85±0.68	569
	Reef Slope	
5B	17.00	1
CCH	60.67±6.55	6
BLL	63.12±4.47	8
BRT	43.25±9.45	4
PM	65.25±6.22	4
CE	49.00	1
All sites	57.04±3.56	24

N=number of urchins measured in five transects; SE=standard error.

Urchins from zones **RW** and **RC** were similar in size and larger than urchins from zone **NRW** (Fig. 3).

Size frequency distribution of *Diadema* at reef crests varied significantly among zones. The **NRW** size distribution was different from both the **RW** distribution (chi-square=298.81, p<0.01) and the **RC** distribution (chi-square=191.65, p<0.01) which did not differ significantly from one another (chi-square=7.39, p>0.05) and were dominated by 51-70mm urchins (52% at zone **RW** and 49%

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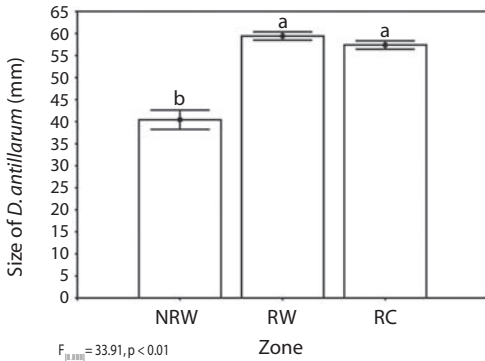
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Fig. 3 Mean sizes (SE) of *Diadema antillarum* at reef crests across zones in Jardines de la Reina during September 2005. Different letters indicate significant differences.

Fig. 3. Tallas promedio (EE) de *Diadema antillarum* por zona en las crestas arrecifales de Jardines de la Reina en Septiembre de 2005. Las letras diferentes indican diferencias significativas.
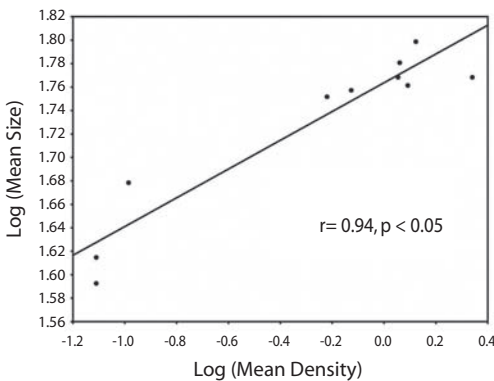

Fig. 4. Positive correlation between mean size and mean density of *Diadema antillarum* across sites at reef crests in Jardines de la Reina during September 2005. Data is presented as log(mean). Equation of line is: log(mean size)=0.1226 log(mean density)+1.7637.

Fig. 4. Correlación positiva entre la talla promedio y la densidad promedio de *Diadema antillarum* por sitios en las crestas arrecifales muestreadas en Jardines de la Reina en Septiembre de 2005. Los datos aparecen representados como el log (media) y la ecuación de la recta es log(talla promedio)=0.1226 log(densidad promedio)+1.7637.

at zone **RC**). In contrast, **NRW** zone showed a higher proportion of individuals in the smallest cohort (58% ≤40mm) particularly in the 31-40mm size class (25%); mid sizes were also well represented in that zone with 23% of urchins in the 51-60mm size class (Fig. 5). The size frequency distribution pooled across all sites was dominated by medium-sized to large urchins with 48% between 51-70mm and individuals from small sizes (≤40mm) were scarce (16%; Fig. 6).

DISCUSSION

Populations of *D. antillarum* were restricted to the reef crests (1-3m depth) in the 40% of surveyed sites in Jardines de la Reina Archipelago. Even when *Diadema* appeared at reef slopes (12-15m depth) population densities were very low (up to three orders of magnitude lower than reef crests). Because of the lack of scientific records about the status of *Diadema* before and after the mass mortality, current urchin abundances can not be compared with historical data. However, if we consider premortality values reported by Hughes *et al.* (1985) and Liddell & Ohlhorst (1986) at similar depths in the north coast of Jamaica, recent densities in Jardines de la Reina are far below those that could potentially exist at such depths before the mortality.

