Influence of wave exposure and habitat complexity in determining spatial variation of the sea urchin *Diadema* aff. *antillarum* (Echinoidea: Diadematidae) populations and macroalgal cover (Canary Islands - Eastern Atlantic Ocean)

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Abstract: *Diadema* aff. *antillarum* performs a key role in organizing and structuring rocky macroalgae assemblages in the Canary Islands; increased sea urchin population density can result in the formation of rocky grounds covered with crustose algae. In the Canary Islands this type of system alternates with non-crustose macroalgal systems. However, understanding of the process controlling formation, persistence and alternation between states is still poor. Moreover, knowledge of spatial and temporal variations of this key herbivore populations are scarce. Here an extensive study of *D*. aff. *antillarum* populations throughout the Canarian Archipelago were presented, with particular emphasis on two main themes: firstly the influence of sea urchin population on non-crustose macroalgal assemblages. Secondly, the spatial variation of adult sea urchin populations at different scales: both on a large scale (between islands and sites with different wave exposure) and on a medium-small scale (between depths and habitats with different characteristics), and including comments regarding human influence on the observed spatial pattern between the studied islands. The main results were: (1) densities of *D*. aff. *antillarum* higher than 4 ind.m^{-2} drastically reduce non-crustose macroalgal cover to under 30%; (2) Tenerife Island comprises the highest urchin densities while El Hierro has been found to have the lowest; (3) wave exposure is a factor determining sea urchin density: more highly exposed sites present lower urchin density and vice versa; (4) rocky grounds covered with crustose algae can be found at greater depth in more highly exposed sites and at shallower depths in lesser exposed sites; (5) when sand percentage over the rocky substrate exceeds 20%, urchin density is limited to under 1 ind.m^{-2} and (6) high relief rocky substrate present higher urchin densities and hence a lower non-crustose macroalgal cover. Rev. Biol. Trop. 56 (Suppl. 3): 229-254. Epub 2009 January 05.

Key words: Canary Islands, *Diadema* aff. *antillarum*, non-crustose macroalgae, wave exposure, habitat complexity.

The importance of herbivorous sea urchins in structuring marine algal assemblages is well known (Lawrence 1975, Lawrence and Sammarco 1982, Dayton and Tegner 1984, Harrold and Pearse 1987). At moderate population densities, sea urchins may alter plant species composition and promote species diversity through selective feeding (Sammarco *et al*. 1974, Sammarco 1982). However, at high densities they can dramatically reduce the non-crustose macroalgae beds of the rocky reefs resulting in formation of 'sea urchin-dominated barren grounds' (Lawrence 1975). The occurrence of such areas has been reported along temperate coastlines (North and Pearse 1970, Estes and Palmisiano 1974, Mann 1977, Scheibling and Stephenson 1984, Miller 1985, Duggins 1989, McShane and Naylor 1991, Vadas and Elner 1992, Andrew 1993, Sala *et al.* 1998, Steneck *et al*. 2002, Guidetti *et al.*

2003) and subtropical coastlines (Aguilera *et al.* 1994, Alves *et al.* 2003, Brito *et al.* 2004, Tuya *et al.* 2004a, 2004b, Hernández 2006), as well as in tropical regions (Ogden *et al.* 1973, Sammarco 1982, Hay 1984, John *et al.* 1992, McClanahan 2000).

In the eastern Atlantic oceanic islands, and particularly in the Canary Islands, the density of the b-form of *Diadema antillarum* Philippi, 1845 (Lessios *et al.* 2001) can often reach more than 12 ind.m^{-2} and it is spread throughout the entire Archipelago (Aguilera *et al.* 1994, Brito *et al.* 2001, Tuya *et al.* 2004a, Hernández 2006). As in other sites around the globe, loss of macroalgal beds due to urchin grazing activity produces lower species diversity (Herrera 1998, Garrido 2003) and lack of habitat suitable for feeding and breeding fish (Brito *et al.* 2004, Tuya *et al.* 2005). Therefore, urchin barrens are unproductive habitats, where primary productivity is more than two orders of magnitude lower than at reefs dominated by algal beds in temperate regions (see Chapman 1981). At the latitude where the Canary Islands lies, between tropical and temperate waters, macroalgae are the main biological engineers on rocky reefs and no coral reef formations occur. Consequently, high macroalgal cover is a well-known indicator of good benthic conservation status (Hernández *et al.* 2007a).

On temperate and subtropical rocky coasts world wide, subtidal habitats are often characterized by one of two community states: algae bed/kelp forest or sea urchin barren (Estes and Palmisiano 1974, Lawrence 1975, Sala and Zabala 1996, Guidetti *et al.* 2003, Folke *et al.* 2004, Tuya *et al.* 2004a, Hernández *et al.* 2007a). When urchins are abundant in barrens their intense grazing denudes the seabed of all but encrusting red coralline algae such as *Hydrolithon* and *Neogonolithon*, and brown encrusting algae *Pseudolithoderma adriaticum* (Sangil *et al.* 2006a, 2006b, Sangil unpublished data). In spite of the high densities of this keystone sea urchin throughout the Canary Islands, relatively large areas that remain without urchins or where urchins are found in very low densities have been discovered (Brito *et*

al. 1984, 2004, Bacallado *et al.* 1987, Garrido 2003, Tuya *et al.* 2004a, Tuya and Haroun 2006, Hernández *et al.* 2007a). In such areas, the algal beds are characterized by brown algae and dominated by the unbranched brown algae *Lobophora variegata,* that occupies 80% of the substrate and can reach 50 m depth (Tuya and Haroun 2006, Sangil *et al.* 2006a, 2006b, Hernández *et al.* 2007a).

Habitat complexity is an important factor influencing *Diadema* grazing (Ogden 1976, Lee 2006), as also holds true for other sea urchin species (Andrew 1993), since complex habitats provide urchins with refuge from predation (Ebling *et al.* 1966, Ogden 1976, Levitan and Genovese 1989, McClanahan and Kurtis 1991). The availability of refuges and the urchins' so called cryptic behavior seems to help promote survival of recruits in complex rocky areas (Carpenter 1984, Verlaque 1984, Bak 1985, Hunte and Younglao 1988, Levitan and Genovese 1989, Sala and Zabala 1996, Tomas *et al.* 2004) and probably contributes to the high adult population density typically found in these habitats (Hernández 2006, Hernández *et al.* 2006, Clemente *et al.* 2007). Therefore, the availability of shelter can be viewed as a major factor influencing the distribution of urchin barrens (Andrew 1993).

Gradients in the physical environment may produce variability in the abundance and distribution of urchin populations simply as a consequence of the space available or of the different physiological tolerances of the species (Ogden 1976, Levitan and Genovese 1989, Andrew 1993). This kind of segregation often occurs at relatively large spatial scales (Gaines and Lubchenco 1982, Barry and Dayton 1991, Dunson and Travis 1991). At smaller scales (within habitats), physical factors may play an important role in regulating the intensity of biological interactions which define invertebrate abundance (Hawkins 1981, Hawkins and Hartnoll 1983, Lubchenco 1983, Sousa 1984, 1985, Connell and Keough 1985). Consequently, environmental conditions play an important role in spatial heterogeneity of marine assemblages at different scales,

from local patchiness to variation along bio-geographic gradients (Levin 1992, Menge and Sutherland 1987, Hixon and Menge 1991, Menge 2000, Fraschetti *et al.* 2005).

The mechanisms that bring about patchiness have been studied in other regions of the world (Lubchenco 1983, Hawkins and Hartnoll 1983, Connell and Keough 1985, Hay 1991, Bennedetti-Cechi and Cinelli 1995) but few studies concerning habitat complexity have been carried out with urchins in subtidal marine environments (McClanahan 1994, Lee 2006, Clemente *et al.* 2007). Since depth, wave exposure and habitat complexity are believed to affect *D.* aff. *antillarum* distribution and abundance (Alves *et al.* 2001, Hernández 2006, Clemente *et al.* 2007, Tuya *et al.* 2007), any deductions made by urchin population studies must be made knowing the species' basic variation in relation to these environmental variables.

Here we present a data set, recorded throughout the Canarian Archipelago over a six year study period and 125 sites, which aims to promote a better understanding of spatial variation at different scales. This study assesses *D.* aff. *antillarum* populations (density); cover of urchin barrens versus macroalgae; and habitat-complexity. Variation is studied at different spatial scales (amongst islands, and amongst areas of different wave exposure, depth, and habitat complexity).

