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Relationships between rocky-reef fish assemblages, the sea urchin *Diadema antillarum* and macroalgae throughout the Canarian Archipelago

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ABSTRACT: *In situ* visual surveys using a hierarchical sampling design were carried out at 36 sublittoral rocky locations along the central-east Atlantic Canarian Archipelago to find relationships among (1) benthic primary producers, (2) the demographic structure of the herbivorous sea urchin *Diadema antillarum* Phillipi and (3) the trophic structure of coastal fish communities. Our correlation approach displayed a relationship between the lack of large macroinvertebrate-eating predatory fish and the increase in density of sea urchins, in addition to a decrease in fish richness. In contrast, increases in fast-growing plankton-feeding fish species were detected. The size structure of *D. antillarum* is dominated by small-to-intermediate sized sea urchins in environments with a high density of individuals, whereas low sea urchin density locations are characterized by the dominance of large sized individuals. The physical complexity of the substrate seems to play an important role in determining the local patchiness of *D. antillarum*. Finally, a non-linear decrease in the percentage of fleshy macroalgal cover with increasing density of *D. antillarum* was observed. We therefore propose *D. antillarum* as a key herbivorous species, which plays an important role in determining the structure of shallow, hard-substratum, infralittoral benthic communities throughout the Canary Islands.

KEY WORDS: Urchin-fish interactions · Trophic cascades · *Diadema antillarum* · Sea urchins · Fish assemblages · Macroalgae · Canary Islands

INTRODUCTION

Large, shallow, rocky areas, previously covered by fleshy erect algae, are transformed by sea urchins into overgrazed substrates dominated by encrusting coralline algae and algal turfs. These so-called urchin-grazed barrens are often termed bare substrates (e.g. Mann 1982, McClanahan & Sala 1997, Kingsford & Battershill 1998, Sala et al. 1998, Shears & Babcock 2003). These environments have been widely described in coastal temperate reefs (Vukovic 1982, Verlaque 1987, Andrew & Underwood 1989, Francour 1994, Sala & Zabala 1996, Sala et al. 1998, Babcock et al. 1999, Pinnegar et al. 2000, Shears & Babcock 2003), as well as in tropical coral reefs (e.g. Hay 1984, McClanahan & Kurtis 1991, Jackson 2001). These authors explain this as a direct consequence of an increase in inshore fishing pressure, since removal of target top predators (e.g. carnivorous fishes) can result in top-down trophic cascades and indirect effects on coastal marine assemblages (Sala et al. 1998, Pinnegar et al. 2000, Shears & Babcock 2003). These studies mainly compare hard-substratum systems within long-established Marine Protected Areas (MPAs) with non-protected zones subjected to artisanal fisheries (Pinnegar et al. 2000, Shears & Babcock 2003).

Disturbances to the inshore areas of the Canarian Archipelago have increased due to the expanding

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tourist industry and the increased demand of fishery resources (Bortone et al. 1991, Falcón et al. 1996). However, no empirical evidence of the effect of these disturbances is available, as there are no data on the nearshore fish populations during the pre-development era of the 1960s (Falcón et al. 1996). Personal observations and several local studies have suggested that the long-spined sea urchin *Diadema antillarum* Philippi has experienced a significant increase in abundance throughout the central-east Atlantic (FAO fisheries region #34) in the last decades (Casañas et al. 1998, Alves et al. 2001, Tuya et al. 2004b). Although *D. antillarum* has been extensively studied in the western Atlantic, where it has a great impact on benthic community structure (e.g. Sammarco et al. 1974, Carpenter 1981, 1984, Lessios 1988), little research has been undertaken in the eastern Atlantic to link the demographic structure of this echinoid species with the abundance and biomass of rocky-reef fish assemblages in the Canarian Archipelago. Moreover, no study has addressed the above along with the coastal trophic cascades within this area (Pinnegar et al. 2000).

The general aim of this study was therefore to determine whether there is an association between the structure of *Diadema antillarum* populations and the community structure of macroalgae and fish. This potential association was examined by quantifying the structure and spatial patterns of *D. antillarum* populations throughout the Canarian Archipelago, and relating this to the fish assemblage structure and macroalgae cover.

MATERIALS AND METHODS

Experimental design and sampled locations. Since the dynamics of populations involved in trophic interactions operate at different spatial scales (see the review by García-Charton & Pérez-Ruzafa 1999), we adopted a multiscaled perspective through a hierarchical sampling design with randomly positioned study locations throughout the Canarian Archipelago (Underwood 1997, Kingsford & Battershill 1998). We selected 4 random locations of rocky substrate in each of the 8 islands of the Archipelago (Fig. 1), with the exception of Chinijo (a group of small islets) and El Hierro Island, where 7 and 5 locations were surveyed, respectively. Furthermore, within each location we randomly sampled 2 sites separated by hundreds of meters in order to increase spatial replication at a small spatial-scale (Kingsford & Battershill 1998). The locations are referred to numerically (1 to 36) and correspond to the geographic locations described in Fig. 1.

All subtidal sampling was conducted from February to May 2003, between 10 and 18 m depth, along rocky bottoms with similar slope to minimize the effect of habitat type on the distribution and patchiness of assemblages (García-Charton & Pérez-Ruzafa 1999). Visibility ranged between 8 and 20 m; water temperature between 18 (eastern islands) and 20°C (western islands). Unfortunately, no capture and fishing effort data from the artisanal coastal fisheries are available to assign a fishing status to each location (Bas et al. 1995, Pajuelo & Lorenzo 1995).

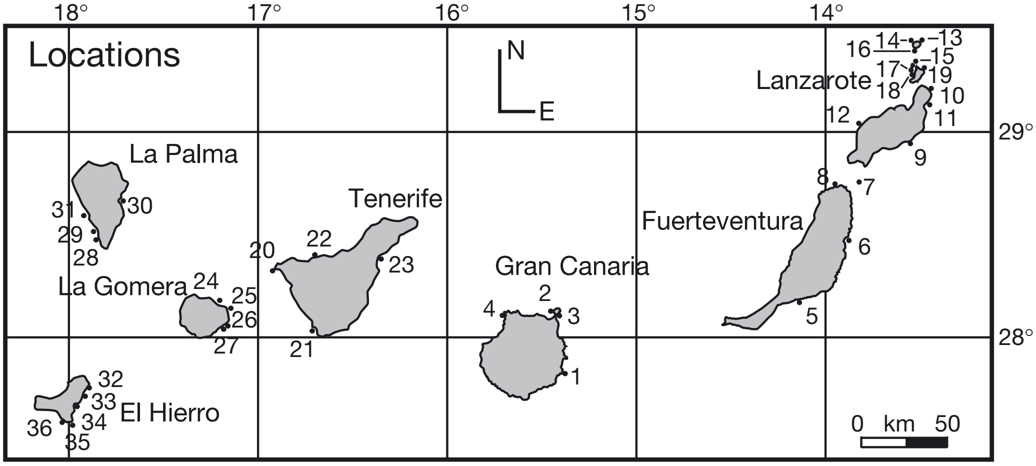

Fig. 1. The Canarian Archipelago showing sampling locations at each island

Code	Location
1	El Cabròn
2	Canteras
3	Puerto deportivo Las Palmas
4	Sardina
5	Caleta Fuste
6	Puerto Rosario
7	Lobos
8	Corralejo
9	Puerto Naos
10	Orzola
11	Arrieta
12	Timanfaya
13	Miraflores
14	Greta
15	Roque
16	Puerto Viejo
17	Veril del Agua
18	Ganado
19	Playa Lambra
20	Teno
21	Christianos
22	Garachico
23	Naútico
24	Hermigua
25	Puntallana
26	Escollera San Sebastián
27	San Sebastián
28	Puntalarga
29	Vuelta Toro
30	Escollera Sta. Cruz Palma
31	Charco Verde
32	Caleta
33	Unelco
34	Bonanza
35	El Rincón
36	Tacoron