Similar results have been recently reported for several locations around the Cuban archipelago, suggesting a country wide pattern of low population density at mid depth reefs. Alcolado *et al.* (unpublished data) recorded very low densities (0.01-0.1 ind./m^2) at reef slopes in Jardines de la Reina (same region of present study but different sampling sites) Eastern Bahía de Cochinos, south-central Cuba (<0.05 ind./m^2) and María La Gorda, southwestern end of Cuba (<0.05 ind./m^2) where Guardia *et al.* (2004a) found no urchins at similar depths. *Diadema* was also absent at reef slopes, except

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NRW Zone
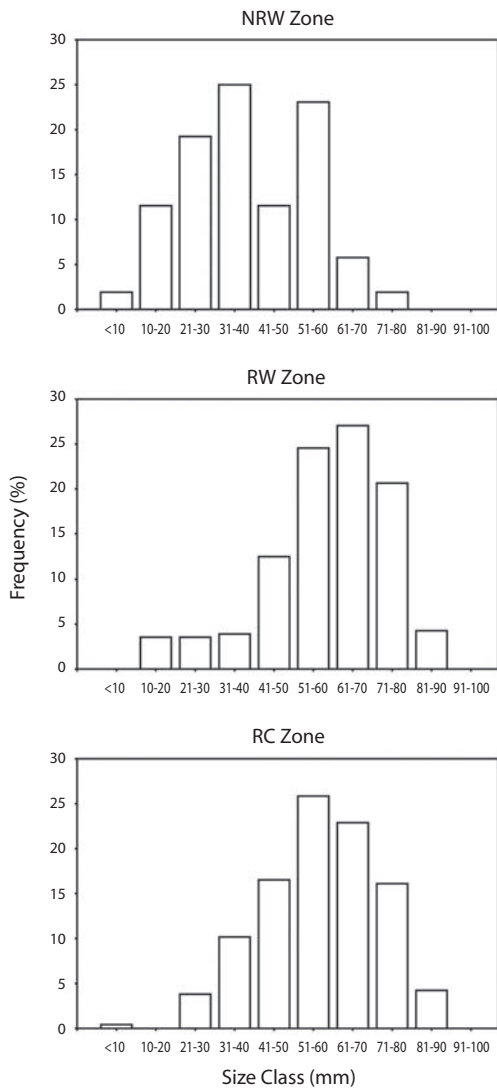

RW Zone

RC Zone

Fig. 5. Size frequency distribution of *Diadema antillarum* at reef crests at each study zone in Jardines de la Reina during September 2005.

Fig. 5. Distribución de frecuencia de talla de *D. antillarum* por zonas en las crestas arrecifales muestreadas en Jardines de la Reina en Septiembre de 2005.
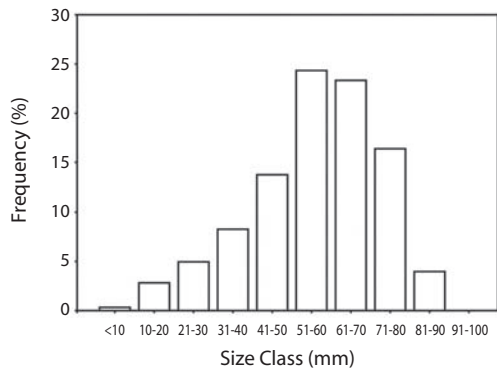

Fig. 6. Size-frequency distribution of *Diadema antillarum* pooled across all sites in Jardines de la Reina during September 2005.

Fig. 6. Distribución de frecuencia de talla acumulada de *D. antillarum* en todos los sitios muestreados en Jardines de la Reina en Septiembre de 2005.

al. 2004b) and Punta del Este, southwestern Cuba (Williams & Polunin 2001). In contrast, reef slope populations from the north coast of Havana, where *Diadema* appears to be more abundant at mid depths, showed higher levels of population density, reaching up to 0.63 ind./m^2 (Alcolado *et al.* unpublished data).