MATERIALS AND METHODS

Study site: oceanographic features of the Canary Islands. The Canary Islands are situated between 27.68° - 29.58° N and 18.28° - 14.58° W on the eastern border of the North Atlantic subtropical gyre. Emerging from the oceanic basin as a result of successive overlays of volcanic material to form an independent set of islands with a water depth of around 2000 m between them, the Canarian Archipelago comprises seven major islands and four islets called the 'Archipelago Chinijo' located at its northeastern side.

The eastern boundary of the archipelago is separated 90 km from the coast of African and it extends about 400 km further west. This geographical location between the cool, nutrient-rich water from the north-west African coastal upwelling, and the warmer, nutrient-poor open ocean waters, means that the Canary Islands are considered a 'Coastal Transition Zone' (Barton *et al.* 1998). In addition, the archipelago itself acts as an obstacle to both the Canary Current, which flows NNE to SSW through the archi-pelago, and to the Trade Winds; thus giving rise to a variety of mesoscale phenomena that have strong implications for the productivity of the region (Molina and Laatzen 1986, Barton 1994, Arístegui *et al.* 1997). This particular geographical situation creates an oceanographic gradient across the archipelago, where differences in sea water temperature (≈ 2ºC), nutrients and primary productivity are found between its eastern and western boundaries (Barton *et al.* 1998, Davenport *et al.* 2002). Therefore, the islands marine assemblages consist of a combination of tropical and temperate species which varies according to its location within the oceanographic gradient (algae: Sansón *et al.* 2001; invertebrates: Moro-Abad *et al.* 2003; vertebrates: Brito *et al.* 2001).

Exposure to wave action is a strong force in segregating urchin species at the scale between islands (Tuya *et al.* 2007). Differences between coastal orientations and seasons are found amongst islands. The shape of the island and orientation against the waves create different degrees of wave exposure along the different islands coastlines, which present different susceptibility to the incidence of storms, both linked to swell and sea wave events. The normal wave pattern consists of sea waves from a NNE direction, which have an annual average height of 1.4 m and a frequency of 9.5 s between waves. Sea waves are more frequent from late autumn until early spring. NNE sea swells are abundant throughout the year, also associated with 18 to 22 km/h NNE and NE winds. However, stronger swells, originated in the Northern Atlantic, become more frequent

between October and March and approach the islands from NNW and NW with an annual wave height ranging between 2 and 3 m and a frequency of 18 s between waves (Yanes *et al.* 2006). According to the different spatial behavior of the swell, differences in terms of average annual height between the northern, western and eastern-southeastern coasts are found. There are also spatial differences between average wave height and frequency along the northern and western coastlines which are exposed to non local swells. Eastern, southeastern and southern coasts of the islands are sheltered from strong swells; these coastlines face waves which are on average smaller than those in coastlines with other orientations (e.g. Tenerife: Pérez *et al.* 2003, Yanes *et al.* 2006).

Sampling methods

Sea urchins and algal assemblages. At each locality the belt transect method was used, in which a continuous area along a line transect is surveyed to count all *D.* aff. *antillarum* individuals, providing estimates of sea urchin population density. In the Mediterranean Sea, this simple technique has been successfully carried out to estimate population density of the sea urchins *Arbacia lixula* and *Paracentrotus lividus* (Harmelin *et al.* 1980, Turón *et al.* 1995, Sala and Zabala 1996). However, in the present study certain modifications have made this technique more suitable for the benthic communities investigated (Hernández *et al.* 2007a). Shorter transects of 10 x 2 m were used, allowing for more replicates; at least eight randomly placed replicates were carried out at each site with a minimum distance of 10 m between replicates. Transects were run parallel to the coast line using a metric tape at a depth range preestablished between 0.5 m and 25 m. The percentage of non-crustose macroalgal cover was visually determined in each 20 m^2 transect. Dominant algal assemblage was recorded in all sampled sites and five separate morpho-functional algal groups were considered following Guidetti (2006) ((a) algal turf; (b) unbranched-erect macroalgae; (c) branched-erect macroalgae; (d) calcified-erect macroalgae) and modifications by Hernández *et al.* (2007) ((e) crustose macroalgae) (Table 1)). These groupings facilitate the ecological interpretation of algal assemblages influenced by *D.* aff. *antillarum*, since species with similar morphotype and phenology tend to react similarly (Dethier 2001).

Experimental design and data analysis

Influence of sea urchin population density on algal assemblages. The influence of sea urchin populations on algae assemblage was determined using data from 125 sites (one survey and at least eight replicates per site) around the Canarian Archipelago (Fig. 1; Table 2) over the period between 2001 and 2006. Log-linear relationships between sea urchin *D.* aff. *antillarum* density (ind.m^{-2}) and non-crustose macroalgal cover (%) were assessed. Regression models were performed using the SPSS-14 statistical package.

To assess the effect of urchin density on non-crustose macroalgal cover, a one-way Permutational ANOVA was performed with 'Sea Urchin Density' as the factor with 6 density categories (1: 0-2 ind. m^{-2}; 2: 2-4 ind. m^{-2}; 3: 4-6 ind. m^{-2}; 4: 6-8 ind. m^{-2}; 5: 8-10 ind. m^{-2}; 6: >10 ind. m^{-2}), using PRIMER 6 & PERMANOVA + software.

Large scale spatial variation: Influence of archipelagic gradient and wave exposure. To assess spatial variation over a scale of kilometers, a total of 125 sites were sampled between 2001 and 2006 throughout the entire archipelago: 28 in La Palma, 20 in El Hierro, 13 in La Gomera, 24 in Tenerife, 10 in Gran Canaria, 9 in Fuerteventura and 21 in Lanzarote and the islets (La Graciosa, Montaña Clara, Alegranza and Roque del Este) (Fig. 1; Table 2). Sites were chosen from two different wave exposure categories and sampling was done in a depth band between 0.5 m and 25 m. A variety of different degrees of exposure can be found on an island due to its local topography.

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Non-crustose macroalgae			
Turf	Unbranched erect	Branched erect	Calcified erect
Amphiroa spp.	*Colpomenia sinuosa*	*Asparagopsis taxiformis*	*Corallina elongata*
Asparagopsis taxiformis (tetrasporofite)	*Hydroclathrus clathratus*	*Cystoseira abies-marina*	*Liagora ceranoides*
Ceramium echionotum	*Lobophora variegata*	*Cystoseira compressa*	*Liagora tetrasporifera*
Cottoniella filamentosa	*Padina pavonica*	*Cystoseira foeniculacea*	
Cianophytes (unidentified)		*Cystoseira* sp.	
Caulerpa webbiana		*Dasya baillouviana*	
Filaments (unidentified)		*Dictyota cervicornis*	
Gelidiopsis intricata		*Dictyota crenulata*	
Herposiphonia secunda		*Dictyota dichotoma*	
Jania adhaerens		*Dictyota fasciola*	
Jania pumila		*Dictyota pfaffii*	
Lophocladia trichoclados		*Dictyota* sp1.	
Polysiphonia furcellata		*Dictyota* sp2.	
Psedochlorodesmis furcellata		*Galaxaura rugosa*	
Pseodotetraspora marina		*Hypnea spinella*	
Sphacelaria cirrosa		*Laurencia* spp.	
Spyridia hypnoides		*Pterosiphonia pennata*	
Wrangelia penicillata		*Sargassum desfontainesii*	
		Sargassum sp.	
		Stypocaulon scoparium	
		Stypopodium zonale	
Crustose macroalgae			
Crutose coralline algae (unidentified)			
Lithothamnium coralloides			
Mesophyllum canariense			
Pseudolithoderma adriaticum			

However to make the analysis simpler, these were grouped in two main levels of wave exposure. As described above in section 2.1, following criteria set out by Pérez *et al.* (2003) and Yanes *et al.* (2006), this simplification facilitates the ecological interpretation of results:

- High exposure: sites located on the north and northwest side of the islands and islets, affected by trade winds and swells from NNE-NE and frequently affected by NNW-NW swells, as well as sites only affected by NNW-NW swells. This exposure is characterized by an annual average wave height of about 3 m.

