

Spatial patterns and response to wave exposure of shallow water algal assemblages across the Canary Archipelago: a multi-scaled approach

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ABSTRACT: We conducted a mensurative survey to investigate spatial variability and the effect of wave exposure at a range of spatial scales including islands (100s of km apart), locations within islands (10s of km apart), and sites within locations (100s of m apart), on the composition, abundance and distribution of shallow water algal assemblages across subtidal hard bottoms of the Canary Archipelago (eastern Atlantic). A multi-scaled hierarchical sampling design provided the framework for quantifying the variation among samples due to spatial scale and level of wave exposure. Randomly placed 50 × 50 cm squares were deployed in shallow rocky-reefs to assess community structure and dominance. Non-parametric multivariate techniques, as well as univariate tests, provided evidence to collectively suggest that shallow water algal assemblages differed between protected (leeward) and exposed (windward) shores, with a consistency of effects across islands, while different spatial scales were also involved in the variability and patchiness of these assemblages. In this sense, differences were clearly taxon and/or group-specific. In general, the presence and abundance of frondose furoid species was greater on exposed shores than on protected shores, whereas turf-algae dominated along the protected shores of each island. Dissimilarities between islands with regard to the overall algal assemblage generally increased with the distance between islands. In particular, the presence and abundance of furoid species was greater in the eastern islands, while turf and bush-like algae increased in the western islands. The large-scale gradient of the oceanographic conditions in an east-to-west direction across the Canary Archipelago provided a partial explanation for this observation although some inconsistencies were observed in the overall regional pattern.

KEY WORDS: Algae · Phytobenthic assemblages · Hierarchical design · Spatial variability · Wave exposure · PERMANOVA · Canary Islands

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INTRODUCTION

Differences in environmental conditions play an important role in landscape heterogeneity at different scales ranging from local patchiness to variation along biogeographic gradients (Levin 1992, Tilman & Kareiva 1997, Fraschetti et al. 2001, 2005, Garrabou et al. 2002). Consequently, linkages across multiple scales are increasingly being considered by ecologists (Brown 1995, Fraschetti et al. 2005). The use of macroecology to reconcile biogeography and ecology has

hitherto focused mainly on terrestrial systems (Boero 1999), with rare applications of these concepts to marine habitats (Fraschetti et al. 2001). Most studies have focused on a narrow range of spatial scales in a limited number of habitats (Fraschetti et al. 2005). In this sense, linkages between local geography and ecological features have seldom been considered with respect to the composition, distribution and structure of subtidal assemblages on rocky reefs.

The main biological engineers of temperate rocky reefs are macroalgae (Steneck et al. 2002, Graham

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2004). The existence of algae is influenced by pre-recruitment processes (Hoffmann & Ugarte 1985, Andrew & Veijo 1998, Coleman 2003), environmental conditions (e.g. wave exposure) (Santelices 1990, Coleman 2003, Taylor & Schiel 2003), post-recruitment biotic processes (Underwood & Jernakoff 1981, Jernakoff 1983, Benedetti-Cecchi & Cinelli 1994), and physical stress and disturbance (Kennelly 1987, Kendrick 1991). The role played by different processes operating at different scales in the composition, distribution and structure of algal assemblages is a growing field of interest, and remains largely untested in the majority of coastal areas (Fraschetti et al. 2005). In this context, hierarchical spatially structured sampling programs provide a means of partitioning and quantifying the magnitude of variation at different spatial scales (Underwood & Chapman 1996, Underwood 1997, Menconi et al. 1999, Benedetti-Cecchi 2001, Benedetti-Cecchi et al. 2003, Anderson & Millar 2004, Dethier & Schoch 2005, Frascchetti et al. 2005).