Fish assemblage structure. Non-cryptic fish populations (size >2 cm) were sampled by means of visual census techniques. At each sampling site within each location, 4 replicates of 25 m long transects were haphazardly laid during daylight hours. The abundance and size (total length to the nearest 2 cm) of each fish species within 2 m of either side of the transects (100 m^2) was recorded on waterproof paper by a SCUBA diver, according to standard procedures (Brock 1982, Lincoln-Smith 1988, 1989, Kingsford & Battershill 1998). Fish belonging to the genera *Seriola*, *Gobius*, and *Trachurus* could not be identified to species visually and were recorded as the genera. Nevertheless, each was then treated as a distinct species in the statistical analyses. Estimation of fish abundance was based on a modification of the method presented by Harmelin-Vivien et al. (1985). Therefore, when fish were grouped in schools larger than 20 individuals, their numbers were estimated according to 6 abundance classes (20–40, 40–70, 70–150, 150–300, 300–700, >700).

We calculated the following for each location: (1) the species richness (*S*), (2) the Shannon-Wiener (*H'*) diversity index and (3) Pielou's evenness or electivity index (*J'*) (Ludwig & Reynolds 1988). Biomass of each species was calculated using the available length–weight relationships for the Canarian Archipelago and from other published and web-based sources (www.fishbase.org). In the cases where length–weight information did not exist for a given species, the parameters from similar bodied congeners were used (Friedlander & DeMartini 2002). Lengths were first estimated by assigning each fish to the midpoint of its observed size range (Miller & Gerstner 2002). All measured biotic variables were calculated to a 100 m^2 area.

Despite the lack of rigorous knowledge of potential predators of *Diadema antillarum* along the Canaries, fish species were grouped for statistical procedures into 5 trophic groups (see Table 1) based on previously published diet and feeding habit information (www.fishbase.org), using a similar criterion to that reported for the Atlantic (Jennings et al. 1995) and the Mediterranean (Bell & Harmelin-Vivien 1983). The 5 groups are: (1) Macroinvertebrate feeders and piscivorous feeders (MaF&PFs), (2) Macroinvertebrate feeders (MaFs), (3) Microinvertebrate feeders (MiFs), (4) Planktivorous (Ps) and (5) Omnivorous (Os). Therefore, *Diadema antillarum* can be consumed only by the MaF&PFs and MaFs groups. Both groups are top predators highly targeted by fishermen throughout the Canarian Archipelago.

Structure of *Diadema antillarum* populations and macroalgal coverage. The abundance and size class of all *Diadema antillarum* individuals were visually estimated by SCUBA divers using haphazardly located 2 × 2 m (4 m^2) quadrats in each site (n = 8) within each location (Ruitton et al. 2000). Sea urchins were grouped into 4 size classes (Class 1 <1.5 cm test diameter without spines, Class 2 between 1.5 and 3.5 cm, Class 3 between 3.5 and 5.5 cm and Class 4 >5.5 cm) (Casañas et al. 1998). Urchin-grazed barrens were classified for further analysis into 4 categories according to mean density (Casañas et al. 1998) (<2, 2 to 4, 4 to 8 and >8 ind. m^{-2}).

The percentage of fleshy macroalgal cover (mainly frondose brown species belonging to the genera *Cystoseira*, *Sargassum*, *Lobophora* and *Dictyota*) was visually quantified within each quadrat (Dethier et al. 1993, Benedetti-Cecchi et al. 1996). Final values were expressed as percentages.

Habitat complexity. To assess the effect of the intermediate-to-small spatial-scale substrate complexity on the local dispersion patterns of *Diadema antillarum*, we counted the number of big (>1 m) and medium (0.2 to 1 m) boulders and crevices in each quadrat, using an approach similar to that reported for the western Mediterranean (García-Charton & Pérez-Ruzafa 1998) and Madeira Island (Alves et al. 2001). We also obtained the index of rugosity of the substratum through the rope-and-chain technique by using two 1 m long tapes with a perpendicular distribution within each quadrat (Luckhurst & Luckhurst 1978, Kingsford & Battershill 1998).

Statistical analysis. Square-root transformed data of fish abundance was analysed using non-metric multidimensional scaling (nMDS) (Clarke 1993), by means of the PRIMER© statistical package, to assess the differences in fish community structure among locations. The 1-way ANOSIM (analysis of similarities) permutation test was used to find the significance of the difference between the locations surveyed within the eastern islands and those along the western islands. The SIMPER procedure was used to identify the contribution of individual species to differences between both groups of islands.

A 3-way nested ANOVA design was used to test for differences in the mean sea urchin density among islands (10^4 to 10^5 m), locations within islands (10^3 to 10^4 m) and sites within locations (10^2 m). Both factors 'locations' and 'sites' were random factors, while 'islands' was considered fixed.

Variance-to-mean ratios (s^2/x, index of dispersion, sensu Ludwig & Reynolds 1988) were calculated to assess the local spatial dispersion pattern (uniform/clumped/random) of total *Diadema antillarum* individuals for each location. These values were compared to a 2-tailed χ^2_{n-1} distribution to test for departures from randomness, following a Poisson distribution as a measure of the spatial pattern (Ludwig & Reynolds 1988).

Table 1. Mean abundance (n = 8, 100 m^2) of fish species at the 36 surveyed locations throughout