- Low exposure: sites located on the east, south or southeast side of the islands and islets, normally affected by trade winds waves and sometimes by swells from

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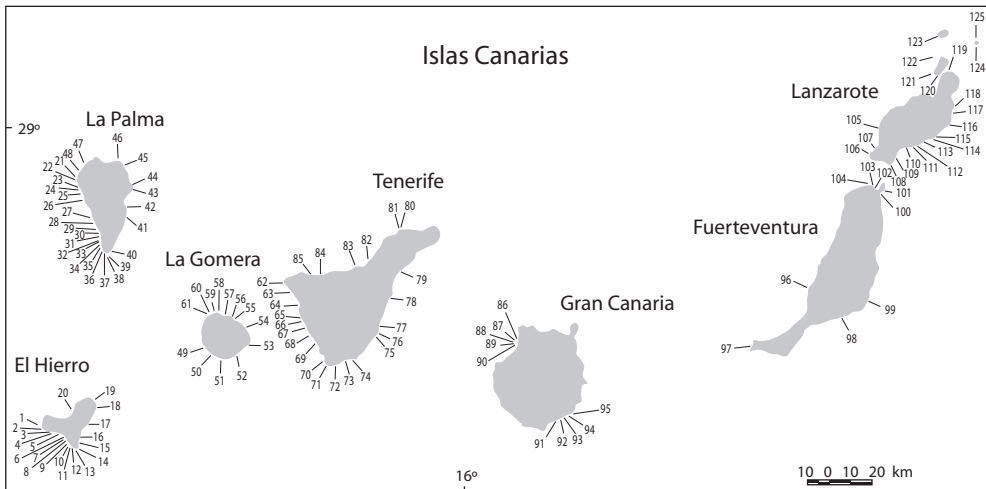
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Fig. 1. Study sites across the Canary Islands including Marine Protected Areas (MPAs). Numbers correspond to the different sites listed in Table 2. [Mar Calmas-MPA from 6 to 14; La Palma-MPA from 28 to 37; La Graciosa-MPA from 119 to 125].

NNE-NE but not affected by NNW-NW swells. This exposure is characterized by an annual average wave height of about 1.4 m.

In order to contrast sea urchin density and barren cover among islands (I) and degrees of wave exposure (E), we performed distance-based permutational ANOVAs (Anderson 2001) rather than carrying out a traditional univariate ANOVA. In these analyses the F-statistics are calculated but p-values are obtained by permutation, thus avoiding any assumption about the nature of the distribution of the original variables (Anderson 2001, Anderson and ter Braak 2003). A three-way design was performed when analysing urchin density and noncrustose macroalgal cover, in which 'I, island' was treated as a fixed factor with seven levels (1: El Hierro; 2: La Palma; 3: La Gomera; 4: Tenerife; 5: Gran Canaria; 6: Fuerteventura; 7: Lanzarote and islets); 'E, exposure' as a fixed factor with two levels (1: High exposure and 2: Low exposure); and 'Site' as a random factor nested in the interaction 'I x E'. All analyses were based on Euclidean distances of the original raw data, with all p-values obtained using 4999 permutations of the appropriate

exchangeable units (Anderson and ter Braak 2003). Significant terms in the full model were examined individually using appropriate *a posteriori* pairwise comparisons. The computer programme PRIMER 6 & PERMANOVA+ (www.primer-e.com) was used to perform the analyses described above.

Medium-small scale spatial variation: Influence of depth, sedimentation, rugosity, slope and substratum diversity. To assess spatial variation at a scale of meters, depth and main habitat-complexity variables which recur in the bibliography were identified: (1) sedimentation (Alves *et al*. 2001, Díez *et al.* 2003, Erikson and Bergström 2005), (2) topographic complexity or rugosity of the substrate (Luckhurst and Luckhurst 1978, Robert and Ormond 1987, Jennings *et al.* 1996 McClanahan 1994), (3) slope (Alves *et al*. 2001, Díez *et al*. 2003), (4) substratum diversity (Gratwicke and Speight 2005). The effect of each variable on *D.* aff. *antillarum* density was tested using field data collected in 1112 belt transects (of 20 m^2 each, totaling 22240 m^2 of surveyed area) from the 125 sites performed throughout the entire Canarian Archipelago

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TABLE 2

List of the surveyed sites in the Canary Islands including wave exposure and mean values and range
of Diadema *aff.* antillarum *densities*

Island	MPA	Site #	Site name	Wave exposure[*]	D. aff. antillarum Mean density (N/m²)	Range (N/m²)
EL HIERRO		1	Baja de Anacón	1	0.13	0.00-0.60
		2	Laja de Orchilla	2	0.16	0.00-0.50
		3	Punta La Palometa	2	0.01	0.00-0.05
		4	Punta de Los Mozos	2	0.07	0.00-0.25
		5	Punta de Los Lances	2	0.22	0.05-0.40
	Mar de Las Calmas-MPA	6	Punta de Tecorón	2	0.36	0.05-0.95
		7	Cueva del Diablo	2	0.20	0.05-0.45
		8	Punta de Las Lapillas	2	0.08	0.00-0.35
		9	Punta de Las Cañas	2	0.21	0.10-0.40
		10	Roque Chico	2	0.03	0.00-0.10
		11	La Gabarra	2	0.08	0.00-0.25
		12	Punta de Los Frailes	2	0.05	0.00-0.30
		13	Cueva de Los Frailes	2	0.03	0.00-0.15
		14	La Herradura	2	0.09	0.00-0.25
		15	Muelle de La Restinga	2	0.04	0.00-0.15
		16	Los Joraditos	1	0.10	0.00-0.30
		17	Roque de La Bonanza	1	0.07	0.00-0.25
		18	La Caleta	1	0.62	0.00-1.10
		19	Tamaduste	1	0.04	0.00-0.15
		20	Punta Grande	1	0.80	0.05-2.45
LA PALMA		21	Punta Llanadas	1	0.12	0.05-0.20
		22	Punta Gorda	1	2.97	0.75-4.10
		23	Playa de Las Vinagreras	1	1.77	1.15-2.50
		24	Callao Nuevo	1	1.78	0.50-3.40
		25	El Roque	1	2.37	1.30-4.05
		26	Morro Negro	2	2.55	1.05-3.50
		27	La Bombilla	2	3.05	1.40-4.25
	La Palma-MPA	28	Punta Bogullos	2	2.96	0.40-5.60
		29	El Faro	2	2.92	0.50-6.60
		30	Playa de El Remo	2	1.11	0.20-1.80
		31	Punta de El Remo	2	1.88	1.15-2.80
		32	Punta Banco	2	2.09	0.80-3.45
		33	Dos Hermanas	2	0.93	0.50-1.55
		34	Los Andenes	2	0.56	0.30-0.85
		35	Siete Islas	2	0.15	0.00-0.75
		36	La Resbaladera	2	0.77	0.15-1.90
		37	Punta Larga	2	0.07	0.00-0.25
		38	Fuencaliente (Malpique)	2	6.40	6.40-10.05
		39	El Faro de Fuencaliente	2	0.30	0.30-4.20

TABLE 2 (Continued)
List of the surveyed sites in the Canary Islands including wave exposure and mean values and range
of Diadema *aff.* antillarum *densities*

| Island | MPA | Site # | Site name | Wave exposure* | D. aff. antillarum | |
					Mean density (N/m^2)	Range (N/m^2)
LA PALMA		40	Las Cabras	2	0.25	0.00-0.65
		41	La Bajita	2	8.20	6.15-10.65
		42	Los Cancajos	2	7.92	3.85-11.75
		43	Puerto Trigo	2	4.89	1.60-6.85
		44	Puerto Paja	1	4.35	0.04-11.60
		45	Puerto Espíndola	1	3.32	2.00-4.45
		46	La Fajana	1	0.07	0.00-0.20
		47	Roque Santo Domingo	1	0.11	0.00-0.40
		48	Lomada Grande	1	1.16	0.00-3-85
LA GOMERA		49	Roque de Iguala	2	2.04	0.55-3.50
		50	Punta Narices	2	2.90	0.45-5.50
		51	Punta Becerro	2	2.94	0.20-5.35
		52	Playa de Suárez	2	3.18	0.05-7.10
		53	Punta Los Canarios	1	5.71	1.75-10.60
		54	Punta Majona	1	4.03	1.40-7.20
		55	Roque de Agulo	1	3.33	3.00-3.95
		56	Playa de San Marcos	1	2.57	1.75-3.70
		57	Punta Sardina/La Sepultura	1	3.47	2.75-4.55
		58	Punta de Los Órganos	1	2.01	1.50-2.80
		59	Los Órganos	1	1.43	0.90-2.05
		60	Roques de Arguamul	1	2.17	1.75-2.60
		61	Playa de Santa Catalina	1	0.01	0.00-0.05
TENERIFE		62	Teno	2	6.34	2.65-9.90
		63	Masca	2	7.64	5.95-10.15
		64	Los Gigantes	2	6.03	3.40-9.55
		65	El Acuario	2	5.12	3.05-10.25
		66	Cueva de Los Cerebros	2	5.65	1.35-10.35
		67	La Tixera	2	5.84	4.55-8.35
		68	La Caleta	2	6.46	3.75-11.50
		69	El Balito	2	7.51	5.05-9.65
		70	El Palm-Mar	2	5.62	3.50-8.15
		71	Punta Rasca	2	3.95	2.65-5.50
		72	Las Galletas	2	5.17	3.35-6.55
		73	Agua Dulce	2	5.96	4.70-7.10
		74	La Tejita	2	4.84	2.25-7.35
		75	La Jaquita	2	13.57	6.35-17.45
		76	Abades	2	9.07	4.60-12.20
		77	El Porís de Abona	2	4.58	2.70-7.80
		78	Punta Prieta	2	8.75	7.85-10.60