The Canary Islands lie between 100 and 600 km off the north-west coast of Africa (~28°N) and comprise 7 major islands, as well as a group of small islets (Chinijo Archipelago) (Fig. 1). Nearshore waters of north-western Africa are characterized by almost year-round wind-driven upwelling that brings cold, nutrient-rich sub-surface waters to the surface, extending as a 50 to 70 km band along the shore (Davenport et al. 2002). Consequently, the Canarian Archipelago lies in the transition between the oligotrophic open ocean and the northwest African upwelling (so-called Northwest African Coastal Transition Zone [NACTZ]). Large spatial variation in sea surface temperature (SST) occurs across an east–west gradient perpendicular to the African coast (Davenport et al. 2002), with an average difference of 2°C between the eastern and western islands (Barton et al. 1998, Davenport et al. 2002). As a result, marine assemblages for islands 100s of km apart are subjected to different oceanographic conditions and regimes of ‘bottom-up’ effects (sensu Menge 2000) that produce qualitative and quantitative differences between the eastern and western islands, as has been observed for demersal fish (Tuya et al. 2004a). At the same time, persistent trade winds induce strong turbulence (swell and wind) on exposed north and northeast facing shores, while south and southwest facing shores are more sheltered.

Islands have provided valuable systems to test hypotheses about the effect of environmental hetero-

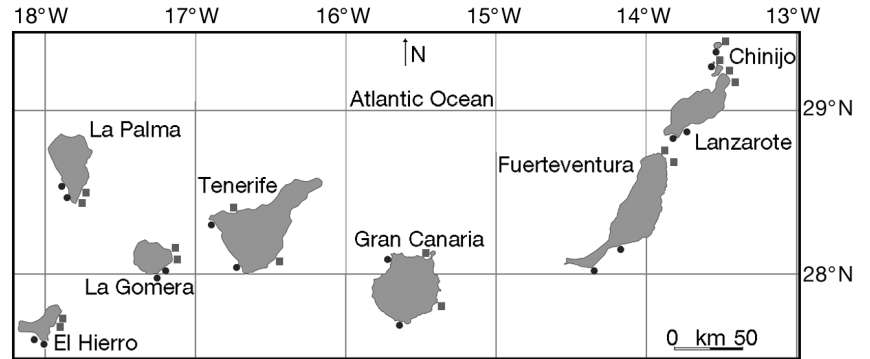


Fig. 1. Study locations within islands. ●: locations protected from the NE-swell. ■: locations exposed to the NE-swell

geneity on the spatial patterns of natural subtidal assemblages (Benedetti-Cecchi et al. 2003, Lindgarth & Gamfeldt 2005, Micheli et al. 2005). We took advantage of the natural conditions across the Canarian Archipelago to assess the role played by environmental factors in determining the composition, structure and organization of shallow water algal assemblages on rocky reefs. In this sense, we conducted a mensurative, multi-scaled, observational experiment (sensu Underwood 1997, Anderson & Millar 2004, Frascchetti et al. 2005) to study the effects of: the degree of wave exposure and spatial variability associated with a hierarchy of spatial scales—ranging from (1) islands (100s of km apart), to (2) locations within islands (10s of km apart), and (3) sites within locations (100s of m apart)—on the composition, abundance and distribution of shallow water algal assemblages in a regional context (<1000 km). More specifically, we tested the hypothesis that the role of wave exposure is significant in determining the structure and organization of shallow water algal assemblages, and assessed the consistency of this pattern across the islands constituting the Canarian Archipelago. Since frondose furoid algae may be considered as temperate-water elements of the shallow subtidal zone (Lüning 1990, Steneck et al. 2002), whereas turf and bush-like algae are more common in tropical waters (Lüning 1990), we additionally hypothesized that the presence and abundance of furoid algae should be greater in the eastern islands, while turf and bush-like algae should increase in the western islands. Algae can be expected to be more susceptible to disturbance by wave action and/or be less able to recover after disturbance, when other factors make the environment stressful. As a result, we predicted that the effects of wave exposure would interact with variability among islands, and that the different algal taxa and/or algal groups would show different patterns in this regard.

MATERIALS AND METHODS

Area of study and sampling design. The study was carried out on basaltic rocky bottoms between 2 and 8 m deep on the Canarian Archipelago (28°N, eastern Atlantic Ocean), during March 2005. In this region, the long-spined black sea urchin *Diadema antillarum* (Philippi) plays a key role in the structure of subtidal rocky reefs (Tuya et al. 2004a), transforming areas previously covered by erect algae to unvegetated substrates. In general, water turbulence inhibits considerably the presence of *D. antillarum* within the first meters of the subtidal throughout the eastern Atlantic (Alves et al. 2001). As a result, the distribution of benthic communities along the bathymetric axis usually shows a clear vertical zonation pattern. Within the shallowest zone, extensive stands of algal assemblages dominate the community, with a scarce presence of *D. antillarum* (densities typically range between 0 and 1 ind. m⁻²). Intensive grazing by *D. antillarum* produces clear interfaces between these shallow water algal stands and deeper areas devoid of vegetation (densities usually range between 2 and 12 ind. m⁻², Tuya et al. 2004a). The contribution of other herbivorous fauna to the organization of subtidal reefs is negligible compared to *D. antillarum* (Tuya et al. 2004b). For example, echinoid species such as *Paracentrotus lividus* or *Arbacia lixula* are found at low densities across all the Canary Islands, in contrast to the nearby Mediterranean Sea.

