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The key role of the sea urchin *Diadema* aff. *antillarum* in controlling macroalgae assemblages throughout the Canary Islands (eastern subtropical Atlantic): an spatio-temporal approach

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Abstract

Diadema aff. *antillarum* perform a key role in organizing and structuring rocky macroalgae assemblages in the Canary Islands. Densities of *D.* aff. *antillarum* higher than

2 individuals m^{-2} are found to drastically reduce non-crustose macroalgal cover to under 30 % and wave exposure appears as a major factor determining sea urchin density, which decreases with exposure level. Substrates containing > 20 % sand limit urchin to under one individual m^{-2} , but high relief rocky habitats show higher density. Moreover, several anthropogenic factors (number of islanders and tourists per coastal perimeter, and number of operational fishing boats) were positively correlated with urchin abundance. A trend of increasing urchin density through time was found, although well structured marine systems found at Mar de Las Calmas Marine Protected Area and at the no-take area of La Graciosa Marine Protected Area do not seem to follow this general trend.

Key words: Canary Islands, *Diadema* aff. *antillarum*, non-crustose macroalgae, spatio-temporal variability, urchin-stable-state, *Lobophora*-stable-state, MPA

1. Introduction

The importance of herbivorous sea urchins in structuring marine algal assemblages is well known (Lawrence, 1975; Harrold and Pearse, 1987). At moderate population densities, sea urchins may alter plant species composition and promote species diversity through selective feeding (Sammarco, 1982). However, at high densities they can dramatically reduce non-crustose macroalgal beds resulting in the formation of ‘sea urchin-dominated barren grounds’ (Lawrence, 1975). The occurrence of such areas has been reported along temperate coastlines (North and Pearse, 1970; Andrew, 1993; Scheibling and Hennigar, 1997; Sala et al., 1998; Guidetti 2006) and subtropical coastlines (Brito et al., 1984; Alves et al., 2001; Brito et al., 2004; Hernández, 2006), as well as in tropical regions (Ogden et al., 1973; Sammarco, 1982; McClanahan, 1994).

1 In the eastern Atlantic oceanic islands, and particularly in the Canary Islands, the
2 density of the genetically differenced ‘b-form’ of the species *Diadema antillarum* defined
3 by Lessios et al. (2001) (here called *D. aff. antillarum*) can reach more than 12
4 individuals m⁻² and it is spread throughout the entire Archipelago (Brito et al., 1984; Brito
5 et al., 2004; Tuya et al., 2004; Hernández, 2006). Loss of macroalgal beds produces
6 lower species diversity (Herrera, 1998) and loss of habitat suitable for feeding and
7 breeding fish (Brito et al., 2004). Therefore, it is well known that urchin barrens are
8 unproductive habitats, where primary productivity is more than two orders of magnitude
9 lower than at comparable reefs dominated by algal beds in temperate regions (see
10 Chapman, 1981). At this latitude between tropical and temperate waters, macroalgae are
11 the main biological engineers on rocky reefs and no coral reef formations occur.
12 Consequently, high macroalgal cover is a well-known indicator of good benthic
13 conservation status (Hernández et al., 2007a).

14 On temperate and subtropical rocky coasts, subtidal habitats are often characterized
15 by one of two community states: algal bed/kelp forest or sea urchin barren (Lawrence,
16 1975; Sala et al., 1998; Guidetti 2006; Hernández et al., 2007a). Algal beds in the Canary
17 Islands are characterized by brown algae and *Lobophora variegata* is the most common
18 species. Other widespread algae are the genus *Dictyota*, *Cystoseira* and *Sargassum*
19 (Sansón et al., 2001; Sangil et al., 2006; Hernández et al., 2007a). When urchins are
20 abundant in barrens their intense grazing denudes the seabed of all but encrusting red
21 coralline algae such as *Hydrolithon* and *Neogonolithon*, and brown encrusting
22 *Pseudolithoderma adriaticum* (Sangil et al., 2006). In spite of the high densities of this
23 keystone urchin throughout the Canary Islands, relatively large areas remain with low
24 urchin densities (Brito et al., 1984; Brito et al., 2004; Tuya and Haroun, 2006; Hernández

et al., 2007a), where *Lobophora variegata* dominates, occupying 80% of the substrate and reaching 50 m depth (Tuya and Haroun, 2006; Sangil et al., 2006; Hernández et al., 2007a).

Occasionally, relevant events such as high recruitment or mass mortality, which alter the adult urchin population, might be noted (Ebert, 1983; Pearse and Hines, 1987; Scheibling and Hennigar, 1997; Lessios, 1988) and these events could be relevant in mediating transitions between alternate states. Mass mortality events have been recorded for different sea urchin species in widespread areas of the world (Pearse et al., 1977; Lessios, 1988; Scheibling and Hennigar, 1997), however no such event has been recorded in the eastern Atlantic, where high densities of urchins and barrens have persisted over the decades (Brito et al., 1984; Hernández, 2006). Experimental urchin exclusions have been performed in the Canary Islands, providing evidence that erect macroalgae have the potential to recolonise encrusting coralline barren areas (Brito et al., 2004). Also shallow rocky bottoms sporadically exposed to storm waves / swell (i.e. high hydrodynamic events) have been found to allow algal growth by removing urchins or restricting the scope of their movement so that they form compliant aggregations (JC. Hernández and S. Clemente personal observation).

Habitat complexity is an important factor influencing *Diadema* grazing (Lee, 2006), as well as for other sea urchin species (Andrew, 1993), since complex habitats provide urchins with refuge from predation (Levitan and Genovese, 1989). The availability of refuges and the urchins' so called cryptic behavior seems to help promote survival of recruits in complex rocky areas (Levitan and Genovese, 1989) and probably contributes to the high adult population density typically found in these habitats (Hernández et al., 2006a, Hernández 2006; Clemente et al., 2007). Gradients in the physical environment

may produce spatial heterogeneity of marine assemblages at different scales simply as a consequence of the space available or of the different physiological tolerances of the species (Levitan and Genovese, 1989; Andrew, 1993). However, few habitat complexity studies 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 *Diadema* aff. *antillarum* distribution and abundance (Alves et al., 2001; Hernández, 2006; Clemente et al., 2007), any interpretation of changes in urchin populations must be made with knowledge of the species' basic variation in relation to these environmental variables.

Here we present a medium-term data set, recorded throughout the Canarian Archipelago over seven years and 125 sites that aim to improve the understanding of spatial variation at different scales. This study assesses *Diadema* aff. *antillarum* populations, cover of urchin barren vs. macroalgae and habitat-complexity. Variation is studied on different spatial scales (islands and areas of different wave exposure, human pressure, depth, and habitat complexity); as well as on different temporal scales. During the course of the sampling period a strong urchin recruitment event was detected due to noticeable seawater warming during 2003 and 2004 in the Canary Islands (Hernández, 2006; Hernández et al., 2006a). A re-sample of study sites was performed after the recruitment event to detect whether the effect of this phenomenon was spread throughout the Canary Islands' Marine Protected Areas (MPAs) and Highly Fished Areas (HFAs).

2. Material and Methods

2.1. Study site: oceanographic features of the Canary Islands

The Canary Islands are situated between latitude 27.68-29.58 N and longitude 18.28-14.58 W on the eastern border of the North Atlantic Ocean's subtropical gyre. Emerging from the oceanic basin as a result of successive overlays of volcanic material to form an independent set of islands, the Canarian Archipelago comprises seven major islands and four islets. The eastern boundary of the archipelago is separated from the coast of the African mainland by a distance of 90 km 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 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, as well as to the Trade Winds; thus giving rise to a variety of mesoscale oceanographic phenomena that have strong implications for the productivity of the region (Barton et al., 1998). This particular geographical situation creates an oceanographic gradient across the archipelago, where differences in sea water temperature ($\approx 2^{\circ}\text{C}$), nutrients and primary productivity are found between its eastern and western boundaries (Barton et al., 1998). Therefore, the islands' marine assemblages consist of a combination of tropical, subtropical and temperate species which varies according to its location within the oceanographic gradient (Sansón et al., 2001; Brito et al., 2001).

Exposure to wave action is a strong force in segregating urchin species (Tuya et al., 2007). The shape of the island and its orientation against the waves creates different degrees of wave exposure along the different coastlines. The normal wave pattern consists of sea waves from NNE, which have an annual average height of 1.4 m and a frequency of 9.5 s. NNE swells are abundant throughout the year and more frequent from

autumn to spring, also associated with NNE and NE winds. Otherwise swells originating in the Northern Atlantic become more frequent between October and March and approach the islands from NNW and NW, with an annual wave height between 2-3 m and a frequency of 18 s (Yanes et al., 2006). According to the different spatial behavior of swells, differences in terms of average annual height and frequency of waves between the northern, western and eastern-southeastern coasts are found. Eastern, southeastern and southern coasts of the islands are sheltered from NNW-NW strong swells and face waves that are on average smaller than those received by northern and western coastlines, which are exposed to non-local swells (Yanes et al., 2006).

2.2. Sampling methods: sea urchins and algal assemblages

At each site the belt transect method was used to count all *Diadema* aff. *antillarum* individuals thus providing estimates of sea urchin population density. Transects of 10 x 2 m, suitable for the benthic communities investigated (Hernández et al., 2007a), were used with at least 8 replicates per site. Transects were run parallel to the coastline using a metric tape at depths of 0.5-25 m, with a minimum distance between replicates of 10 m. Percentages of non-crustose macroalgae and barren cover were estimated *in situ* by randomly placing 3-5 quadrats per transect. Barren cover was defined as total surface covered by crustose macroalgae and bare rock (modified from Guidetti, 2006). Dominant algal assemblage was recorded in all sites considering five morpho-functional groups (Guidetti, 2006): (a) algal turf; (b) unbranched-erect macroalgae; (c) branched-erect macroalgae; (d) calcified-erect macroalgae and (e) crustose macroalgae (Table 1). These groupings facilitate the ecological interpretation of algal assemblages influenced by *D. aff. antillarum*.

1

2 2.3. Sampling design and data analysis

3 2.3.1. Influence of sea urchin population density on algal assemblages

4 The influence of urchin populations on algae assemblages was assessed using data
5 from 125 sites around the Canary Islands (Fig. 1; see table 1 in Supplementary materials)
6 over the period 2001-2006. Log-linear relationships between urchin density (individuals
7 m⁻²) and non-crustose macroalgal cover (%) were performed using SPSS-14 statistical
8 package.