Trophic group Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Omnivorous															
Sparisoma (*Euscarus*) *cretense*	13.38	0.25	5.00	0.25	0.13	0.13	0.75	0.38	1.25	0.38	0.50	0.25	1.88	5.88	10.00
Diplodus sargus cadenati	1.25	4.38	15.50	1.50	0.88	–	7.88	–	0.13	1.88	–	–	–	–	1.25
Diplodus vulgaris	0.63	1.13	6.00	0.88	–	–	2.75	–	0.13	–	1.13	–	–	–	2.50
Diplodus annularis	0.25	–	–	–	–	0.25	–	–	–	–	–	–	–	–	–
Microinvertebrate feeders															
Thalassoma pavo	14.63	30.25	28.50	14.00	26.38	0.13	15.00	26.38	4.25	15.63	14.00	53.63	45.00	30.88	97.13
Abudefduf luridus	12.25	22.50	12.50	11.88	12.38	7.38	9.25	19.88	7.50	2.50	6.00	22.75	25.00	18.75	12.75
Canthigaster rostrata	2.13	1.25	0.25	1.25	1.00	1.88	0.63	0.13	0.25	–	1.50	0.50	–	–	–
Scorpaena maderensis	0.13	0.25	–	0.13	0.25	–	0.13	0.75	0.38	0.25	–	–	0.63	–	–
Sphoroides spengleri	2.25	0.38	–	–	–	0.25	0.00	–	–	–	–	–	–	–	–
Apogon imberbis	–	–	–	0.13	–	–	–	–	0.13	–	–	–	–	–	–
Gobius sp.	0.38	–	0.13	–	–	–	–	–	–	–	–	–	–	–	–
Planktivorous															
Boop boops	–	–	2.00	–	462.50	1.25	–	–	2.50	–	–	262.50	18.75	18.75	565.00
Chromis limbatus	121.25	–	112.25	43.88	100.50	6.25	145.13	32.75	37.50	–	10.00	19.25	15.00	2.50	0.50
Athrerina presbyter	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Macroinvertebrate feeders															
Coris julis	18.75	–	–	1.75	–	0.63	1.50	0.38	7.38	–	0.38	3.00	0.38	5.63	1.38
Oblada melanura	–	–	10.00	0.13	–	–	–	–	–	–	2.50	–	–	–	–
Mullus surmuletus	–	–	–	0.88	0.13	–	–	–	–	–	2.50	–	–	–	–
Pomadasys incisus	–	–	–	–	–	–	–	–	1.00	–	–	–	–	–	–
Aulostomus strigosus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Centrolabrus trutta	–	1.13	1.00	–	–	–	–	–	–	9.63	–	–	0.50	1.75	1.88
Aluterus sp.	–	–	–	–	–	–	–	–	–	–	5.00	–	–	–	–
Stephanolepis hispidus	0.25	0.25	0.13	–	–	2.00	–	–	–	–	–	–	–	–	–
Bothus podas maderensis	–	–	0.13	–	–	–	–	–	–	–	–	–	–	–	–
Chilomycterus atringa	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Xyrichthys novacula	–	–	–	–	–	–	–	–	–	–	0.13	–	–	–	–
Heteropriacanthus cruentatus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Lithognathus mormyrus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Myrichthys pardalis	–	0.13	–	–	–	–	–	–	–	–	–	–	–	–	–
Macroinvertebrate feeders and piscivorous															
Sphyraena viridensis	22.50	–	–	–	–	–	–	–	–	1.00	–	–	–	–	–
Pseudocaranx dentex	–	–	0.75	–	–	–	–	–	–	–	–	–	–	–	–
Serranus atricauda	0.50	–	–	–	–	–	–	0.25	–	–	–	0.63	0.38	0.38	–
Mycteroperca fusca	0.13	0.13	0.13	0.25	–	–	–	–	–	–	–	–	–	0.25	–
Diplodus cervinus	0.63	0.25	–	0.50	0.13	–	1.00	–	–	–	–	–	0.63	–	0.25
Sarda sarda	–	–	–	–	–	–	–	–	–	–	–	–	–	9.38	0.75
Seriola sp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Kyphosus sectator	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Spondyliosoma cantharus	–	–	–	–	–	0.13	–	–	–	–	–	–	–	–	–
Serranus cabrilla	0.13	–	–	0.25	–	0.25	0.38	–	–	–	–	–	–	–	–
Bodianus scrofa	–	–	–	–	–	–	0.13	–	–	–	–	0.13	0.40	–	–
Synodus synodus	–	0.75	0.38	0.38	0.13	0.25	–	–	–	–	0.13	–	–	–	–
Serranus scriba	0.38	0.13	–	0.13	–	0.38	–	–	–	–	–	–	–	0.13	0.13
Scorpaena porcus	0.13	0.25	0.13	–	–	–	–	0.50	–	–	–	–	–	–	–
Epinephelus marginatus	–	–	–	–	–	–	–	–	–	–	–	–	0.13	–	–
Dentex sp.	0.50	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Dicentrarchus labrax	–	–	0.50	–	–	–	–	–	–	–	–	–	–	–	–
Gymnothorax unicolor	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Muraena augusti	–	–	–	–	0.13	–	–	–	–	–	–	–	0.25	–	–
Pagrus auriga	–	–	–	0.13	–	–	–	–	–	–	–	–	0.13	–	–
Synodus saurus	–	–	0.13	0.13	–	–	–	–	–	–	–	–	–	–	–
Muraena helena	0.13	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Pagrus pagrus	0.13	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Labrus bergylta	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.13
Balistes carolinensis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Squatina squatina	–	–	–	–	–	–	–	–	–	–	–	–	0.13	–	–
Taenuria grabata	–	–	–	–	–	–	–	–	–	–	–	–	–	0.13	–
Trachinus draco	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

the Canarian Archipelago. Locations numbered as in Fig. 1. Ov. m. ab. = overall mean abundance

