

## **Influence of *Diadema antillarum* populations (Echinodermata: Diadematidae) on algal community structure in Jardines de la Reina, Cuba**

Félix Martín Blanco<sup>1</sup>, Lídice Clero Alonso<sup>1</sup>, Gaspar González Sansón<sup>2</sup> & Fabián Pina Amargós<sup>1</sup>

1. Centro de Investigaciones de Ecosistemas Costeros, Ministerio de Ciencia, Tecnología y Medio Ambiente. Cayo Coco, Morón, Ciego de Ávila, CP 69400, Cuba; felix.martin79@gmail.com, fabian@ciec.fica.inf.cu, lclero@yahoo.es
2. Centro de Investigaciones Marinas, Universidad de la Habana. Calle 16, # 114 e/ 1ra y 3ra, Miramar, Playa, Ciudad de La Habana, CP. 11300, Cuba; gaspargonzalez2001@yahoo.es

Received 10-VIII-2010.      Corrected 09-I-2011.      Accepted 08-II-2011.

**Abstract:** The 1983-1984 mass mortality of *Diadema antillarum* produced severe damages on Caribbean reefs contributing to substantial changes in community structure that still persist. Despite the importance of *Diadema* grazing in structuring coral reefs, available information on current abundances and algal-urchin interactions in Cuba is scarce. We analyzed spatial variations in *Diadema* abundance and its influence on algal community structure in 22 reef sites in Jardines de la Reina, in June/2004 and April/2005. Urchins were counted in five 30x2m transects per site, and algal coverage was estimated in randomly located 0.25m side quadrats (15 per site). Abundances of *Diadema* were higher at reef crests (0.013-1.553 ind/m<sup>2</sup>), while reef slope populations showed values up to three orders of magnitude lower and were overgrown by macroalgae (up to 87%, local values). Algal community structure at reef slopes were dominated by macroalgae, especially *Dictyota*, *Lobophora* and *Halimeda* while the most abundant macroalgae at reef crests were *Halimeda* and *Amphiroa*. Urchin densities were negatively and positively correlated with mean coverage of macroalgae and crustose coralline algae, respectively, when analyzing data pooled across all sites, but not with data from separate habitats (specially reef crest), suggesting, along with historical fish biomass, that shallow reef community structure is being shaped by the synergistic action of other factors (e.g. fish grazing) rather than the influence of *Diadema* alone. However, we observed clear signs of *Diadema* grazing at reef crests and decreased macroalgal cover according to 2001 data, what suggest that grazing intensity at this habitat increased at the same time that *Diadema* recruitment began to be noticeable. Furthermore, the excessive abundance of macroalgae at reef slopes and the scarcity of crustose coralline algae seems to be due by the almost complete absence of *D. antillarum* at mid depth reefs, where local densities of this urchin were predominantly low. Rev. Biol. Trop. 59 (3): 1149-1163. Epub 2011 September 01.

**Key words:** *Diadema antillarum*, algal community structure, algal-urchin relationships, herbivory, Jardines de la Reina, Cuba.

The 1983-1984 mass mortality of *Diadema antillarum* Philippi, 1845 in the Caribbean produced significant damages on many coral reefs of the region. Several reefs around the wider Caribbean became rapidly overgrown by macroalgae after depletion of this major herbivore (Hughes *et al.* 1985, Liddell & Ohlhorst 1986, De Ruyter van Steveninck

& Breeman 1987, Levitan 1988, Carpenter 1990) and experienced substantial changes in benthic community structure that still persist (Hughes 1994, Hughes *et al.* 1999, Aronson & Precht 2000, 2006, Edmunds & Carpenter 2001, Knowlton 2001, Bellwood *et al.* 2004, Carpenter & Edmunds 2006, Mumby *et al.* 2006). The increasingly decline of reef corals

in the absence of *D. antillarum* emphasize the impact of limited functional redundancy of Caribbean reef ecosystems (Bellwood *et al.* 2004) and demonstrate that Caribbean reefs lost a key component of resilience at the time of *Diadema* die-off. Accordingly, the recovery of *D. antillarum* populations across the entire Caribbean during the last decade has been associated with decrease macroalgal cover and enhanced coral cover and recruitment (Aronson & Precht 2000, Edmunds & Carpenter 2001, Miller *et al.* 2003, Weil *et al.* 2005, Carpenter & Edmunds 2006, Myhre & Acevedo-Gutiérrez 2007) showing that a phase reversal from macroalgal to coral dominance could be possible if former levels of herbivory resume (Carpenter & Edmunds 2006, Mumby 2009).

Although there are no historical records about the status of *Diadema* populations in Cuban reefs before die-off (only one paper about methodological aspects was published, Herrera-Moreno *et al.* 1981), and no scientific papers reported the consequences of the mortality in coral reefs, today it is well documented that several Cuban reefs are overgrown by macroalgae, which are generally more abundant than corals at shallow and mid depth reefs (Alcolado *et al.* 2001, Caballero & Guardia 2003, Guardia *et al.* 2004a, b, 2006, Caballero *et al.* 2006, Clero-Alonso *et al.* 2006, Pina-Amargós *et al.* 2006). Fore reef habitats from Jardines de la Reina represent a clear example of macroalgal dominated/coral depauperate ecosystems; Pina-Amargós *et al.* (2006) reported mean cover of macroalgae of 32% and 58% at reef crests and reef slopes respectively and <20% of coral cover at both habitats.

In spite of the importance of *Diadema* as a keystone species in structuring coral reefs, available information about population abundances and its influence on algal community structure in Cuban reefs is scarce. The most complete data come from surveys of the Atlantic and Gulf Rapid Reef Assessment (AGRRA) carried out at 199 reef sites around the Cuban archipelago from 1999 to 2003 (Alcolado *et al.* unpublished data), but little is discussed about algal-urchin interactions at surveyed reefs by

the authors, which reassessed South Western Cuban sites corresponding to Los Canarreos Archipelago in 2007 (Alcolado *et al.* 2009) and only focused on the impact of hurricanes and coral diseases affecting studied reefs, neglecting the importance of algal-urchin interactions and the impact of a long period of reduced herbivory (urchins and fishes) despite an apparent recent recovery of *Diadema* in some reefs, as reported by the authors, and the enforcement of fish protection in Canarreos Marine Reserve. In a broader study, Williams & Polunin (2001) analyzed relationships between algal cover and grazers at seven locations across the Caribbean including two areas in Cuban Western reefs, but their conclusions are limited to mid depth reefs (12-15m), thus urchin grazing effects remain unclear in Cuban shallow reefs though Caballero *et al.* (2009) contribution, in which benthic community structure and urchin densities were studied closely at shallow and mid depth reefs from the North coast of Havana.

The present report analyzes spatial variations in population abundance of *D. antillarum* and its influence on algal community structure by exploring algal-urchin relationships (percent cover of algae vs densities of *Diadema*) and examining linked patterns of abundance of algal functional groups at different spatial scales within and adjacent to a Marine Reserve in Jardines de la Reina Archipelago, Cuba. We therefore expected that densities of *D. antillarum* would be negatively correlated with macroalgal cover and positively with algal turf and crustose coralline algae at fore reefs habitats, considering that because of Jardines de la Reina is located far from human settlements and two thirds of the archipelago constitute a No-Take Marine Reserve with an effective protection, the study area can be consider as a “quasi-pristine” zone where nutrient concentrations and fish assemblages have been not affected by human impacts, thus they are not responsible for macroalgal overgrowth. This assumption is supported by the results of Pina-Amargós *et al.* (2006) who reported average fish biomass inside the Marine Reserve of 152g/m<sup>2</sup> at reef crests and 118g/m<sup>2</sup> at reef