Data collected from Cuban reef slopes and those of other recent studies in the Caribbean region at similar depths (Haley & Solandt 2001, Moses & Bonem 2001 in Jamaica; Williams & Polunin 2001 in Barbados, Belize, Grand Cayman and Jamaica; Chiappone *et al.* 2002 in Florida Keys; Lessios 2005 in Panama; Carpenter & Edmunds 2006 in Jamaica, St. Croix, Grenada, Barbados, Bonaire and Belize; Debrot & Nagelkerken 2006 in Curaçao) show that western Atlantic mid-depth populations of *D. antillarum* are still far from recovery, despite simultaneous increases in shallow reef populations observed in Jamaica (Aronson & Precht 2000, Edmunds & Carpenter 2001, Haley & Solandt 2001), St. Croix (Miller *et al.* 2003) and earlier in Barbados (Hunte & Young-lao 1988) indicated the possible beginning of a full population recovery in the Caribbean. Such a recovery has been recently documented

in one site (0.01 ind./m^2), in Sabana-Camagüey Archipelago, north-central Cuba (Alcolado *et al.* unpublished data), and absent at all sampled locations in Punta Francés, southwestern Cuba (Williams & Polunin 2001, Guardia *et*

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in Costa Rica (Alvarado *et al.* 2004, Myhre & Acevedo-Gutiérrez 2007), Puerto Rico (Weil *et al.* 2005) Barbados (Macintyre *et al.* 2005, Carpenter & Edmunds 2006), Curaçao (Debrot & Nagelkerken 2006), Dominica (Steiner & Williams 2006), Jamaica, St. Croix, Grenada, Bonaire, Belize (Carpenter & Edmunds 2006), Venezuela (Noriega *et al.* 2006) and Yucatan (Jordán-Garza *et al.* 2008).

Results from reef crest populations in Jardines de la Reina (this study) are consistent with those presented by Carpenter & Edmunds (2006), who reported that dense populations of *D. antillarum* now occur at both local and regional scales in the Caribbean. Mean population densities recorded in Jardines de la Reina shallow reefs by this study are higher than those reported by Alcolado *et al.* (unpublished data) at similar depths in Eastern Bahía de Cochinos, south-central Cuba ($\approx$0.075 ind./m^2); Gulf of Batabanó, southwestern Cuba ($\approx$0.83 ind./m^2) and Archipelago Sabana-Camagüey, north-central Cuba (<0.2 ind./m^2). The maximum site level densities recorded by these authors at the reef crests of "Las Doce Leguas" in Jardines de la Reina were slightly lower (0.93 ind./m^2 in Caballones Centro and 0.94 ind./m^2 in Cayo Grande Este) than present densities at neighbor reefs. Because of different sites and sampling methodology, no statistical comparisons were possible. Only one site studied by Alcolado *et al.* (Canal de las Mulatas) located westward, out of the keys of "Las Doce Leguas" and closer to mainland showed a comparatively high density of *Diadema* (2.11 ind./m^2), similar to the highest density recorded at present study (2.18 ind./m^2).

On the other hand, abundances of *D. antillarum* recorded at Jardines de la Reina (this study) are lower than those recorded by Alcolado *et al.* (unpublished data) at Playa Franceses, north coast of Havana, which represents the highest value reported for Cuban shallow reefs until now (8.1 ind./m^2). The increase in more than 5 ind./m^2 at this site between 1997 and 2003 indicates successful recruitment and population persistence along time. However, due to the sampling method used at this site

(1m^2 quadrats) or maybe a bias in the way the quadrats were placed, density values reported by these authors at this site could be an overestimate. As Moses & Bonem (2001) pointed out, given the tendency of the species to aggregate, estimates of density using this method can reach >10 ind./m^2 in one sampling unit, while surrounding abundances may be close to zero. Results from all other shallow reef sites in the north coast of Havana surveyed by Alcolado *et al.* (unpublished data) using a different sampling method (10x1m transects) support this idea, since urchin densities (even being among the highest of the study, up to 0.77 ind./m^2) were one order of magnitude lower than Playa Franceses's abundance and are into conformity with population pattern observed at shallow reefs studied by those authors around Cuba. Thus, population densities from Playa Franceses's should be resurveyed in order to provide a better estimate of current population status.