9 2.3.2. Large scale spatial variation: influence of wave exposure and human pressure in 10 sea urchin archipelagic distribution

11 To assess spatial variation over a scale of kilometers, a total of 125 sites were
12 sampled between 2001-2006 throughout the entire archipelago (Fig.1; see table 1 in
13 Supplementary materials). Sites were chosen from two different wave exposure levels.
14 Different degrees of exposure can be found on an island due to its local topography,
15 which can be simplified into two main levels, as described in section 2.1 following Yanes
16 et al. (2006):

17 - High exposure: sites located on the north or northwest side of the islands and islets,
18 affected by trade winds and swells from NNE-NE and often by NNW-NW swells, as well
19 as sites only affected by NNW-NW swells (see table 1 in Supplementary materials).

20 - Low exposure: sites located on the east, south or southeast side of the islands and
21 islets normally affected by trade winds waves and swells from NNE-NE and not by
22 NNW-NW swells (see table 1 in Supplementary materials).

23 In order to contrast sea urchin density and barren cover among islands and degrees of
24 exposure to wave action, we performed distance-based permutational ANOVAs

(Anderson, 2001). A three way design was performed when analysing urchin density and barren cover, in which ‘Island’ (I) was treated as a fixed factor with seven levels; ‘Exposure’ (E) as a fixed factor with two levels and ‘Site’ (S) 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 4.999 permutations of the appropriate exchangeable units (Anderson, 2001). Significant terms in the full model were examined individually using appropriate *a posteriori* pairwise comparisons. The software PRIMER 6 & PERMANOVA+ was used to perform these analyses.

Relationships between sea urchin density and factors that define human and fishing pressure (number of islanders and tourists per island perimeter, and number of fishing boats) were analysed. Logarithmic and linear models were performed using the SPSS 14.0 statistical package. Information on human and fishing pressure in the Canary Islands was obtained from Gobierno de Canarias (www.gobcan.es), National Spanish Network of Marine Protected Areas (www.mapya.es/rmarinas/) and Bas et al. (1995); data previously used by Tuya et al. (2006a). Similar data have been used by other authors to provide a useful depiction of anthropogenic pressure and resource exploitation (Hawkins and Roberts, 2004). Data from Gran Canaria Island were not included in the regression due to proximity of sampling sites (see Fig. 1).

2.3.3. *Medium-small scale spatial variation: influence of depth, sedimentation, topographic relief, slope and substratum diversity*

To assess spatial variation at a scale of meters, depth and four main habitat-complexity variables were identified:

-Sedimentation (Díez et al., 2003): estimated as the percentage of rock covered by sand at each transect and assigned to categories of (1) 0%; (2) 1- 10%; (3) 10 - 20%; and (4) more than 20%.

-Topographic relief (McClanahan, 1994): visually estimated at each transect, considering contour height in relation to linear surface area, as (1) flat surface; (2) less than 1 m; (3) between 1-3 m; and (4) high relief, more than 3 m.

-Slope (Díez et al., 2003): measured at each transect as the inclination of the substrate in degrees, using an angle meter with a weight as a pendulum, and then assigned to the categories (1) 0°; (2) from 0° to 45°; (3) more than 45°; and (4) 90°.

-Substratum diversity (Gratwicke and Speight, 2005): considered as the substrate type or combination of substrates visually identified at belt transects. We categorized them as: (1) bed rock; (2) boulders from 5-100 cm; (3) a combination of bed rock and boulders.

The influence of each habitat-complexity variable on *Diadema* aff. *antillarum* density and barren cover was tested using field data collected in 1112 belt transects performed throughout the entire Canarian Archipelago (Fig. 1). We performed three way distance-based permutational ANOVAs (Anderson, 2001), in which 'Island' was treated as a fixed factor with seven levels. Habitat-complexity variables were treated as fixed factors with four levels each for 'Sand' (Sa), 'Topographic relief' (TR) and 'Slope' (Sl) and three levels for 'Substrate diversity' (SD). 'Site' was treated as a random factor nested within the interaction 'Island x habitat-complexity variable'.

2.3.4. Temporal variation: effects of sea urchin population expansion throughout the Archipelago (MPAs vs HFA)

To temporally monitor sea urchin density, three sites were chosen (Fig. 1; see table 1 in Supplementary materials). Abades was the most sampled site with three years of

1 monthly sampling from February 2002 to February 2005, and some additional seasonal
2 sampling in 2005-2006. Masca was sampled monthly from February 2002 to March 2003
3 and Boca Cangrejo from January 2004 to February 2005. In Boca Cangrejo, further data
4 were collected in selected months of 2005, as well as seasonally in 2006. Year to year
5 variations in urchin density and barren cover were tested, between Abades and Masca
6 (2002 to 2003) and between Abades and Boca Cangrejo (2004 and 2005), with the factor
7 ‘Year’ (Y) treated as a fixed factor and ‘Site’ (S) as a random factor.

8 Sea urchin population outbreaks were detected at two sites in Tenerife (Abades and
9 Boca Cangrejo) during 2004 and 2005. These two instances of proliferation can both be
10 related to increases in water temperature (Hernández, 2006; Hernández et al., 2006a) and
11 provided the opportunity to study how the response of urchin populations varied across
12 the Canarian Archipelago. A total of 24 sites, for which previous data were available,
13 were revisited during 2006 to assess the effect of the detected outbreak in different areas:
14 7 sites in Mar de Las Calmas MPA (El Hierro), 11 sites in Tenerife HFA and 6 sites in La
15 Graciosa MPA (Lanzarote and northern islets) (Fig. 1; see table 1 in Supplementary
16 materials). Seasonal and spatial variations in adult density and barren cover were
17 analyzed using a three way Permutational ANOVA. The orthogonal factor ‘Outbreak
18 event’ (O) was treated as a fixed with two levels of variation: (1) before and (2) after the
19 event; Island (I) as a fixed factor with three levels: (1) Mar de Las Calmas-MPA, (2)
20 Tenerife-HFA and (3) La Graciosa-MPA; and ‘Site’ (S) as a random factor nested within
21 ‘Island’ with 24 levels. While Mar de Las Calmas-MPA had large areas dominated by
22 *Lobophora variegata* before the outbreak, La Graciosa-MPA and Tenerife-HFA showed
23 dense barrens of *Diadema* aff. *antillarum* (Brito et al., 2004; Hernández et al., 2007a).

3. Results

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

A highly significant log-linear relationship was detected between sea urchin 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 of algal cover at the lowest urchin densities, in which higher variability in the dominant morpho-functional algal group also occurs. At intermediate densities this variability decreased sharply and at a threshold density of about 4 individuals m^{-2} non-crustose macroalgal cover remains below 30%, with crustose macroalgae clearly the dominant algal group (Fig. 2). In general, when urchin densities exceed 4.5 individual 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 when urchin densities were below 6.5 individuals m^{-2} (Fig. 2).

3.2. Spatial variation at large scale: effect of wave exposure on sea urchin populations

High variability in *Diadema* 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 the factor 'Exposure' (Table 2A). *A posteriori* pairwise analyses showed that the maximum sea urchin densities were recorded at Tenerife island, which differs significantly from the medium densities registered in Lanzarote-La Graciosa ($t = 2.42$, $p < 0.05$), 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 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 $t = 6.64$ respectively, $p < 0.01$) (Fig. 3A₁).

Results concerning the factor 'Exposure' show that sites with high levels of exposure to wave action maintained significantly lower *D. aff. antillarum* densities (2.27 ± 0.14 individuals m^{-2}) than those less exposed (3.49 ± 0.12 individuals m^{-2}) (Fig. 3A₂). There were also differences in urchin densities between sites at each island (Table 2A).

The assessment of barren ground cover across the Archipelago showed a significant interaction of factors 'Island x Exposure' (Table 2B). Barren ground cover differed depending on level of exposure to wave action in relation to each island considered, as shown by *a posteriori* pairwise analyses. The only island for which differences were obtained was Tenerife, where barren cover was found to be significantly higher at less exposed sites ($t = 2.92$, $p < 0.01$) (Fig. 3B). 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-La Graciosa ($t = 1.60$, $p = 0.13$) (Fig. 3B). On the other hand, differences at the scale of factor 'Site (Island)' were also significant (Table 2B), differing in the % of barren ground cover between sites at each island.

3.3. Spatial variation at large scale: interaction between sea urchin and humans

A significant log-linear relationship was detected between sea urchin density and number of islander's resident along the coastal perimeter (Fig. 4A). The scatter plot of sea urchin density versus number of islanders per coastal perimeter showed Tenerife's more populated coastal perimeter also had the highest sea urchin density. A low significant linear relationship was detected between sea urchin density and number of

tourist per coastal perimeter (Fig. 4B), and a low significant log-linear relationship was found between sea urchin density and number of fishing boats (Fig. 4C).

3.4. Spatial variation at medium-small scale

3.4.1. Depth

When assessing the variability of *D. aff. antillarum* density with depth, the scatter plot showed higher variability in urchin density at shallower depths (<7m) 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 individuals m^{-2} previously reported to drastically reduce non-crustose macroalgal cover, was not reached at highly exposed sites at depths less than about 7 m, while at less exposed sites this density is common in shallower water (~3 m) (Fig. 5).

3.4.2. Sedimentation

Permutational ANOVA analysis showed a significant effect of the factor ‘Sedimentation’ over *D. aff. antillarum* densities, as well as of the factor ‘Island’ (Table 3A). *A posteriori* pairwise analyses showed urchin density to be significantly lower on substrates where sand was >20 % compared to those without any sand ($t = 2.82$, $p < 0.01$), 1-10 % ($t = 2.13$, $p < 0.05$) and 10-20 % ($t = 1.87$, $p < 0.05$) (Fig. 6A). Variations at the scale of ‘Site (Island x Sedimentation)’ were obtained (Table 3A), differing urchin density between sites at each island in relation to the sedimentation level considered.

Analyses showed no significant effect of either ‘Sedimentation’ or the interaction of factors ‘Island x Sedimentation’ on barren cover, although differences at the level of ‘Island’ and ‘Site (Island x Sedimentation)’ were still found (Fig. 6A; Table 3B).

3.4.3. Topographic relief

Permutational ANOVA analysis showed both ‘Island’ and ‘Topographic relief’ (TR) had highly significant effects on *D. aff. antillarum* density (Table 4A). *A posteriori* pairwise analyses showed urchin density to be significantly higher at the highest TR level (4) than in habitats with lower TR: 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 4A), meaning that urchin density differed between sites at each island in relation to the rugosity level.