TABLE 2 (Continued)
List of the surveyed sites in the Canary Islands including wave exposure and mean values and range
of Diadema *aff.* antillarum *densities*

| Island | MPA | Site # | Site name | Wave exposure* | D. aff. antillarum | |
					Mean density (N/m^2)	Range (N/m^2)
TENERIFE		79	Boca Cangrejo	2	6.06	3.24-8.20
		80	Punta Hidalgo	1	0.00	0.00-0.00
		81	Punta Hidalgo 2	1	4.21	2.00-5.60
		82	Martiánez	1	8.48	6.10-11.25
		83	La Rapadura	1	4.41	3.25-5.25
		84	La Consolación	1	3.77	1.70-5.50
		85	La Hondura	1	5.17	2.55-7.05
GRAN CANARIA		86	Punta El Cardonal	1	3.37	2.60-4.10
		87	El Juncal	1	1.76	1.15-2.50
		88	Punta del Tumas	1	0.97	0.75-1.35
		89	Playa de Las Nieves	1	0.36	0.00-0.85
		90	Muñón de Dios	1	1.06	0.15-2.30
		91	Punta del Tarajalillo	2	0.30	0.10-0.40
		92	Playa Corral del Espino	2	2.45	0.50-3.95
		93	Puntilla de La Caleta	2	2.33	1.60-3.00
		94	Playa de La Caleta	2	2.27	0.45-4.35
		95	Las Casillas	2	0.73	0.10-1.15
FUERTEVENTURA		96	Ajúi	1	0.06	0.00-0.15
		97	Punta de Jandía	1	0.00	0.00-0.00
		98	Jinijinamar	2	1.05	0.00-2.30
		99	Jacomar	2	4.39	3.10-6.40
		100	El Queso	2	0.02	0.00-0.15
		101	El Marrajito	2	0.06	0.00-0.25
		102	Baja de Fefo	2	5.79	3.20-9.65
		103	El Calamareo	2	3.01	1.45-6.25
		104	Veril del Morrajo	2	1.41	0.00-4.90
LANZAROTE and ISLETS		105	El Golfo	1	0.04	0.00-0.15
		106	Punta Limones	2	4.31	2.80-6.00
		107	Playa Flamingo	2	3.77	3.00-6.00
		108	El Pasito	2	2.00	0.90-4.70
		109	Puntagorda	2	3.54	2.60-4.60
		110	Puerto Calero	2	2.97	1.10-5.25
		111	Puerto del Carmen (sur)	2	6.98	2.00-13.30
		112	Puerto del Carmen	2	5.78	3.65-8.60
		113	Playa de Los Pocillos	2	3.86	3.30-4.25
		114	Hoyas Hondas	2	1.07	0.50-1.80
		115	Playa Matagorda	2	3.63	2.95-4.55
		116	Playa Honda	1	3.18	2.50-4.00
		117	Los Cocoteros	1	7.05	4.70-8.90

TABLE 2 (Continued)

List of the surveyed sites in the Canary Islands including wave exposure and mean values and range
of Diadema *aff.* antillarum *densities*

Island	MPA	Site #	Site name	Wave exposure[*]	D. aff. antillarum	
					Mean density (N/m^2)	Range (N/m^2)
LANZAROTE and ISLETS	La Graciosa-MPA	118	Mala	1	5.70	4.00-7.70
		119	Punta Fariones	1	2.76	0.00-4.80
		120	Caleta del Sebo	2	0.16	0.00-1.00
		121	Montaña Amarilla	2	3.72	2.10-5.60
		122	Cuevas Coloradas	2	6.19	3.90-10.30
		123	Punta La Mareta	2	6.55	3.80-9.20
		124	Roque del Este (sur)	2	1.12	0.00-4.40
		125	Roque del Este (Norte)	1	0.03	0.00-0.15

*Wave exposure: 1 = highly exposed sites, always affected by waves and swell (NE-NNE) and periodically exposed to NNW swells; 2 = lesser exposed sites or thoses exposed only to NNE waves. At least 160 m^2 of area sampled at each site. All sites were used in the analysis of small and large scale spatial variation.

(Fig. 1). The habitat-complexity variables were described as follows:

- Sedimentation: measured as the percentage of sand over the rocky substrate and categorized from 1 to 4: (1) 0%; (2) 1 to 10%; (3) 10 to 20%; and (4) more than 20%.
- Rugosity: measured as the ratio of actual surface area in relation to linear surface area (belt transect size: 20 m²): (1) flat surface; (2) less than 1m; (3) between 1 and 3m; and (4) high relief more than 3 m.
- Slope: measured as the inclination of the substrate in degrees. (1) 0˚; (2) from 0˚ to 45˚; (3) more than 45˚ and less than 90º; and (4) 90˚.
- Substrate diversity: evaluated as the substrate type or combination of substrata found in belt transects. We categorized them as: (1) bed rock substrate; (2) boulder substrate between 5 and 100 cm; (3) a combination of bed rock and boulder substrate.

In order to assess the influence of habitat-complexity variables on sea urchin density, we performed distance-based permutational ANOVAs (Anderson 2001). A three-way design was performed when analysing urchin density and biomass, in which 'Island' I was treated as a fixed factor with seven levels, grouped by geographic location from west to east (1: El Hierro; 2: La Palma; 3: La Gomera; 4: Tenerife; 5: Gran Canaria; 6: Fuerteventura; 7: Lanzarote and islets). Habitat complexity variables were treated as fixed factors with four levels each for 'Sand' (S), 'Rugosity' (R) and 'Slope' (S) and three levels for 'Substrate diversity' (SD). 'Site' was treated as a random factor nested within the interaction 'Island x habitat complexity variable'.

RESULTS

Influence of sea urchin populations on algal assemblages throughout the Canary Islands

A highly significant log-linear relationship was detected between sea urchin *D.* aff. *antillarum* density and non-crustose macroalgal cover (Fig. 2). The scatter plot of sea urchin density versus non-crustose macroalgal cover showed more variability in percentage
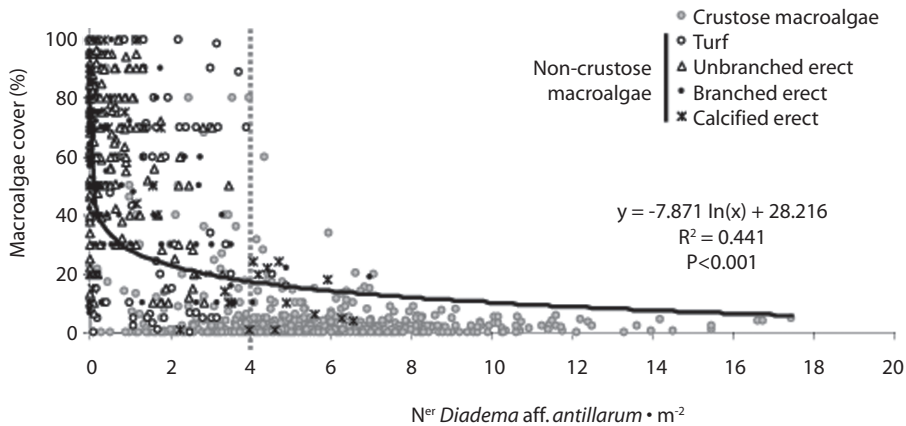
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Fig. 2. Log-linear relationship between sea urchin abundance and macroalgal cover.

of algal cover at the lowest urchin densities (0-4 ind.m^{-2}), at these densities higher variability in the dominant morpho-functional algal group also occurred. At intermediate densities this variability decreased sharply and at a threshold density of about 4 ind.m^{-2} non-crustose macroalgal cover remained below 30%, with crustose macroalgae clearly the dominant algal group (Fig. 2). In general, when urchin densities exceed 4.5 ind.m^{-2}, turf, unbranched-erect and branched-erect macroalgae did not appear as dominant (Fig. 2). Calcified-erect macroalgae only appeared as the dominant algae in cases where urchin densities were

lower than 6.5 ind. m^{-2} (Fig. 2). The list of species found for each morpho-functional group is presented on Table 1, with 18 identified algal turf species, four unbranched-erect species, 21 branched-erect, three calcified-erect and four crustose macroalgae identified species.