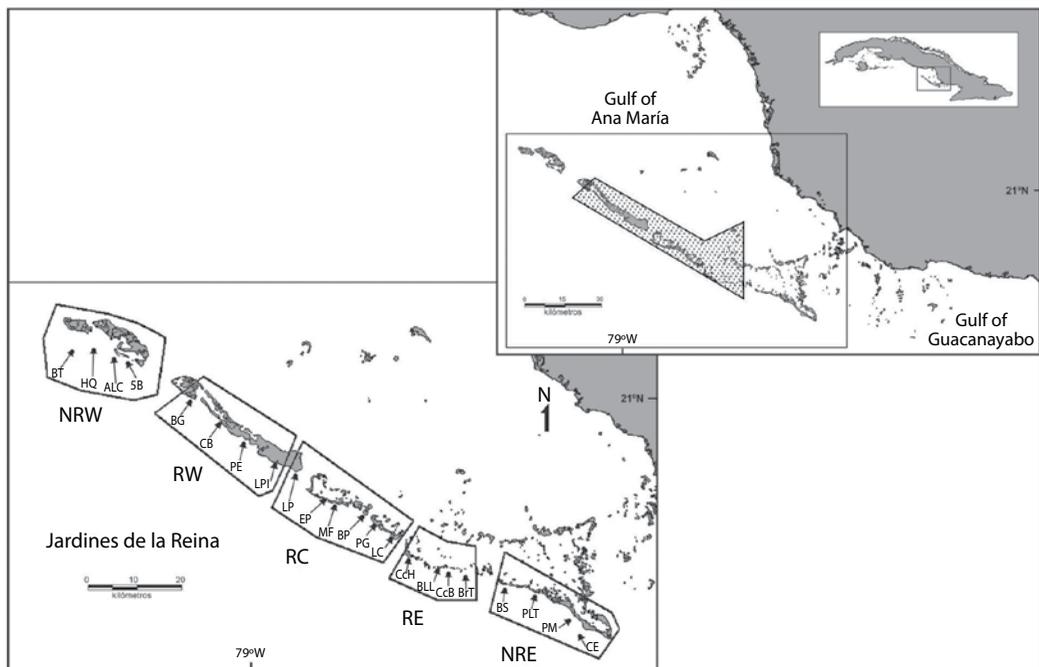
slopes with local values of 220-380g/m<sup>2</sup> and 240-270g/m<sup>2</sup> respectively and those reported by González de Zayas *et al.* (2006) who pointed out that nutrient concentrations were into conformity with oligotrophic water standards reported for the Caribbean.

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<sup>2</sup>) 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 are 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), with large stands of



**Fig. 1.** 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.

dead *Acropora palmata* and some interspersed live colonies comprising the main component of three dimensional structure, and reef slopes (12-15m the shallow reef slope and 20-30m the deep reef slope) with *Siderastrea siderea* and *Agaricia agaricites* as dominant species of coral assemblages.

**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 and April 2005. Counts of *D. antillarum* were performed at each sampling time in five 30x2m transects located parallel to 10 reefs crests (specifically in the front part) and 21 shallow reef slopes, all distributed along 22 sampling sites (Fig. 1; see Martin-Blanco *et al.* 2010 for GPS references of sites).

Percent cover of algae was estimated in 0.25m side quadrats (n=15) which were randomly located at the same sites and habitats surveyed for urchins densities. Algal functional groups were categorized as macroalgae (fleshy, foliose and filamentous algae with frond >1cm tall plus *Halimeda* spp.), algal turf (mixed species assemblages of filamentous algae with canopy height <1cm) and crustose coralline algae.

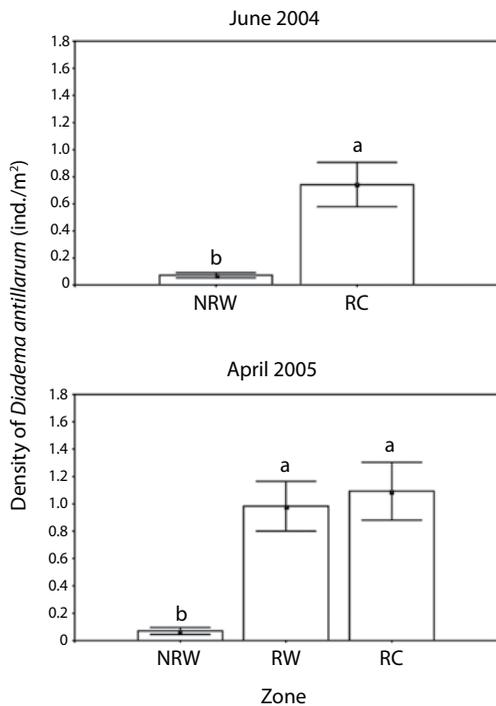
Data collected from sites were grouped in pre-determined zones, three within the Marine Reserve and two (Westward and Eastward) adjacent to the Marine Reserve (Fig. 1). The zone classifying criteria was based on the existing different degrees of protection in the Marine Reserve regarding that protection decreases from RC, RW, RE to NRW and NRE which show a higher human activity. That information 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 as mentioned in the Introduction section. Densities 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 suggested by the log-mean vs log-variance relationship

(Taylor's Law) for conformity to the assumptions 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.

Percent cover of each algal functional groups was compared among zones and between habitats with a two way balanced ANOVA (reef slope data from **RE** and **NRE** were not included in the analysis because comparable reef crests do not exist in shallow depths at corresponding sites from those zones) and the Student-Newman-Keuls test for post-hoc comparisons at each sampling time. Data were transformed using the  $\log_{10}(x+1)$  transformation for conformity to statistical assumptions. An additional one way ANOVA was performed with all zones included to compare macroalgal coverage at reef slopes. Pearson's correlation coefficient was used to determine whether mean coverage of algal functional groups were correlated with mean densities of *Diadema* at each sampling time at two spatial scales (i.e. with data pooled across all reef crest and reef slope sites and data from reef crests and reef slopes by separate). All statistical analyses were performed using STATISTICA 6.0.

## RESULTS

**Urchin abundance:** Abundances of *D. antillarum* were highest at reef crests during the study. Mean population densities were up to three orders of magnitude higher than those recorded at reef slopes (local values up to 1.553ind/m<sup>2</sup> at **LP** in April 2005). Average densities of *Diadema* varied significantly among zones at reef crests ( $F_{(1,28)}=36.434$ ,  $p<0.01$ , in June 2004;  $F_{(2,46)}=36.522$ ,  $p<0.01$ , in April 2005; Fig. 2) and were significantly higher within the Marine Reserve at each sampling time (0.741ind/m<sup>2</sup> and 0.982ind/m<sup>2</sup> at **RC** in June 2004 and April 2005 respectively and 1.092ind/m<sup>2</sup> at **RW** in April 2005). Densities from reef slopes ranged from 0.010-0.070ind/m<sup>2</sup> in June

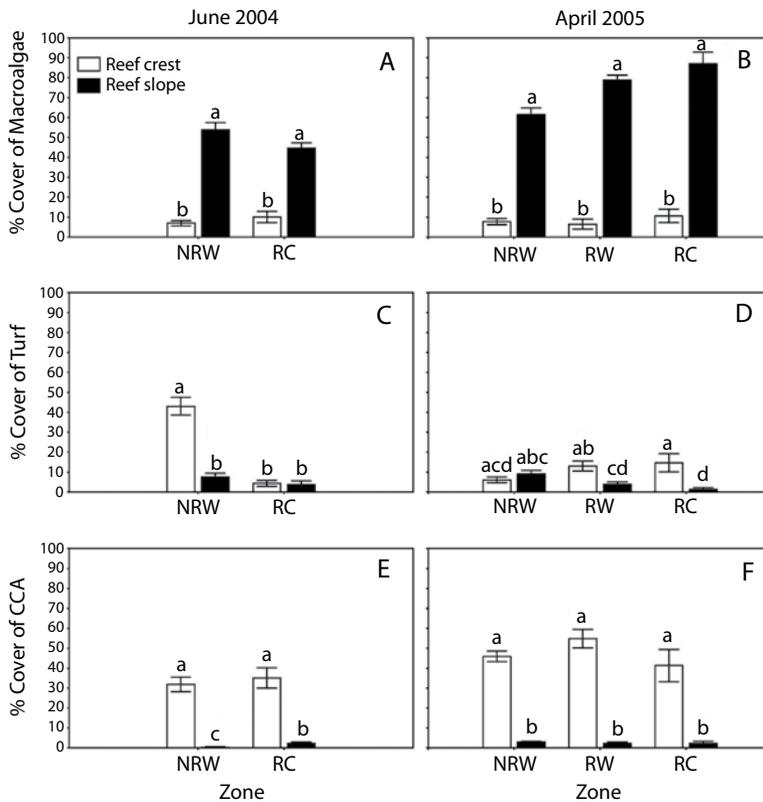


**Fig. 2.** Mean population densities (SE) of *Diadema antillarum* at reef crests across zones in Jardines de la Reina at each sampling time. Different letters indicate significant differences.