When analysing barren cover, a significant effect of TR and highly significant effects of factors ‘Island’ and ‘Site (Island x TR)’ were obtained (Table 4B). *A posteriori* tests showed significant differences in percentage of barren cover between sites within the highest TR (4); which had a higher percentage of barren cover than at lower levels 1 ($t = 1.87$, $p < 0.05$), 2 ($t = 3.16$, $p < 0.01$) and 3 ($t = 1.92$, $p < 0.05$) (Fig. 6B).

3.4.4. Slope

Permutational ANOVA analyses showed no significant effect of ‘Slope’ or the interaction ‘Island x Slope’ on *D. aff. antillarum* density and on percentage of barren cover. However, differences at the level of ‘Island’ and ‘Site (Island x Sedimentation)’ were always found to be significant (see table 2 in Supplementary material).

3.4.5. Substrate diversity

There were no significant effects of factor ‘Substrate’ or even of the interaction ‘Island x Substrate’ on urchin density and barren cover, although differences at the levels of ‘Island’ and ‘Site (Island x Sedimentation)’ were significant (see table 3 in Supplementary material).

3.5. Temporal variation in sea urchin populations

3.5.1. Medium term monitoring

Sea urchin densities exceed 4 individuals m^{-2} at all studied sites and sampling periods, with higher values at Abades than at Masca and Boca Cangrejo. While the range of densities registered at each site was more stable from 2002 to 2005, Abades and Boca Cangrejo sites showed a trend of substantial increase of densities during 2005 and 2006 (Fig. 7A). Analyses comparing urchin density over the studied years showed significant effects of both main factors 'Year' and 'Site' (Table 5A). *A posteriori* tests showed that densities recorded in 2002 and 2004 ($t = 0.37$, $p = 0.81$) differed (02 vs. 05: $t = 23.32$, $p < 0.05$; 02 vs. 06: $t = 24.25$, $p < 0.05$; 04 vs. 05: $t = 39.74$, $p < 0.05$ and 04 vs. 06: $t = 368.45$, $p < 0.01$) from those collected in 2005 and 2006 at all sites ($t = 4.84$, $p = 0.13$) (Fig. 7A).

Percentages of barren cover remained high (above 80 %) over the whole duration of the study with slight variability between sites (Fig. 7B). Analyses comparing this variable over the years showed significant effects of the interaction 'Year x Site' (Table 5B), with percentages differing in relation to the site (Table 5B).

3.5.2. Analysis of the sea urchin outbreak

A two-way Permutational ANOVA was used to assess the seasonal and spatial variations of a population 'outbreak' across the Canarian Archipelago. A significant effect of the interaction 'Outbreak event x Island' on urchin density was obtained (Table 6A), differing urchin density before and after the reported event in relation to the island considered (Fig. 8A and 9). *A posteriori* pairwise analyses of this interaction showed densities recorded before compared to after the event were significantly different at El Hierro where urchin density was lower after the event ($t = 4.79$, $p < 0.01$), and at Tenerife where urchin density was found to be higher after the event ($t = 4.21$, $p < 0.01$), (Figs. 8A

and 9). In La Graciosa there was an increase in urchin density but the *a posteriori* test did not show the difference to be significant ($t = 1.79$, $p = 0.14$) (Figs. 8A and 9).

Similarly, in terms of percentage barren cover, there was shown to be a significant effect of the main factor 'Island' as well as of the interaction of factors 'Outbreak event x Site (Island)' (Table 6B), with these variables differing before and after the reported event in relation to the site considered at each island (Fig. 8B).

4. Discussion

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

Diadema aff. *antillarum* exhibits a key role in controlling fleshy macroalgae on rocky bottoms of the eastern Atlantic Islands (Madeira, Salvajes, Canary Islands) as demonstrated by various authors in recent years (Alves et al., 2001; Brito et al., 2004; Tuya et al., 2004; Hernández et al., 2007a). However, the urchin barren state was noticed long before in the Canary Islands (Brito et al., 1984).

In general, at a density of 4 individuals m^{-2} , non-crustose percentage cover of macroalgal assemblages is drastically reduced to around 30 % or less. 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 individuals m^{-2} . Filamentous algae and articulate coralline assemblages have been seen to maintain a low presence on densely populated barrens. At an urchin density above 2 individuals m^{-2} , non-crustose macroalgal cover is drastically reduced below 15 %, and at densities above 4 individuals m^{-2} it 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; Tuya and Haroun, 2006; Sangil et al., 2006), we consider a threshold density of 2 individuals m^{-2} in a rocky subtidal habitat to represent an urchin barren ground in the Canary Islands. When urchin density exceeds 4 individuals m^{-2} it could be considered a degraded urchin barren where non-macroalgae beds can develop. Definitions of these thresholds are useful with regard to conservation strategies, as they allow one 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 (Brito et al., 2004). Once a habitat is in the barren state, urchins can survive indefinitely by feeding upon animals, coralline algae, microbial films and drift algae (Hernández et al., 2007b).

Compared to typical urchin barrens elsewhere in the world (Chapman 1981; Pearse and Hines 1987; Valentine and Johnson, 2005; Guidetti and Dulčić, 2007), barrens in the Canary Islands appear to be maintained by sea urchins at relatively low densities (≈ 2 individuals m^{-2}). Their movement rate and food consumption rate, which involves grazing large areas of rocky substrate at night, could explain these differences. Through its movements and potentially large grazing grounds, *Diadema antillarum* can efficiently remove its preferred macroalgal species (Carpenter, 1981). In the oligotrophic Caribbean waters mean urchin densities around 10 individuals m^{-2} were recorded (Bak et al., 1984; see review in Lessios, 1988) and high abundances were noticed before a mass mortality event (Lessios, 1988). In similar oligotrophic conditions, the limited ‘nutrient’ resources

provided by waters surrounding the Canary Islands are not enough to maintain high urchin populations, but, as already stated, a relatively low urchin density is able to maintain a barren habitat. Despite limited nutrient supply in the Caribbean, the high abundance of urchins recorded in the area could be due to the increased habitat complexity created by corals which benefit the urchins (Lee, 2006), as also shown in this study in the case on rocky bottoms (see section 4.3 below).

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

Diadema aff. *antillarum* is spread across the entire Canarian Archipelago, with noticeable spatial variation in density. However, there is no a clear pattern to show oceanographic gradient affecting species distribution. Other authors have postulated that the extent of overfishing at each particular island determines urchin density (Tuya et al., 2004), and overfishing is thought to be a general problem in the Canaries (Brito et al., 1984; Falcón et al., 1996). The highest urchin densities were recorded in Tenerife, the island that supports high number of locals and tourists, denoting more pollution, more fishing pressure and less conservation of the marine environment. El Hierro, the smallest island, has less 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). Gran Canaria showed less dense urchin populations, as would be expected considering the human pressure and high level of fishing effort (Bortone et al., 1991; Bas et al., 1995; Tuya et al., 2006a). Although, skewed sampling distribution in this island may be underestimating the real density.

Spatial variation and patchiness found at each island illustrate that other environmental factors are controlling and influencing sea urchin abundance. Of particular importance is the existence of great water depths very close to the breakers. For example, in El Hierro Island, 50 m offshore the water is 50 m deep, therefore waves conserve much of their initial energy up to the breakpoint (Yanes et al., 2006). Consequently, NW-NNW sea swells seems to affect urchin populations more than trade winds, and the incidence of storms determines their 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 previously noted in the Caribbean (Debrot and Nagelkerken, 2006). Consequently, general urchin distribution is controlled by wave force and island slope that affects the energy of the wave. Protected coasts have calmer waters that promote urchin larvae retention and increased water temperature that enhances larval metamorphosis and settlement (Hernández, 2006), while at exposed sites larvae tend to get washed away. Such has been noticed for *Strongylocentrotus purpuratus* in capes and headlands due to high upwelling flow (Ebert and Russell, 1988).

4.3. Does habitat complexity affect sea urchin distribution?

Different patterns of variation in urchin populations and macroalgae have been reported at the studied areas with regard to depth. Areas with higher hydrodynamics show greater urchin density in the deeper band between 14-20 m water depth. In less exposed areas denser populations appear between 5-11 m. Depth limits recorded here agree with the theoretical model described by Tuya et al. (2007) who performed hydrodynamic experiments in a flow tank to estimate depth-limits beyond which urchin species can not withstand unidirectional waves. Density accumulation below certain depth limit could be

1 explained as a migratory strategy of urchins which tend to form fronts just below the
2 algal stand, as has been observed in *Strongylocentrotus droebachiensis* (Lauzon-Guay
3 and Scheibling, 2007). Along sheltered coasts, algal beds exist only at the shallower level
4 and urchin biomass accumulates in this band where more food is available. However,
5 along exposed coasts high urchin densities appear at greater depth but just below the algal
6 stand. Hydrodynamics allows algal growth by removing *Diadema* by dislodgement,
7 preventing its grazing activity (Tuya et al., 2007) or limiting their movement. Wave
8 action is therefore an important force limiting urchin grazing and density, and is the
9 mechanism that maintains shallow water algal stands throughout the Canary Islands
10 (Tuya and Haroun, 2006) and other places (Alves et al., 2001; Lauzon-Guay and
11 Scheibling, 2007).

12 Another important factor limiting urchin density is the percentage of sand or
13 sedimentation, as other studies have demonstrated on rocky reef organisms (Airoldi
14 2003). Levels above 10-20 % sand keep urchin densities below 2 individuals m⁻². The
15 combined effects of water motion and sediment scouring the substrate can weaken the
16 attachment between urchin and substrate as well as impairing their mobility.

17 Surveys revealed that substrate topographic relief and *Diadema* density were
18 positively related, as has been noted in the Caribbean (Lee, 2006). Increasing habitat
19 complexity by adding physical structure significantly increased the proportion of urchins,
20 while low habitat complexity was found to permit macroalgal-dominated reefs. High
21 topographic relief provides more suitable habitat on which urchins can reside
22 (Hernández, 2006) and these areas can support denser populations, as noted by Clemente
23 et al. (2007) in barren grounds of Tenerife. Future conservation strategies need to
24 consider habitat complexity, since certain habitats are potentially occupied by higher

1 numbers of urchins and are likely to present high resistance to restoration due to positive
2 feedback mechanisms that stabilize the system (Knowlton, 2004). Furthermore, it is
3 important to consider that human actions along the coast such as the construction of piers,
4 harbours, jetties and artificial reefs, could act as a potential stepping stone for spread of
5 this urchin. Artificial substrates such as these offer high relief habitat space and a
6 sheltered area for larval settlement, which means they can encourage and support large
7 urchin populations (Herrera, 1998).