Permutational ANOVA results revealed a highly significant effect of the factor 'Sea Urchin Density' over percentage of macroalgae cover (F= 292.42, p<0.001) (Fig. 3). *A posteriori* pairwise analyses showed that at the lowest levels of urchin density (0-2 ind.m^{-2}) maximum percentages of macroalgal cover were recorded. This cover differs significantly
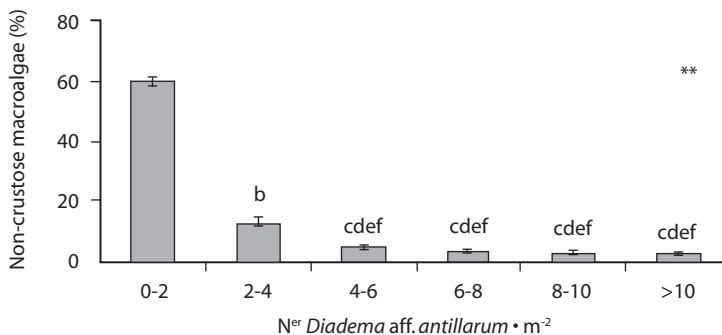

Fig. 3. Comparison of mean non-crustose macroalgal cover (± SE) at different abundances of *Diadema* aff. *antillarum,* including data from 125 sites studied. There was no significant difference between means with identical letters (pairwise analysis). ** = p < 0.01.

from the lower values recorded at urchin densities ranging from 2-4 ind.m^{-2} (t = 21.03, p<0.01) and from the lowest macroalgal cover registered at urchin density levels of 4-6, 6-8, 8-10 and >10 ind.m^{-2} (t = 23.164, p<0.01; t = 20.03, p<0.01; t = 13.22, p<0.01 and t=11.565, p<0.01, respectively) although macroalgal cover at the four highest urchin density levels were not found to differ significantly from one another (p>0.01 in all cases) (Fig. 3).

Spatial variation at large scale

Archipelagic gradient and effect of wave exposure on sea urchin populations. High variability in *D.* aff. *antillarum* population density throughout the Canarian Archipelago was detected. Permutational ANOVA results revealed a highly significant effect of the main factor 'Island' and to a lesser extent of factor 'Exposure' on urchin density (Table 3a). *A posteriori* pairwise analyses showed that the maximum sea urchin densities were recorded at Tenerife island, and these densities differ significantly from those registered in Lanzarote islets (t = 2.42, p<0.05), La Gomera (t = 3.14, p<0.01), La Palma (t = 4.01, p<0.01), Fuerteventura (t = 3.83, p<0.01) and Gran Canaria (t = 4.16, p<0.01). El Hierro comprised the lowest urchin densities, which were significantly different from those recorded on the other islands (t = 8.07, p<0.01; t = 5.44, p<0.01; t = 8.36, p<0.01; t = 4.09, p<0.01; t = 1.94, p<0.05 and t = 6.64, p<0.01, respectively) (Fig. 4a). Results concerning the factor
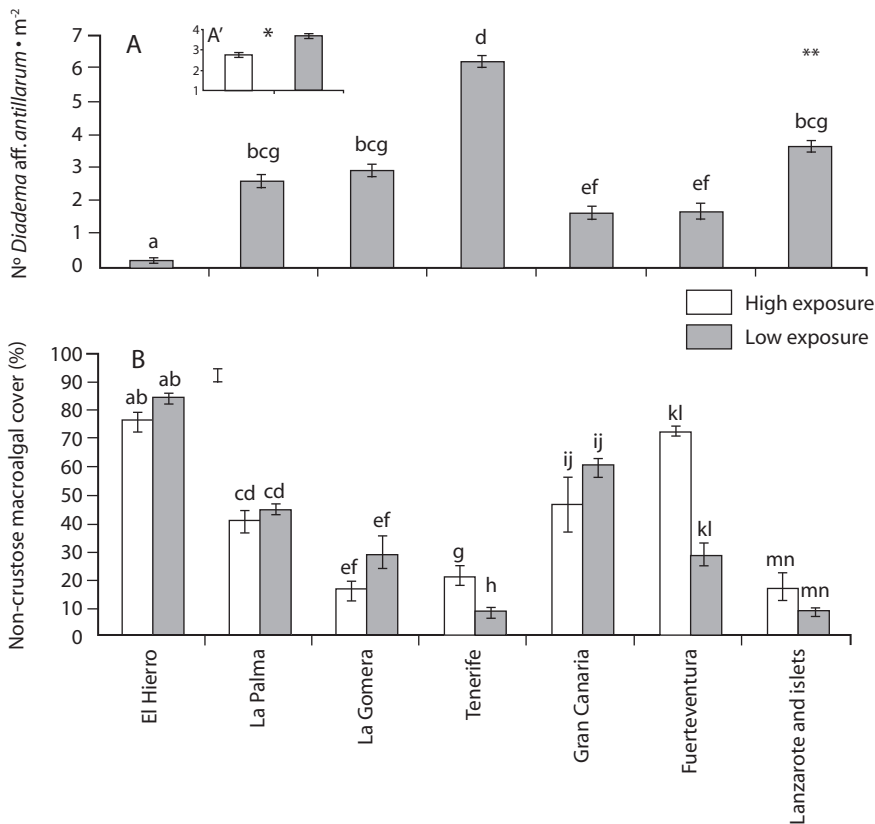

Fig. 4. (A) Comparison of mean sea urchin abundance (± SE) among Islands and (A') at different wave exposure. (B) Comparison of mean percentage of non-crustose macroalgal cover (± SE) among Islands and wave exposure. There was no significant difference between means with identical letters (pairwise analysis). ns= not significant; * = p < 0.05; ** = p < 0.01.

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'Exposure' show that sites with high levels of exposure to wave action (N=44 sites) maintained significantly lower *D.* aff. *antillarum* densities (2.27 ± 0.14 ind.m^{-2}) than those with low exposure levels (N=81 sites) (3.49 ± 0.12 ind.m^{-2}) (Fig. 4a'). There were also differences in urchin densities between sites at each island when the nested factor 'Site (Island)' was taken into consideration (Table 3a).

The assessment of non-crustose macroalgal cover across the Archipelago showed a significant interaction of factors 'Island x Exposure' (Table 3b). Non-crustose macroalgal cover differed depending on level of exposure to wave action in relation to each island considered, as shown by the *a posteriori* pairwise analyses. The only island for which significant differences were obtained was Tenerife, where non-crustose macroalgal cover was found to be higher at highly exposed sites (t = 2.92, p<0.01) (Fig. 4b). No significant differences were obtained at El Hierro (t = 1.25, p = 0.23), La Palma (t = 0.10, p = 0.93), La Gomera (t = 0.99, p = 0.34), Gran Canaria (t = 0.43, p =

0.68), Fuerteventura (t = 1.90, p = 0.09) and Lanzarote islets (t = 1.60, p = 0.13) (Fig. 4b). On the other hand, differences at the scale of nested factor 'Site (Island)' were also significant (Table 3b), differing the percentage of non-crustose macroalgal cover between sites at each island.

Spatial variation at medium-small scale

Depth. When assessing the variability of *D. antillarum* density with depth, the scatter plot showed higher variability in urchin density at shallower depths (<7 m) for those sites less exposed to wave action (Fig. 5). At highly exposed sites urchin density hardly varied in shallow water but variability was found to increase with depth (Fig. 5). The critical threshold of 4 ind.m^{-2} previously reported to drastically reduce non-crustose macroalgal cover, was not reached at highly exposed sites at depths shallower than about 7 m, while at less exposed sites this density is common in shallower waters (~3 m) (Fig. 5).

