

## Spatial variation patterns of subtidal seaweed assemblages along a subtropical oceanic archipelago: Thermal gradient vs herbivore pressure

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### ABSTRACT

The structure and composition of subtidal rocky seaweed assemblages were studied at 69 sites on the Canary Islands (northeastern Atlantic). This group of islands are situated at the southern boundary of the warm temperate region and adjacent to the cold waters from the northwest African coastal upwelling, which creates a difference of almost 2 °C in surface seawater temperature from the eastern to the western islands. This thermal variation allows an examination of the transition between the warm temperate and the tropical regions along this longitudinal gradient together with the hypothesised Fucales-dominated assemblages towards the eastern islands in contrast to the Dictyotales-dominated assemblages towards the western ones. Environmental and biological parameters were considered in order to investigate which were the main factors explaining spatial variation along the gradient in a multi-scaled approach. Although seventy-nine macroalgae were identified, 87.63% of the total mean cover was due to six taxa (*Lobophora variegata*, nongeniculate corallines, *Canistrocarpus cervicornis*, *Jania adhaerens*, *Cystoseira abies-marina* and *Pseudolithoderma adriaticum*). At a large scale, sea urchin density explained the highest variation in seaweed assemblages (26.94%), and its pattern of distribution across the islands. The expected pattern of distribution according to the upwelling distance only occurred in restricted areas of the Canarian Archipelago in absence of herbivore pressure and habitat degradation. Spatial variations within islands (medium scale) were mainly related to wave exposure, while at a small scale these were mostly due to the degree of sedimentation.

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### 1. Introduction

Island biota are often considered unique because they are exposed to unpredictable patterns of colonization/extinction that depend on distance from other sources of colonists and on the size of the island, and because the islands also provide different habitats of those of the mainland, regardless of any possible effect of size and isolation (MacArthur and Wilson, 1967; Benedetti-Cecchi et al., 2003). The composition of the colonizing marine biota on islands is directly influenced by the patterns of ocean circulation, as currents and other oceanographic phenomena such as upwellings (Lüning, 1990; Whittaker and Fernández-Palacios, 2007), and dispersal abilities of each species ultimately conditioning the pool of organisms that reach any oceanic island (Hoek, 1984). Consequently, benthic assemblages

on islands may be exclusive and its structure not necessarily reproduces that of the neighbouring continent because they can exhibit alternative environmental conditions, as surface seawater temperature, wave exposure, depth, sedimentation and substratum (Schils and Coppejans, 2003; Goldberg and Kendrick, 2004).

The structure and composition of subtidal seaweed assemblages fluctuate at several spatial and temporal scales (Schneider, 1994). The role played by different processes operating at different scales on macroalgal assemblages is a growing field of interest and remains largely untested in the majority of shore areas (Fraschetti et al., 2005; Tuya and Haroun, 2006; Sales and Ballesteros, 2009). Thus, sampling programmes have been designed to provide a means of partitioning and quantifying the magnitude of variation at different spatial scales (Anderson and Millar, 2004; Dethier and Schoch, 2005; Fraschetti et al., 2005; Connell, 2007; Olabarría et al., 2009; Smale et al., 2011). 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 (Levitán and Genovese, 1989; Andrew, 1993; Benedetti-Cecchi, 2001).

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Island chains have provided valuable systems to test hypotheses about the effect of environmental heterogeneity on the spatial patterns of subtidal assemblages (Goldberg and Kendrick, 2004; Sales and Ballesteros, 2009). Island groups placed hundreds of kilometres apart can show differences in subtidal seaweed assemblages, as a consequence of changes in oceanographic conditions related to a latitudinal gradient (Vroom and Page, 2006; Tribollet and Vroom, 2007; Smale et al., 2010), or to a longitudinal gradient in island groups situated perpendicularly to a local upwelling or oceanic current (Schils and Coppejans, 2003). The shape and size of an island and its orientation against the waves create different degrees of wave exposure between sites situated tens of kilometres apart, while other parameters as depth, sedimentation and substrata change within a site at a smaller spatial scale (Cheroske et al., 2000; Díez et al., 2003; Goldberg and Kendrick, 2004; Spatharis et al., 2011). Finally, the density of herbivores, which is also regulated by a set of variables at different spatial scales, affects the structure and composition of seaweed assemblages (Schiel et al., 1995; Cheroske et al., 2000).

Local upwellings give rise to longitudinal temperature gradients, which at a regional scale can affect to seaweed assemblages. The Canarian Archipelago is situated at the southern boundary of the Northeastern Atlantic Warm Temperate Region (NAWTR), the biogeographic region with the highest seaweed richness on this side of the Atlantic Ocean (Hoek, 1984; Lüning, 1990). The Canarian marine flora consists of an ensemble of species with different biogeographical affinities, i.e. endemisms from NAWTR (31%), tropical and subtropical (30%), cosmopolitan (19%) and cold temperate (16%) (Sansón et al., 2001). Its geographical location in the North Atlantic current system has facilitated the seaweed colonization and the Canary Islands have been considered as a crossroads for marine propagule dispersion (Pakker et al., 1996).

This simultaneous occurrence of characteristic macroalgae from both warm temperate and tropical regions has also been reported for Canarian marine fauna assemblages (Brito and Ocaña, 2004; Hernández et al., 2008). The geographical location of the Canarian Archipelago between cold waters from the northwest African coastal upwelling and the warmer open ocean waters creates a difference of almost 2 °C in surface seawater temperature from the eastern to the western islands (Braun and Molina, 1984; Barton et al., 1998). This seawater thermal variation allows the examination of the transition between the warm temperate and the tropical region along the longitudinal gradient which crosses this group of islands. Consequently, it may be predicted that structure of subtidal seaweed assemblages on rocky substrata would vary from east to west in the archipelago following the temperature gradient. Based on macroalgal morpho-functional groups, Tuya and Haroun (2006) analyzed the role played by wave exposure in shallow waters on the Canarian seaweed assemblages, and subsequently Hernández et al. (2008) examined the role of sea urchin densities. However, there are no studies which try to disentangle the main environmental factors affecting the structure and composition of assemblages considering all macroalgal species. The aim of this paper is to test which of the selected factors (upwelling influence, wave exposure, depth, sedimentation, substratum and sea urchins) are driving the present distribution of shallow subtidal rocky seaweed assemblages between 5 and 20 m depth along the Canary Islands.

## 2. Materials and methods

### 2.1. Study area

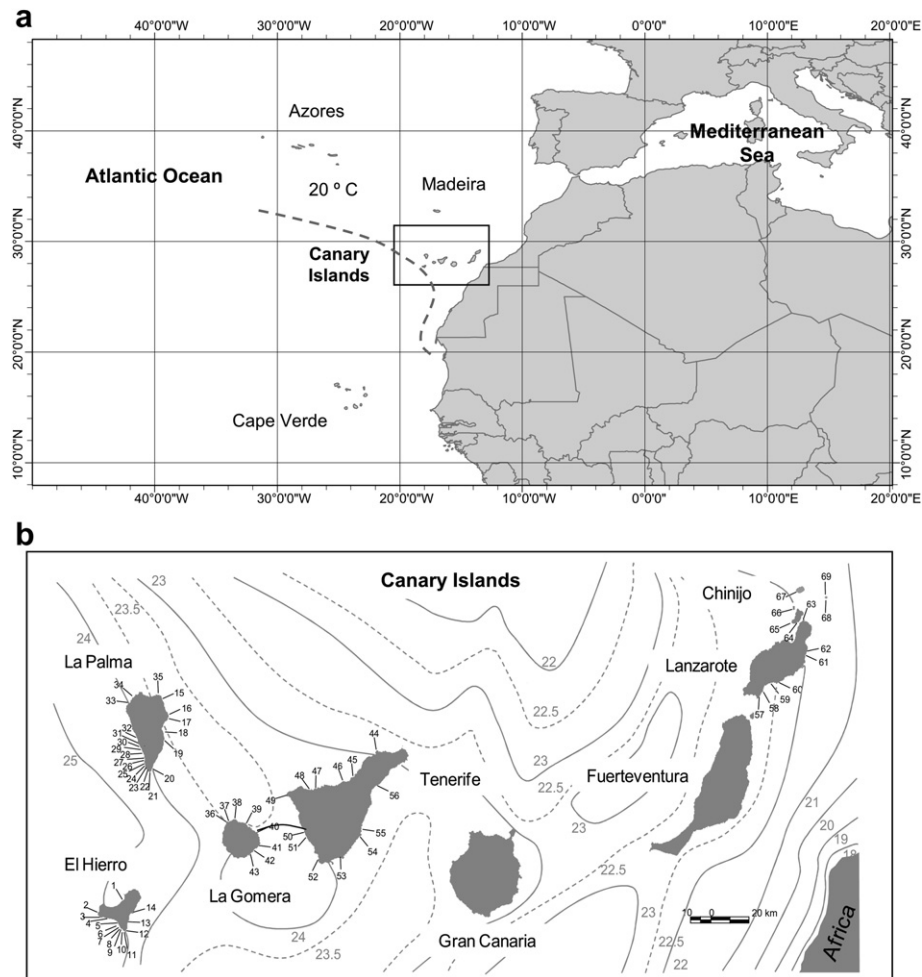
The Canarian Archipelago is constituted by seven major islands and a group of islets in the northeast known as Chinijo Archipelago. It is situated between latitude 27.68–29.58N and longitude

18.28–14.58W on the eastern border of the North Atlantic Ocean's subtropical gyre (Fig. 1). The islands emerged from the oceanic basin as a result of successive volcanic activity. They are 90 km from the shore of the African mainland extending about 400 km further west. This particular geographical situation creates an oceanographic gradient across the archipelago, where surface seawater temperature varies between 17 and 19 °C in March–April and 23–25 °C in September–October (Barton et al., 1998), with differences of about 2 °C between its eastern and western boundaries (Fig. 1).