2004, while the lowest local value in April 2005 was 0.003ind/m<sup>2</sup> (see Table 2 in Martín-Blanco *et al.* 2010 for detailed information on abundance and distribution patterns). *Diadema* was found at only six of nine sites surveyed in June 2004 and absent at all in 42% of 19 sites surveyed in April 2005. The maximum site level density (0.133ind/m<sup>2</sup>) occurred in April 2005, but there was only one site showing this value.

**Community structure and algal-urchin relationships:** Algal community structure varied significantly between habitats at each sampling time. Percent cover of macroalgae was significantly higher at reef slopes, where densities of *D. antillarum* were zero or near zero during the study ( $F_{(1,146)}=200.14$ ,  $p<0.01$ , in June 2004;  $F_{(1,201)}=236.35$ ,  $p<0.01$ , in April 2005; Fig. 3 A, B). Mean coverage

of macroalgae at reef slopes was 44% in June 2004 and 62% in April 2005, with local values up to 67% and 87% respectively (Table 1). In contrast, the amount of substratum occupied by macroalgae at reef crests averaged 10% at each sampling time (Table 1). Except by percent cover of macroalgae at **NRW** zone which was higher than value from **NRE** zone in June 2004 and percent cover of macroalgae at **RW** zone which was higher than values from **NRW** and **RE** zones in April 2005 when comparing all zones at reef slopes (data not shown), no differences were found with any of the two ANOVA tests in macroalgal cover among zones during the study; the zone-habitat interaction was not significant either. Abundances of algal turf differed between habitats ( $F_{(1,146)}=50.73$ ,  $p<0.01$ ) and between zones ( $F_{(1,146)}=62.82$ ,  $p<0.01$ ) in June 2004, being significantly higher at reef crests (Fig. 3 C), pattern that was held across zones but was stronger at **NRW** zone in June 2004, as demonstrated by the significant zone-habitat interaction ( $F_{(1,146)}=30.42$ ,  $p<0.01$ ). The pattern of higher coverage of algal turf at reef crests held in April 2005 ( $F_{(1,201)}=12.30$ ,  $p<0.01$ ; Fig. 3 D) and showed a significant zone-habitat interaction ( $F_{(2,201)}=10.15$ ,  $p<0.01$ ) but mean values did not varied among zones. Percent cover of crustose coralline algae varied between habitats at each sampling time ( $F_{(1,146)}=373.61$ ,  $p<0.01$ , in June 2004;  $F_{(1,201)}=274.59$ ,  $p<0.01$ , in April 2005) being higher at reef crests (Fig. 3 E, F). Mean values differed among zones only in June 2004 ( $F_{(1,146)}=5.95$ ,  $p<0.05$ ) and the zone-habitat interaction was not significant during the study. Algal community structure at reef crests, where *Diadema* was more abundant, was dominated by crustose coralline algae (mean values of 30% in June 2004 and 46% in April 2005, Table 1) while macroalgae occupied the major amount of substratum at reef slopes during the study. Macroalgal cover at reef slopes was dominated by *Dictyota* sp., *Lobophora* sp. and *Halimeda* sp. at each sampling time while the most abundant at reef crests were *Halimeda* sp. and *Amphiroa* sp. (Table 2).



**Fig. 3.** Mean coverage (SE) of macroalgae (A, B), algal turf (C, D) and CCA=crustose coralline algae (E, F) at fore reef habitats across studied zones in Jardines de la Reina at each sampling time. Reef slope data from **RE** and **NRE** zones were not included because comparable reef crests do not exist at corresponding sites in shallow depths from those zones. Different letters indicate significant differences.

Correlations between percent cover of algal functional groups and the abundance of *D. antillarum* indicated a significant association among variables when analyzing data pooled across all sites. Densities of *D. antillarum* were negatively and positively correlated with mean coverage of macroalgae and crustose coralline algae, respectively, during the study (Fig. 4 A, B, E, F) while mean coverage of algal turfs showed no significant pattern of variation in relation to *Diadema* abundances at this spatial scale (Fig. 4 C, D). Partial correlations with data from reef crests and reef slopes by separate yielded no significant relationships among algal functional categories and

*Diadema* densities in most cases (Table 3). Only the percent cover of crustose coralline algae showed a significant positive relationship with the abundance of *Diadema* but Pearson's correlation coefficient was too low (Table 3).

## DISCUSSION

Surveys from shallow and mid depth reefs in Jardines de la Reina showed that patterns of abundance of *D. antillarum* in the study zone are similar than those reported by Alcolado *et al.* (unpublished data) around Cuba. Data collected from reef slopes in Jardines de la Reina and those from other Cuban locations indicate a

TABLE 1  
Mean percent cover ( $\pm$ SE) of algal functional categories at fore reef sites in Jardines de la Reina (2004-2005)