16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	Ov. m.ab.
3.00	0.75	4.88	0.13	0.88	13.38	12.13	3.63	1.88	20.63	25.38	77.38	6.25	19.00	0.88	49.38	14.38	29.63	16.63	20.75	172.75	14.833
1.00	2.50	0.50	–	–	2.63	3.13	50.38	–	–	1.13	0.13	0.13	–	2.25	13.75	–	0.25	–	1.50	0.25	3.170
8.88	5.38	–	–	–	35.50	0.13	2.63	–	–	–	0.63	–	–	2.75	–	–	2.50	–	3.25	–	2.132
–	–	–	–	–	–	–	0.50	–	–	–	–	–	–	–	–	–	–	–	–	–	0.028
31.63	14.25	16.88	12.00	102.38	18.63	13.00	44.38	45.00	67.75	13.75	79.50	40.75	52.50	11.13	466.88	536.25	396.50	47.38	97.25	286.63	78.059
19.75	27.88	2.25	11.75	174.75	38.50	34.13	47.50	53.75	50.13	46.63	25.00	39.25	65.00	21.00	57.50	186.25	68.50	106.25	29.00	74.75	38.410
0.50	0.38	0.13	0.25	2.88	5.63	3.25	2.50	1.50	0.13	2.38	3.13	1.75	2.00	4.38	2.25	10.25	3.25	4.38	3.00	4.75	1.927
0.63	0.25	–	0.25	0.13	0.25	–	0.13	–	–	0.13	0.38	0.25	–	0.25	0.38	0.50	–	0.75	0.25	0.25	0.212
–	–	–	–	0.38	–	0.13	–	–	–	–	–	0.13	–	–	–	–	0.25	–	0.13	–	0.108
–	–	–	–	–	–	–	0.13	–	–	–	–	–	–	–	–	1.50	0.25	–	–	–	0.059
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.014
–	–	–	125.00	18.75	–	–	155.00	55.00	51.25	256.25	–	–	32.50	325.00	–	68.88	–	137.50	–	–	71.066
39.38	69.00	13.88	8.63	201.25	28.50	–	76.25	201.25	130.00	35.63	0.63	263.75	276.25	17.38	4.88	1.38	24.50	100.00	20.25	12.13	60.323
–	–	–	–	–	–	37.50	–	–	–	–	–	–	–	17.50	–	–	–	281.25	–	–	9.340
0.13	0.63	11.00	–	9.38	–	–	–	3.00	–	–	–	–	–	–	1.50	2.63	0.50	5.13	1.00	4.13	2.226
–	2.50	–	–	–	–	–	10.00	5.00	2.50	0.13	–	5.00	5.00	9.00	–	–	13.00	–	12.88	–	2.156
2.25	–	–	–	–	0.13	–	56.38	–	–	1.50	–	0.13	–	4.25	–	–	3.63	–	–	–	1.993
–	–	–	–	43.75	–	–	2.88	–	–	–	–	–	–	–	–	–	–	–	–	–	1.323
–	–	–	–	0.25	0.25	–	–	0.25	–	–	0.25	1.13	0.63	–	4.50	4.13	6.38	2.75	12.38	1.75	0.962
–	–	4.00	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.552
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.13	0.142
–	–	–	–	–	–	–	–	–	–	–	0.88	–	–	–	–	–	–	–	0.88	0.13	0.125
–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.13	–	–	–	–	–	–	0.007
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.25	–	–	0.007
–	–	–	–	–	–	–	–	–	0.13	–	–	–	–	–	–	–	–	–	–	–	0.007
–	–	–	–	–	–	–	–	–	–	–	–	–	0.13	–	–	–	–	–	–	–	0.003
–	–	–	–	–	–	–	0.13	–	–	–	–	–	–	–	–	–	–	–	–	–	0.003
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.003
–	–	–	–	–	–	–	–	–	–	40.88	–	–	–	–	–	–	–	–	4.75	–	1.920
–	–	–	–	–	–	–	18.00	–	–	3.25	0.25	–	–	–	–	0.50	6.25	–	0.13	–	0.809
–	0.25	0.13	–	1.13	1.50	–	–	1.88	3.00	0.25	–	1.13	0.38	–	1.63	1.50	0.75	0.63	0.25	1.25	0.493
0.13	–	0.25	–	0.13	0.25	–	–	–	0.13	–	0.38	1.75	0.75	0.25	0.25	7.63	0.13	2.63	0.25	0.13	0.441
0.13	–	–	0.25	–	0.13	0.75	–	1.00	–	–	1.75	1.38	0.50	–	–	0.38	2.38	0.25	0.50	–	0.354
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.281
–	–	–	–	–	–	–	8.75	–	–	–	0.25	–	–	0.25	–	–	–	–	–	–	0.257
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4.00	–	–	3.00	–	0.194
–	–	–	–	6.00	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.170
–	–	–	–	–	0.13	–	0.13	1.38	0.13	–	–	–	–	–	–	–	–	–	0.13	–	0.080
0.13	–	–	0.25	–	–	–	–	–	–	–	–	–	–	–	0.25	1.00	–	0.13	0.25	0.13	0.077
–	–	–	0.13	–	0.13	–	–	–	–	–	0.25	0.13	–	0.13	–	–	–	–	–	–	0.076
0.38	–	0.13	–	–	0.75	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.069
–	–	–	–	–	–	–	–	–	0.13	–	–	–	–	–	–	–	–	–	–	–	0.031
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.25	–	0.25	–	0.13	–	0.021
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.014
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.014
–	–	–	–	–	–	–	–	–	–	–	–	0.25	–	–	0.13	0.13	–	–	–	–	0.014
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.13	0.014
–	–	–	–	–	0.13	0.13	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.014
–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.25	–	–	–	–	–	–	0.014
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.25	–	–	–	–	0.010
–	–	–	–	0.25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.010
–	–	0.13	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.007
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.13	–	–	–	0.003
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.003
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.003
–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.13	–	–	–	–	–	–	0.003

One-way ANOVA models on pooled unbalanced data for all surveyed locations were used to test the effects of 4 defined categories of barrens on differences in the mean total abundance and biomass of each considered fish trophic assemblage. Since no transformation rendered homogeneous variances, the level of significance considered was 0.01 instead of 0.05 (Underwood 1981). Furthermore, multiple comparisons were tested using the Tamhane T2 test via the SPSS© software.

To evaluate the spatial relationships between the density of *Diadema antillarum* sea urchins at each location and (1) their size structure, (2) the fleshy macroalgal cover and (3) the fish species richness, we performed regression models (Underwood 1997). In addition, we carried out correlation analyses between (1) the structure of *D. antillarum* populations and the abundance and biomass of each fish trophic group at each location, and (2) the local dispersion patterns of sea urchin abundance and the measured complexity of the habitat.

RESULTS

Fish assemblages

A total of 55 fish species were observed from the 288 visual surveys that we conducted during the sampling period at the 36 sampling locations along the Canary Islands (Table 1). The plankton-feeders *Chromis limbatus* and *Boop boops* were the most abundant pelagic schooling species. The wrasse *Thalassoma pavo*, damselfish *Abudefduf luridus* and parrotfish *Sparisoma cretense* were, in decreasing order, the most abundant species of the demersal nearshore fish assemblage (mean density for the entire study >10 ind. 100 m^{-2}, Table 1). Furthermore, *S. cretense*, *T. pavo* and *A. luridus* were detected at all locations (100% occurrence frequency), while *C. limbatus* and *Canthigaster rostrata* were observed in 91 and 88% of the locations, respectively. The average number of species per location (*S*, Table 2) varied between 3.63 (Playa Lambra, Location 19) and 11 at El Rincón (Location 35). Mean species diversity (*H*′, Table 2) fluctuated between 0.33 (El Roque, Location 15) to 0.72 at Los Cristianos (Location 21), and evenness (*J*′, Table 2) between 0.40 (Charco Verde, Location 31) and 0.79 (Puerto Rosario and Los Cristianos, Locations 6 and 21). Finally, mean total fish biomass ranged between 1790.69 g 100 m^{-2} at Puerto

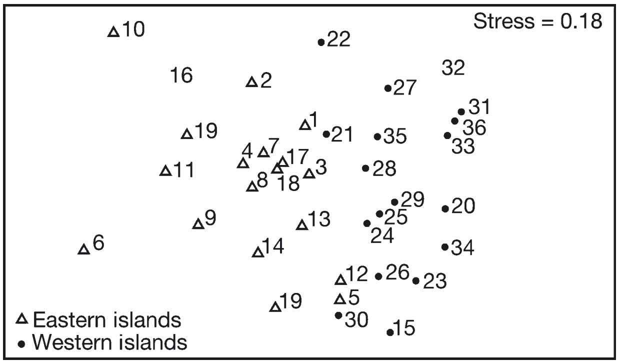

Fig. 2. nMDS plot ordination of the fish species abundance data matrix for all locations sampled

Table 2. Fish descriptive statistics 100 m^{-2} (diversity indices) and the mean total fish biomass 100 m^{-2} for each location studied