8
9 *4.4. Persistence of algal / urchin states and influence of recent urchin demographic*
10 *outbreak throughout the Canary Islands*

11 'Barren ground' and '*Lobophora* bed' states exhibit a high degree of persistence and
12 stability in the Canary Islands (Brito et al., 1984; Bortone et al., 1991; Hernández et al.,
13 2007a). However, the area occupied by each system clearly differs. Barren grounds are
14 spread over the entire archipelago and can reach 50 m depth, whereas *Lobophora* beds
15 only appear in large areas of rocky bottom (0-60 m) in El Hierro and southwestern La
16 Palma, and in the rest of the archipelago they are restricted to shallow areas where wave
17 action keeps urchin grazing activity at a very low intensity.

18 The monthly variation in urchin density in shallow waters found by Tuya et al.
19 (2006b) agrees with our results in which wave exposure is related to adult density.
20 However, our depth range study shows that this variation only occurs in shallow waters.
21 The persistence of the high urchin densities even where little food remains may be down
22 to a continuous larval supply (Hernández et al., 2006b) and the absence of urchin's main
23 predators. Overfishing creates a trophic cascade effect which allows urchins to flourish,
24 as seen in Tenerife (Clemente et al., 2007). In addition, enrichment of coastal waters with

sewage effluent due to high human activity (amino acid enrichment) adds significantly to the nutrition received by urchins (North and Pearse, 1970), and recent sea water warming may have also increased *Diadema* larval settlement (Hernández et al., 2006a; Hernández, 2006) by increasing larvae develop. Other areas around the world have shown continuation of barren states (Chapman, 1981; Valentine and Johnson, 2005) although mass mortality events have also occurred (Lessios, 1988; Scheibling and Hennigar, 1997). No mass mortality event has been found to have occurred in the Canary Islands over the last decades (Brito et al., 1984; Lessios, 1988), not even during the early 80s when a huge mortality took place in the western Atlantic and eliminated almost the entire Caribbean *Diadema antillarum* population (see review in Lessios, 1988). Some factors may have kept the eastern species free of disease. The Atlantic Ocean itself acts as barrier and the two populations have been separate for about 2 million years (Lessios et al., 2001). Moreover, the high urchin density found on the Caribbean before the mortality event (Sammarco, 1982; Bak et al., 1984; Lessios, 1988) and in other areas involving other urchin species (Pearse et al., 1977; Scheibling and Hennigar, 1997) compared to the low densities in barrens of the Canary Islands, lends itself to disease propagation.

During 2005 and 2006 an increase in water temperature around the Canaries caused a sudden outbreak in the urchin population by assisting larval settlement (Hernández, 2006; Hernández et al., 2006a); but the effects were clearly variable across the Archipelago. Densities increased after the demographic outbreak in barren areas in Tenerife and at most sites in Lanzarote, except in a no-take area in La Graciosa MPA where lower urchin density and higher non-crustose macroalgal cover were recorded after the outbreak. Due to protection policies introduced at the site 11 years ago, urchin predators are gradually becoming more abundant, which will ultimately help alleviate the barren situation.

1 Although, this is a seemingly promising result, barren grounds have still persisted at this
2 site. On El Hierro very low urchin densities and high cover of *Lobophora* were recorded
3 before the outbreak event and no change in urchin density or percentage barren cover was
4 detected. A comparison of this result with the latter, demonstrates that the system's
5 degree of resilience to an outbreak event is dependent on how well structured the system
6 is, which means that no disturbance has altered any trophic levels. El Hierro was well
7 structured before the event, with high macroalgae cover and abundant fish predators
8 (Bortone et al., 1991; Hernández, et al., 2007a), which has provided the island protection
9 against the general trend toward an increase in urchin density.

10 Algal beds have persisted on El Hierro for decades, even before the implementation
11 of the MPA (Brito et al., 1984; Bortone et al., 1991). The *Lobophora* state seems to act as
12 a buffer against urchin domination trend in the Canary Islands (Hernández, 2006), due
13 either to a well structured system where predators control urchins or simply because
14 *Lobophora* beds are not suitable for larval settlement or urchin growth. It has been
15 speculated that predation at El Hierro (Bortone et al., 1991; Falcón et al., 1996; Tuya et
16 al., 2004) controls urchin population by 'top down forces', although specific experiments
17 are needed to verify this hypothesis. As noted by Sala (2006) and Guidetti and Sala
18 (2007), a well structured system seems to be resilient as it is shielded from external
19 human impacts and sea water warming (Knowlton, 2004). *Lobophora* algal beds seem to
20 be resistant to various biotic and abiotic perturbations, a situation comparable to that of
21 kelp in temperate regions (Sutherland, 1981). Additionally, the higher sea water
22 temperatures surrounding the western islands combined with the general increase in
23 temperature detected in the Canary Islands (Hernández, 2006) could be favouring the

development and persistence of the tropical *Lobophora variegata* beds, by aiding its settlement and growth.

In conclusion, *Diadema* aff. *antillarum* abundance clearly determines barren grounds distribution and algal beds dominated by *Lobophora* in the Canary Islands. Extension and persistence of both barrens and algal stands appear to be related to certain environmental factors, as well as to anthropogenic disturbances. The latter points out the importance of protection measures such as MPAs and the need to implement of restrictive fishing policies that help promote healthy systems which in turn control urchin populations.

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Tables and figures captions:

Table 1. List of algae species surveyed at the sampling sites in the Canary Islands. Categorized as non-crustose (turf; unbranched erect; branched erect and calcified erect) and crustose macroalgae.

Table 2. Results of three ways Permutational ANOVA comparing (A) density (individuals m⁻²) of *Diadema* aff. *antillarum* and (B) barren 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 1 supplementary material).

Table 3. Results of three ways Permutational ANOVA comparing (A) density (individuals m⁻²) of *Diadema* aff. *antillarum* and (B) barren 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 1 supplementary material).

Table 4. Results of three ways Permutational ANOVA comparing (A) density (individuals m⁻²) of *Diadema* aff. *antillarum* and (B) barren 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 topographic relief level (1= flat; 2=<1m; 3= 1-3m; 4= high relief), and 125 sites of the Canarian Archipelago (Table 1 supplementary material).

Table 5. *Diadema* aff. *antillarum*. Summary of the factorial two ways Permutational ANOVA to assess significant differences in (A) abundance of adult *D.* aff. *antillarum*

individuals; and (B) percentage barren cover between sampling years (Y) and sites (S: Abades, Boca Cangrejo and Masca) surveyed from 2002 to 2006 and their interactions.

Table 6. Results of three ways Permutational ANOVA comparing (A) density (individuals m⁻²) of *Diadema* aff. *antillarum* and (B) barren cover (%) before and after an outbreak event and between three areas (1: El Hierro-MPA (Marine Protected Areas); 2: Tenerife-HFA (Highly Fished Areas); 3: La Graciosa-MPA) and 24 sites of the Canarian Archipelago (Table 1 supplementary material).

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

Figure 2. Log-linear relationship between sea urchin (*Diadema* aff. *antillarum*) abundance and macroalgal cover.

Figure 3. (A1) Comparison of mean sea urchin (*Diadema* aff. *antillarum*) abundance (\pm SE) at different wave exposure and (A2) among Islands. (B) Comparison of mean percentage barren cover (\pm SE) among Island. There was no significant difference between means with identical letters (pairwise analysis). * = $p < 0.05$; ** = $p < 0.01$.

Figure 4. (A) Log-linear relationship between number of islanders per coastal perimeter and sea urchin (*Diadema* aff. *antillarum*) abundance. (B) Linear relationship between number of tourists per coastal perimeter and sea urchin abundance. (C) Log-linear relationship between number of fishing boats and sea urchin abundance. [H: El Hierro; P: La Palma; G: La Gomera; T: Tenerife; GC: Gran Canaria; F: Fuerteventura; L: Lanzarote

e islotes]. GC was not included in the analysis as sampled sites were all in close proximity and therefore did not represent the total coastal perimeter.

Figure 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. Dashed lines shows start depth of urchin barrens. Curved line shows depth range where the maximum abundances of urchins were found.

Figure 6. Effects of two habitat complexity variables (A: sedimentation, B: topographic relief) on mean (\pm SE) abundance of *Diadema* aff. *antillarum* and percentage barren cover. Data were analysed using Permutational Anova. There was no significant difference between means with identical letters (pairwise analysis). ns: not significant. * = $p < 0.05$; ** = $p < 0.01$.

Figure 7. Five years monthly temporal variation in (A) mean adult urchin (*Diadema* aff. *antillarum*) abundance (\pm SE); and (B) mean barren cover (\pm SE), in three sites of Tenerife Island (Masca, Abades and Boca Cangrejo).

Figure 8. Effects of a massive recruitment event on (A) mean (\pm SE) *Diadema* aff. *antillarum* abundance; (B) barren cover, in three areas of the Canary Islands from west to east (Mar de las Calmas-MPA; Tenerife-HFA (Highly Fished Areas); La Graciosa-MPA). Data were analysed using Permutational Anova.

Figure 9. *Diadema* aff. *antillarum* general log-linear increment of populations density after a high recruitment event, as a function of initial density registered at HFA and MPA sites throughout the Canarian Archipelago. H: Mar Calmas MPA, RE: Roque del Este site located on La Graciosa-MPA.