Zone/Site	June 2004						April 2005											
	Macroalgae			Turf			CCA			Macroalgae			Turf			CCA		
	R. Slope	R. Crest	R. Slope	R. Crest	R. Slope	R. Crest	R. Slope	R. Crest	R. Slope	R. Crest	R. Slope	R. Crest	R. Slope	R. Crest	R. Slope	R. Crest	R. Slope	R. Crest
N	BT	67.5 $\pm$ 6.8	3.3 $\pm$ 1.8	0	58.3 $\pm$ 8.3	0	21.3 $\pm$ 6.2	50.7 $\pm$ 9.8	2.0 $\pm$ 0.9	0.7 $\pm$ 0.7	3.3 $\pm$ 1.6	1.3 $\pm$ 0.8	55.3 $\pm$ 2.6					
R	HQ	51.1 $\pm$ 5.7	9.0 $\pm$ 2.8	16.0 $\pm$ 4.3	50.0 $\pm$ 7.0	0.7 $\pm$ 0.7	25.3 $\pm$ 4.1	64.7 $\pm$ 4.5	6.3 $\pm$ 2.3	22.3 $\pm$ 4.4	5.0 $\pm$ 2.1	2.3 $\pm$ 0.7	44.3 $\pm$ 4.3					
W	ALC	N/A	N/A	N/A	N/A	N/A	N/A	72.3 $\pm$ 2.5	22.9 $\pm$ 4.4	7.0 $\pm$ 1.8	1.2 $\pm$ 0.9	4.3 $\pm$ 0.4	28.7 $\pm$ 7.2					
	5B	43.0 $\pm$ 4.9	8.7 $\pm$ 1.5	6.1 $\pm$ 2.6	20.7 $\pm$ 3.0	0.2 $\pm$ 0.2	49.0 $\pm$ 5.7	59.3 $\pm$ 5.0	3.0 $\pm$ 1.4	8.0 $\pm$ 3.0	13.7 $\pm$ 4.3	4.0 $\pm$ 1.0	52.0 $\pm$ 5.2					
	BG	N/A	N/A	N/A	N/A	N/A	N/A	N/A	24.7 $\pm$ 6.9	N/A	15.0 $\pm$ 4.9	N/A	34.3 $\pm$ 6.3					
R	CB	N/A	N/A	N/A	N/A	N/A	N/A	73.8 $\pm$ 2.8	4.7 $\pm$ 1.6	3.72.3	19.04.4	3.0 $\pm$ 1.0	50.7 $\pm$ 4.7					
W	PE	N/A	N/A	N/A	N/A	N/A	N/A	83.9 $\pm$ 3.5	8.3 $\pm$ 4.7	4.0 $\pm$ 1.1	7.0 $\pm$ 1.5	1.7 $\pm$ 0.6	59.0 $\pm$ 8.2					
	LPI	N/A	N/A	N/A	N/A	N/A	N/A	58.5 $\pm$ 3.0	N/A	3.3 $\pm$ 1.5	N/A	3.7 $\pm$ 0.8	N/A					
	LP	51.8 $\pm$ 3.0	5.0 $\pm$ 2.0	2.0 $\pm$ 1.4	5.3 $\pm$ 2.0	2.7 $\pm$ 1.0	29.3 $\pm$ 5.4	N/A	3.0 $\pm$ 2.1	N/A	3.0 $\pm$ 1.8	N/A	49.7 $\pm$ 7.6					
	EP	N/A	N/A	N/A	N/A	N/A	N/A	87.5 $\pm$ 3.3	N/A	4.7 $\pm$ 1.9	N/A	1.3 $\pm$ 0.8	N/A					
R	MF	37.5 $\pm$ 3.5	15.2 $\pm$ 5.0	5.3 $\pm$ 3.5	3.3 $\pm$ 2.3	2.0 $\pm$ 1.0	41.0 $\pm$ 8.6	87.0 $\pm$ 5.8	10.7 $\pm$ 3.3	1.3 $\pm$ 0.9	14.7 $\pm$ 4.6	2.3 $\pm$ 1.0	41.3 $\pm$ 8.0					
C	BP	N/A	17.7 $\pm$ 4.3	N/A	23.7 $\pm$ 6.0	N/A	15.3 $\pm$ 2.4	N/A	13.0 $\pm$ 3.7	N/A	11.3 $\pm$ 3.5	N/A	38.0 $\pm$ 6.3					
	PG	N/A	N/E	N/A	N/E	N/A	N/E	35.7 $\pm$ 4.7	N/E	7.3 $\pm$ 2.6	N/E	0.3 $\pm$ 0.3	N/E					
	LC	N/A	N/E	N/A	N/E	N/A	N/E	60.8 $\pm$ 5.0	N/E	15.7 $\pm$ 4.5	N/E	8.7 $\pm$ 2.3	N/E					
	CCH	N/A	N/E	N/A	N/E	N/A	N/E	N/A	N/E	N/A	N/E	N/A	N/E					
R	BLL	N/A	N/E	N/A	N/E	N/A	N/E	61.3 $\pm$ 4.4	N/E	1.7 $\pm$ 0.9	N/E	9.7 $\pm$ 1.7	N/E					
E	CRB	N/A	N/E	N/A	N/E	N/A	N/E	31.3 $\pm$ 2.6	N/E	16.3 $\pm$ 2.3	N/E	9.3 $\pm$ 2.2	N/E					
	BRT	N/A	N/E	N/A	N/E	N/A	N/E	60.3 $\pm$ 6.4	N/E	0	N/E	4.0 $\pm$ 1.8	N/E					
	BS	40.5 $\pm$ 5.3	N/E	6.0 $\pm$ 2.3	N/E	7.0 $\pm$ 2.5	N/E	58.1 $\pm$ 2.6	N/E	14.0 $\pm$ 1.6	N/E	0	N/E					
N	PLT	29.3 $\pm$ 5.1	N/E	6.7 $\pm$ 4.1	N/E	12.0 $\pm$ 4.2	N/E	63.0 $\pm$ 3.8	N/E	14.0 $\pm$ 2.4	N/E	5.7 $\pm$ 0.7	N/E					
R	PM	34.8 $\pm$ 4.4	N/E	9.0 $\pm$ 3.7	N/E	2.4 $\pm$ 1.0	N/E	65.3 $\pm$ 5.9	N/E	7.7 $\pm$ 3.4	N/E	9.7 $\pm$ 2.7	N/E					
E	CE	N/A	N/E	N/A	N/E	N/A	N/E	48.6 $\pm$ 5.4	N/E	19.0 $\pm$ 2.9	N/E	6.3 $\pm$ 1.8	N/E					
	All sites	44.4 $\pm$ 2.0)	9.8 $\pm$ 1.4	6.4 $\pm$ 1.1	26.9 $\pm$ 3.1	3.4 $\pm$ 0.7	30.2 $\pm$ 2.6	62.3 $\pm$ 1.4	9.6 $\pm$ 1.3	8.4 $\pm$ 0.7	9.5 $\pm$ 1.1	4.3 $\pm$ 0.4	45.7 $\pm$ 2.1					

SE=Standard error; R. Slope=Reef Slope; R. Crest=Reef Crest; CCA=Crustose coralline algae; N/A=Data not available; N/E=Habitat does not exist.

TABLE 2  
Mean coverage ( $\geq 0.3\%$ ) of macroalgal genera at fore reef sites in Jardines de la Reina (2004-2005)

June 2004			April 2005		
Habitat (number of sites)	% cover	SE	Habitat (number of sites)	% cover	SE
<b>Reef slope (n=8)</b>			<b>Reef slope (n=18)</b>		
Dictyota	24.9	5.5	Dictyota	29.9	7.5
Lobophora	10.1	2.8	Lobophora	17.0	5.8
Halimeda.	5.4	2.1	Halimeda	5.9	3.0
Styopodium	1.3	1.0	Sargassum	3.9	1.8
Sargassum	0.9	0.3	Jania	1.5	1.6
Amphiroa	0.7	0.5	Amphiroa	1.3	1.5
Anadyomene	0.3	0.2	Anadyomene	1.2	1.0
<b>Reef crest (n=6)</b>			Styopodium	0.8	0.9
Halimeda	5.2	2.4	<b>Reef crest (n=10)</b>		
Amphiroa	3.3	1.7	Halimeda	4.8	2.4
Laurencia	0.4	0.3	Amphiroa	0.9	0.5
Dictyota	0.3	0.2	Laurencia	0.6	0.3
Galaxaura	0.3	0.2	Dictyota	0.5	0.2
			Galaxaura	0.3	0.2

SE=Standard error.