Exposure to waves varies within the islands according to shoreline orientation. The normal wave pattern consists of sea waves from NNE, which have an annual mean 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. There are differences in mean annual height and frequency of waves between the northern, western and eastern-southeastern shores. Eastern, southeastern and southern shores 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 shorelines, which are exposed to non-local swells (Braun and Molina, 1984; Yanes et al., 2006). Shallow bottoms are characterized by a seascape of rocky platforms, large stones, pebbles and sandy patches (Yanes, 1990).

### 2.2. Collection of data

Fieldwork was conducted by SCUBA diving at 69 sites along six islands (the small Chinijo Archipelago was considered a unique island) (Fig. 1), from May 2004 to May 2007, in rocky reefs between 5 and 20 m depth. Each site was sampled once. Macroalgal assemblages are dominated throughout the year by perennial species (Wildpret et al., 1987) and preliminary data on temporal turnover did not show significant variation. Six random photographs (5 m apart replicates) were obtained at each of the three depth levels: 5–10 m, 10–15 m and 15–20 m. The occurrence of sandy bottoms prevented us from studying the deepest level in some sites, resulting in a total of 1038 samples. Percentages of cover were estimated from the photographic analysis of each quadrat (25 × 25 cm) following Littler and Littler (1985) and Murray (2001). Richness (as number of species) and the Shannon–Wiener index for diversity were calculated per sample (Shanon and Weaver, 1949). At each site and level main macroalgal species were identified and annotated *in situ*, and if necessary collected to be identified later in the laboratory. Species were usually identified *in situ* and only filamentous blue-green algae ('cyanophytes'), non-geniculate corallines and small filamentous ceramiales were not identified to species level. Six environmental parameters (upwelling distance, wave exposure, sedimentation, depth, substratum and sea urchin density) were obtained from each sample. Upwelling distance refers to the relative position of each site from an imaginary line parallel to the west African coast where upwelling is situated and was calculated using a Geographic Information System (GIS). Wave exposure data were obtained from oceanic buoys ([www.puertos.es](http://www.puertos.es)) and simplified for each site as 'exposed' (annual mean wave height > 1.4 m) or 'semiexposed' (annual mean wave height < 1.4 m). Sedimentation was estimated as the percentage of rock covered by sand (Díez et al., 2003; Erikson and Bergström, 2005). Substratum was categorized in three types: (1) rocky platform; (2) boulders and rocks > 0.5 m diameter; and (3) small rocks < 0.5 m diameter. At each site, individuals of *Diadema* aff. *antillarum* were counted using the belt transect method described in Hernández et al. (2008) providing estimates of sea urchin density. Transects of 10 × 2 m parallel to the shoreline were used with at least nine replicates per site, three at each depth level.



**Fig. 1.** Map of the study region in the Warm Temperate Northeastern Atlantic: (a) Location of the Canary Islands next to the southern border of the 20 °C winter-isotherm, usually accepted as the boundary between warm temperate and tropical regions. (b) Sampling sites in the Canary Islands: El Hierro (1–14), La Palma (15–35), La Gomera (35–43), Tenerife (44–56), Lanzarote (57–63) and Chinijo (64–69), indicating surface seawater temperature in the summer 2007 (adapted from [www.aemet.es](http://www.aemet.es)).

### 2.3. Data analysis

A draftsman plot (Clarke and Gorley, 2006) was performed with the environmental and biological variables matrix in order to detect possible skewness of the variables and/or strong correlation among pairs of variables. Depth, sedimentation and sea urchin density were square-root transformed, while upwelling distance was fourth-root transformed. Substrata data were not transformed. The statistical significance of Pearson correlations between variables did not exceed  $p = 0.5$ , and consequently all variables were retained in the environmental matrix.

The Distance-based Linear Model routine (DistLM) (Legendre and Anderson, 1999) was applied in order to analyse and model the relationship between seaweed data and environmental factors, and it is based on similarity matrices using the Bray–Curtis index for the biological data and Euclidean distance for the environmental variables. The selection criterion and selection procedure used were step-wise and adjusted  $R^2$ , using 9999 permutations. Seaweed cover values were square-root transformed and the environmental matrix (with previous transformations) was used as the predictor variable worksheet. A Distance-based redundancy analysis (dbRDA, McArdle and Anderson, 2001) plot was made to allow the visualization of the samples ordination according to the multivariate regression model previously generated by applying DistLM.

In order to study the structure of seaweed assemblages a permutational multivariate analysis of variance (PERMANOVA) was performed (Anderson et al., 2008). The analysis was based in Bray–Curtis resemblance measure after square-root transformed matrix using 4999 permutations. Additionally, richness, diversity and species cover (for species with more than 1% mean cover) were studied using permutational ANOVAs, based on Euclidean distances of the square-root transformed data using 4999 permutations of the appropriate exchangeable units (Anderson, 2001; Anderson and ter Braak, 2003). Significant terms in the full model were examined individually using appropriate a posteriori pairwise comparisons (Anderson, 2004). When the number of possible permutations was not large, Monte Carlo  $p$ -values ( $n = 4999$ ) were instead obtained by random sampling from the asymptotic permutations distribution (Anderson and Robinson, 2003).

#### 2.3.1. Spatial variation between islands

To assess spatial variation over a scale of hundreds of kilometres in the composition and structure of seaweed assemblages, richness, diversity and cover of dominant species (>1% mean cover) along the set of islands a two-way model were performed, in which 'island' was treated as a fixed factor (6 levels: El Hierro, La Palma, La Gomera, Tenerife, Lanzarote, Chinijo), and 'site' (69 levels: see Fig. 1) as a random factor nested in 'island'.

**Table 1**

Macroalgae found in the sublittoral seaweed assemblages studied in the 69 sites along a set of islands in the Canarian Archipelago, from the westernmost island (El Hierro) to the easternmost (Chinijo). Relative macroalgae cover, richness and diversity (mean  $\pm$  S.E.) for each island and the whole Canarian Archipelago ( $n = 1038$ ).