TABLE 3

Results of three-way Permutational ANOVA comparing (A) density of Diadema *aff.* antillarum *(n° ind.m $^{-2}$) and (B) non-crustose macroalgal cover (%) between the 7 islands (1. El Hierro; 2. La Palma; 3. La Gomera; 4. Tenerife; 5. Gran Canaria; 6. Fuerteventura; 7. Lanzarote and islets), two different levels of wave exposure (1. high wave exposure; 2. low wave exposure), and 125 sites across the Canarian Archipelago (Table 2)*

A. Density	Df	MS	F	P (perm)
Island (I)	6	405.46	12.15	0.001
Wave exposure (E)	1	131.42	4.10	0.040
I x E	6	28.63	0.86	0.545
Site (I x E)	111	37.19	18.31	0.001
Residual	987	2.03		
Total	1111			
B. Macroalgal cover				
I	6	66881.00	18.24	0.001
E	1	5203.10	0.70	0.422
I x E	6	8521.40	2.32	0.038
Site (I x E)	111	4087.80	18.94	0.001
Residual	987	215.80		
Total	1111			

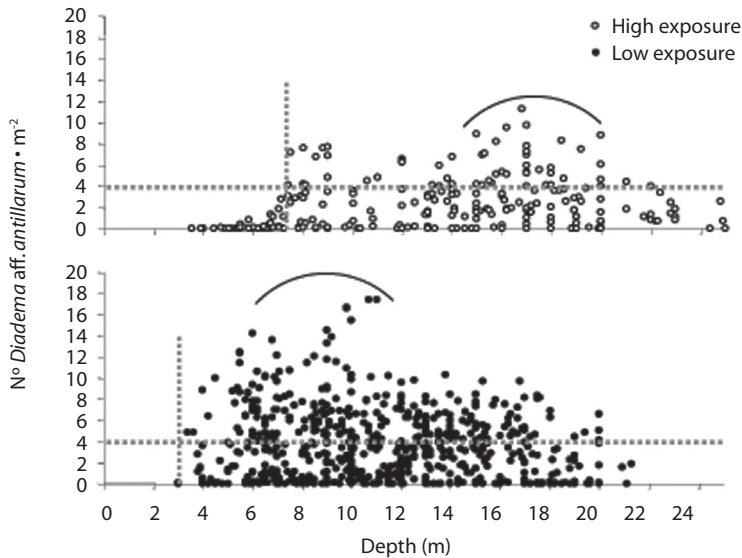Rev. Biol. Trop. (Int. J. Trop. Biol. ISSN-0034-7744) Vol. 56 (Suppl. 3): 229-254, December 2008

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Fig. 5. Dispersion diagrams illustrating abundance of *Diadema* aff. *antillarum* in the depth range studied (0.5-25m), in conditions of high and low wave exposure. Each point in the figure is a replicate. Dashed lines show border depth of urchin barrens. Curved line shows depth range where the maximum abundance and biomass of urchins were found.

Sedimentation. Permutational ANOVA analysis showed a significant effect of the factor 'Sedimentation' and 'Island' over *D*. aff. *antillarum* density (Table 4a). *A posteriori* pairwise analyses showed urchin density to be significantly lower on substrates where the percentages of sand was >20% compared to substrates where sand constituted 0% (t = 2.82, p<0.01), 1-10% (t = 2.13, p<0.05) and 10-20% (t = 1.87, p<0.05) (Fig. 6a). Variations at the local scale of 'Site (Island x Sedimentation)' were obtained (Table 4a), differing urchin density between sites at each island in relation to the sedimentation level considered.

Permutational ANOVA analysis showed no significant effect of either 'Sedimentation' or the interaction of factors 'Island x Sedimentation' on percentage of non-crustose macroalgal cover, although differences at the level of 'Island' and 'Site (Island x Sedimentation)' were still found (Fig. 6a; Table 4b).

Rugosity. Permutational ANOVA analysis showed that both 'Island' and 'Rugosity' had highly significant effects on *D. antillarum* density (Table 5a). *A posteriori* pairwise

analyses showed urchin density to be significantly higher at the highest rugosity level (4) than in habitats with lower rugosities: level 1 (t = 5.17, p<0.01), 2 (t = 4.67, p<0.01) and 3 (t = 3.15, p<0.01) (Fig. 6b). Moreover, differences with regard to the factor 'Site (Island x Rugosity)' were significant (Table 5a), meaning that urchin density differed between sites at each island in relation to the rugosity level. *A posteriori* pairwise analyses showed that sea urchin densities recorded at maximum rugosity level (4) were significantly higher (t = 5.17, p<0.01; t = 4.67, p<0.01 and t = 3.15, p<0.01) that those recorded at rugosity levels 1, 2 and 3 (t = 0.85, p = 0.40; t = 2.19, p = 0.09; t = 1.38, p = 0.17) (Fig. 6b).

When analysing non-crustose macroalgal cover, permutational ANOVA analysis showed a significant effect of 'Rugosity'. Highly significant effects of factors 'Island' and 'Site (Island x Rugosity)' were obtained (Table 5b). *A posteriori* tests showed significant differences in percentage of non-crustose macroalgal cover amongst sites within the highest rugosity level (4); which had a lower percentage of non-crustose macroalgal cover than at rugosity levels 1

TABLE 4

Results of three-way Permutational ANOVA comparing (A) density of Diadema *aff.* antillarum *(nº indv · m ⁻²) and (B) non-crustose macroalgal cover (%) between the 7 islands (1. El Hierro; 2. La Palma; 3. La Gomera; 4. Tenerife; 5. Gran Canaria; 6. Fuerteventura; 7. Lanzarote and islets), four different sedimentation levels (1=0; 2=1-10%; 3=10-20%; 4=>20%), and 125 sites across the Canarian Archipelago (Table 2)*

A. Density	Df	MS	F	P (perm)
Island (I)	6	246.06	19.82	0.001
Sand (S)	3	36.25	2.89	0.029
I x S	18	11.21	0.85	0.631
Site (I x S)	237	19.94	12.96	0.001
Residual	847	1.54		
Total	1111			
B. Macroalgal cover				
I	6	52668.00	41.69	0.001
S	3	1783.80	1.40	0.235
I x S	18	1993.50	1.49	0.07
Site (I x S)	237	2002.60	10.24	0.001
Residual	847	195.50		
Total	1111			

TABLE 5

Results of three-way Permutational ANOVA comparing (A) density of Diadema *aff.* antillarum *(nº ind.m ⁻²) and (B) non-crustose macroalgal cover (%) between the 7 islands (1. El Hierro; 2. La Palma; 3. La Gomera; 4. Tenerife; 5. Gran Canaria; 6. Fuerteventura; 7. Lanzarote and islets), four different rugosity level (1= flat; 2= <1m; 3= 1-3m; 4= high relief), and 125 sites of the Canarian Archipelago (Table 2)*

A. Density	df	MS	F	P (perm)
Island (I)	6	389.35	35.92	0.001
Rugosity (R)	3	110.70	10.30	0.001
I x R	18	14.45	1.24	0.214
Site (I x R)	251	16.16	10.77	0.001
Residual	833	1.50		
Total	1111			
B. Macroalgal cover				
I	6	47084.00	33.93	0.001
R	3	4182.50	3.04	0.03
I x R	18	1183.10	0.79	0.707
Site (I x R)	251	2065.30	10.46	0.001
Residual	833	197.39		
Total	1111			