Although our results can not explain the relative importance of mechanisms affecting abundance patterns of *D. antillarum* populations in Jardines de la Reina; observed differences in mean densities seem to be the result of local factors regulating recruitment processes rather than those responsible for inadequate larval supply or post-settlement mortality. The higher abundance of *Diadema* at **RW** and **RC** zones may be explained by the numerical contribution (to the overall density) of local densities from sites **BG**, **LP** and **BP** which are located on the west margins of major channels between keys (Pasa de Boca de Guano, Pasa de Caballones and Pasa de Boca de Piedra respectively). These sites are under the influence of a higher water flow generated by tide-driven currents circulating through those important channels and hence they might be exposed to a major larval supply when larvae are transported in the water column to the inner and outer waters of the platform as a result of diurnal tide cycles. Furthermore, the pattern of prevailing surface current in the archipelago is from east to west (González de Zayas *et al.* 2006). Thus, this water circulation pattern acting synergistically with tide-driven processes

could produce a major larval retention at the west margins of those channels, enhancing urchin recruitment at reefs mentioned above. In addition, the apparently higher abundance of *Diadema* (author's observations) in the margins of small channels that locally bisect reef crests, reinforce that discussed above and seems to be determined by the same processes acting in a shorter spatial scale. Results from shallow reefs of Curaçao also support our findings since more abundant populations of *D. antillarum* occurred at the entrance of coastal lagoon as reported by Debrot & Nagelkerken (2006). Future research should be addressed to determine rates of recruitment as well as variations in the abundance and size structure of *Diadema* among different zones within the reef crest and between both the west and the east sides of channels between keys. Although **PE** (site with the highest mean density) receives no influence of major channels, it is close to a communicating channel that allows a substantial water exchange between the Gulf of Ana María and the adjacent Caribbean Sea; thus the explanation discussed above is also applicable to this site.

Availability of refuges is one factor that can potentially influence on *D. antillarum* populations; since more rugose reefs can support higher urchin populations by providing shelters from predation, differences in habitat structural complexity could lead to differences in numbers of *Diadema* (Haley & Solandt 2001). In addition, the biomass and structure of sea urchins assemblages is greatly dependent on three-dimensional structure of the habitat (Lee 2006). However, it is unlikely that sheltering represents a limited resource at the reef crests surveyed in June 2004 because rugosity not only was similar among studied zones in June 2004 (present study) but also among the same sites and zones analyzed by Pina-Amargós *et al.* (2008) in April 2005, September, 2005 and December 2005 using the semi-quantitative scale. Furthermore, considering that the power of Pearson´s correlation test, performed to analyze the association between mean values of rugosity and mean population densities of *Diadema*, was acceptably high (Power=0.81), the lack of significance in such association obtained from the test, support the idea that sheltering is not a limited resource, at least at the reef crests surveyed in June 2004. However, more detailed studies (with more replicate samples) should be conducted toward analyzing the influence of habitat structural complexity on *Diadema* population density in order to improve understanding of distribution patterns at a greater spatial scale.

Although juvenile *D. antillarum* could be competitively excluded by adult *E. lucunter* and *E. viridis* (Shulman 1990), *Diadema* recruitment could be facilitated by the presence of *E. lucunter* as their mean densities were positively correlated. Given the propensity of *Diadema* larvae to settle in areas cleared of filamentous algae (Bak 1985), grazing activity of *E. lucunter* and its consequent benefit to *Diadema* recruitment, might be more important than possible competitive exclusion in post-settlement stages of small juvenile *Diadema* at the reefs crests of Jardines de la Reina. Because correlations do not prove causality, long term experimental studies considering recruitment should be carried out in the future to corroborate our findings. However, the pattern we found was consistent with that obtained by Lessios (1988, 1995) in the echinoid exclusion and inclusion experiments performed in the San Blas Archipelago, Panamá. Due to the absence of *T. ventricosus* in surveyed reefs during this study, no facilitation by this species has influenced the recruitment of *Diadema*, as has been suggested in Jamaica by Aronson & Precht (2000) and Haley & Solandt (2001).