Macroalgae	El Hierro	La Palma	La Gomera	Tenerife	Lanzarote	Chinijo	Canary Islands
<i>Cyanophyta</i>							
<i>cyanophytes</i>	1.49 $\pm$ 0.17	0.05 $\pm$ 0.01	0.10 $\pm$ 0.02	...	0.12 $\pm$ 0.05	0.32 $\pm$ 0.13	0.43 $\pm$ 0.04
<i>Rhodophyta</i>							
<i>Acrosymphyton purpuriferum</i> (J. Agardh) Sjöstedt	0.003 $\pm$ 0.003	...	1.06 $\pm$ 0.45	...	...	...	0.13 $\pm$ 0.05
<i>Acrosorium venulosum</i> (Zanardini) Kylin	...	...	0.0007 $\pm$ 0.0007	...	...	...	0.00009 $\pm$ 0.00009
<i>Amphiroa</i> spp.	0.30 $\pm$ 0.05	0.10 $\pm$ 0.02	0.37 $\pm$ 0.07	...	0.08 $\pm$ 0.02	...	0.16 $\pm$ 0.01
<i>Asparagopsis taxiformis</i> (Delile) Trevisan	0.26 $\pm$ 0.10	0.37 $\pm$ 0.11	0.86 $\pm$ 0.21	0.19 $\pm$ 0.19	0.007 $\pm$ 0.005	...	0.32 $\pm$ 0.05
<i>Asparagopsis taxiformis</i> (sporophyte)	...	0.006 $\pm$ 0.005	...	0.01 $\pm$ 0.01	0.01 $\pm$ 0.001	0.02 $\pm$ 0.006	0.005 $\pm$ 0.002
<i>Ceramium echionotum</i> J. Agardh	...	...	...	...	...	0.008 $\pm$ 0.006	0.0007 $\pm$ 0.0005
<i>Corallina elongata</i> Ellis et Solander	0.01 $\pm$ 0.003	0.65 $\pm$ 0.20	0.77 $\pm$ 0.33	...	0.01 $\pm$ 0.008	0.006 $\pm$ 0.005	0.34 $\pm$ 0.08
<i>Cottoniella filamentosa</i> (Howe) Børgesen	0.37 $\pm$ 0.12	0.11 $\pm$ 0.04	0.01 $\pm$ 0.01	...	0.02 $\pm$ 0.01	0.01 $\pm$ 0.008	0.13 $\pm$ 0.03
<i>Dasya baillouviana</i> (Gmelin) Montagne	0.05 $\pm$ 0.03	0.03 $\pm$ 0.01	...	...	...	...	0.02 $\pm$ 0.01
<i>Dasya hutchinsiae</i> Harvey	...	0.002 $\pm$ 0.001	0.005 $\pm$ 0.003	...	0.04 $\pm$ 0.02	...	0.005 $\pm$ 0.002
Filamentous ceramiales	0.29 $\pm$ 0.06	0.43 $\pm$ 0.06	0.22 $\pm$ 0.05	0.97 $\pm$ 0.24	0.33 $\pm$ 0.10	0.23 $\pm$ 0.06	0.39 $\pm$ 0.03
<i>Galaxaura rugosa</i> (Ellis et Solander) Lamouroux	...	...	...	...	...	0.26 $\pm$ 0.16	0.02 $\pm$ 0.01
<i>Ganonema farinosum</i> (Lamouroux) Fan et Wang	...	...	0.06 $\pm$ 0.06	...	...	...	0.007 $\pm$ 0.007
<i>Ganonema lubricum</i> Afonso-Carrillo, Sansón et Reyes	...	...	1.83 $\pm$ 0.74	...	...	...	0.23 $\pm$ 0.09
<i>Gayliella</i> cf. <i>flaccida</i>	...	0.0002 $\pm$ 0.0002	...	...	...	...	0.00009 $\pm$ 0.00009
<i>Gelidiopsis intricata</i> (C. Agardh) Vickers	0.05 $\pm$ 0.021	0.17 $\pm$ 0.03	0.01 $\pm$ 0.005	0.03 $\pm$ 0.02	0.02 $\pm$ 0.007	0.03 $\pm$ 0.01	0.08 $\pm$ 0.01
<i>Gelidium pusillum</i> (Stackhouse) Le Jolis	...	...	0.0007 $\pm$ 0.0007	...	...	...	0.00009 $\pm$ 0.0009
<i>Haliptilon virgatum</i> Garbary et Johansen	...	0.001 $\pm$ 0.0009	...	...	...	...	0.0004 $\pm$ 0.0003
<i>Herposiphonia secunda</i> (C. Agardh) Ambronn	...	...	...	...	...	0.003 $\pm$ 0.001	0.0002 $\pm$ 0.0001
<i>Heterosiphonia crispella</i> (C. Agardh) Wynne	...	0.01 $\pm$ 0.006	...	...	...	...	0.004 $\pm$ 0.002
<i>Hypnea spinella</i> (C. Agardh) Kützing	0.0003 $\pm$ 0.0003	0.01 $\pm$ 0.008	0.001 $\pm$ 0.001	...	0.004 $\pm$ 0.004	0.01 $\pm$ 0.008	0.008 $\pm$ 0.003
<i>Jania adhaerens</i> Lamouroux	0.88 $\pm$ 0.15	3.15 $\pm$ 0.36	1.33 $\pm$ 0.16	0.51 $\pm$ 0.10	0.92 $\pm$ 0.20	0.44 $\pm$ 0.12	1.70 $\pm$ 0.14
<i>Jania pumila</i> Lamouroux	0.04 $\pm$ 0.02	0.0002 $\pm$ 0.0002	0.004 $\pm$ 0.001	...	...	...	0.01 $\pm$ 0.005
<i>Laurencia majuscula</i> (Harvey) Lucas	...	0.01 $\pm$ 0.008	...	...	...	...	0.004 $\pm$ 0.003
<i>Laurencia</i> s.l. spp.	0.0003 $\pm$ 0.0003	0.0006 $\pm$ 0.0006	0.0007 $\pm$ 0.0007	...	0.0009 $\pm$ 0.0009	0.001 $\pm$ 0.001	0.0006 $\pm$ 0.0003
<i>Liagora canariensis</i> Børgesen	...	...	1.79 $\pm$ 0.74	...	...	...	0.22 $\pm$ 0.09
<i>Liagora ceranoides</i> Lamouroux	0.001 $\pm$ 0.001	...	...	...	...	...	0.0004 $\pm$ 0.0004
<i>Liagora distenta</i> (Mertens) Lamouroux	...	...	0.07 $\pm$ 0.03	...	...	...	0.009 $\pm$ 0.004
<i>Liagora tetrasporifera</i> Børgesen	0.005 $\pm$ 0.002	...	...	0.01 $\pm$ 0.01	...	...	0.002 $\pm$ 0.001
<i>Lophocladia trichoclados</i> (C. Agardh) Schmitz	0.06 $\pm$ 0.04	0.35 $\pm$ 0.11	1.15 $\pm$ 0.48	...	0.02 $\pm$ 0.02	...	0.29 $\pm$ 0.07
Nongeniculate corallines	8.24 $\pm$ 0.84	29.62 $\pm$ 1.37	33.79 $\pm$ 2.43	39.86 $\pm$ 2.94	19.94 $\pm$ 1.49	32.09 $\pm$ 2.03	25.05 $\pm$ 0.77
<i>Peyssonnelia</i> spp.	...	0.35 $\pm$ 0.10	0.61 $\pm$ 0.26	0.01 $\pm$ 0.01	...	...	0.21 $\pm$ 0.05
<i>Plocamium cartilagineum</i> (Linnaeus) Dixon	...	...	0.0007 $\pm$ 0.0007	...	...	...	0.00009 $\pm$ 0.00009
<i>Pterosiphonia pennata</i> (C. Agardh) Falkenberg	...	...	...	...	...	0.02 $\pm$ 0.02	0.002 $\pm$ 0.001
<i>Spyridia hypnoides</i> (Bory) Papenfuss	...	0.001 $\pm$ 0.001	...	...	0.01 $\pm$ 0.009	0.10 $\pm$ 0.06	0.01 $\pm$ 0.005
<i>Tricleocarpa cylindrica</i> (Ellis et Solander) Huisman et Borowitzka	...	...	0.03 $\pm$ 0.02	...	...	...	0.004 $\pm$ 0.003
<i>Thuretella schousboei</i> (Thuret) Schmitz	...	...	0.09 $\pm$ 0.09	...	...	...	0.01 $\pm$ 0.01
<i>Wrangelia argus</i> (Montagne) Montagne	...	0.001 $\pm$ 0.0008	0.72 $\pm$ 0.24	...	...	...	0.09 $\pm$ 0.03

(continued on next page)

Table 1 (continued)