Figure 1

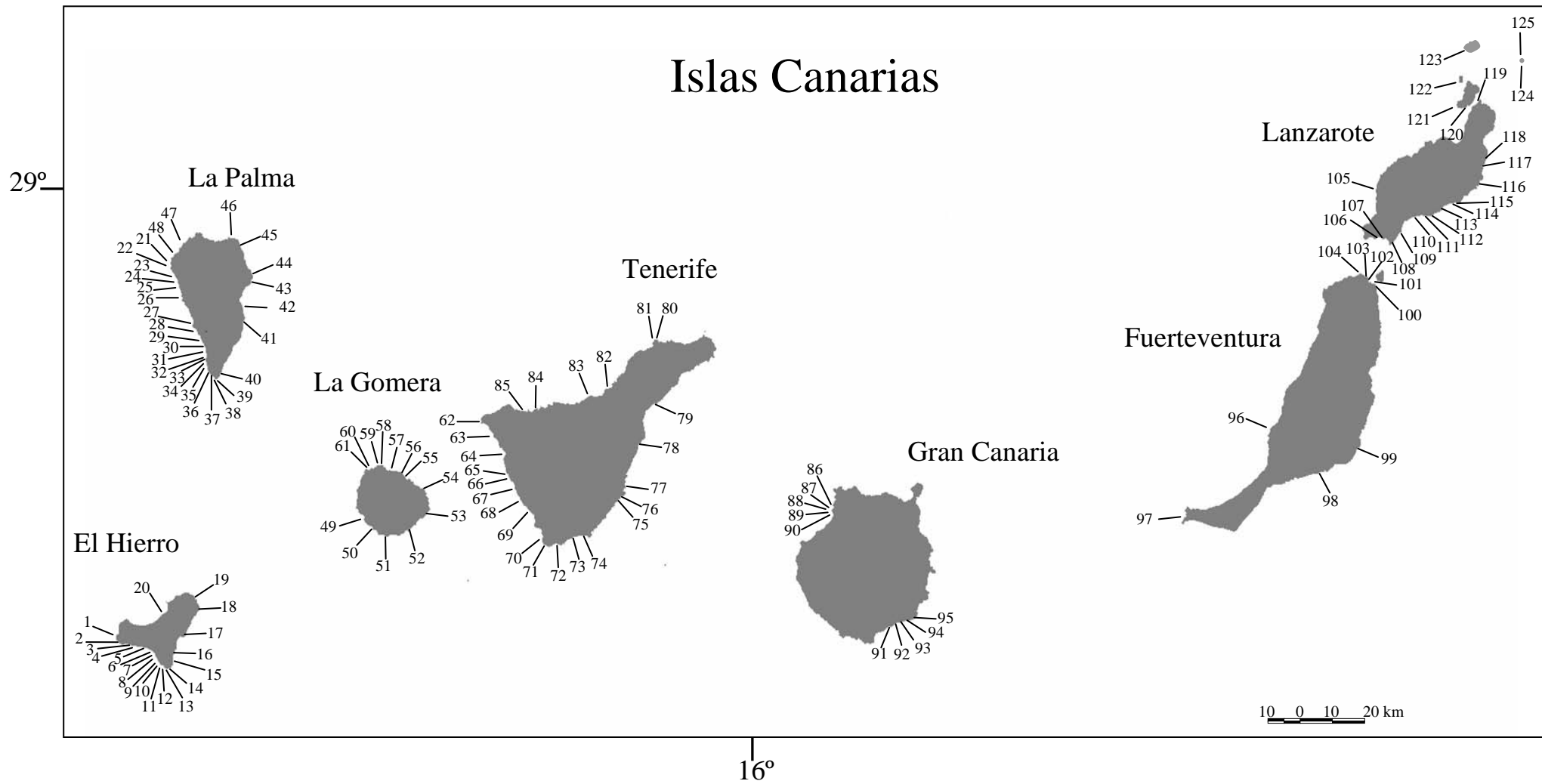
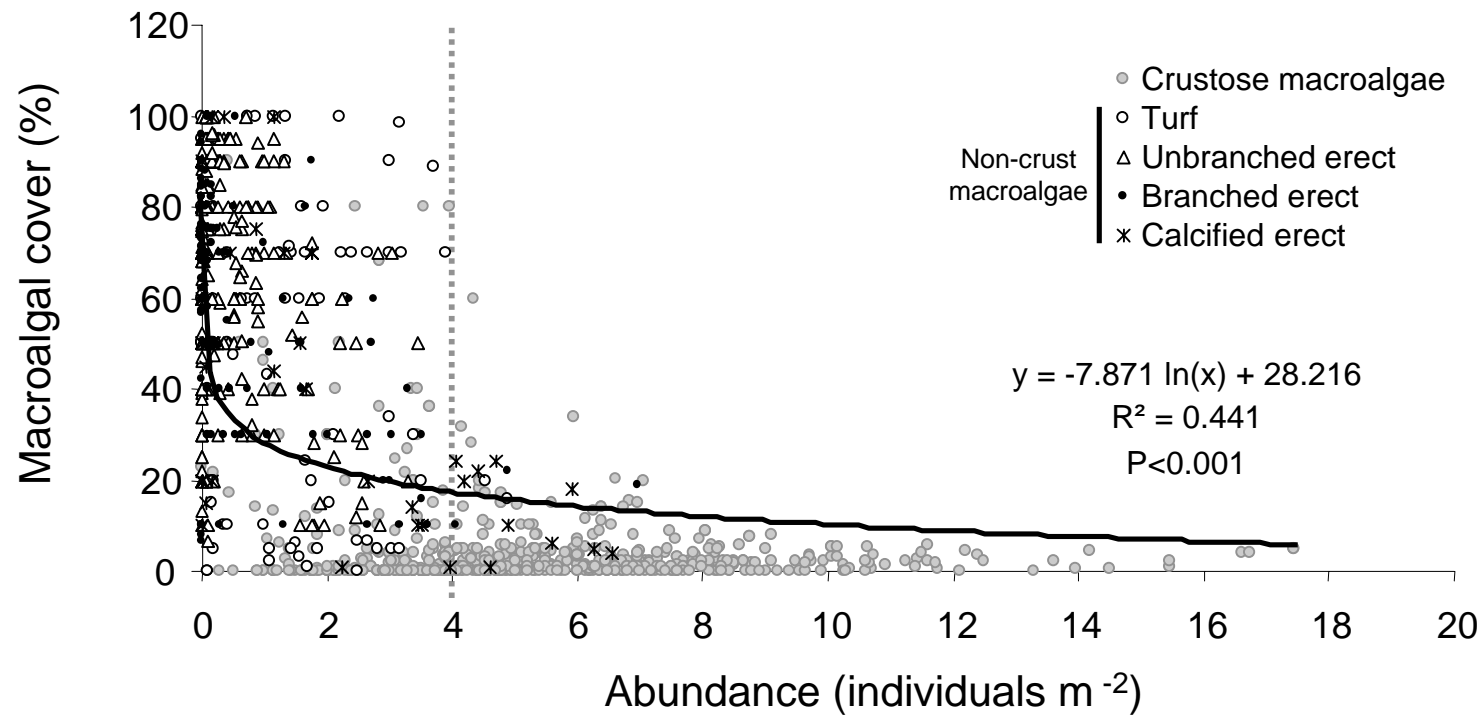