Location	Mean richness (*S*)	Mean *H*′	Mean *J*′	Mean total biomass (g 100 m^{-2})
1	9.38	0.48	0.49	38791.77
2	7.13	0.52	0.62	8748.67
3	7.75	0.60	0.68	18019.14
4	7.13	0.57	0.70	5948.24
5	5.38	0.35	0.49	54084.67
6	4.88	0.52	0.79	1790.69
7	6.13	0.44	0.58	14615.08
8	3.88	0.39	0.72	5736.43
9	4.88	0.42	0.61	4022.55
10	4.13	0.45	0.76	5213.51
11	4.50	0.48	0.75	6080.94
12	4.88	0.34	0.54	46819.77
13	4.88	0.34	0.53	10343.88
14	4.88	0.38	0.53	28824.78
15	5.75	0.33	0.43	76004.25
16	6.63	0.56	0.70	8556.03
17	4.38	0.36	0.57	8979.03
18	5.75	0.52	0.70	6226.89
19	3.63	0.35	0.74	16174.77
20	4.34	0.47	0.57	61879.26
21	8.50	0.72	0.79	16759.84
22	5.38	0.48	0.69	9200.79
23	8.88	0.69	0.75	47716.55
24	7.38	0.55	0.63	26452.58
25	5.63	0.51	0.70	28852.35
26	7.00	0.53	0.64	63742.73
27	7.13	0.52	0.63	28461.93
28	8.38	0.49	0.53	21910.56
29	6.88	0.48	0.58	24367.52
30	8.50	0.44	0.49	9931.08
31	8.50	0.37	0.40	51682.82
32	10.25	0.56	0.55	37106.93
33	10.13	0.52	0.51	68604.10
34	8.38	0.46	0.50	43931.60
35	11.00	0.69	0.67	62164.81
36	7.38	0.49	0.58	61269.15
	6.65 ± 1.97	0.48 ± 0.09	0.62 ± 0.10	28583.77 ± 22358.48

Rosario (Location 6) and 76 004.25 g 100 m^{-2} at El Roque (Location 15), while average total fish biomass per location (n = 36) was 28 583.77 ± 22 358.48 g 100 m^{-2} (mean ± standard deviation) for the entire study.

The 2-dimensional nMDS (Fig. 2) performed on the fish abundances revealed a separation of the locations that lie within the eastern islands (left-side of the plot) from those within the western islands (right-side of the plot). This difference was statistically demonstrated by the 1-way ANOSIM permutation test ($r = 0.32$, $p = 0.001$). Since 2 main groups of islands can therefore be biogeographically differentiated along an east–west gradient through the Canaries, we proceeded to analyze the fish species data from the eastern and western islands separately. As the SIMPER procedure indicated, percentages of contribution to dissimilarities (%) between both groups of islands were partially due to large differences in the abundances of a few low trophic-level fish species (*Chromis limbatus* – 7.20 %, *Coris julis* – 5.36 %, *Diplodus sargus cadenati* – 5.02 %, *D. vulgaris* – 4.78 % and *Oblada melanura* – 4.65 %).

Structure of *Diadema antillarum* populations

The mean density of *Diadema antillarum* for the overall study (Table 3) was 2.92 ± 3.75 ind. m^{-2} (mean ± standard deviation, n = 36), which fluctuated between a minimum of 0 at several locations and a maximum of 13.92 ± 4.48 ind. m^{-2} at Teno (Location 20). As indicated by 3-way nested ANOVA, the distribution of *D. antillarum* showed statistical differences among locations within islands (Table 4).

Significant non-parametric Spearman correlations were detected between the mean % frequency of the Size classes 2, 3 and 4 and the local density of *Diadema antillarum* individuals for all studied locations ($R_S = 0.56$ for Size class 2, $R_S = 0.51$ for Size class 3 and $R_S = -0.39$ for Size class 4). However, no significant relation was observed for newly settled recruits of *D. antillarum* (Size class 1), as no recruits were recorded throughout the study. The non-linear relations between the mean density of *D. antillarum* at each location and the 3 size classes are graphically illustrated in Fig. 3. Locations with low sea urchin density were therefore dominated by large-sized (Size class 4) individuals, while small-sized sea urchins (Size class 2) were found in high abundances along well-developed urchin-dominated barrens (>8 ind. m^{-2}). Finally, the presence of intermediate-sized individuals (Size class 3) was maximal at intermediate sea urchin density (6 to 8 ind. m^{-2}).

Overall, *Diadema antillarum* exhibited a uniform dispersion pattern at only 2 locations, both at El Hierro Island (Locations 32 and 34, Table 3). On the other hand, *D. antillarum* showed random dispersion patterns at 75 % of studied locations, which were locations practically devoid of sea urchins (<1 ind. m^{-2}) or well-developed barrens with a high abundance of individuals (>8 ind. m^{-2}) (Table 3). The remaining locations (19 %) with clumped patterns were found at locations with small-to-intermediate density values (1 to 2 ind. m^{-2}), except Location 7 (Lobos), where we detected a clumped pattern along a barren with high sea urchin abundance.

Table 3. *Diadema antillarum*. Mean abundance (n = 16, m^{-2}), standard deviation (SD), index of dispersion (id) and spatial distribution pattern for each studied location. Significant non-parametric correlations (R_S) with the measured attributes of the physical complexity of the rocky substrate are also displayed. $^{**}p < 0.01$

Location	Mean density (ind. m^{-2})	SD	id (s^2/x)	Spatial distribution pattern	Significant R_S
1	0.03	0.12	0.48	Random	
2	0.00	0.00	–	–	
3	0.10	0.22	0.48	Random	
4	5.17	1.64	0.52	Random	
5	7.61	1.82	0.44	Random	
6	0.89	0.74	0.61	Random	
7	8.33	5.24	3.29	Patchy	0.81^{a**}
8	6.19	3.20	1.65	Random	
9	5.67	2.12	0.79	Random	
10	0.00	0.00	–	–	
11	1.66	1.81	1.98	Patchy	0.91^{c**}
12	10.31	3.46	1.16	Random	
13	9.25	2.86	0.89	Random	
14	0.08	0.31	1.25	Random	
15	0.00	0.00	–	–	
16	4.95	2.94	1.75	Random	
17	4.45	2.32	1.21	Random	0.74^{c**}
18	0.00	0.00	–	–	
19	10.41	3.49	1.17	Random	
20	13.92	4.48	1.44	Random	
21	1.29	2.41	4.50	Patchy	
22	0.15	0.35	0.82	Random	
23	0.01	0.09	0.56	Random	
24	2.55	1.84	1.33	Random	
25	2.90	1.51	0.79	Random	
26	0.28	0.37	0.49	Random	
27	0.38	0.72	1.36	Random	
28	2.43	3.15	4.08	Patchy	0.98^{b**}
29	2.89	2.79	2.69	Patchy	0.78^{c**}
30	0.29	0.36	0.45	Random	
31	0.67	0.97	1.40	Random	
32	0.91	0.47	0.24	Uniform	
33	0.23	0.43	0.80	Random	
34	0.18	0.21	0.25	Uniform	
35	0.04	0.13	0.42	Random	
36	0.91	1.38	2.09	Patchy	0.60^{a**}
Total	2.92	3.75			

[a] Significant correlation with no. of large boulders
[b] Significant correlation with no. of large crevices
[c] Significant correlation with no. medium crevices

Table 4. *Diadema antillarum*. Results of nested ANOVA comparing mean densities among islands, locations and sites. $^{**}p < 0.01$

Source of variation	df	MS	*F*
Island	7	197.63	0.89
Location (Island)	24	222.01	55.92**
Site (Location(Island))	32	3.97	1.17
Error	448	3.39	

We found significant positive correlations between the distribution of *Diadema antillarum* individuals and the physical attributes of the rocky substrate only in those locations where *D. antillarum* exhibited patchy dispersion patterns, with the exception of Location 17 (Veril del Agua) (Table 3). However, no significant correlations were obtained for the rugosity of the substrate or for the depth.