Macroalgae	El Hierro	La Palma	La Gomera	Tenerife	Lanzarote	Chinijo	Canary Islands
<i>Wrangelia penicillata</i> (C. Agardh) C. Agardh	0.01 ± 0.01	0.002 ± 0.002	0.001 ± 0.001	...	...	...	0.005 ± 0.003
<i>Phaeophyceae</i>							
<i>Canistrocarpus cervicornis</i> (Kützting) De Clerck	2.51 ± 0.37	1.71 ± 0.27	5.46 ± 1.22	0.19 ± 0.04	0.62 ± 0.24	...	2.00 ± 0.21
<i>Colpomenia sinuosa</i> (Roth) Derbès et Solier	...	0.14 ± 0.05	0.01 ± 0.007	...	...	...	0.05 ± 0.01
<i>Cystoseira abies-marina</i> (Gmelin) C. Agardh	0.03 ± 0.01	2.11 ± 0.61	...	6.96 ± 1.98	...	0.01 ± 0.008	1.34 ± 0.28
<i>Cystoseira compressa</i> (Esper) Gerloff et Nizamuddin	0.04 ± 0.01	0.35 ± 0.09	0.003 ± 0.002	0.50 ± 0.43	0.009 ± 0.009	...	0.18 ± 0.04
<i>Cystoseira foeniculacea</i> (Linnaeus) Greville	...	...	...	...	0.04 ± 0.04	0.10 ± 0.08	0.01 ± 0.009
<i>Cystoseira</i> sp.	...	...	...	...	...	6.91 ± 1.60	0.59 ± 0.15
<i>Dictyopteris polypodioides</i> (De Candolle) Lamouroux	...	0.006 ± 0.003	...	...	...	...	0.002 ± 0.001
<i>Dictyota ciliolata</i> Kützting	...	0.001 ± 0.001	...	...	...	...	0.0007 ± 0.0007
<i>Dictyota dichotoma</i> (Hudson) Lamouroux	0.008 ± 0.003	0.17 ± 0.05	0.05 ± 0.02	0.25 ± 0.13	...	...	0.09 ± 0.02
<i>Dictyota fasciola</i> (Roth) Lamouroux	...	0.01 ± 0.01	0.01 ± 0.005	...	...	...	0.008 ± 0.004
<i>Dictyota implexa</i> (Desfontaines) Lamouroux	...	0.01 ± 0.01	...	...	...	...	0.003 ± 0.003
<i>Dictyota cf. jamaicensis</i>	0.04 ± 0.01	0.007 ± 0.007	...	...	...	...	0.01 ± 0.004
<i>Dictyota cf. pfaflii</i>	0.18 ± 0.04	0.28 ± 0.05	0.02 ± 0.01	0.27 ± 0.08	0.36 ± 0.16	0.40 ± 0.15	0.24 ± 0.03
<i>Dictyota</i> sp1	...	0.005 ± 0.004	0.01 ± 0.01	...	...	...	0.003 ± 0.002
<i>Dictyota</i> sp2	0.007 ± 0.004	0.89 ± 0.17	0.003 ± 0.001	...	...	...	0.32 ± 0.06
<i>Halopteris scoparia</i> (Linnaeus) Sauvageau	0.005 ± 0.004	0.25 ± 0.10	0.01 ± 0.008	...	0.04 ± 0.01	0.10 ± 0.08	0.10 ± 0.03
<i>Hydroclathrus clathratus</i> (C. Agardh) Howe	0.01 ± 0.005	...	0.003 ± 0.003	...	...	...	0.003 ± 0.001
<i>Lobophora variegata</i> (Lamouroux) Oliveira	69.72 ± 2.38	24.30 ± 1.64	12.72 ± 2.13	6.92 ± 1.53	0.18 ± 0.43	6.76 ± 1.57	28.56 ± 1.17
<i>Nemacystus hispanicus</i> (Sauvageau) Kylin	...	...	0.0007 ± 0.0007	...	...	...	0.00009 ± 0.00009
<i>Padina pavonica</i> (Linnaeus) Thivy in Taylor	0.005 ± 0.002	0.09 ± 0.02	0.13 ± 0.06	0.02 ± 0.01	0.01 ± 0.005	...	0.05 ± 0.01
<i>Pseudolithoderma adriaticum</i> (Hauck) Verlaque	...	1.43 ± 0.23	1.22 ± 0.24	2.23 ± 0.62	1.67 ± 0.12	1.62 ± 0.17	1.16 ± 0.10
<i>Rosenvingea intricata</i> (J. Agardh) Børgesen	...	...	0.009 ± 0.005	...	...	...	0.001 ± 0.0007
<i>Sargassum desfontainesii</i> (Turner) C. Agardh	...	0.008 ± 0.005	...	0.11 ± 0.11	...	...	0.01 ± 0.009
<i>Sargassum</i> sp1.	0.18 ± 0.03	0.96 ± 0.18	0.003 ± 0.002	0.16 ± 0.12	0.11 ± 0.05	0.38 ± 0.16	0.45 ± 0.07
<i>Sargassum</i> sp2.	0.0009 ± 0.0009	2.70 ± 0.53	...	0.11 ± 0.11	...	...	0.99 ± 0.19
<i>Sphacelaria cirrosa</i> (Roth) C. Agardh	...	...	...	...	...	0.05 ± 0.03	0.005 ± 0.002
<i>Stypopodium zonale</i> (Lamouroux) Papenfuss	0.23 ± 0.09	0.12 ± 0.06	0.35 ± 0.12	1.04 ± 0.57	...	0.03 ± 0.01	0.23 ± 0.06
<i>Taonia atomaria</i> (Woodward) J. Agardh	...	0.03 ± 0.01	...	0.11 ± 0.11	...	...	0.02 ± 0.01
<i>Zonaria tournefortii</i> (Lamouroux) Montagne	...	1.17 ± 0.48	...	...	...	...	0.42 ± 0.17
<i>Chlorophyta</i>							
<i>Acetabularia parvula</i> Solms-Laubach	...	...	0.01 ± 0.009	...	...	...	0.001 ± 0.001
<i>Caulerpa racemosa</i> (Forsskål) J. Agardh	0.001 ± 0.001	...	...	...	...	...	0.0004 ± 0.0004
<i>Caulerpa webbiana</i> Montagne	...	...	...	...	0.0009 ± 0.0009	...	0.00009 ± 0.00009
<i>Chaetomorpha</i> spp.	...	...	...	0.01 ± 0.01	...	...	0.0009 ± 0.00009
<i>Cladophora liebetruthii</i> Grunow	0.003 ± 0.002	0.002 ± 0.002	...	...	0.30 ± 0.17	...	0.03 ± 0.017
<i>Dasycladus vermicularis</i> (Scopoli) Krasser	...	...	0.04 ± 0.01	...	...	...	0.005 ± 0.001
<i>Ernodesmis verticillata</i> (Kützting) Børgesen	0.002 ± 0.002	...	...	0.04 ± 0.03	...	...	0.004 ± 0.003
<i>Microdictyon calodictyon</i> (Montagne) Kützting	0.0009 ± 0.0009	0.005 ± 0.005	...	...	...	...	0.002 ± 0.001
<i>Pseudochlorodesmis furcellata</i> (Zanardini) Børgesen	0.01 ± 0.004	0.04 ± 0.008	0.01 ± 0.003	0.33 ± 0.08	0.07 ± 0.006	...	0.06 ± 0.007
<i>Pseudotetraspora marina</i> Wille	1.40 ± 0.25	0.007 ± 0.003	0.007 ± 0.005	...	...	...	0.34 ± 0.06
Richness	5.73 ± 0.17	5.90 ± 0.10	6.26 ± 0.23	4.04 ± 0.19	5.46 ± 0.23	6.54 ± 0.25	5.77 ± 0.07
Diversity	0.57 ± 0.02	0.73 ± 0.02	0.71 ± 0.04	0.62 ± 0.04	0.63 ± 0.03	0.63 ± 0.04	0.66 ± 0.01

### 2.3.2. Spatial variation within islands: the role of wave exposure

To assess spatial variation over a scale of tens of kilometres, differences in richness, diversity and cover of dominant species between localities according to wave exposure degree were tested by a three-way model, in which 'island' and 'wave exposure' (2 levels: semiexposed and exposed) were treated as fixed factors and 'site' as a random factor nested within the interaction 'island × wave exposure'.

### 2.3.3. Spatial variation between and within localities: the effects of sedimentation, depth and substrate

To assess spatial variation over a scale of metres, differences in richness, diversity and cover of dominant species between samples, according to habitat complexity variables (sedimentation, depth and substratum) were tested by a three-way model, in which 'island' was treated as a fixed factor. Habitat complexity variables were treated as fixed factors ['sedimentation' (3 levels: <5%, 5–30%, and >30%), 'depth' (3 levels: 5–10, 10–15, 15–20 m), and 'substratum' (3 levels: rocky platform, boulders and rocks, and small rocks)]. 'Site' was treated as a random factor nested within the interaction 'island × habitat complexity variable'.

### 2.3.4. The role of sea urchin density on seaweed assemblages

To assess the relation between sea urchin density and differences in richness, diversity and cover of dominant seaweed species between samples, a one-way model was performed, in which 'sea urchin density' was treated as a fixed factor (5 levels: 0–0.15, 0.15–2, 2–4, 4–6, >6 urchins.m<sup>-2</sup>). Large-scale spatial variation of sea urchin density was tested by a two-way model permutational ANOVA, based on Euclidean distances of data set and using 4999, in which 'island' was treated as a fixed factor and 'site' as a random factor nested in 'island'.

Statistical descriptives were performed using the SPSS 15.0 for Windows statistical package (SPSS, Chicago, IL, USA), while regressions, multivariate and univariate analysis were performed using PRIMER-E® v.6 +PERMANOVA+ ([www.primers-e.com](http://www.primers-e.com); Clarke and Gorley, 2006). The tables of main tests and a posteriori comparisons can be found in the online version as [Supplementary material](#).

## 3. Results

### 3.1. Composition of seaweed assemblages and species cover

Seventy-nine macroalgae (1 Cyanophyta, 39 Rhodophyta, 29 Phaeophyceae and 10 Chlorophyta) were identified in subtidal seaweed assemblages studied (Table 1). Six macroalgae contributed with 87.63% to the total mean cover per site: *Lobophora variegata* (41.84%), nongeniculate corallines (36.68%), *Canistrocarpus cervicornis* (2.93%), *Jania adhaerens* (2.49%), *Cystoseira abies-marina* (1.96%) and *Pseudolithoderma adriaticum* (1.69%). The remainder macroalgae exhibited very low cover (<1%). Mean cover percentages of all macroalgae identified, per island and for the whole archipelago, are showed in Table 1.

### 3.2. Relationships between seaweed assemblages and environmental factors

DistLM analysis shows a significant relationship between biological and environmental data when considering predictor variables individually (Table 2). All the studied parameters show significant relationship to the macroalgae data. Sea urchin density (26.94%), upwelling distance (11.66%), and sedimentation (6.81%) explain the highest percentage of variation in composition and cover of subtidal seaweed assemblages. The factors substratum,

**Table 2**

Results of DistLM (distance-based linear model routine). (A) Tests for relationships between individual environmental variables and biological data. (B) Tests for relationships between environmental and biological data considering all environmental variables integrated in a multiple regression model.

(A) Marginal test				
Variable	Pseudo-F	p	% var.	
Depth	8.998	0.0001	0.86	
Upwelling distance	136.77	0.0001	11.66	
Wave exposure	20.03	0.0001	1.89	
Sedimentation	75.821	0.0001	6.81	
Herbivore density	382.17	0.0001	26.94	
Substrate	29.19	0.0001	2.73	
(B) Sequential test				
Variable	Pseudo-F	p	% var.	com. % var
Herbivore density	410.140	0.0001	22.51	22.51
Upwelling distance	137.080	0.0001	11.59	34.10
Sedimentation	88.653	0.0001	6.79	40.90
Substrate	16.175	0.0001	0.87	41.78
Wave exposure	19.004	0.0001	1.57	43.36
Depth	8.998	0.0003	0.86	44.22