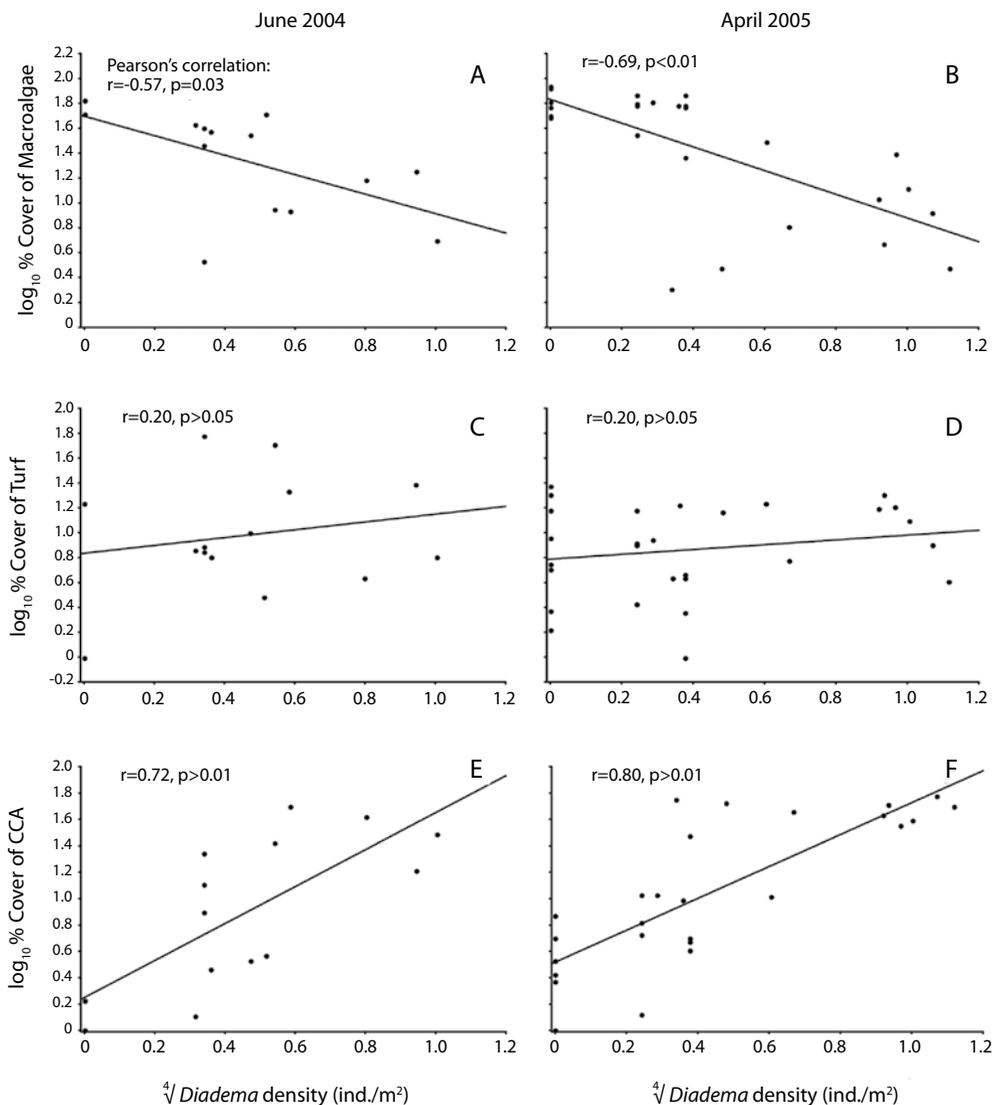
TABLE 3  
Relationship between density of *D. antillarum* and percent cover of algal functional categories at reef habitats by separate in Jardines de la Reina (2004-2005)

Habitat/Variables	June 2004			April 2005		
	r (X,Y)	P	n	r (X,Y)	p	n
<b>Reef crest</b>						
X vs Y <sub>Macroalgae</sub>	0.49	0.32	6	0.20	0.57	10
X vs Y <sub>Turf</sub>	-0.71	0.11	6	0.46	0.18	10
X vs Y <sub>CCA</sub>	-0.08	0.87	6	0.13	0.72	10
<b>Reef slope</b>						
X vs Y <sub>Macroalgae</sub>	-0.59	0.12	8	-0.43	0.08	18
X vs Y' <sub>Turf</sub>	0.16	0.71	8	0.01	0.98	18
X vs Y' <sub>CCA</sub>	0.55	0.16	8	0.53	0.02*	18

X= $\sqrt[4]{}$ mean density of *Diadema*; Y= $\log_{10}$ (mean cover); Y'= $\log_{10}$ (mean cover+1); CCA=crustose coralline algae; r=Pearson's correlation coefficient; p=probability value; n=number of sites; \*=statistical significance.

country wide pattern of low population density at mid depth reefs; whereas densities recorded at reef crests (this study) are among the highest reported around the Cuban Archipelago (Martín-Blanco *et al.* 2010). The pattern of higher population density inside the Marine Reserve

at studied reefs contrasts with that reported by Harborne *et al.* (2009) in The Bahamas, where abundances of *Diadema* were higher outside the Exuma Cays Land and Sea Park. Observed differences in mean densities at reef crests in Jardines de la Reina seem to be the result of



**Fig. 4.** Relationship between density of *D. antillarum* and percent cover of macroalgae (A, B), algal turf (C, D) and CCA=crustose coralline algae (E, F) across all fore reef sites in Jardines de la Reina during the study. Data is presented as  $\log_{10}(\text{mean})$  vs  $\sqrt[4]{\text{mean}}$  in A & B and  $\log_{10}(\text{mean} + 1)$  vs  $\sqrt[4]{\text{mean}}$  from C-F. Equation of line is: A ( $\log_{10}(\% \text{ cover}) = 1.6965 - 0.7828\sqrt[4]{\text{density}}$ ), B ( $\log_{10}(\% \text{ cover}) = 1.8312 - 0.9530\sqrt[4]{\text{density}}$ ), C ( $\log_{10}(\% \text{ cover}) = 0.8344 + 0.3140\sqrt[4]{\text{density}}$ ), D ( $\log_{10}(\% \text{ cover}) = 0.7871 + 0.1930\sqrt[4]{\text{density}}$ ), E ( $\log_{10}(\% \text{ cover}) = 0.2499 + 1.4013\sqrt[4]{\text{density}}$ ), F ( $\log_{10}(\% \text{ cover}) = 0.5173 + 1.2095\sqrt[4]{\text{density}}$ ).

local factors regulating recruitment processes rather than those responsible for inadequate larval supply or post-settlement mortality (see Martín-Blanco *et al.* 2010 for a detailed discussion on abundances and size structure of *D. antillarum* in the studied zone at both habitats).

Our results emphasize the importance of *Diadema* grazing in top-down processes on reef ecosystems. The associations between algal coverage and the abundance of *D. antillarum* (negative in the case of macroalgae and positive in the case of crustose coralline

algae) suggest that algal community structure in Jardines de la Reina depends, in part, on the influence of *Diadema* in an overall scale. Although correlations do not prove causality, there is some evidence that highlights the role of *Diadema* in the control of macroalgae at surveyed reefs. Considering that the protection inside the reserve has been enhanced through time and no major disturbances have occurred in the area, thus fish assemblages and nutrient concentrations remain unaltered, our data and those reported by Pina-Amargós *et al.* (2006) are reliable enough to support our interpretations. However, some manipulative experiments should be done to corroborate our inference that *Diadema* is, at present, an important factor on macroalgal cover at reef slopes.

The excessive abundance of macroalgae at reef slopes seems to be due by the almost complete absence of *D. antillarum* at mid depth reefs, where local densities of this urchin were predominantly low ( $<0.07 \text{ ind/m}^2$  in 95% of surveyed reef slopes during the study). In addition, the higher dominance of macroalgae (up to 87% cover) and the scarcity of crustose coralline algae ( $<4\%$  cover as mean value) at this habitat suggest that grazing intensity at reef slopes is under threshold levels required to maintain the algal community in a cropped state. As pointed out by Szmant (2002), when a reef has a high algal standing crop, it can be inferred that in some point in time, the algal production has exceeded the capacity of the heterotrophic community to consume it. In consequence, the level of grazing needed to return to coral dominance would differ dramatically from that needed to maintain the former coral dominated system (Mumby 2009).