Diadema antillarum versus fleshy macroalgae cover

Mean densities of total *Diadema antillarum* individuals and mean fleshy macroalgal coverage (mainly large brown macroalgae) showed an overall negative correlation in the studied locations. A non-linear decrease in the mean percentage of fleshy macroalgal cover with increasing mean density of *D. antillarum* was thus observed (Fig. 4). Hence, high fleshy macroalgal cover was found only in those locations where *D. antillarum* was absent or at low densities (<2 ind. m^{-2}). In contrast, locations with a high density of *D. antillarum* (>8 ind. m^{-2}) showed a complete lack of macroalgal cover.

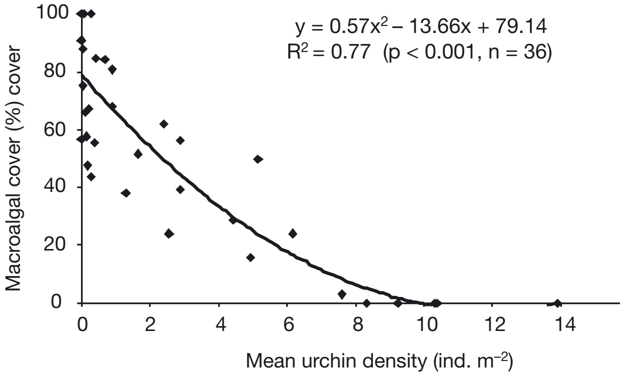

Fig. 4. *Diadema antillarum*. Non-linear regression between the mean density of total individuals and mean percentage of algal cover at each location

Fish assemblages versus *Diadema antillarum* density

Overall, subtidal rocky-bottom fish species richness decreased slightly with an increase in the mean density of *Diadema antillarum* individuals for both the east and west island groups (Fig. 5).

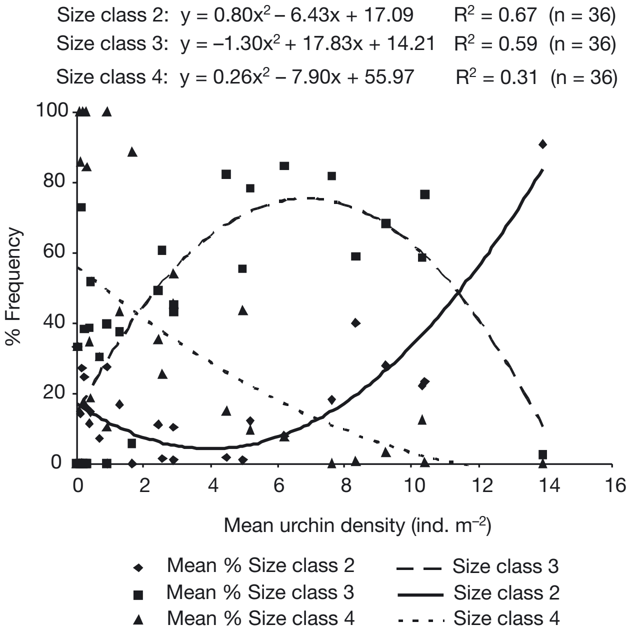

Fig. 3. *Diadema antillarum*. Relationships between the mean % frequency of each size class and mean total density of individuals at each location

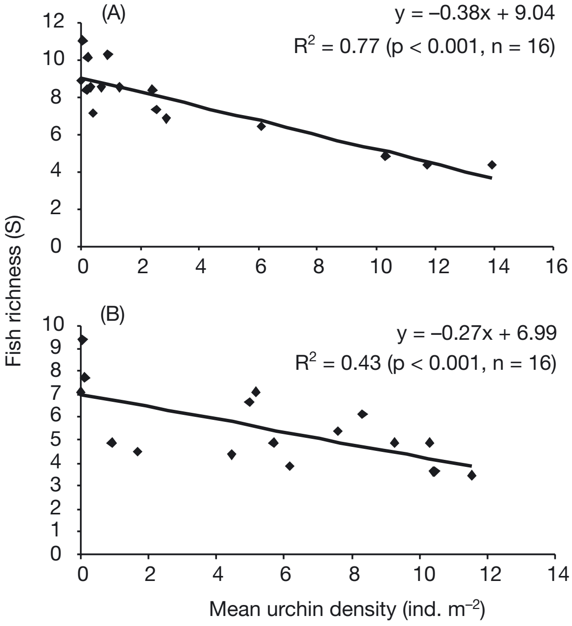

Fig. 5. *Diadema antillarum*. Relationship between the overall mean density of individuals and rocky-reef fish assemblage richness. (A) Western islands, (B) eastern islands

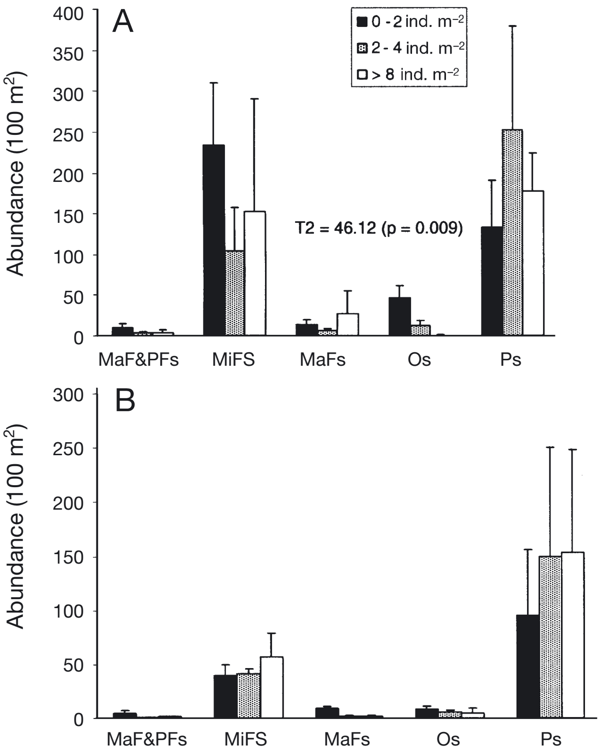

Fig. 6. Total mean abundance of the 5 considered trophic groups with regard to the defined categories of urchin-grazed barrens. Error bars represent SE of means. Above bars: significant results ($p < 0.01$) of T2 Tamhane *a posteriori* multiple comparisons. (A) Western islands, (B) eastern islands. MaF&PFs: macroinvertebrate feeders and piscivorous, MaFs: macroinvertebrate feeders, MiFs: microinvertebrate feeders, Ps: planktivorous, Os: omnivorous