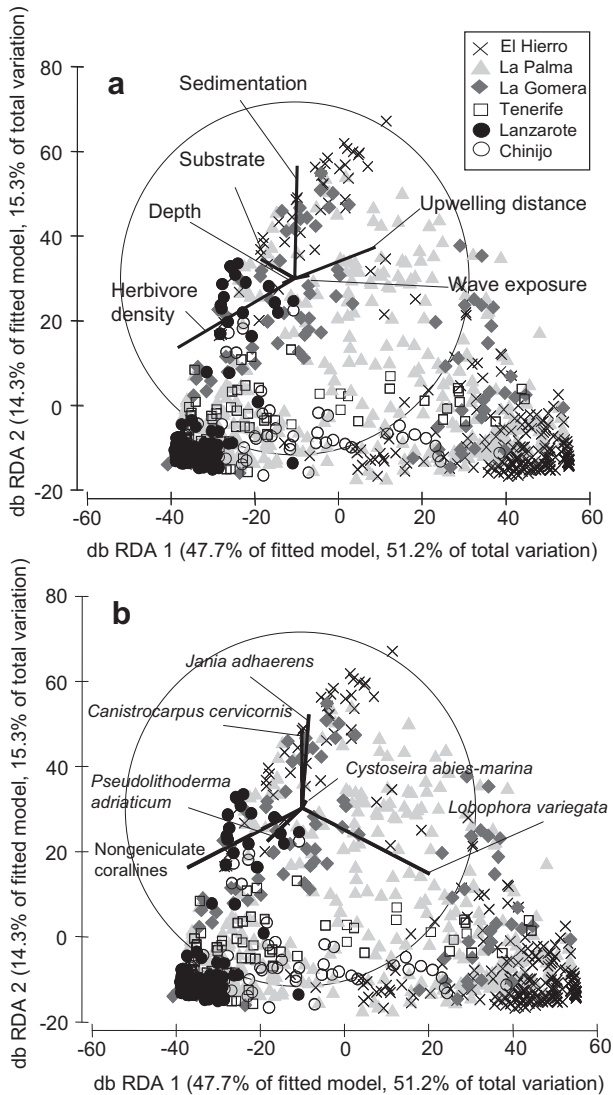
wave exposure and depth only explain a low amount of variation in the macroalgae data matrix (2.73, 1.89 and 0.86%, respectively) (Table 2A). When considering the environmental factors together, that is, when adding sequentially these variables in a model in order to predict the composition of seaweed assemblages, the first chosen factor is sea urchin density, followed by upwelling distance and so on (see Table 2B). The total variation in the composition and percent cover of assemblages explained by all 6 environmental variables is 44.22% (Table 2B).

dbRDA plots allow the visualization of the relationship between biological and environmental variables (Fig. 2). Environmental variables and subtidal macroalgae are represented in the plots as overlaid vectors. The environmental variables that are more strongly related to the first dbRDA axis are upwelling distance (positively related) and sea urchin density and substratum (negatively related). On the other hand, the variable more related (positively) to the second dbRDA axis is sedimentation. The species *Lobophora variegata* is strongly positively related to the first axis, while nongeniculate corallines and *Pseudolithoderma adriaticum* are negatively related. *Canistrocarpus cervicornis* and *Jania adhaerens* show a positive relationship with the second axis.

With regards to the seaweed assemblages sampled in different islands, most of the samples from the westernmost island (El Hierro) have a positive relationship to upwelling distance and to *Lobophora variegata*, and therefore a negative relationship to sea urchin density, while most of the samples from islands Tenerife and Lanzarote appear to be positively related to sea urchin density and crustose macroalgae (nongeniculate corallines and *Pseudolithoderma adriaticum*). Samples from La Palma, La Gomera and Chinijo show more heterogeneous relationships with environmental factors and species cover. Samples that are positively related to sedimentation and *Canistrocarpus cervicornis* and *Jania adhaerens* appear in different islands (Fig. 2).

### 3.3. Spatial variation between islands

High variability in composition and structure of seaweed assemblages along the group of islands was detected. There was a highly significant effect of the main factor 'island' ( $F = 7.790$ ,  $p = 0.0002$ ), and 'site' ( $F = 23.178$ ,  $p = 0.0002$ ). A posteriori pairwise analyses showed significant differences between the island situated most far away to upwelling (El Hierro) and the remainder



**Fig. 2.** Distance-based redundancy analysis (dbRDA). (a) Relationships between the ordination of the sites based on species cover and environmental factors. (b) Direction of increasing abundances of the six macroalgae with the highest mean cover (>1%) in the rocky subtidal seaweed assemblages studied ( $n = 1038$ ).

islands ( $p < 0.001$ ), and also for some island pairwise analyses (Table 3). The dbRDA plots (Fig. 2) show differences between islands are mainly related to cover of *Lobophora variegata* and nongeniculate corallines.

Richness and diversity mean values are not significantly different between islands (Table 1). On the contrary, differences were detected between localities (richness:  $F = 21.009$ ,  $p = 0.0002$ ; diversity:  $F = 18.018$ ,  $p = 0.0002$ ).

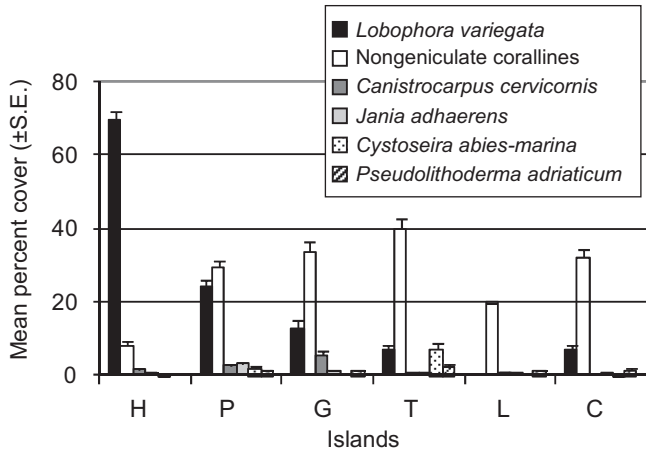
Cover of the most abundant macroalgae (mean cover >1%) varied along the island chain (Fig. 3), with *Lobophora variegata*, nongeniculate corallines, *Canistrocarpus cervicornis* and *Jania adhaerens* showing significant differences between islands ( $F = 15.086$ ,  $p = 0.0002$ ;  $F = 4.372$ ,  $p = 0.003$ ;  $F = 2.762$ ,  $p = 0.030$ ;  $F = 2.625$ ,  $p = 0.038$ ; respectively). All species studied showed, however, significant differences for 'site' ( $p < 0.0002$ ). *Lobophora variegata* exhibited maximum cover values in El Hierro ( $69.72 \pm 2.38\%$ ) and minimum in Lanzarote ( $0.18 \pm 0.43\%$ ). Nongeniculate corallines showed the highest cover values in Tenerife ( $39.86 \pm 2.94\%$ ) while the lowest in El Hierro ( $8.24 \pm 0.84\%$ ). *Canistrocarpus cervicornis* registered the highest cover values in La Gomera ( $5.46 \pm 1.22\%$ ), and it was absent in Chinijo. And finally, *J. adhaerens* presented maximum cover values in La Palma ( $3.15 \pm 0.36\%$ ) and minimum in Tenerife ( $0.51 \pm 0.10\%$ ). A posteriori pairwise analyses for these species are showed in Table 3.

#### 3.4. Spatial variation within islands: the role of wave exposure

The results revealed a high significant effect of the factor 'wave exposure' in richness and diversity. Richness increased with wave exposure. The highest values ( $6.74 \pm 0.11$  macroalgae per sample) were detected in exposed shores, while the lowest ( $5.16 \pm 0.09$ ) were observed in semiexposed shores. Diversity showed the same pattern, with the highest values ( $0.83 \pm 0.02$ ) on exposed shores and the lowest ( $0.56 \pm 0.01$ ) on semiexposed ones. Considering the most abundant macroalgae, only *Cystoseira abies-marina* showed significant differences in cover related to exposure to wave action, varying from  $0.0007 \pm 0.0007\%$  at semiexposed shores to  $3.46 \pm 0.71\%$  at exposed shores. *Lobophora variegata* and *Canistrocarpus cervicornis* showed a significant interaction of factors 'island  $\times$  wave exposure', which indicates that the wave exposure effect differs with the island. Thus, *L. variegata* from El Hierro and La Palma registered its highest cover in semiexposed shores, but showed the opposite pattern in La Gomera, Tenerife and Chinijo (Fig. 4). Nevertheless, a significant posteriori differences was found

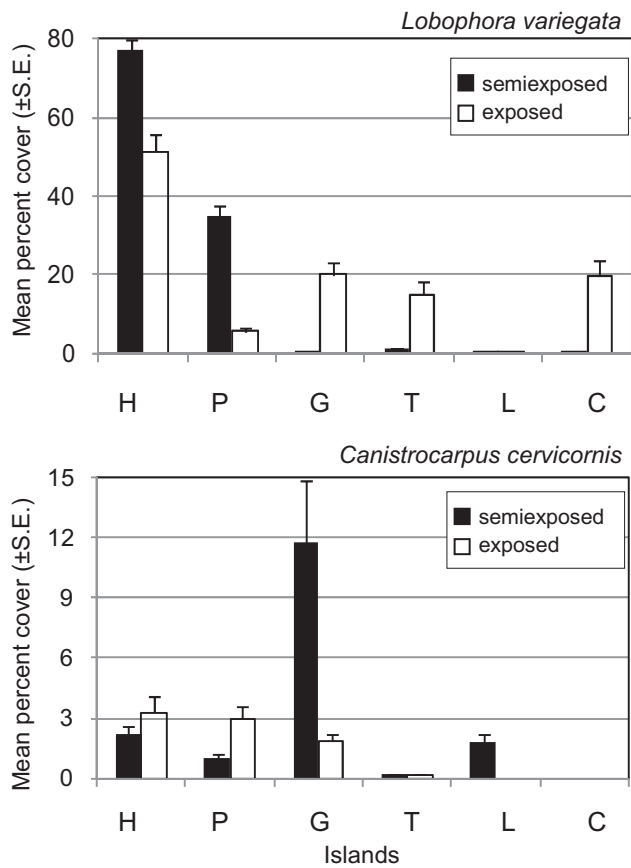
**Table 3**  
Results of Permutational ANOVA pairwise analysis. Effects of the factor 'island' on composition and structure of assemblages and cover of *Lobophora variegata*, nongeniculate corallines, *Canistrocarpus cervicornis* and *Jania adhaerens*.