Considering values of herbivorous fish biomass (Acanthurids + Scarids) reported by Pina-Amargós *et al.* (2002) in the studied zone (mean biomass= $31.8 \text{ g/m}^2$  and maximum biomass= $56.7 \text{ g/m}^2$ ) and that dominant macroalgae from reef slopes (*Dictyota*, *Lobophora* and *Halimeda*) are those readily consumed by *Diadema* (reviewed in Szmant 2002) and less palatable to herbivorous fishes (Hay 1997; Author's pers. observ.), one likely explanation

to the lack of herbivory at mid depth reefs in Jardines de la Reina could be the absence of *D. antillarum* at this habitat. Furthermore, since macroalgal cover did not vary among zones (two way ANOVA results with balanced data; Fig. 3 A, B) and results from the additional ANOVA, yielded no differences in macroalgal abundances among all zones (except by percent cover from **RW** zone which was significantly higher than those from **NRW** and **RE**) potential higher abundances of herbivorous fish inside the Marine Reserve (author's pers. observ.) appear to make no difference in macroalgal control inside and outside the Marine Reserve. Parrotfishes and surgeonfishes appear to play a critical role in preventing phase shifts to macroalgae but when presented with intact stands of macroalgae, their ability to remove the algae may be limited (Bellwood *et al.* 2006). In contrast to Mumby *et al.* (2007) observations about trophic cascades resulting in reductions of macroalgal cover inside Marine Reserves, positive effects expected from reserve-driven trophic interactions in Jardines de la Reina, via the increase of fish grazing, are not strong enough to prevent macroalgal overgrowth and enhance coral recruitment at mid depth reefs in the largest of Caribbean Marine Reserves. Neither highly diverse fish assemblages and mature food webs, nor the presence of abundant herbivorous fish in Jardines de la Reina Marine Reserve appear to increase resilience at surveyed reef slopes without suitable functional redundancy in the absence of *D. antillarum* at the time of this study.

Similar results have been reported from other Cuban reefs at the same depth; Guardia *et al.* (2004a) recorded high percentages of macroalgae from diving sites in Maria La Gorda, southwestern end of Cuba ( $\approx 50\%$  from spoor and grove and patch reefs sites) and a high dominance of *Dictyota* and *Lobophora* at all over the reef; patterns that seem to be associated, as mentioned by the authors, with the significant scarcity of *D. antillarum*. Present results are also into conformity to that obtained by Williams & Polunin (2001) at several locations in the Caribbean, including two

locations from the Isle of Youth, Southwestern Cuba (a Marine Reserve at Punta Francés and a non protected zone at Punta del Este). Their findings indicate that, even in locations where herbivorous fish are abundant (mean biomass=9.3g/m<sup>2</sup>) there is an upper limit to the amount of substrate that can be grazed with sufficient intensity for upright macroalgae to be excluded in the absence of *Diadema*; suggesting that those reefs would previously have been dependent on *Diadema* grazing. The fact that mean biomass of herbivorous fish reported by Pina-Amargós *et al.* (2002) at the studied zone in Jardines de la Reina was three times higher than average biomass reported by Williams & Polunin (2001) and that coral reefs from Jardines de la Reina still show higher percentages of macroalgae, suggest that the role of *D. antillarum* in the control of macroalgae needs to be considered when analyzing algal community structure in Jardines de la Reina coral reefs. Results from the North coast of Havana (H.P. Caballero 2007, pers. comm.) reinforce this idea since percent covers of macroalgae (24-67%) recorded from reef slopes, where abundances of *Diadema* reach up to 0.63ind/m<sup>2</sup> and fish assemblages are highly affected by overfishing (mean overall fish biomass=4g/m<sup>2</sup> and mean herbivorous fish biomass=1.7g/m<sup>2</sup>; H.P. Caballero 2007, pers. comm.), are comparatively lower than those recorded in Jardines de la Reina at the same habitat (29-87%; this study). In addition, algal species composition from the North coast of Havana contrasts with that from Jardines de la Reina; as Clero-Alonso 2007 (pers. comm.) the abundance of filamentous algae in Havanan reefs, specially *Cladophora* and *Cladophoropsis*, is higher than that observed in Jardines de la Reina, where they are rare, what illustrate different components of herbivory between locations and highlights the higher intensity of *Diadema* grazing in the North coast of Havana, where not only macroalgal species preferred by this urchin are less abundant, but also the percent cover of the entire macroalgal community. However, different biophysical conditions from northern reefs (e.g. different wave exposure) should be

considered for generalizations regarding differential effects on algal communities independently of urchin grazing.

On the other hand, partial correlations with data recorded from reef crests and reef slopes by separate, indicate no significant associations between algal coverage and the abundance of *D. antillarum* at this spatial scale. Data from reef crests suggest that algal community structure at this habitat is being shaped by the synergistic action of other factors (e.g. fish grazing) rather than the influence of *Diadema* grazing alone. If we consider average biomass of herbivorous fish (86.6g/m<sup>2</sup>) reported by Pina-Amargós *et al.* (2002) from reef crests in Jardines de la Reina and that abundances of upright macroalgae at this habitat are naturally limited by physical factors (e.g. wave action), we cannot discount the role of fish grazing as a key component of herbivory at these sites. Certainly, in shallow reefs, where herbivorous fish are more abundant, grazing by fishes alone can maintain the algal community in a cropped state (Carpenter 1986, Lewis 1986, Bruggemann *et al.* 1994). Nevertheless, we observed clear signs of *Diadema* grazing at shallow reefs (large patches of bare substrate around *Diadema* aggregations and sparse macroalgal cover), where urchin abundances were moderately high (up to 1.553ind/m<sup>2</sup>) and percent covers of algae preferred by *Diadema* were very low (<6%). Additionally, current abundances of macroalgae at reef crests in Jardines de la Reina (<10% cover) are comparatively lower than those reported by Pina-Amargós *et al.* (2006) at the studied area (32% cover; average values from data recorded in 2001), what suggests, together with recent observations of new recruits of *A. palmata* (F. Pina-Amargós 2010, pers. comm.), that grazing intensity have increased at the same time that *Diadema* recruitment began to be noticeable ( $\approx$ 3-4 years before our surveys took place; Martín-Blanco *et al.* 2010).

Although our results cannot explain the relative importance of *Diadema* grazing and correlation evidence do not prove a cause and effect hypothesis, the recovery of *D. antillarum* across the Caribbean and its association with

reduced macroalgal cover and enhanced coral recruitment at shallow reefs (Miller *et al.* 2003, Weil *et al.* 2005, Carpenter & Edmunds 2006, Myhre & Acevedo-Gutiérrez 2007) along with prior experimental studies (Ogden *et al.* 1973, Sanmarco *et al.* 1974, Carpenter 1981, 1986, Sanmarco 1980, 1982), support our hypothesis on the functional role of *D. antillarum* in mediating the removal of macroalgae at surveyed reefs. However, further experimental studies should be addressed to determine the importance of *Diadema* grazing and fish grazing by separate in order to improve our understanding about the structure and functioning of these ecosystems in which three dimensional structure of coral assemblages still persists. Since assemblages of reef fish and sea urchins are highly dependent on three dimensional structure of reef habitats (Hixon & Beets 1993, Aguilar *et al.* 1997, González-Sansón *et al.* 1997, Friedlander & Parrish 1998, Jones *et al.* 2004, Idjadi & Edmunds 2006, Lee 2006) and fish/urchin grazing reduces macroalgal cover and promotes coral recruitment which in turn can help to maintain three dimensional structure (Aronson & Precht 2000, Bellwood *et al.* 2004, Carpenter & Edmunds 2006, Mumby 2006, 2009, Mumby *et al.* 2006, Mumby *et al.* 2007), positive feed backs resulting in coral community recovery might be expected to occur in Jardines de la Reina as *Diadema* populations continue to increase and the reserve gets older for cascading interactions to be effective. Considering that conservation driven processes contributing to coral reef ecosystems recovery may take long periods of time to be effective (McClanahan 2000, Rodwell *et al.* 2003, Russ & Alcala 2004, McClanahan *et al.* 2005, 2007) and that recovery of *D. antillarum* is still limited to shallow depths in Jardines de la Reina, additional management actions such as restoration programs should be implemented in favor of those reefs where urchin populations are scarce and macroalgal occupied space limits coral recruitment, specially at reef slopes.

## ACKNOWLEDGMENTS

The authors are thankful to the staff of Azulmar for logistical support on Jardines de la Reina, specially to Giuseppe Omegna (Pepe) its manager and Noel López. To WWF Canada for funding this research and to E. Sala, Director of the Center for Marine Biodiversity and Conservation of the Scripps Institution of Oceanography, for partial funding and logistics. We thank the Ministry of Science, Technology and Environment for funds and logistics, especially C. Pazos Alberdi, R. Gómez Fernández, A. Zúñiga Ríos. Infinite thanks to CIEC's staff for supporting us in doing research on Jardines de la Reina, specially to L. Hernández Fernández, A. Zayas Fernández, W. Acosta de la Red, A. Jiménez del Castillo, M. Lazarte Llanes. We also want to thanks P.M. Alcolado, H.P. Caballero, Y. Lezcano, for assistance in bibliography and especial considerations.