Figure 2



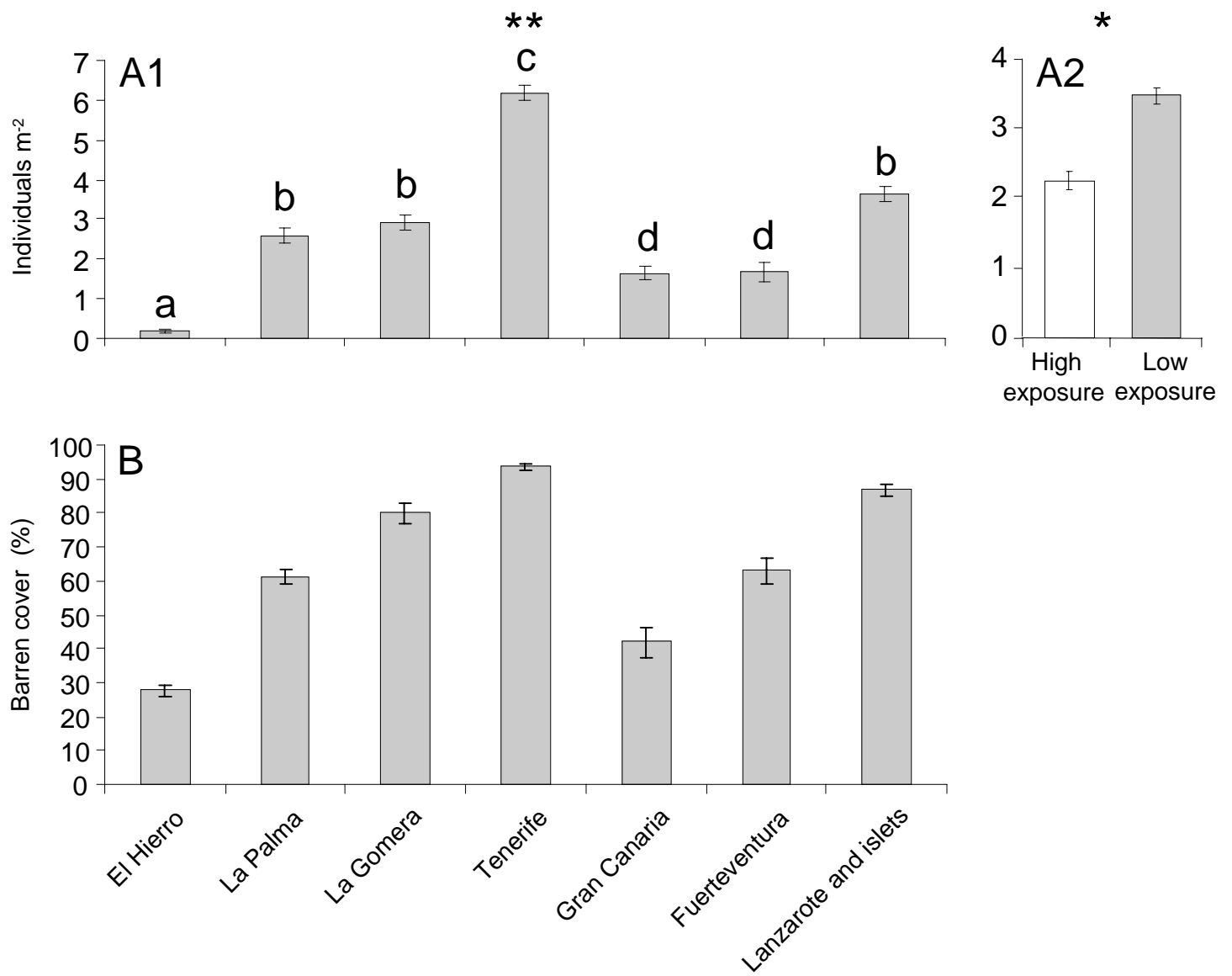


Figure 3

Figure 4

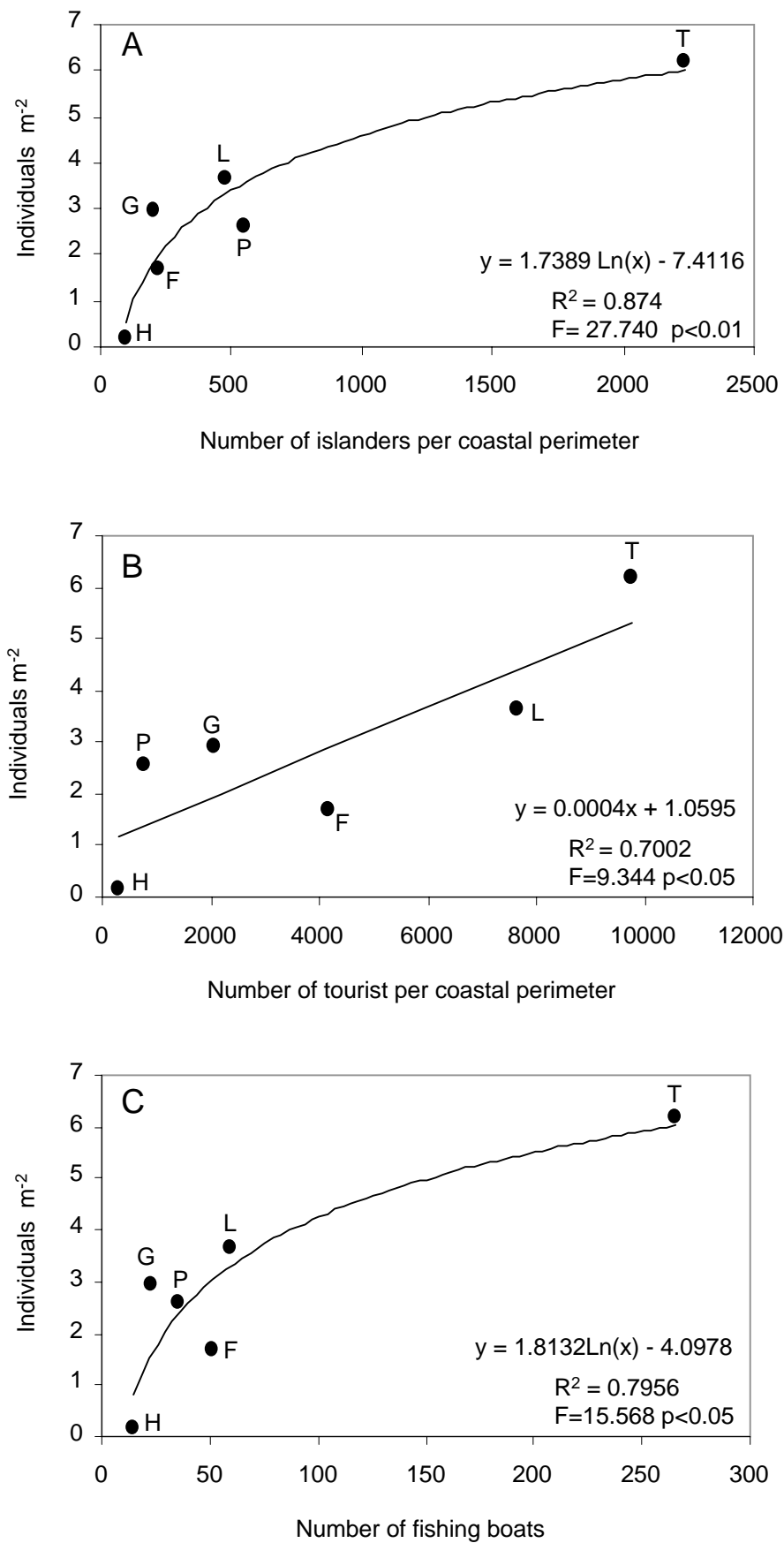


Figure 5

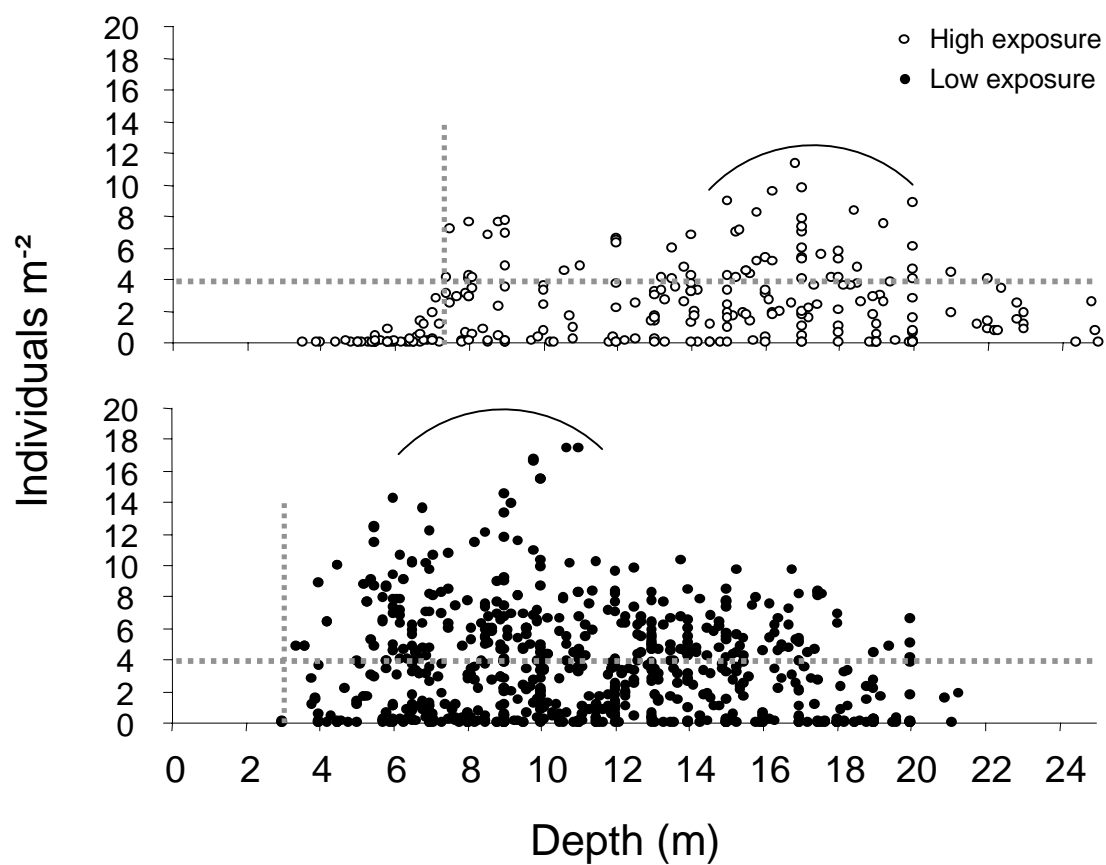
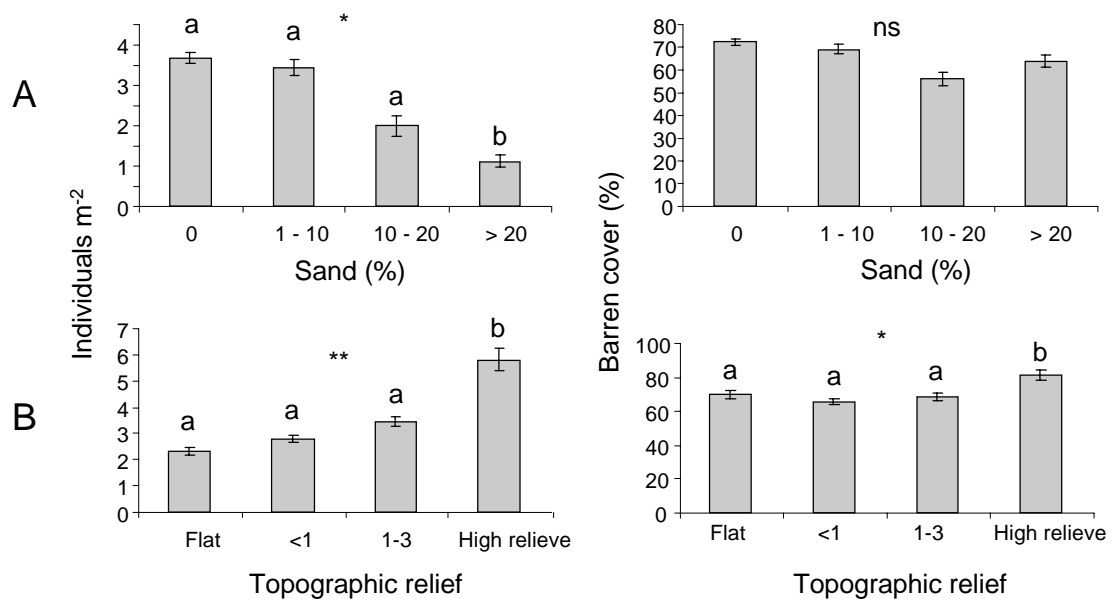