Groups	Total cover		<i>Lobophora variegata</i>		Nongeniculate corallines		<i>Canistrocarpus cervicornis</i>		<i>Jania adhaerens</i>	
	t	P	t	P	t	P	t	P	t	P
El Hierro vs La Palma	3.906	0.0002	4.528	0.002	3.187	0.003	0.673	0.521	2.991	0.026
El Hierro vs La Gomera	3.331	0.0008	4.264	0.0008	2.931	0.007	1.015	0.321	1.55	0.133
El Hierro vs Tenerife	4.638	0.0002	5.611	0.0002	5.764	0.0006	1.918	0.078	0.480	0.650
El Hierro vs Lanzarote	4.731	0.0002	5.199	0.0002	1.915	0.066	1.586	0.124	0.291	0.769
El Hierro vs Chinijo	3.764	0.0002	4.291	0.001	3.646	0.002	1.975	0.044	0.346	0.730
La Palma vs La Gomera	1.328	0.131	1.185	0.251	0.227	0.819	1.762	0.076	0.704	0.504
La Palma vs Tenerife	2.076	0.003	2.314	0.027	1.656	0.113	1.568	0.152	2.383	0.032
La Palma vs Lanzarote	2.803	0.0002	2.418	0.019	1.086	0.291	1.271	0.225	1.818	0.074
La Palma vs Chinijo	1.769	0.018	1.582	0.123	0.211	0.839	1.733	0.103	1.344	0.184
La Gomera vs Tenerife	1.379	0.096	0.884	0.743	1.004	0.330	2.813	0.006	2.288	0.037
La Gomera vs Lanzarote	1.875	0.014	1.398	0.407	1.103	0.292	2.370	0.028	1.349	0.202
La Gomera vs Chinijo	1.307	0.136	0.522	0.608	0.008	0.994	2.752	0.014	1.061	0.299
Tenerife vs Lanzarote	2.214	0.002	1.157	0.328	2.742	0.016	0.024	0.936	0.045	0.970
Tenerife vs Chinijo	1.367	0.059	0.404	0.742	1.178	0.267	1.638	0.069	0.923	0.393
Lanzarote vs Chinijo	1.434	0.098	1.715	0.057	1.534	0.135	0.837	0.987	0.472	0.453



**Fig. 3.** Mean percent cover ( $\pm$ S.E.) of the six macroalgae with the highest cover ( $>1\%$ ) in each studied island: El Hierro (H), La Palma (P), La Gomera (G), Tenerife (T), Lanzarote (L), and Chinijo (C) ( $n = 1038$ ).

only for La Palma and Chinijo. *Canistrocarpus cervicornis* showed the highest cover at semiexposed localities in La Gomera and Lanzarote, but in El Hierro, La Palma and Tenerife the highest cover was reached at exposed shores (Fig. 4). However, a significant posteriori differences was detected only for La Gomera.

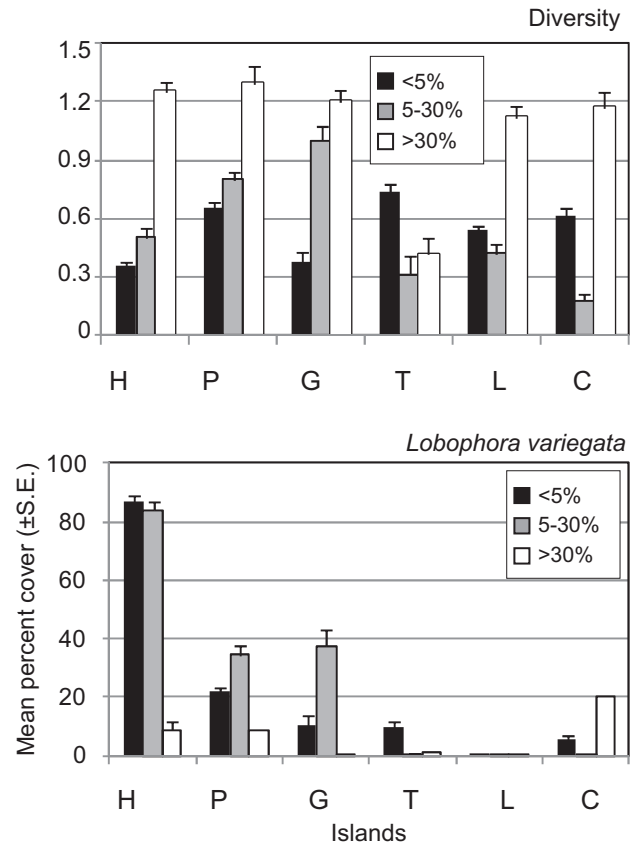


**Fig. 4.** Mean percent cover ( $\pm$ S.E.) of *Lobophora variegata* and *Canistrocarpus cervicornis* in semiexposed and exposed habitats of each studied island: El Hierro (H), La Palma (P), La Gomera (G), Tenerife (T), Lanzarote (L), and Chinijo (C) ( $n = 1038$ ).

3.5. Spatial variation between and within localities: the effects of sedimentation, depth and substratum

Results revealed a high significant effect in richness of the factor 'sedimentation'. Richness registered low mean values at  $<5\%$  and  $5\text{--}30\%$  of rock covered by sand with  $5.18 \pm 0.08$  and  $5.58 \pm 0.12$  macroalgae per sample respectively, and high at sedimentation  $>30\%$  with  $8.55 \pm 0.19$ . A posteriori analyses showed significant differences in richness between the highest sedimentation level ( $>30\%$  of rock covered by sand) and the remainder levels. Concerning diversity, a significant interaction of factors 'island  $\times$  sedimentation' was detected. For all the islands, except Tenerife, the highest cover values were registered with the highest sedimentation level (Fig. 5). A posteriori differences were found between  $<5\%$  vs  $>30\%$  and  $5\text{--}30\%$  vs  $>30\%$  pairwise analyses for El Hierro, La Palma and Lanzarote, and between  $5$  and  $30\%$  vs  $>30\%$  for Chinijo.

The most abundant macroalgae, only *Canistrocarpus cervicornis* and *Jania adhaerens* showed differences in cover related to the level of rock covered by sand. The highest cover for *Canistrocarpus* and *Jania* ( $9.29 \pm 1.26\%$  and  $3.44 \pm 0.59\%$ , respectively) were obtained with the highest level of sedimentation, while low and intermediate levels registered the lowest cover ( $0.36 \pm 0.08\%$  and  $1.66 \pm 0.59\%$ , for *C. cervicornis*;  $0.12 \pm 0.02\%$  and  $0.39 \pm 0.20\%$  for *J. adhaerens*). A posteriori pairwise analyses found differences for  $<5\%$  vs  $>30\%$  levels in *Canistrocarpus* as well as *Jania*. Cover of *L. variegata* showed a significant interaction of factors 'island  $\times$  sedimentation'. *Lobophora variegata* presented its maximum cover in zones with low or intermediate effect of sand,



**Fig. 5.** Diversity and mean percent cover ( $\pm$ S.E.) of *Lobophora variegata* in the three sedimentation (% rock covered by sand) levels of each studied island: El Hierro (H), La Palma (P), La Gomera (G), Tenerife (T), Lanzarote (L), and Chinijo (C) ( $n = 1038$ ).



except in the eastern islands of Lanzarote and Chinijo (Fig. 5). However, a posteriori analyses detected differences only in the western island of El Hierro for <5% vs >30% and for 5–30% vs >30%.

For the factor 'depth', no significant differences were found in richness, diversity and cover of the most abundant species.

Finally, the diversity of seaweed assemblages was the unique parameter that exhibited significant relationship with the type of substratum, showing an interaction of factors 'island × substratum'. The highest values in diversity from the islands El Hierro, La Gomera and Chinijo, were reached on small rocks, while from La Palma, and Lanzarote were measured on rocky platforms and from Tenerife on boulders and rocks (Fig. 6). A posteriori analyses only found significant differences for boulders and rocks vs small rocks in El Hierro and La Gomera.

### 3.6. The role of sea urchin density on seaweed assemblages

Richness and diversity in seaweed assemblages showed highly significant differences in relation to density of the sea urchin *Diadema* aff. *antillarum* (richness:  $F = 48.336$ ,  $p = 0.0002$ ; diversity:  $F = 57.936$ ,  $p = 0.0002$ ). Richness varied from  $6.88 \pm 1.13$  macroalgae with the lowest herbivore density (0–0.15 urchins.m<sup>-2</sup>) to  $4.42 \pm 0.38$  macroalgae with the highest densities (>6 urchins.m<sup>-2</sup>) (Fig. 7). Pairwise comparisons showed that all densities were significantly different from each other, except for 2–4 vs 4–6 urchins.m<sup>-2</sup>. Similarly, diversity varied from the lowest density to 0.38 ± 0.02 with the highest one (Fig. 7). A posteriori analyses found differences for all pairwise analyses, except for 2–4 vs 4–6 urchins.m<sup>-2</sup>.