## RESUMEN

A pesar de la importancia del forrajeo de *Diadema* en la estructuración de los arrecifes de coral, la información disponible sobre la actual abundancia de algas y de las interacciones de erizos en Cuba es escasa. Por lo tanto, se analizan las variaciones espaciales en la abundancia de *Diadema antillarum* y su influencia sobre las algas en 22 arrecifes en Jardines de la Reina, en junio/2004 y abril/2005. Los erizos se muestrearon en recorridos de 30x2m (5/sitio) y las algas en cuadrículas de 0.25m de lado (15/sitio). Las densidades de *Diadema* fueron mayores en las crestas arrecifales (0.013-1.553ind/m<sup>2</sup>) mientras que las pendientes mostraron valores hasta tres ordenes de magnitud menor y presentaron un cubrimiento excesivo de macroalgas (hasta 87%), siendo las más abundantes *Dictyota*, *Lobophora* y *Halimeda*. Las densidades de erizos estuvieron correlacionadas negativa y positivamente con el cubrimiento de macroalgas y algas costrosas, respectivamente, en el análisis global, pero no en hábitats separados (especialmente en crestas), sugiriendo, conjuntamente con la biomasa histórica de peces, que la estructura de las comunidades en las crestas está determinada por la acción sinérgica de otros factores (herbivoría de peces) más que por la influencia de *Diadema* solo. No obstante, se observaron indicios del forrajeo de *Diadema*, y el cubrimiento de macroalgas disminuyó desde 2001, lo cual sugiere que la

intensidad de la herbivoría aumentó al mismo tiempo que el reclutamiento de *Diadema*.

**Palabras clave:** *Diadema antillarum*, estructura de las comunidades de algas, relaciones alga-erizo, herbivoría, Jardines de la Reina, Cuba.

## REFERENCES

- Aguilar, C., G. González-Sanasón, J. Angulo & C. González. 1997. Variación espacial y temporal de la ictiofauna en un arrecife de coral costero de la región noroccidental de Cuba. I: Abundancia total. Rev. Invest. Mar. 18: 223-232.
- Alcolado, P.M., R. Claro, B. Martínez-Daranas, G. Menéndez-Macia, P. García-Parrado, K. Cantelar, M. Hernández & R. del Valle. 2001. Evaluación ecológica de los arrecifes coralinos del oeste de Cayo Largo del Sur, Cuba: 1998-1999. Bol. Invest. Mar. Costeras 30: 25-32.
- Alcolado, P.M., D. Hernández-Muñoz, H.P. Caballero, L. Busutil, S. Perera & G. Hidalgo. 2009. Efectos de un inusual período de alta frecuencia de huracanes sobre el bentos de arrecifes coralinos. Rev. Cienc. Mar. Costeras 1: 73-94.
- Appeldoorn, R.C. & K.C. Lindeman. 2003. A Caribbean-wide survey of marine reserves: spatial coverage and attributes of effectiveness. Gulf. Caribb. Res. 14: 139-154.
- Aronson, R.B. & W.F. Precht. 2000. Herbivory and algal dynamics on the coral reef at Discovery Bay, Jamaica. Limnol. Oceanogr. 45: 251-255.
- Aronson, R.B. & W.F. Precht. 2006. Conservation, precaution, and Caribbean reefs. Coral Reefs 25: 441-450.
- Bellwood, D.R., T.P. Hughes, C. Folke & M. Nyström. 2004. Confronting the coral reef crisis. Nature 429: 827-833.
- Bellwood, D.R., T.P. Hughes & A.S. Hoey. 2006. Sleeping functional group drives coral-reef recovery. Curr. Biol. 16: 2434-2439.
- Bruggemann, J.H., M.J.H. Vanoppen & A.M. Breeman. 1994. Foraging by the stoplight parrotfish *Sparisoma viride* I. Food selection in different socially determined habitats. Mar. Ecol. Prog. Ser. 106: 41-55.
- Caballero, H.P. & E. de la Guardia. 2003. Arrecifes de coral utilizados como zonas de colectas para exhibiciones en el Acuario Nacional de Cuba. I. Costa noroccidental de la Habana, Cuba. Rev. Invest. Mar. 24: 205-220.
- Caballero, H.P., D. Rosales & A. Alcalá. 2006. Estudio diagnóstico del arrecife coralino del Rincón de Guanabo, Ciudad de la Habana, Cuba. I. Corales, esponjas y gorgonáceos. Rev. Invest. Mar. 27: 49-59.
- Caballero, H.P., P.M. Alcolado & A. Semidey. 2009. Condición de los arrecifes de coral frente a costas con asentamientos humanos y aportes terrígenos: el caso del litoral habanero, Cuba. Rev. Cienc. Mar. Costeras 1: 49-72.
- Carpenter, R.C. 1981. Grazing by *Diadema antillarum* Philippi and its effects on the benthic algal community. J. Mar. Res. 39: 747-765.
- Carpenter, R.C. 1986. Partitioning herbivory and its effects on coral reef algal communities. Ecol. Monogr. 56: 345-36.
- 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.
- Carpenter, R.C. & P.J. Edmunds. 2006. Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. Ecol. Lett. 9: 271-280.
- Clero-Alonso, L., F. Pina-Amargós, L. Hernández-Frenández, F. Martín-Blanco, D. Zúñiga-Ríos, S. Cowling, A.K. Brady & S. Caldwell. 2006. Biota acuática del norte de la provincia de Ciego de Ávila, p. 182-206. In F. Pina-Amargós (ed.). Ecosistemas costeros: biodiversidad y gestión de los recursos naturales. Compilación por el XV Aniversario del Centro de Investigaciones de Ecosistemas costeros (CIEC). CUJAE, Ciudad de la Habana, Cuba.
- De Ruyter van Steveninck, E.D. & A.M. Breeman. 1987. Deep water populations of *Lobophora variegata* (Phaeophyceae) on the coral reef of Curaçao: influence of grazing and dispersal on distribution patterns. Mar. Ecol. Prog. Ser. 38: 241-250.
- Edmunds, P.J. & R.C. Carpenter. 2001. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. P. Natl. Acad. Sci. USA. 98: 5057-5071.
- Friedlander, A.M. & J.D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J. Exp. Mar. Biol. Ecol. 224: 1-30.
- Guardia, E., A.P. Valdivia & P. González-Díaz. 2004a. Estructura de las comunidades bentónicas en la zona de buceo de María La Gorda, Ensenada de Corrientes, Sureste de la Península de Guanahacabibes, Cuba. Rev. Invest. Mar. 25: 103-111.