Responses of algae to environmental variability are best tested using a functional group approach rather than specific species (Steneck & Dethier 1994). Fleshy, canopy-forming, algae were categorized into 3 morphological groups, taking into account the algal form groups reported in the literature (Steneck & Dethier 1994, Fowler-Walker & Connell 2002, Garrahou et al. 2002, McClanahan et al. 2003), especially those from the nearby Mediterranean (Ruitton et al. 2000), as well as on our own experience. Turf algae (TA) consist of small cushion-shaped and filamentous species, usually <5 cm in height, such as *Codium* spp., *Colpomenia sinuosa*, *Dasycladus vermicularis* and, principally, *Lobophora variegata*. Bush-like algae (BA) are sheet-shaped, jointed non-crustose calcareous and thick, leathery species (e.g. *Asparagopsis* spp., *Corallina elongata*, *Dyctiota* spp., *Padina pavonica*, *Stypocaulon scoparium*, *Styopodium zonale*, *Taonia atomaria*, *Zonaria tournefortii*, etc.), from 1 to 15 cm in height, which constitute either large algal cushions or thin sheets with mixtures of algal species. Corticated, large, canopy-forming brown macrophytes (BM) are erect, frondose, coarsely branched fucoid species (the genera *Cystoseira* and *Sargassum*), usually >15 cm in height, and

in general forming low diversity algal stands. Understorey algae were excluded from the surveys as their coverage is hard to determinate, and a meticulous investigation of the whole substratum is too time-consuming. However, crustose coralline algae (e.g. the genera *Lithothamnion*, *Lithophyllum*, *Neogoniolithon*, *Titanoderma*, etc.) were counted when not overgrown by other algae.

Our sampling design tested the effect of the degree of wave exposure to the dominant, trade wind induced NE swells (categorized as high versus low exposure, i.e. exposed or windward versus protected or leeward shores; see Lindegarth & Gamfeldt 2005 for a discussion of this topic) around each of the 7 islands constituting the Canary Islands, as well as a group of small islets, the 'Chinijo Archipelago', to the north of Lanzarote (Fig. 1). We selected a total of 32 locations across the Canarian Archipelago as spatial replicates of the 16 defined treatments (2 degrees of wave exposure × 8 islands), with 2 locations (10s of km apart) per treatment (Fig. 1). Exposed locations directly received the prevailing swells and winds from the northeast, whereas protected locations lay to the south, on the opposite side of each island (Fig. 1). Swells from the south are significantly rarer (Martín Ruiz 2001). Additionally, we surveyed 2 randomly selected sites between 10 and 100 m apart within each location. As a result, a hierarchical, structured, sampling design (sensu Underwood 1997, Fraschetti et al. 2005) provided the framework for quantifying the variation among samples due to 3 spatial scales and 2 levels of wave exposure at a regional scale (<1000 km).

Sampling and data analysis. At each site, a SCUBA-diver quantified *in situ* the percent cover of algae in four 50 × 50 cm squares (0.25 m²), following point-square procedures with a grid of 121 points per square. Squares, several meters apart, were randomly laid out. This is a rapid, non-destructive technique used to assess community structure and dominance of sessile biota (Fowler-Walker & Connell 2002, McClanahan et al. 2003). Final values for each taxon were expressed as percentages. Taxa present in less than a 4% cover were omitted. Unidentified filamentous turf consisted principally of red algae belonging to the families Ceramiaceae and Rhodomelaceae.