Cover of the most abundant macroalgae (Fig. 7) presented significant differences according to sea urchin density (*Lobophora variegata*  $F = 111.08$ ,  $p = 0.0002$ ; nongeniculate corallines  $F = 158.58$ ,  $p = 0.0002$ ; *Canistrocarpus cervicornis*  $F = 13.58$ ,  $p = 0.0002$ ; *Jania adhaerens*  $F = 11.71$ ,  $p = 0.0002$ ; *Cystoseira abies-marina*  $F = 9.842$ ,  $p = 0.0002$ ; and *Pseudolithoderma adriaticum*  $F = 37.29$ ,  $p = 0.0002$ ). *Lobophora variegata* varied from  $52.87 \pm 2.51\%$  with densities of 0.5–2 urchins.m<sup>-2</sup> to  $0.67 \pm 0.12\%$  with more than 6 urchins.m<sup>-2</sup>. Pairwise comparisons showed that all densities were significantly different from each other. Nongeniculate corallines presented the highest cover ( $47.72 \pm 2.47\%$ ) with >6 urchins.m<sup>-2</sup>, while the lowest ( $10.57 \pm 0.66\%$ ) with 0–0.15 urchins.m<sup>-2</sup>. A posteriori analyses found differences for all densities, except for 2–4 vs 4–6 urchins.m<sup>-2</sup>. *Canistrocarpus cervicornis*

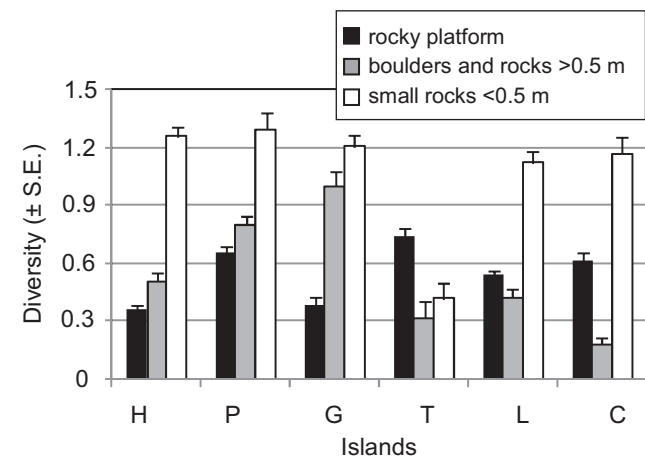


Fig. 6. Mean diversity (±S.E.) in the three types of substrates examined (rocky platform, boulders-rocks, and small rocks) of each studied island: El Hierro (H), La Palma (P), La Gomera (G), Tenerife (T), Lanzarote (L), and Chinijo (C) ( $n = 1038$ ).

cover varied from  $3.40 \pm 0.65\%$  (0.15–2 urchins.m<sup>-2</sup>) to  $0.005 \pm 0.002\%$  (>6 urchins.m<sup>-2</sup>), with significant differences for all pairwise densities, except 0–0.15 vs 0.15–2 urchins.m<sup>-2</sup> and 2–4 vs 4–6 urchins.m<sup>-2</sup>. *Jania adhaerens* presented maximum cover ( $2.63 \pm 0.28\%$ ) with 0–0.15 urchins.m<sup>-2</sup> and minimum ( $0.15 \pm 0.03\%$ ) with >6 urchins.m<sup>-2</sup>, and pairwise comparisons

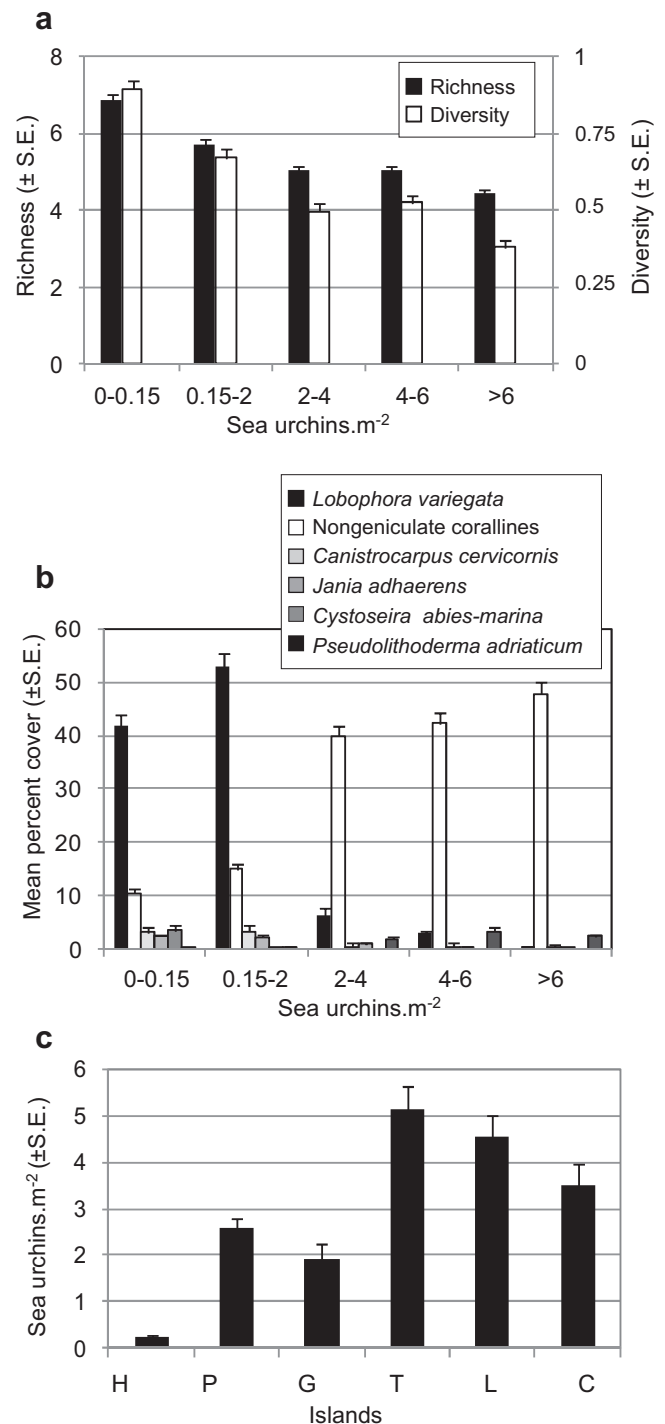


Fig. 7. Sea urchin density. (a) Mean richness (number of species ± S.E.) and mean diversity (±S.E.) of macroalgae for each herbivore density interval. (b) Mean percent cover (±S.E.) of the six macroalgae with the highest covers (>1%) for each herbivore density interval. (c) Mean density of *Diadema* aff. *antillarum* (±S.E.) per each studied island: El Hierro (H), La Palma (P), La Gomera (G), Tenerife (T), Lanzarote (L), and Chinijo (C) ( $n = 1038$ ).

showed that all densities were significantly different from each other, except 0–0.15 vs 0.15–2 and 2–4 vs 4–6 urchins.m<sup>-2</sup>. *Cystoseira abies-marina* occurred only with low density, reaching the highest cover (3.67 ± 0.75%) with 0–0.15 urchins.m<sup>-2</sup>, and showed significant differences for lower pairwise densities. Finally, *P. adriaticum* exhibited maximum cover (3.41 ± 0.62%) with 4–6 urchins.m<sup>-2</sup> and minimum (0.05 ± 0.01) with 0–0.15 urchins.m<sup>-2</sup>. A posteriori analyses found differences for all densities, except for 2–4 vs >6, and 4–6 vs >6 urchins.m<sup>-2</sup>.

Results of densities of the sea urchin *Diadema* aff. *antillarum* revealed highly significant effects of the factors 'island' ( $F = 6.63$ ,  $p = 0.0002$ ) and 'site' ( $F = 13.26$ ,  $p = 0.0002$ ). Sea urchin densities varied from maximum values of 5.13 ± 0.50 urchins.m<sup>-2</sup> in the central island Tenerife to minimum values of 0.23 ± 0.05 urchins.m<sup>-2</sup> in the western island El Hierro (Fig. 7). Pairwise comparisons in sea urchin density for the factor 'island' showed significant differences between El Hierro and the remainder islands and for La Palma vs Tenerife and La Gomera vs Tenerife.

#### 4. Discussion

The structure and composition of shallow rocky seaweed assemblages of the Canarian Archipelago differ greatly from those of neighbouring continental shores. On the mainland, few Laminariales or Fucales are the engineering species in the seaweed assemblages at this warm temperate region (Dangeard, 1949; Ballesteros and Pinedo, 2004). To the south of the NAWTR the *Cystoseira* beds dominate the seascape on non-human influenced rocky bottoms (Ballesteros, 1989). However, in the Canary Islands, the engineering species on pristine subtidal rocky bottoms are both warm temperate Fucales (i.e. *Cystoseira*, *Sargassum*) and tropical Dictyotales (i.e. *Canistrocarpus*, *Dictyota*, *Lobophora*, *Styopodium*, *Zonaria*) (Wildpret et al., 1987), being *Lobophora variegata* the widest dominant element reported in tropical and subtropical seaweed assemblages (Ruyter van Steveninck and Breman, 1987; Vroom and Page, 2006). The environmental conditions due to the geographic position of the Canaries at the eastern limit of the North Atlantic Ocean's subtropical gyre, allow the development of assemblages with tropical characteristics different from those of the nearby warm temperate mainland.