Figure 6



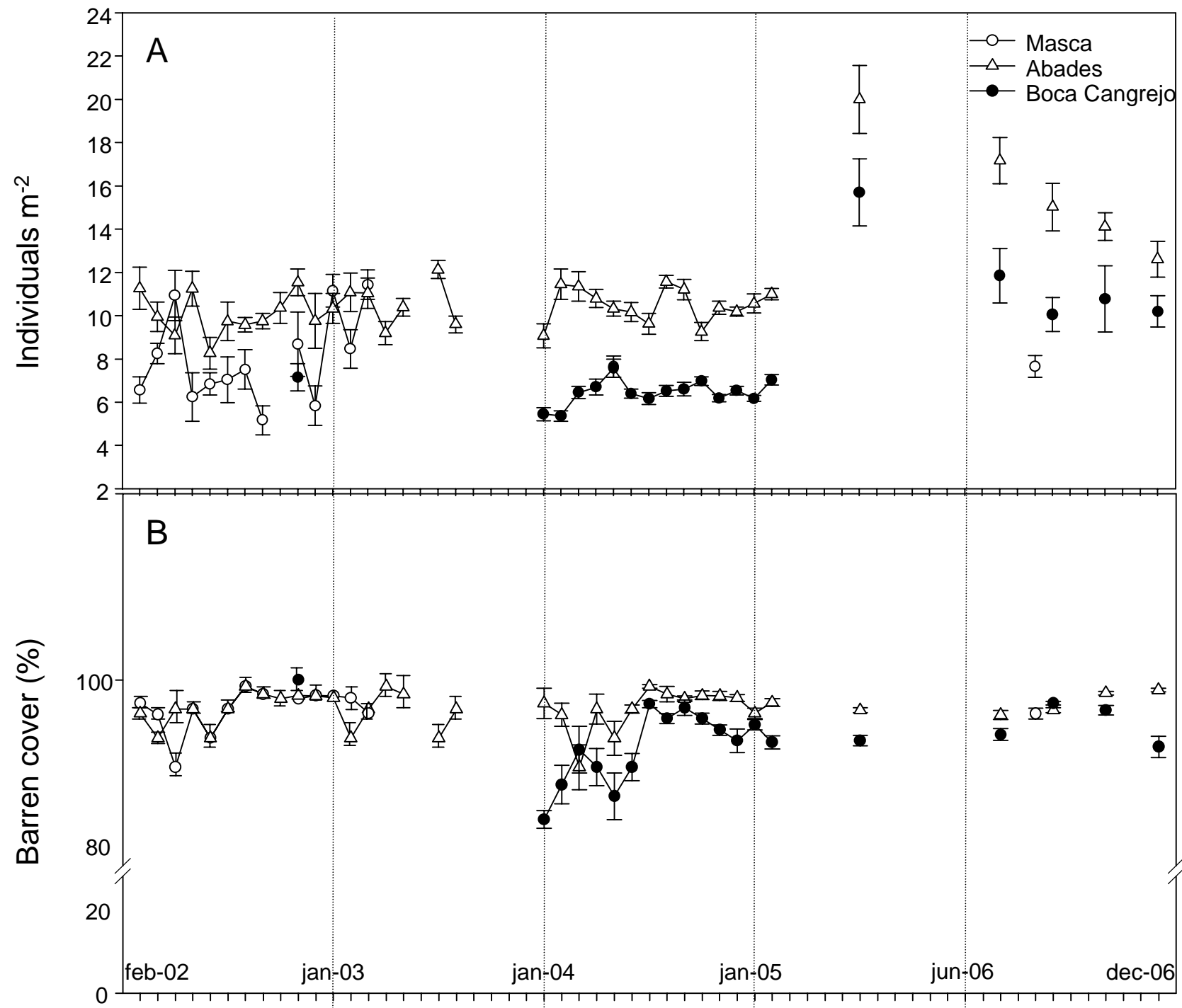


Figure 7

Figure 8

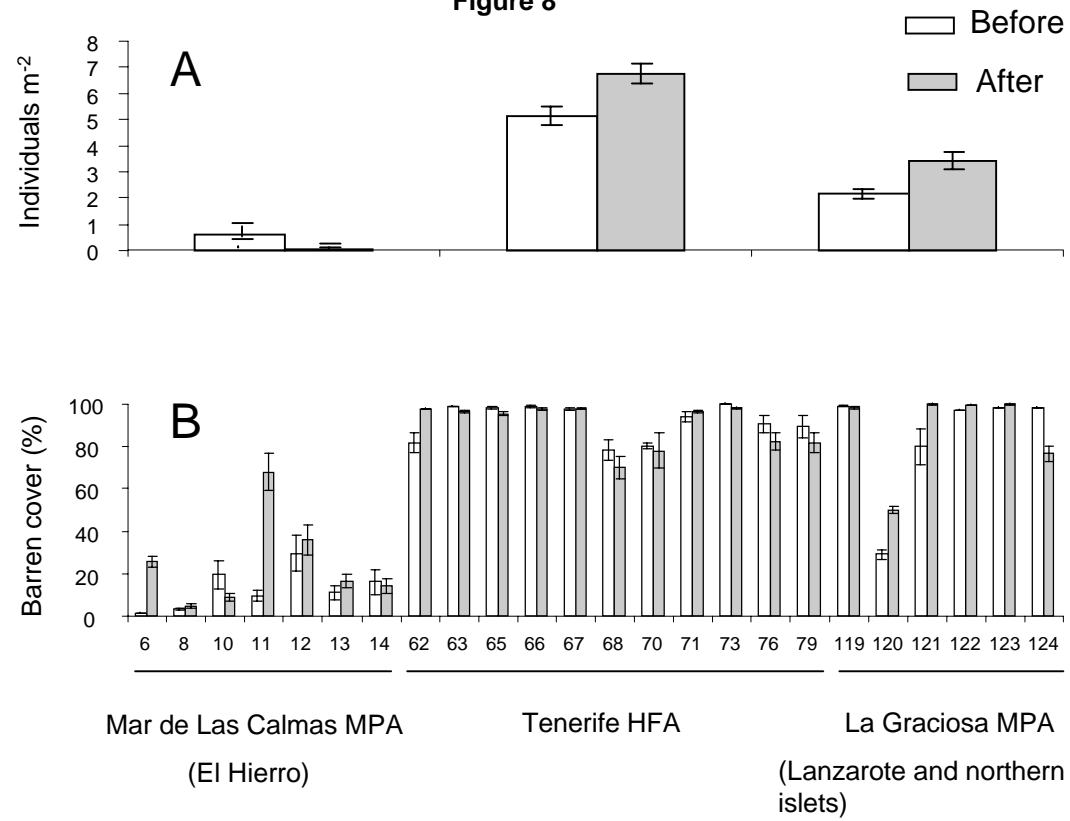


Figure 9

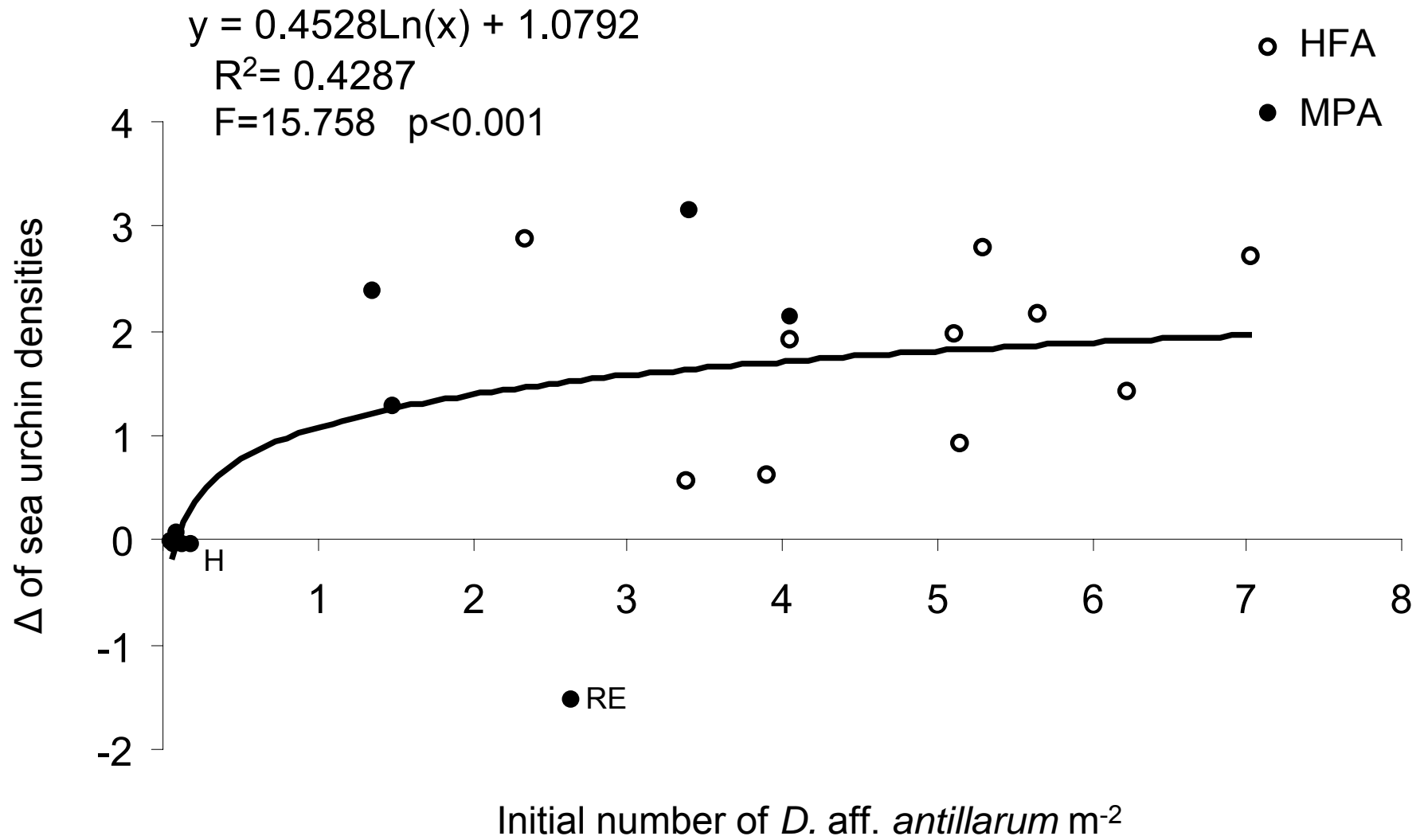


Table 1

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

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. Barren				
I	6	66881	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			

Table 3

A. Density	df	MS	F	P (perm)
Island (I)	6	246.06	19.82	0.001
Sand (Sa)	3	36.25	2.89	0.029
I x Sa	18	11.209	0.85	0.631
Site (I x Sa)	237	19.941	12.96	0.001
Residual	847	1.5387		
Total	1111			
B. Barren				
I	6	52668	41.69	0.001
Sa	3	1783.8	1.40	0.235
I x Sa	18	1993.5	1.49	0.07
Site (I x Sa)	237	2002.6	10.24	0.001
Residual	847	195.5		
Total	1111			

Table 4

A. Density	df	MS	F	P (perm)
Island (I)	6	389.35	35.92	0.001
Topographic relief (TR)	3	110.70	10.30	0.001
I x TR	18	14.45	1.24	0.214
Site (I x TR)	251	16.16	10.77	0.001
Residual	833	1.50		
Total	1111			
B. Barren				
I	6	47084	33.93	0.001
TR	3	4182.5	3.04	0.03
I x TR	18	1183.1	0.79	0.707
Site (I x TR)	251	2065.3	10.46	0.001
Residual	833	197.39		
Total	1111			

Table 5

A. Density	df	MS	F	P (perm)
Year (Y)	3	414.14	48.97	0.005
Site (S)	1	710.18	96.26	0.001
Y x S	3	8.45	1.15	0.321
Residual	434	7.38		
Total	441			
B. Barren				
Year (Y)	3	166.55	1.46	0.370
Site (S)	1	189.67	13.48	0.003
Y x S	3	113.84	8.09	0.001
Residual	434	14.071		
Total	441			

Table 6

A. Density	df	MS	F	P (perm)
Outbreak (O)	1	90.06	3.62	0.160
Area (A)	2	1330	33.79	0.001
Site (A)	21	40.58	8.27	0.001
O x A	2	25.31	3.95	0.033
O x Site (A)	21	6.47	1.32	0.139
Residual	451	4.90		
Total	498			
B. Barren				
Outbreak (O)	1	1827.10	0.87	0.441
Area (A)	2	2.4613E5	61.49	0.001
Site (A)	21	4138.60	24.96	0.001
O x A	2	2121	1.78	0.218
O x Site (A)	21	1227.20	7.40	0.001
Residual	451	165.81		
Total	498			

Tables supplementary material

Table 1. List of the surveyed sites in the Canary Islands. [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 those exposed only to NNE waves]. At least 200 m² of area sampled at each site. All sites were used in the analysis of small and large scale spatial variation. [* Sites used for long-term monitoring; † Sites used for recent outbreak analysis; N: total of transect at each sampling time].