Differences in the trophic structure of the fish assemblages were observed between the eastern and western islands with regard to the 4 barren categories (Figs. 6 & 7). However, significant differences were detected by 1-way ANOVA ($p < 0.01$, Figs. 6 & 7) only in the mean total abundance and biomass of omnivorous fish species from the western islands, as a consequence of the large and heterogeneous variances associated with the values of mean total abundance and biomass. Nonetheless, the mean biomass of MaF&PFs is about 9 and 10 times greater in low-urchin density rocky environments (<2 ind. m^{-2}) than in well developed urchin-grazed barrens (>8 ind. m^{-2}) for the eastern and western Canary Islands (Fig. 7), respectively. Likewise, the mean biomass of omnivorous fish species (mainly the parrotfish *Sparisoma cretense*) for the western and eastern islands was 6 and 2 times greater, respectively, in barrens with low densities of sea urchins that in heavily-grazed barrens. In contrast, the mean biomass of fast-growing plankton-feeding species (e.g. *Chromis limbatus*, *Atherina presbyter*) in overgrazed barrens (>8 ind. m^{-2}) is approximately twice that observed in locations either devoid of or with very low density of *Diadema antillarum* sea urchins for the eastern islands, and 3 times greater for the western islands (Fig. 7).

The above-mentioned results are corroborated by the significant non-parametric Spearman correlation coefficients found between the overall mean densities of *Diadema antillarum* individuals and the mean total abundance and biomass of the 5 considered trophic groups (Table 5). Significant negative correlations were observed for both macroinvertebrate-feeder groups (MaF&PFs and MaFs), as well as for the omnivorous fish group. In addition, the significant correlations between mean abundance and biomass of the 5 considered trophic groups and the 4 defined size classes of *D. antillarum* (Table 6) seem to indicate an inverse relationship between the mean abundance and biomass of macroinvertebrate-feeders registered per location and the mean % frequency of the small-to-intermediate size classes. On the other hand, we recorded several significant positive correlations between sea urchin density and total mean abundance and biomass of plankton-feeders (Table 5).

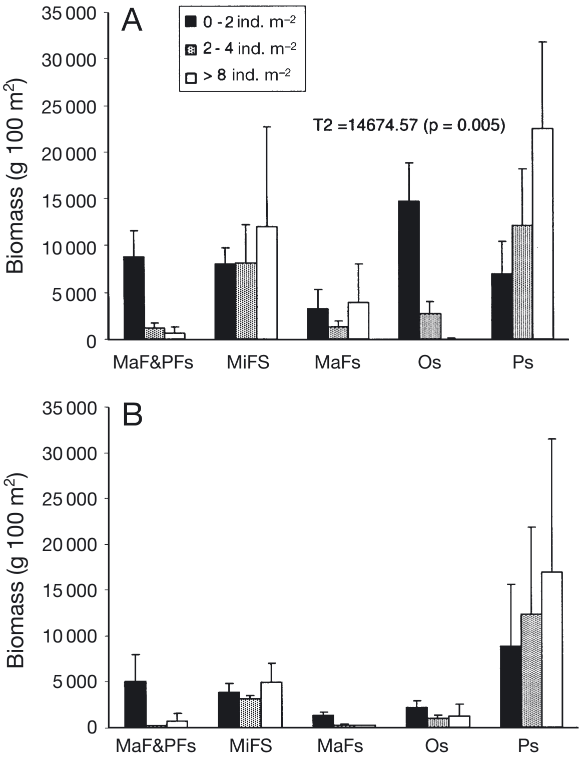

Fig. 7. Total mean biomass of the 5 considered trophic groups with regard to the defined categories of urchin-grazed barrens. Error bars represent SE of means. Above bars: significant results ($p < 0.01$) of T2 Tamhane *a posteriori* multiple comparisons. (A) Western islands, (B) eastern islands. MaF&PFs: macroinvertebrate feeders and piscivorous, MaFs: macroinvertebrate feeders, MiFs: microinvertebrate feeders, Ps: planktivorous, Os: omnivorous

Table 5. *Diadema antillarum*. Significant non-parametric Spearman correlation coefficients and levels of significance (in parentheses) of correlations between the mean density of individuals per location and the mean total abundance and biomass of the 5 defined fish trophic groups. Dashed lines indicate no significant relationship

	Overall Archipelago (n = 36)		Eastern islands (n = 19)		Western islands (n = 17)	
	Mean total abundance	Mean total biomass	Mean total abundance	Mean total biomass	Mean total abundance	Mean total biomass
MaF&PFs	−0.31 (0.060)	−0.44 (0.006)	–	−0.46 (0.047)	–	–
MiFs	–	–	–	–	–	–
MaFs	−0.41 (0.013)	−0.30 (0.067)	−0.65 (0.002)	−0.58 (0.009)	–	–
Os	−0.48 (0.003)	−0.52 (0.001)	−0.55 (0.013)	−0.58 (0.009)	–	−0.45 (0.065)
Ps	–	0.34 (0.042)	0.45 (0.052)	0.45 (0.050)	–	–

Table 6. *Diadema antillarum*. Significant non-parametric Spearman correlation coefficients and levels of significance (in parentheses) of correlations between the mean % of frequency of the 4 size classes and the mean total abundance and biomass of the 5 defined fish trophic groups. Dashed lines indicate no significant relationship

	Mean total abundance					Mean total biomass				
	MaF&PFs	MiFs	MaFs	Os	Ps	MaF&PFs	MiFs	MaFs	Os	Ps
Overall Canarian Archipelago (n = 36)										
Size class 1	–	–	–	–	–	–	–	–	–	–
Size class 2	–	–	–	–	–	–	–	–	–	–
Size class 3	–	–	−0.60 (0.000)	–	–	−0.48 (0.003)	–	−0.54 (0.003)	–	–
Size class 4	–	–	–	–	–	–	–	–	–	–
Western islands (n = 17)										
Size class 1	–	–	–	–	–	–	–	–	–	–
Size class 2	–	–	–	–	–	–	–	−0.49 (0.041)	–	–
Size class 3	–	–	–	–	–	−0.45 (0.067)	–	–	–	–
Size class 4	–	–	–	–	–	–	–	–	–	–
Eastern islands (n = 19)										
Size class 1	–	–	–	–	–	–	–	–	–	–
Size class 2	–	–	−0.64 (0.008)	–	0.59 (0.015)	–	–	−0.58 (0.017)	–	–
Size class 3	–	–	−0.71 (0.002)	–	–	−0.57 (0.020)	–	−0.64 (0.007)	–	–
Size class 4	–	–	–	–	–	–	–	–	–	–

DISCUSSION

Our study represents another case in which low abundance and biomass of top predatory fish seem to be related to high densities of sea urchins and in turn, to low cover of fleshy macroalgae. These results suggest that a trophic-cascade may exist in the Canarian Archipelago, as has been demonstrated in other locations worldwide such as the Mediterranean (Sala & Zabala 1996, Sala et al. 1998), tropical coral-reef habitats (Hay 1984, McClanahan & Muthiga 1988, McClanahan & Shafir 1990) and kelp-dominated areas (Andrew & Choat 1982, Bernstein et al. 1983, Steneck 1997, Babcock et al. 1999, Shears & Babcock 2003). We suggest that this cascade is at least partially related to overfishing of large macroinvertebrate-eating fish (Duggins 1980, Tegner & Dayton 1981, Breen et al. 1982, Tegner & Levin 1983, Hay 1984, McClanahan & Muthiga 1988, McClanahan & Shafir 1990, McClanahan 1992, McClanahan et al. 1994, Sala & Zabala 1996, Babcock et al. 1999); although no data on fishing intensity in this area is available to support this assumption, as artisanal fishermen sell their captures directly to local markets without any sort of governmental control (Bas et al. 1995, Pajuelo & Lorenzo 1995). The increased prevalence of urchin-dominated barrens throughout the Canarian Archipelago could be therefore considered as one symptom of long-standing intense use (e.g. overfishing) of the littoral (Sala & Zabala 1996, Sala et al. 1998, Babcock et al. 1999, Pinnegar et al. 2000, Shears & Babcock 2003).