Since abundances of *D. antillarum* were relatively high at several reef crests in Jardines de la Reina, low densities observed at **NRW** zone might be unrelated to low numbers of larvae in the water column. Inadequate larval supply due to poor fertilization success caused by low densities of upstream reproducing adults (the Alle effect) has been reported as the most likely explanation for the lack of recruitment of *Diadema* in the Caribbean (Lessios 1988, 1995, 2005, Hughes 1994, Edmunds & Carpenter

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2001, Miller *et al.* 2003) but considering abundances from **RW** and **RC** zones, it could be agreed that upstream populations have reached such levels of population density that they are able to produce enough larvae to overcome mortality in the planktonic stage and therefore an adequate larval supply to sustain recruitment at surveyed reefs. Thus, *Diadema* populations from **NRW** zone seem to be limited, in part, by oceanographic features of the reefs in question and could be conditioned by the presence of *E. lucunter* that might provide suitable substrata for larval settlement as discussed above. However, the size frequency distribution of *D. antillarum* at this zone indicates successful recruitment and that in spite of low densities, juvenile *Diadema* persist along time.

Mean test sizes showed the same pattern of variation as mean densities of *D. antillarum* across zones, being higher within the marine reserve where abundances reached the maximum values. These results are consistent with the positive relationship found between size and density across sites at the present study. Contrary to our finding, an inverse relationship between size and density has been well documented for the species by Carpenter (1981) and Levitan (1988, 1989, 1991) who pointed out the ability of *Diadema* to reduce body size when density increases and therefore food is limited. Considering abundance patterns and size frequency distributions, the association we found appear to be the result of a recent recruitment event at reefs from **NRW** zone as suggested by the high proportion of urchins with sizes ≤40 mm encountered in that zone (Fig. 4).

Given that growth rate of *D. antillarum* slows down as the test diameter increase (Ogden & Carpenter 1987), estimation of age in adult sea urchins, could lead to inaccurate results, even when food is not limited. However, the size frequency distribution pooled across all sites, in association with the fact that the maximum test diameter of the species has not been attained (about 100mm; Ogden & Carpenter 1987), indicates that recruitment of *D. antillarum* populations in Jardines de la Reina began to be noticeable few years (≈3

years) before the survey took place, suggesting that *Diadema* was depleted in the past and population is recovering now.

Because of the lack of scientific information about abundances of *D. antillarum* in Jardines de la Reina before 2001 [data reported by Alcolado *et al.* (unpublished data)] and the complete lack of information about size structure before the present study it is impossible to arrive to more detailed conclusions about its population dynamics. Nevertheless, our study shows that environmental conditions across the best conserved of the four archipelagos around Cuba, one of the best conserved and also the largest marine reserve in the Caribbean, appear to enhance larval recruitment and survival in post-settlement stages of *D. antillarum*, suggesting that recovery is undergoing in Jardines de la Reina and that if a sustained increase in population densities occurs, the patterns we found and those from other particular reefs around Cuba could become in a country wide recovery of the species, contributing to the wider Caribbean population.

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RESUMEN

La mortalidad de *Diadema antillarum* en 1983-1984 afectó más del 93% de la población del Caribe. Aunque no existen datos publicados sobre el estado de sus poblaciones en arrecifes cubanos antes y después de la mortalidad, se conoce anecdóticamente que fueron afectadas. En el presente trabajo se analizan las variaciones espaciales de la abundancia y estructura de tallas de *D. antillarum* en 22 arrecifes frontales en Jardines de la Reina, para lo cual se realizaron cinco recorridos de 30x2m en cada sitio entre Junio de 2004 y Septiembre de 2005. Las densidades de *Diadema* fueron mayores en las crestas arrecifales (0.08-2.18 ind./m^2) mientras que en las pendientes fueron hasta tres órdenes de magnitud menor y la densidad máxima fue 0.13 ind./m^2. Las crestas con mayor abundancia de *Diadema* están ubicadas en los márgenes de las grandes pasas existentes entre cayos donde el reclutamiento parece estar favorecido por las condiciones oceanográficas locales y facilitado por la abundancia de *Echinometra lucunter*. La distribución de frecuencia de tallas de *Diadema* sugiere que el reclutamiento comenzó a ser notable aproximadamente tres años antes del muestreo, indicando que en el pasado sus poblaciones estuvieron afectadas y ahora están recuperándose.

Palabras clave: *Diadema antillarum*, recuperación de erizos marinos, densidad poblacional, estructura de tallas, Jardines de la Reina, Cuba.

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