- Guardia, E., P. González-Díaz & S. Castellanos-Iglesias. 2004b. Estructura de la comunidad de grupos bentónicos sésiles en la zona de buceo de Punta Francés, Cuba. *Rev. Invest. Mar.* 25: 81-90.
- Guardia, E., P. González-Díaz, A. Valdivia & O. González-Ontivero. 2006. Estructura y salud de la comunidad de corales en el arrecife de la zona de buceo de Cayo Levisa, Archipiélago Los Colorados, Cuba. *Rev. Invest. Mar.* 27: 197-208.
- González-Sansón, G., C. Aguilar, J. Angulo & C. González. 1997. Variación espacial y estacional de la ictiofauna en un arrecife de coral costero de la región noroccidental de Cuba. II: Diversidad. *Rev. Invest. Mar.* 18: 233-240.
- González de Zayas, R., A. Zúñiga-Ríos, O. Camejo-Cardoso, L.M. Batista-Tamayo & R. Cárdenas-Murillo. 2006. Atributos físicos del ecosistema Jardines de la Reina, p. 296-351. In F. Pina-Amargós (ed.). Ecosistemas costeros: biodiversidad y gestión de los recursos naturales. Compilación por el XV Aniversario del Centro de Investigaciones de Ecosistemas Costeros (CIEC). CUJAE, Ciudad de la Habana, Cuba.
- Harborne, A.R., P.G. Renaud, E.H.M. Tyler & P.J. Mumby. 2009. Reduced density of the herbivorous urchin *Diadema antillarum* inside a Caribbean marine reserve linked to increased predation pressure by fishes. *Coral Reefs* 28: 783-791.
- Hay, M.E. 1997. The ecology and evolution of seaweeds-herbivores interactions on coral reefs. *Coral Reefs* 16: 67-76.
- Herrera-Moreno, A., E. Valdés-Muñoz & D. Ibarzábal. 1981. Evaluación poblacional del erizo negro, *Diadema antillarum* Phillipi, mediante un diseño de muestreo aleatorio estratificado, y algunos aspectos de su biología. *Cienc. Biol.* 6: 61-79.
- Hixon, M.A. & J.P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecol. Monogr.* 63: 77-101.
- Hughes, T.P. 1994. Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* 265: 1547-1551.
- Hughes, T.P., B.D. Keller, J.B.C. Jackson & M.J. Boyle. 1985. Mass mortality of the echinoid *Diadema antillarum* Phillipi in Jamaica. *Bull. Mar. Sci.* 36: 377-384.
- Hughes, T.P., A.M. Szmant, R. Steneck, R. Carpenter & S. Miller. 1999. Algal blooms on coral reefs: What are the cause? *Limnol. Oceanogr.* 44: 1583-1586.
- Idjadi, J.A. & P.J. Edmunds. 2006. Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. *Mar. Ecol. Prog. Ser.* 319: 117-127.
- Jones, G.P., M.I. McCormick, M. Srinivasan & J.V. Eagle. 2004. Coral decline threatens fish biodiversity in marine reserves. *P. Natl. Acad. Sci. USA.* 101: 8251-8253.
- Knowlton, N. 2001. Sea urchin recovery from mass mortality: New hope for Caribbean coral reefs? *P. Natl. Acad. Sci. USA.* 98: 4822-4824.
- Lee, S.C. 2006. Habitat complexity and consumer-mediated positive feedbacks on a Caribbean coral reef. *Oikos* 112: 442-447.
- Levitan, D.R. 1988. Algal-urchin biomass responses following the mass mortality of *Diadema antillarum* Phillipi at St. John. *J. Exp. Mar. Biol. Ecol.* 119: 167-178.
- Lewis, S.M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol. Monogr.* 56: 183-200.
- 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.
- Martín-Blanco, F., G. González-Sansón, F. Pina-Amargós & L. Clero-Alonso. 2010. Abundance, distribution and size structure of *Diadema antillarum* (Echinodermata: Diadematidae) in South Eastern Cuban coral reefs. *Rev. Biol. Trop.* 58: 663-676.
- McClanahan, T.R. 2000. Recovery of the coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biol. Conserv.* 94: 191-198.
- McClanahan, T.R. & N.A.J. Graham. 2005. Recovery trajectories of coral reef fish assemblages within Kenyan marine protected areas. *Mar. Ecol. Prog. Ser.* 294: 241-248.
- McClanahan, T.R., N.A.J. Graham, J.M. Calnan & M.A. MacNeil. 2007. Toward pristine biomass: Reef fish recovery in coral reef marine protected areas in Kenya. *Ecol. Appl.* 17: 1055-1067.
- Miller, J.R., A.J. Adams, N.B. Ogden, J.C. Ogden & J.P. Ebersole. 2003. *Diadema antillarum* 17 years after mass mortality: is recovery beginning on St. Croix? *Coral Reefs* 22: 181-187.
- Mumby, P.J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecol. Appl.* 16: 747-769.

- Mumby, P.J. 2009. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28: 761-773.
- Mumby, P.J., J.D. Hedley, K. Zychaluk, A.R. Harborne & P.G. Blackwell. 2006. Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: Fresh insights on resilience from a simulation model. *Ecol. Model.* 196: 131-148.
- Mumby, P.J., A.R. Harborne, J. Williams, C.V. Kappel, D.R. Brumbaugh, F. Micheli, K.E. Holmes, C.P. Dahlgren, C.B. Paris & P.G. Blackwell. 2007. Trophic cascade facilitates coral recruitment in a marine reserve. *P. Natl. Acad. Sci. USA.* 104: 8362-8367.
- Myhre, S. & A. Acevedo-Gutiérrez. 2007. Recovery of sea urchin *Diadema antillarum* populations is correlated to increased coral and reduced macroalgal cover. *Mar. Ecol. Prog. Ser.* 329: 205-210.
- 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: 715-717.
- Pina-Amargós, F. 2008. Efectividad de la Reserva Marina de Jardines de la Reina en la conservación de la ictiofauna. Tesis de Doctorado, Universidad de La Habana, Ciudad de la Habana, Cuba.
- Pina-Amargós, F., P.M. Alcolado, L. Hernández-Fernández, G. González-Sansón, R. González de Zayas, L. Clero-Alonso, K. Cantelar-Ramos & S. González-Ferrer. 2002. Estado de salud de los arrecifes coralinos de Jardines de la Reina. Resultado: Caracterización de los arrecifes coralinos de Jardines de la Reina, p. 1-20. *In* F. Pina-Amargós (ed.). Caracterización y manejo de los ecosistemas marinos en el archipiélago Jardines de la Reina (Informe Final de Proyecto). Centro de Investigaciones de Ecosistemas Costeros (CIEC), Cayo Coco, Ciego de Ávila, Cuba.
- Pina-Amargós, F., L. Clero-Alonso, F. Martín-Blanco, L. Hernández-Frenández, W. Acosta de la Red, L. Cabreja-Ávila, P.M. Alcolado, R.M. Claro, K.R. Cantelar, S.F. González & J.P.G. Artiaga. 2006. Biota marina del ecosistema Jardines de la Reina, p. 396-449. *In* F. Pina-Amargós (ed.). Ecosistemas costeros: biodiversidad y gestión de los recursos naturales. Compilación por el XV Aniversario del Centro de Investigaciones de Ecosistemas Costeros (CIEC). CUJAE, Ciudad de la Habana, Cuba.
- Rodwell, L.D., E.B. Barbier, C.M. Roberts & T.R. McClanahan. 2003. The importance of habitat quality for marine reserve fishery linkages. *Can. J. Fish. Aquat. Sci.* 60: 171-181.
- Russ, G.R. & A.C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138: 622-627.
- Sanmarco, P.W. 1980. *Diadema* and its relationship to coral spot mortality: grazing, competition and biological disturbance. *J. Exp. Mar. Biol. Ecol.* 45: 245-272.
- Sanmarco, P.W. 1982. Effects of grazing by *Diadema antillarum* Philippi (Echinodermata: Echinoidea) on algal diversity and community structure. *J. Exp. Mar. Biol. Ecol.* 65: 83-105.
- Sanmarco, P.W., J.S. Levinton & J.C. Ogden. 1974. Grazing and control of coral reef community structure by *Diadema antillarum* (Echinodermata: Echinoidea): a preliminary study. *J. Mar. Res.* 32: 47-53.
- Szmant, A.M. 2002. Nutrient enrichment on coral reefs: Is it a major cause of coral reef decline? *Estuaries* 25: 743-766.
- Weil, E., J.L. Torres & M. Ashton. 2005. Population characteristics of the sea urchin *Diadema antillarum* in La Parguera, Puerto Rico, 17 years after the mass mortality event. *Rev. Biol. Trop.* 53: 219-231.
- Williams, I.D. & N.V.C. Polunin. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* 19: 358-366.