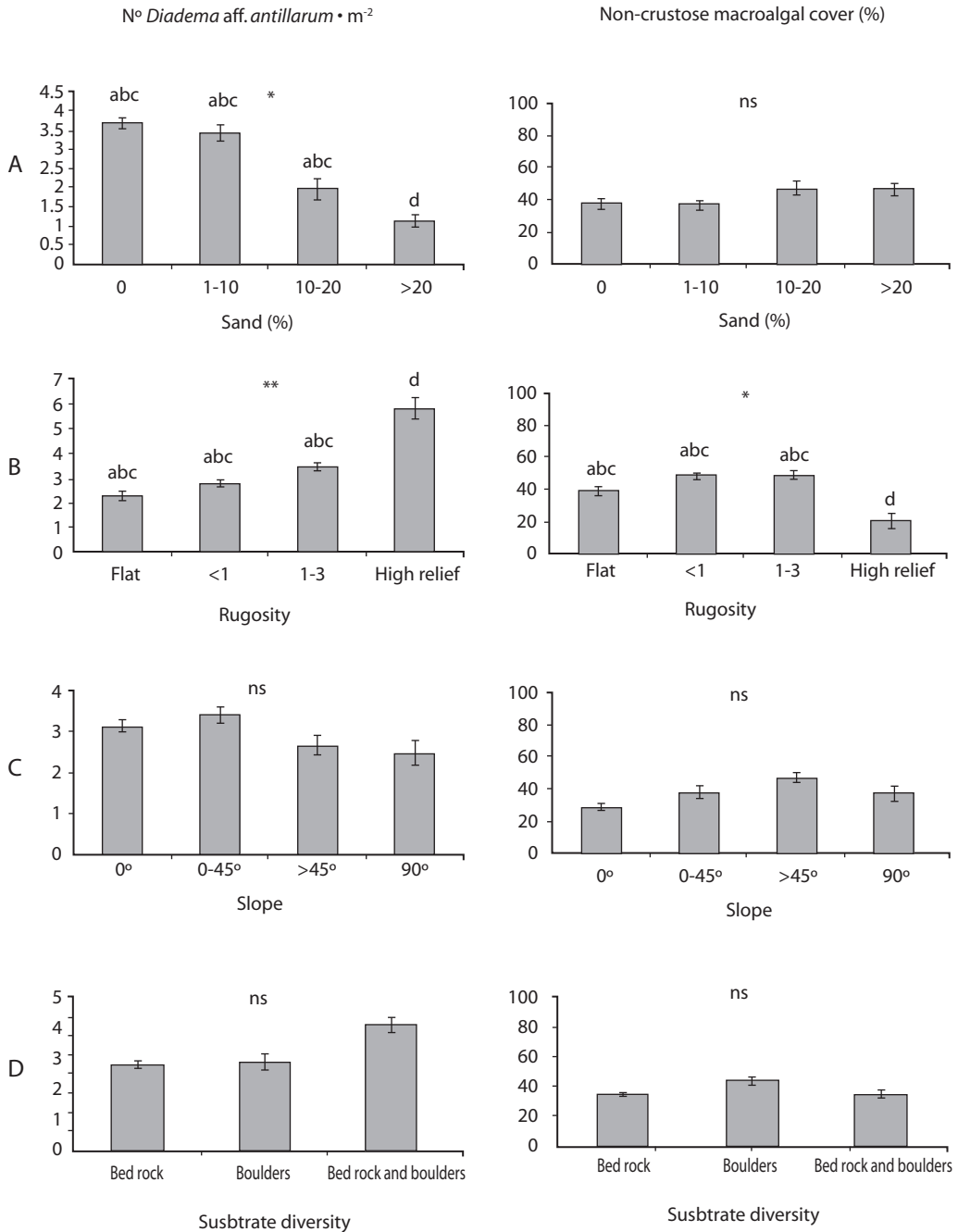N° *Diadema* aff. *antillarum* • m^{-2}

Non-crustose macroalgal cover (%)

Fig. 6. Effects of four habitat complexity variables (A: sedimentation, B: rugosity, C: slope, D: substrate diversity) on mean (± SE) abundance of sea urchins *Diadema* aff. *antillarum* and on percentage of non-crustose macroalgal cover. Data were analysed using Permutational Anova. There was no significant difference between means with identical letters (pairwise analysis). ns: not significant. * = p < 0.05. ** = p < 0.01.

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(t = 1.87, p<0.05), 2 (t = 3.16, p<0.01) and 3 (t = 1.92, p<0.05) (Fig. 6b).

Slope. Permutational ANOVA analyses showed no significant effect of 'Slope', or the interaction 'Island x Slope', neither on *D.* aff. *antillarum* density, nor on percentage of non-crustose macroalgal cover (Fig. 6c; Table 6a,b). However, differences at the level of 'Island' and 'Site (Island x Sedimentation)' were always found to be significant (Table 6a,b).

Substrate diversity.

There was no significant effect of factors 'Substrate' or even the interaction of factors 'Island x Substrate' on urchin population density and percentage of non-crustose macroalgal cover (Fig. 6d, Table 7a, b), although differences at the levels of 'Island' and 'Site (Island x Sedimentation)' were significant (Table 7a, b).

DISCUSSION

Influence of urchin populations on macroalgal assemblages throughout the Canary Islands: barren ground state definition

D. aff. *antillarum* exhibits a key role in controlling fleshy macroalgae on rocky bottoms of the northeastern Atlantic Islands (Madeira, Selvagens, Canary Islands) as demonstrated by numerous authors in recent years (Alves *et al.* 2001, 2003, Brito *et al.* 2004, Hernández 2006, Tuya *et al.* 2006, Hernández *et al.* 2007a). However, the urchin barren state was noticed long before in the Canary Islands (Brito *et al.* 1984, Bacallado *et al.* 1987, Aguilera *et al.* 1994).

In general, in this study we found that at a density of 4 ind.m^{-2}, non-crustose cover of

TABLE 6

Results of three-way Permutational ANOVA designs comparing (A) density of Diadema *aff.* antillarum *(n° ind.m $^{-2}$) and (B) non-crustose macroalgal cover (%) between the 7 islands (1. El Hierro; 2. La Palma; 3. La Gomera; 4. Tenerife; 5. Gran Canaria; 6. Fuerteventura; 7. Lanzarote and islets), four different substrate slopes (1= 0˚; 2= 0-45˚; 3= >45˚; 4= 90˚), and 125 sites across the Canarian Archipelago (Table 2)*

A. Density	df	MS	F	P (perm)
Island (I)	6	218.80	15.69	0.001
Slope (Sl)	3	2.90	0.20	0.891
I x Sl	18	6.09	0.39	0.989
Site (I x Sl)	222	21.49	12.51	0.001
Residual	862	1.72		
Total	1111			
B. Macroalgal cover				
I	6	37744.00	24.54	0.001
Sl	3	3817.20	2.39	0.066
I x Sl	18	2232.70	1.31	0.177
Site (I x Sl)	222	2376.00	13.19	0.001
Residual	862	180.13		
Total	1111			

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Results of three-way Permutational ANOVA designs comparing (A) density of Diadema *aff.* antillarum *(n° ind.m $^{-2}$) and (B) non-crustose macroalgal cover (%) between the 7 islands (1. El Hierro; 2. La Palma; 3. La Gomera; 4. Tenerife; 5. Gran Canaria; 6. Fuerteventura; 7. Lanzarote and islets), three different substrate types (1= bed rock; 2= boulders; 3= bed rock and boulders), and 125 sites across the Canarian Archipelago (Table 2)*

A. Density	df	MS	F	P (perm)
Island (I)	6	152.45	10.12	0.001
Substrate diversity (D)	2	1.54	0.10	0.908
I x D	12	14.49	0.88	0.540
Site (I x D)	170	26.35	13.93	0.001
Residual	921	1.89		
Total	1111			
B. Macroalgal cover				
I	6	25036.00	14.47	0.001
D	2	292.11	0.17	0.844
I x D	12	1810.70	0.96	0.467
Site (I x D)	170	3041.50	15.45	0.001
Residual	921	196.90		
Total	1111			

macroalgal assemblages is drastically reduced below 30% at all studied sites. Nevertheless, the effect over algal cover differs depending on the algal group in question. While crustose macroalgae maintain a high percentage cover with increasing urchin density, others such as branched and unbranched macroalgae virtually disappear at densities around 4 ind.m^{-2}. Filamentous algae and articulate coralline assemblages maintain a low presence on densely populated barrens. At urchin densities from 2-4 ind.m^{-2}, mean non-crustose macroalgal cover is drastically reduced to 15%, and at densities above 4 ind.m^{-2} mean algal cover values barely exceeds 10%. Even though there is spatial variability in this general pattern, due to the particular environmental conditions that may favor recruitment and growth of algae (Sansón *et al.* 2001, Sangil *et al.* 2006a, 2006b, Tuya and Haroun 2006), we consider a threshold density of 2 ind.m^{-2} in a rocky subtidal habitat as an urchin barren ground in the Canary Islands (locally termed "blanquizal"). A similar habitat, where urchin density exceeds

4 ind.m^{-2}, could be considered a degraded urchin barren and non-macroalgae stand is able to develop. Definitions of these thresholds are useful with regard to conservation strategies; they allow to distinguish between habitats with urchins simply present, and habitats dominated by urchins which could be considered 'undesired states' and have high resistance to restoration (Hernández *et al.* 2007a). Barren grounds are continuously invaded by algal spores and propagules but intensive grazing by urchins prevents the establishment of most species and maintains any existing macroalgal assemblage in the early succession stage (Falcón *et al.* 2004). Once a habitat is in the barren state, urchins can probably survive indefinitely by feeding upon animals, coralline algae, microbial films and drift algae (Johnson and Mann 1993, Hernández *et al.* 2007b).