Island	MPA	Site #	Site name	Wave exposure	Density (individuals m ⁻²)	N	Range (individuals m ⁻²)
EL HIERRO	Mar de Las Calmas-MPA	1	Baja de Anacon	1	0.13	10	0.00-0.60
		2	Laja de Orchilla	2	0.16	10	0.00-0.50
		3	Punta La Palometa	2	0.01	10	0.00-0.05
		4	Punta de Los Mozos	2	0.07	10	0.00-0.25
		5	Punta Lajas del Lance	2	0.22	10	0.05-0.40
		6	Punta de Tecoron †	2	0.36	10	0.05-0.95
		7	Cueva del Diablo	2	0.20	10	0.05-0.45
		8	Punta de Las Lapillas †	2	0.08	10	0.00-0.35
		9	Punta de Las Cañas	2	0.21	10	0.10-0.40
		10	Roque Chico †	2	0.03	10	0.00-0.10
		11	La Gabarra †	2	0.08	10	0.00-0.25
		12	Punta de Los Frailes †	2	0.05	10	0.00-0.30
		13	Cueva de Los Frailes †	2	0.03	10	0.00-0.15
		14	La Herradura †	2	0.09	10	0.00-0.25
	15	Muelle de La Restinga	2	0.04	10	0.00-0.15	
	16	Los Joraditos	1	0.10	10	0.00-0.30	
	17	Roque de La Bonanza	1	0.07	10	0.00-0.25	
	18	La Caleta	1	0.62	8	0.00-1.10	
	19	Tamaduste	1	0.04	8	0.00-0.15	
	20	Punta Grande	1	0.80	10	0.05-2.45	
Total surface sampled:						3920 m ²	
LA PALMA	La Palma-MPA	21	Punta Llanadas	1	0.12	8	0.05-0.20
		22	Punta Gorda	1	2.97	8	0.75-4.10
		23	Playa de Las Vinagreras	1	1.77	8	1.15-2.50
		24	Callao Nuevo	1	1.78	8	0.50-3.40
		25	El Roque	1	2.37	8	1.30-4.05
		26	Morro Negro	2	2.55	8	1.05-3.50
		27	La Bombilla	2	3.05	8	1.40-4.25
		28	Punta Bogullos	2	2.96	8	0.40-5.60
		29	El Faro	2	2.92	8	0.50-6.60
		30	Playa de El Remo	2	1.11	8	0.20-1.80
		31	Punta de El Remo	2	1.88	8	1.15-2.80
		32	Punta Banco	2	2.09	8	0.80-3.45
		33	Dos Hermanas	2	0.93	8	0.50-1.55
		34	Los Andenes	2	0.56	8	0.30-0.85
		35	Siete Islas	2	0.15	8	0.00-0.75

	36	La Resbaladera	2	0.77	8	0.15-1.90
	37	Punta Larga	2	0.07	8	0.00-0.25
	38	Fuencaliente (Malpique)	2	6.40	8	6.40-10.05
	39	El Faro de Fuencaliente	2	0.30	8	0.30-4.20
	40	Las Cabras	2	0.25	8	0.00-0.65
	41	La Bajita	2	8.20	8	6.15-10.65
	42	Los Cancajos	2	7.92	8	3.85-11.75
	43	Puerto Trigo	2	4.89	8	1.60-6.85
	44	Puerto Paja	1	4.35	8	0.04-11.60
	45	Puerto Espindola	1	3.32	8	2.00-4.45
	46	La Fajana	1	0.07	8	0.00-0.20
	47	Roque Santo Domingo	1	0.11	8	0.00-0.40
	48	Lomada Grande	1	1.16	8	0.00-3.85
	Total surface sampled:			4480 m²		
LA GOMERA	49	Roque de Iguala	2	2.04	8	0.55-3.50
	50	Punta Narices	2	2.90	8	0.45-5.50
	51	Punta Becerro	2	2.94	8	0.20-5.35
	52	Playa de Suarez	2	3.18	8	0.05-7.10
	53	Punta. Los Canarios	1	5.71	8	1.75-10.60
	54	Punta Majona	1	4.03	8	1.40-7.20
	55	Roque de Agulo	1	3.33	8	3.00-3.95
	56	Playa de San Marcos	1	2.57	8	1.75-3.70
	57	Punta Sardina/La Sepultura	1	3.47	8	2.75-4.55
	58	Punta de Los Organos	1	2.01	8	1.50-2.80
	59	Los Organos	1	1.43	8	0.90-2.05
	60	Roques de Arguamul	1	2.17	8	1.75-2.60
	61	Playa de Santa Catalina	1	0.01	8	0.00-0.05
	Total surface sampled:			2080 m²		
TENERIFE	62	Teno †	2	6.34	10	2.65-9.90
	63	Masca * †	2	7.64	8	5.95-10.15
	64	Los Gigantes	2	6.03	10	3.40-9.55
	65	El Acuario †	2	5.12	10	3.05-10.25
	66	Cueva de Los Cerebros †	2	5.65	14	1.35-10.35
	67	La Tixera †	2	5.84	10	4.55-8.35
	68	La Caleta †	2	6.46	8	3.75-11.50
	69	El Balito	2	7.51	8	5.05-9.65
	70	El Palm-Mar	2	5.62	14	3.50-8.15
	71	Punta Rasca †	2	3.95	8	2.65-5.50
	72	Las Galletas	2	5.17	8	3.35-6.55
	73	Agua Dulce †	2	5.96	8	4.70-7.10
	74	La Tejita	2	4.84	8	2.25-7.35
	75	La Jaquita	2	13.57	13	6.35-17.45
	76	Abades * †	2	9.07	16	4.60-12.20
	77	El Poris de Abona	2	4.58	16	2.70-7.80
	78	Punta Prieta	2	8.75	8	7.85-10.60
	79	Boca Cangrejo * †	2	6.06	16	3.24-8.20
	80	Punta Hidalgo 1	1	0.00	12	0.00-0.00
	81	Punta Hidalgo 2	1	4.21	8	2.00-5.60

	82	Martianez	1	8.48	8	6.10-11.25
	83	La Rapadura	1	4.41	8	3.25-5.25
	84	La Consolación	1	3.77	8	1.70-5.50
	85	La Hondura	1	5.17	8	2.55-7.05
	Total surface sampled:				4900 m²	
GRAN CANARIA	86	Punta El Cardonal	1	3.37	8	2.60-4.10
	87	El Juncal	1	1.76	8	1.15-2.50
	88	Punta del Tumas	1	0.97	8	0.75-1.35
	89	Playa de Las Nieves	1	0.36	8	0.00-0.85
	90	Muñón de Dios	1	1.06	8	0.15-2.30
	91	Punta del Tarajalillo	2	0.30	8	0.10-0.40
	92	Playa Corral del Espino	2	2.45	8	0.50-3.95
	93	Puntilla de La Caleta	2	2.33	8	1.60-3.00
	94	Playa de La Caleta	2	2.27	8	0.45-4.35
	95	Las Casillas	2	0.73	8	0.10-1.15
	Total surface sampled:				1600 m²	
FUERTEVENTURA	96	Ajui	1	0.06	8	0.00-0.15
	97	Punta de Jandia	1	0.00	8	0.00-0.00
	98	Jinijinar	2	1.05	8	0.00-2.30
	99	Jacomar	2	4.39	8	3.10-6.40
	100	El Queso	2	0.02	8	0.00-0.15
	101	El Marrajito	2	0.06	8	0.00-0.25
	102	Baja de Fefo	2	5.79	8	3.20-9.65
	103	El Calamareo	2	3.01	8	1.45-6.25
	104	Veril del Marrajo	2	1.41	8	0.00-4.90
	Total surface sampled:				1440 m²	
LANZAROTE and ISLETS	105	El Golfo	1	0.04	10	0.00-0.15
	106	Punta Limones	2	4.31	8	2.80-6.00
	107	Playa Flamingo	2	3.77	8	3.00-6.00
	108	El Pasito	2	2.00	8	0.90-4.70
	109	Puntagorda	2	3.54	9	2.60-4.60
	110	Puerto Calero	2	2.97	8	1.10-5.25
	111	Puerto del Carmen (Sur)	2	6.98	9	2.00-13.30
	112	Puerto del Carmen	2	5.78	8	3.65-8.60
	113	Playa de Los Pocillos	2	3.86	8	3.30-4.25
	114	Hoyas Hondas	2	1.07	8	0.50-1.80
	115	Playa Matagorda	2	3.63	8	2.95-4.55
	116	Playa Honda	1	3.18	8	2.50-4.00
	117	Los Cocoteros	1	7.05	9	4.70-8.90
	118	Mala	1	5.70	10	4.00-7.70
	119	Punta Fariones †	1	2.76	10	0.00-4.80
	120	Caleta del Sebo †	2	0.16	10	0.00-1.00
	121	Montaña Amarilla †	2	3.72	12	2.10-5.60
	122	Cuevas Coloradas †	2	6.19	10	3.90-10.30
	123	Punta La Mareta †	2	6.55	10	3.80-9.20
	124	Roque del Este (Sur) †	2	1.12	10	0.00-4.40
	125	Roque del Este (Norte)	1	0.03	10	0.00-0.15
	Total surface sampled:				3820 m²	

Table 2. Results of three ways Permutational ANOVA designs comparing (A) density (individuals m⁻²) of *Diadema* aff. *antillarum* and (B) barren 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 1 supplementary material).

A. Density	df	MS	F	P (perm)
Island (I)	6	218.8	15.69	0.001
Slope (Sl)	3	2.896	0.20	0.891
I x Sl	18	6.089	0.39	0.989
Site (I x Sl)	222	21.486	12.51	0.001
Residual	862	1.717		
Total	1111			
B. Barren				
I	6	37744	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	13.19	0.001
Residual	862	180.13		
Total	1111			

Table 3. Results of three ways Permutational ANOVA designs comparing (A) density (individuals m⁻²) of *Diadema* aff. *antillarum* and (B) barren 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 1 supplementary material).

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. Barren				
I	6	25036	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			