Our results suggest, therefore, that macroinvertebrate-eating carnivorous fish (e.g. Sparids and Labrids) act as a controlling force on the *Diadema antillarum* population structure through predation. These species have been widely reported as potential predators of sea urchins (e.g. McClanahan 1995, Sala & Zabala 1996, Sala 1997). The clear, negative relationship between sea urchin density and the mean total abundance (or biomass) of the omnivorous fish group is probably caused by the most abundant omnivorous species (the parrotfish *Sparisoma cretense*) inhabiting, almost exclusively, shallow algal bands throughout the Canarian Archipelago (Bortone et al. 1991, Falcón et al. 1996). Additionally, compensatory increases (sensu Myers & Worm 2003) in fast-growing plankton-feeding coastal fish species (e.g. *Chromis limbatus*) were observed in our study throughout well-developed urchin-dominated barrens of the rocky littoral zones of the Canary Islands.

The high variability in sea urchin density that could not be explained by fish density suggests that other mechanisms also control it. The interaction between sea urchins and coastal fish populations is thus a complex interplay between physical and physiological disturbance, competition, predation and recruitment, which in turn are influenced by stochastic factors (Sala & Zabala 1996). Hence, factors other than predation-based cascades could contribute to the interaction between *Diadema antillarum* and hard-bottom fish populations in the first place and, therefore, to the large variability observed in sea urchin density among locations within islands. Processes including pollution, diseases, large-scale oceanographic events, recruitment and the structural complexity of the rocky substratum (availability of refuges) are also important factors driving the dynamic interaction processes between rocky-bottom fish assemblages and sea urchin populations (Sala et al. 1998).

The size structure of *Diadema antillarum* is dominated by small-to-intermediate sized sea urchins (Size classes 2 and 3) within environments with a high density of individuals. This strategy may buffer the adverse effects of increases in population density and allow exploitation of resources (Levitan 1988, 1991, Karlson & Levitan 1990, Alves et al. 2001). In contrast, low sea urchin density locations are characterized by the dominance of large sized individuals. The lack of potential predators for large sized *D. antillarum* individuals (Size class 4) could explain this fact. This result contrasts with the size-frequency distributions observed by Sala & Zabala (1996) for the edible sea urchin *Paracentrotus lividus* (Lamarck) in the western Mediterranean, where low numbers of large sized sea urchins were recorded within protected areas with high fish density. This is attributable to differences in morphology and therefore to the higher structural complexity of a long-spined sea urchin such as *D. antillarum* versus a short-spined such as *P. lividus*. Predation pressure on *D. antillarum* should be thus concentrated on small-to-intermediate sized individuals (Size classes 1 and 2). Consequently, we propose the existence of a predator 'escape size' (sensu Sala 1997) for the sea urchin *D. antillarum* along the Canarian Archipelago. On the other hand, our correlation-based study has not provided evidence of the existence of different predator groups for differently sized sea urchins, as Sala (1997) has reported for *P. lividus*. Hence, further research should focus on this point by means of direct observations, predation experiments and gut content analyses (McClanahan & Muthiga 1988, McClanahan 1995, Sala & Zabala 1996).

Garrido et al. (2000) have shown that *Diadema antillarum* presents a reproductive peak in the Canarian coasts during the spring months (April to May); this fact may explain the absence of new recruits (Size class 1) in all locations, as we made our observations in late winter.

The physical complexity of subtidal rocky bottoms, at the small-to-intermediate spatial scale measured by our study, seems to play an important role in determining the local patchiness of *Diadema antillarum* populations, when density is intermediate. In contrast, habitat complexity is not important throughout well-developed urchin-grazed barrens (>8 ind. m^{-2}), where *D. antillarum* is randomly distributed and widespread along rocky reefs. We believe that the local complexity of the rocky substrate is therefore important when the populations of *D. antillarum* are under high predator control and, consequently, seek shelter within refuges (e.g. medium and large crevices, inside groups of boulders) during daylight hours to reduce the risk of predation. This crevice-dwelling behavior has been reported in the Caribbean (Carpenter 1981, 1984) and the eastern Atlantic (Tuya et al. 2004a), and is common in other echinoid species in the presence of predators in temperate waters (Andrew & Underwood 1989, Sala & Zabala 1996). Hence, the availability of refuges may be a sufficient condition for the creation of areas of barren habitat (Andrew 1993, Sala & Zabala 1996), even in locations with intense predatory activity such as Location 7 of our study.

The strong negative relationship observed between the percentage of fleshy macroalgal cover (frondose brown algae) and the density of *Diadema antillarum* has also been described in Caribbean waters (Carpenter 1981, Sammarco 1982, Hay 1984, Lessios et al. 2001) and the eastern Atlantic (Alves et al. 2001, Tuya et al. 2004b); as well as for other echinoid species in the western Mediterranean (Sala & Boudouresque 1997), the Kenyan coast (McClanahan et al. 1996), New Zealand (Andrew & Choat 1982, Babcock et al. 1999, Shears & Babcock 2003) and in the north-western Atlantic (Vadas & Steneck 1995). The non-linear decrease in fleshy macroalgal cover with increasing sea urchin density has been reported as the response of algae to the *in situ* manipulation of sea urchin density (Andrew & Underwood 1993, Benedetti-Cecchi et al. 1998). Although the reasons underlying non-linearities are difficult to interpret (Andrew & Underwood 1993, Benedetti-Cecchi et al. 1998), we believe that differences in the quality of algae as food resources for sea urchins could explain this process (Benedetti-Cecchi et al. 1998), since sea urchins are able to detect preferred species (Himmelman & Nédélec 1990). *D. antillarum* displayed clear feeding preferences over the most abundant large brown macroalgae species of the Canary Islands (Tuya et al. 2001). Therefore, individuals can forage only on food resources of high quality if density is low. However, *D. antillarum* has to graze over a wide variety of algal species when density increases, consuming all available algae and leading to a dramatic decrease in macroalgal cover. Although grazing on macroalgae may change with depth (Ruitton et al. 2000), we can consider the long-spined sea urchin *D. antillarum* as a key herbivorous species (Tuya et al. 2004b) that plays an important role in determining fleshy macroalgae cover in rocky subtidal communities of the Canarian Archipelago.

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