Compared to typical urchin barrens elsewhere in the world (Shears and Babcock 2002, Gagnon *et al.* 2004, Johnson *et al.* 2004, Valentine and Johnson 2005, Guidetti and Dulcic 2007), barrens in the Canary Islands

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appear to be maintained by sea urchins at relatively low densities (around 2 ind.m^{-2}). Their movement range and food consumption, that involve grazing large areas of rocky substrate by night (Tuya *et al.* 2001, Tuya *et al.* 2004b), could explain these differences. Through its movements and potential large grazing grounds, *D*. aff. *antillarum* can efficiently remove its preferred macroalgal species (Carpenter 1981). In the oligotrophic Caribbean waters mean urchin densities around 10 ind.m^{-2} were recorded (Bauer 1980, Bak *et al.* 1984 but see extensive review in Lessios 1988) and 'hyperabundance' of this urchin was noticed before a mass mortality event (Hay 1984, Levitan 1992, Lessios 1988). In contrast, the oligotrophic 'bottom up' resource provided by the waters surrounding the Canary Islands is not enough to maintain high populations of the urchin, but as already stated a relatively low urchin density is substantial to maintain a barren habitat. Consequently, it can be seen that the 'bottom up resources' hypothesis does not explain all this variability. An alternative explanation for the hyperabundance of urchins recorded in the Caribbean is that the increased habitat complexity created by corals benefited the urchins (Lee 2006), as we have shown here is also the case on rocky bottoms. The urchin species is also at an advantage situation in terms of self sustaining at high density due to the high degree of body plasticity that it possesses; individual urchins have the potential to adapt their size to suit the quantity of resource available and can thus shrink when food is in short supply (Levitan 1989, 1991).

Actual status of *D*. aff. *antillarum* populations throughout the Archipelago: influence of human pressure and wave exposure

D. antillarum is spread across the entire Canarian Archipelago, with noticeable spatial variation in density and biomass. Tenerife Island had the highest urchin density while El Hierro had the lowest. Lanzarote and northern islets showed the second highest density followed by La Gomera and La Palma. In Gran Canaria and Fuerteventura medium urchin density were recorded. There is not a clear pattern to show oceanographic gradient affecting this species distribution. Other authors have postulated that the extent of overfishing at each particular island determines urchin density (Tuya *et al.* 2004a), in concordance to the general over fishing situation in the Canaries (Aguilera *et al.* 1994, Falcón *et al.* 1996) as it is found here. Gran Canaria showed less dense urchin populations as we could expect considering its human pressure and high level of fishing effort (Bortone *et al.* 1991, Bas *et al.* 1995, Tuya *et al.* 2006). Skewed sampling distribution in this island as well as in Fuerteventura, where number of fishing boats is one of the highest, may be overestimating the real urchin density. The highest urchin densities were recorded in Tenerife, the island that supported a relatively high number of locals and tourists, denoting more pollution, more fishing pressure and less conservation of the marine environment. El Hierro, the smallest island (Bacallado *et al.* 1989), has fewer residents and tourists (Bortone *et al.* 1991), less intense fisheries, as well as MPA-conservation policies, and therefore provides a higher level of conservation along its coastline (Hernández *et al.* 2007a).

Spatial variation and patchiness found at each island illustrate that other environmental factors are controlling and influencing sea urchin abundance. The existence of great water depths very close to the breakers is of particular importance. For example, in El Hierro Island, 50 m off shore the water is 50 m deep, in these circumstances the waves preserve much of their initial energy up to the breakpoint (Yanes *et al.* 2006). Consequently, NW-NNW sea swells seems to affect the urchin population more than trade winds, and the incidence of storms determines urchin distribution as waves induce dislodgement, particularly in this species (Tuya *et al.* 2007). Urchin density also tends to be higher along sheltered coastlines compared to exposed ones, as has been previously noted in Madeira (Alves *et al.* 2001) and in the Caribbean (Debrot and Nagelkerken 2006). Consequently, general urchin distribution is controlled by wave force

and island slope affecting wave energy; more slope implies more wave energy at the breaking point. Protected coasts have calmer waters that benefit retention and concentration of urchin larvae; and increased water temperature that enhances larval metamorphosis and settlement (Hernández 2006). At exposed coastal sites larvae tend to get washed away, as it has been observed in capes and headlands with the species *Strongylocentrotus purpuratus* due to high upwelling flow (Ebert and Russell 1988). Balch *et al.* (1999) also found that calm ocean conditions seem to favor invertebrate larvae settlement.

Does habitat complexity affect sea urchin distribution?

Different patterns of variation in urchin populations and macroalgae related to depth have been reported at the studied areas. Areas with higher hydrodynamics show higher urchin density in the deeper band between 14 and 20 m, and in less exposed areas denser populations appear at depths between 5 and 11 m. Depth-limits recorded here are according to the theoretical model described by Tuya *et al.* (2007), which uses linear wave theory to estimate depth-limits beyond which urchin species can not withstand linear waves. Density and biomass accumulation just below the depth limit could be explained as a migratory strategy of urchins which tend to accumulate forming fronts just below the algal stand, as it has been observed in *Strongylocentrotus droebachiensis* (Lauzon-Guay *et al.* 2006, Lauzon-Guay and Scheibling 2007). Along sheltered coasts, algal beds exist only at the shallower level and urchin biomass accumulates in this band where more food is available. Along exposed coasts high urchin densities appear at greater depth but just bellow the algal stand. Hydrodynamics allows algal growth by removing *Diadema* by dislodgement, by preventing grazing activity (Tuya *et al.* 2007), or by limiting their movement. Wave action is therefore an important force limiting urchin grazing and density, and it is the mechanism that maintains shallow water algal stands throughout the Canary Islands (Tuya and Haroun 2006) and other places (Keats 1991, Lauzon-Guay and Scheibling 2007).

Another important factor limiting urchin density is the sand percentage or sedimentation, as other studies have demonstrated on rocky reef organisms (Airoldi 2003). Percentages above 10-20% of sand keep urchin densities below 2 ind.m^{-2}. Inhibition of algal canopy growth and a decrease in algal recruits create a desolate habitat for urchin grazing activity (Valentine and Johnson 2005). The combined effects of water motion and sediment scouring the substrate can weaken the attachment between urchin and substrate as well as impairing their mobility.

Surveys revealed that substrate rugosity and *Diadema* density were positively related, as has been found in the Caribbean (Lee 2006). Increasing habitat complexity by adding physical structure significantly increased the proportion of urchins, while low habitat complexity was found to permit macroalgal-dominated reefs. These results show that physical structure attracts *Diadema* in the Canary Islands similarly to the case in the Caribbean area (Lee 2006). High topographic relief provides more suitable habitat on which urchins can reside (Hernández 2006) and these areas can support dense urchin populations, as noted by Clemente *et al.* (2007) in barren grounds of Tenerife. There was tendency for urchin density to decrease with slope, but it is thought that this was due mainly to other factors such as rugosity. Sea urchins could inhabit high slope substrate if there was enough rugosity to provide refuge from the wave action. These results imply that future conservation strategies need to consider habitat complexity, since certain habitats are potentially occupied by higher numbers of urchins, and these areas are likely to present high resistance to restoration due to positive feedback mechanisms that stabilize the system (Knowlton 2004). Those positive feedbacks make it difficult to recover perturbed communities where ability to restoration is null (Bellwood et al. 2004, Suding *et al.* 2004).

Furthermore, it is important to consider that human actions along the coast such as the construction of piers, harbors, jetties and artificial reefs, could act as a potential stepping stone for spread of this urchin. Artificial substrates such as these offer high relief habitat space and a sheltered area for larval settlement which means they can encourage and support large urchin populations.

RESUMEN

El erizo *Diadema* aff. *antillarum* juega un papel clave en la organización y estructura de las comunidades de macroalgas de fondos rocosos de las islas Canarias, de forma que altas densidades poblacionales pueden generar blanquizales (área rocosa dominada por macroalgas costrosas). Estos, y los sistemas dominados por macroalgas no costrosas, se alternan en el espacio. Se presenta un estudio de las poblaciones de *D.* aff. *antillarum* en el Archipiélago Canario, con énfasis en dos aspectos: la influencia de las poblaciones del erizo sobre las comunidades de algas no costrosas y la variación espacial de las poblaciones de erizos adultos a gran escala y a media-pequeña escala. Los principales resultados fueron: (1) densidades de *D.* aff. *antillarum* mayores de 4 ind.m^{-2} reducen drásticamente las coberturas de macroalgas no costrosas hasta valores inferiores al 30%; (2) la isla de Tenerife presenta las densidades de erizos más altas mientras que en El Hierro se registraron las menores densidades; (3) la exposición al oleaje es un factor que determina la densidad del erizo; (4) los blanquizales aparecen a mayores profundidades en las localidades más expuestas al oleaje y a menores profundidades en las localidades menos expuestas; (5) cuando el porcentaje de arena sobre el sustrato rocoso supera el 20%, la densidad de erizos se mantiene por debajo de 1 ind.m^{-2} y (6) los sustratos más rugosos albergan mayores densidades de erizos y, por lo tanto, menores coberturas de macroalgas no costrosas.

Palabras clave: islas Canarias, *Diadema* aff. *antillarum*, macroalgas no costrosas, exposición al oleaje, complejidad de hábitat.

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