Significant relationships have been detected between the six studied environmental factors and the structure and composition of the rocky seaweed assemblages. These environmental variables account for 44.22% of the variability in ecological structure in these patchy systems. Sea urchin density (22.51%) was the factor that mainly explained assemblage variability, instead of the expected upwelling distance (11.59%). The other variables, sedimentation (6.79%), substratum (0.87%), wave exposure (1.57%) and depth (0.86%) have a limited influence. The unexplained variability would be related to other parameters not examined in this study (i.e., concentration of nutrients, inclination and texture of substrata, water turbidity, density of other herbivores or pollution).

Only six of the seventy-nine macroalgae contributed significantly to the total seaweed coverage, with nearly 90%. All six species (*Lobophora variegata*, nongeniculate corallines, *Canistrocarpus cervicornis*, *Jania adhaerens*, *Cystoseira abies-marina* and *Pseudolithoderma adriaticum*) are perennial and can be recognized throughout the year, although *C. cervicornis* and *J. adhaerens* survive as prostrate stolons during the winter. The dictyotalean *L. variegata* and the nongeniculate corallines are the most abundant elements occurring under almost all the environmental conditions, while the dictyotalean *C. cervicornis*, the fucallean *C. abies-marina*, the geniculate coralline *J. adhaerens* and the brown crustose *P. adriaticum* do not reach 6% of the whole cover.

*Lobophora variegata* seems to be the main macroalgal erect species in the subtidal of the Canary Islands, as it is in other

tropical–subtropical areas around the world (Littler and Littler, 2000). The abundance of *L. variegata* along this archipelago is in good agreement with the expected pattern of dominance of dictyotalean assemblages in western islands. This large-scale spatial variation shows a positive relationship to upwelling distance and negative to sea urchin density, despite the fact that *L. variegata* exhibits different morphologies according to grazing intensity as well as some allelochemicals which allow its survival under urchin pressure (De Ruyter van Steveninck et al., 1988; Coen and Tanner, 1989; Targett and Arnold, 1998). However, crustose macroalgae (nongeniculate corallines and *Pseudolithoderma adriaticum*) appear positively related to sea urchin density and not related to upwelling distance, occurring mainly in samples from central islands and in a lower extent from eastern islands. The key role of sea urchins on the structure and composition of seaweed assemblages has been well documented (Mann, 1982; Harold and Pearse, 1987; McClanahan and Safir, 1990), as *Diadema* aff. *antillarum* is the main herbivore that controls fleshy macroalgae on rocky bottoms in the eastern Atlantic Islands (Hernández et al., 2008). Our results show that an increase in density of *Diadema* aff. *antillarum* decreases both richness and diversity of seaweed assemblages, reducing the cover of erect macroalgae and supporting a high percentage cover of crustose species. The cover of *L. variegata* is higher than 50% with low sea urchin density, while the cover of crustose macroalgae is near 50% when density is high. Density of the sea urchin is not related to upwelling distance reaching the highest values in the central island Tenerife and the eastern island Lanzarote, a spatial variation also observed by Hernández et al. (2008). The extent of human activities especially overfishing has been considered determinant of sea urchin densities at each particular island of the Canaries (Clemente et al., 2010). Thus, these activities may be postulated as triggering factors in disrupting the expected pattern on structure and composition of seaweed assemblages along this group of islands.

Populations of Fucales (*Cystoseira* and *Sargassum*) are restricted in the Canarian Archipelago, and only show highest cover at determinate exposed areas. The highest mean cover values (~7%) are reached for *Cystoseira* spp. in the eastern island (Chinijo) and for *Cystoseira abies-marina* in the central island (Tenerife), with lower cover in western islands. However in recent decades *Cystoseira* spp. were reported as the engineering seaweeds at exposed rocky bottoms constituting beds with higher values of cover in central and eastern islands (Wildpret et al., 1987; Reyes et al., 2000). With four species (*C. abies-marina*, *Cystoseira compressa*, *Cystoseira foeniculacea* and *Cystoseira* spp.) growing in subtidal habitats, *Cystoseira* is more diverse to the eastern islands coinciding with the highest upwelling influence; while in the western and central islands only two species (*C. abies-marina* and *C. compressa*) are present.

The low cover observed for fucallean algae, which contrast with those of *Lobophora*, can be explained by the progressive reduction that *Cystoseira* beds have suffered due to herbivores pressure and habitat degradation. Available data (Wildpret et al., 1987) show that many of the Canarian localities sampled during this study exhibit a significant reduction or a complete loss of historical extensive *Cystoseira* populations. Most of these localities are situated next to urban or tourist centres where human pressure on the shore is strong. In the Mediterranean, where *Cystoseira* beds also constitute the typical engineering species on rocky bottoms, habitat degradation and eutrophication have been postulated as the major factors explaining the disappearance of *Cystoseira* assemblages during the recent decades (Thibaut et al., 2005; Arévalo et al., 2007; Mangialajo et al., 2008; Sales and Ballesteros, 2009; Sales et al., 2011). Human activities in the Canary Islands, including those that directly determine the density of herbivores, seem to play a pivotal role on the maintenance of subtidal fucallean assemblages,

and consequently changing the expected pattern of dominance of fucalean to the eastern islands.

Both richness and diversity of seaweed assemblages increase significantly from semiexposed to exposed shores according to the increase of heterogeneity due to the detachment of erect macroalgae by the waves (Cheroske et al., 2000; Leliaert et al., 2000; Goldberg and Kendrick, 2004). Among the most abundant species only *Cystoseira abies-marina* exhibits an increase on cover from semiexposed to exposed shores, but as densities of sea urchins decrease in the same way (Hernández et al., 2008), both factors must be jointly considered. Thus, in islands with low densities of sea urchins (i.e., La Palma and El Hierro) cover of *Lobophora variegata* is higher in semiexposed shores, while in the rest of the islands the highest values are reached on exposed shores. Distribution of *C. abies-marina* beds in the Canary Islands was well documented (Wildpret et al., 1987) and as many other Fucales species it mainly grows in the exposed shores (Ballesteros, 1989; Engelen et al., 2005). The variation at medium spatial scale between northern shores (exposed) and southern shores (semiexposed) seems to agree also with the large-scale pattern of variation of seaweeds assemblages to the western islands, with Fucales growing mainly in the north and Dictyotales in the south.

At a small spatial scale, percentage of rock covered by sand (sedimentation) is the single factor that affects significantly the structure and composition of seaweed assemblages. Although the cover of *Canistrocarpus cervicornis* and *Jania adhaerens* differs between islands, there is no relationship to upwelling influence, but increase positively with the sedimentation degree. Richness and diversity of seaweed assemblages increase also with sedimentation, as on rocky–sandy mixed bottoms many perennial species are replaced by ephemeral ones, heightening the diversity and allowing the arrangement of different mosaics of vegetation (Airoldi, 2003; Díez et al., 2003; Erikson and Bergström, 2005). Herbivores do not occur on these habitats, since the sea urchins are excluded with high degrees of sedimentation (Hernández et al., 2008).

Depth (between 5 and 20 m) and substratum (from rocky platform to small rocks) show a scarce influence on the structure and composition of shallow seaweed assemblages. Although depth is a key factor structuring nearshore benthic assemblages around the world (Dayton, 1985; Garrabou et al., 2002), the range 5–20 m depth does not affect significantly the distribution of the assemblages studied. None of the three types of rocky substratum examined generate differences in seaweed assemblages, except in El Hierro and La Gomera, where diversity increases from stable rocky platforms to unstable small rocks. Replacement of perennial by ephemeral species on the smallest substrata, which can be occasionally displaced by storms, explains this variation in diversity (Davis and Wilce, 1987).

The surveys presented here have enhanced our knowledge of benthic assemblages in a transition zone between warm temperate and tropical regions. This island chain is providing a valuable system to analyze the effect of environmental heterogeneity on the spatial patterns of subtidal assemblages. The structure and composition of macroalgal assemblages at shallow rocky bottoms exhibit differences at island level (large scale), between shores with different wave exposure (medium scale) and bottoms with distinct degree of sedimentation, substrata and depth (small scale). Although it was predicted that seaweed assemblages would vary along the islands chain following the temperature gradient, this study highlights the importance of herbivore density, over water temperature, as the major driver of the structure of these subtidal assemblages. Future research is required on the environmental factors affecting the main seaweed assemblages (*Lobophora variegata* dominated beds and nongeniculate coralline bottoms) in habitats with different sea urchins densities, including a more

detailed spatial and temporal approach of the structure and composition of assemblages. Knowing relationships between environmental factors and biological descriptors are important for obtaining information on the current status of Canarian rocky seaweed assemblages and to recognize future changes along the longitudinal temperature gradient.

## 5. Conclusions

The current distribution of subtidal rocky seaweed assemblages along the seawater temperature gradient where the Canary Islands are placed depends on a set of environmental and biological factors. Although sea urchin density has resulted to be the factor explaining the highest percentage of variation in composition and cover of subtidal seaweed assemblages, the expected pattern of distribution (Fucales-dominated assemblages towards the eastern islands versus Dictyotales-dominated assemblages towards the western islands) according to the longitudinal thermal gradient is modified by herbivores, and only evident in protected areas and highly exposed shores.

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## Appendix. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecss.2011.07.004.

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