Hypotheses were tested using multivariate and univariate procedures. To test for differences in the algal community caused by the 2 levels of wave exposure across the hierarchy of spatial scales, we selected non-parametric approaches (Anderson 2001, Anderson & Millar 2004), and applied a mixed analysis technique by combining the semi-parametric, distance based, Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson 2004), and non-metric multidimensional scaling (MDS) ordination (PRIMER soft-

ware; Clarke & Warwick 1994). In both cases, data were transformed to square root and analyses were based on Bray-Curtis dissimilarities. The PERMANOVA incorporated the following factors: (1) 'Wave Exposure' (fixed factor with 2 levels: protected versus exposed), (2) 'Island' (fixed factor with 8 levels corresponding to the 7 islands plus Chinijo Archipelago, and orthogonal to the previous factor), (3) 'Locations' (random factor with 2 levels, nested within the interaction term between 'Islands' and 'Wave exposure') and (4) 'Sites' (random factor with 2 levels, nested within the interaction term between 'Locations', 'Islands' and 'Wave exposure'). PERMANOVA was used to partition variability and provide measures of multivariate variability at different scales in the structured design in a manner analogous to univariate partitioning using ANOVA (Anderson & Millar 2004, Frascchetti et al. 2005). We applied this technique to the overall community dataset, as well as to each of the 3 defined morphological groups of algae. When appropriate, pairwise *a posteriori* comparisons were executed using permutations (Anderson 2004).

To visualize multivariate patterns, non-metric MDS ordinations were carried out. The MDS was applied to 3 different scenarios, gradually increasing the complexity of the analysis: First, we analyzed the algal community structure by considering only the 16 established treatments (8 islands \times 2 levels of wave exposure) by pooling the overall data within each treatment; second, we included replicated locations within each treatment; and third, we included replicated sites within locations for each treatment. Stress values are a measure of goodness of fit of data points in the MDS, and stress equals zero when data are perfectly represented (Clarke & Warwick 1994). If the stress levels are greater than 0.2, plots are considered difficult to interpret. Since an acceptable stress value (<0.14) was only obtained for the first scenario, this was the only analysis we used.

The SIMPER procedure (Clarke & Warwick 1994) was carried out to assess average similarities and dissimilarities within and between treatments, respectively, as well as to identify the contribution of each algal taxon to the differences within and between levels of wave exposure and islands. As a result, prominent taxa contributing to differences between treatments were identified and used in subsequent univariate analyses.

A mixed 4-factor ANOVA univariate model (Underwood 1997) was applied to each of the 3 groups of algae, as well as to the prominent taxa detected by the SIMPER protocol, to test for significant differences attributable to the factors discussed above. Hence, ANOVAs tested the same hypotheses described above for multivariate data, but in a univariate context. When the fac-

tor 'Islands' was significant for some of the ANOVAs, pairwise *a posteriori* Student-Newman-Keuls (SNK) tests were used. Before analysis, the Cochran's test was used to check for homogeneity of variances. Although no transformation rendered homogeneous variances in the majority of cases (Cochran's test, $p < 0.01$), ANOVA was carried out as it is robust to heterogeneity of variances, particularly for large, balanced experiments (Underwood 1997). The significance level was thus set at 0.01 instead of at 0.05 (Underwood 1997).

Finally, we assessed the geographical affinities in the composition and structure of algal assemblages across the Canarian Archipelago by means of a correlation analysis between the average pairwise dissimilarities matrix among islands for the entire dataset and a pairwise matrix containing the minimum lineal distances (in km) between each pair of islands. We used the pairwise average dissimilarities matrix output from both the SIMPER procedure and the PERMANOVA.

RESULTS

A total of 39 algal taxa were observed in the 256 squares conducted at the 32 study locations (Appendix 1, available at www.int-res.com/articles/suppl/m311p015_app.pdf). The prominent taxa within the TA were, in decreasing order, *Lobophora variegata* (40.6% of 256 squares), unidentified filamentous turf (38.6%) and *Jania* spp. (32.4%). The BA group was mainly dominated by *Dyctiota dichotoma* (68.7%), *Padina pavonica* (31.6%) and *Asparagopsis* spp. (21.9%). Finally, the BM group was represented by *Cystoseira* spp. (21.9%) and *Sargassum* spp. (11.3%).

Multivariate analysis

Multivariate techniques revealed large and significant differences in the composition and structure of the algal community for the different factors. Firstly, the multivariate ANOVA performed on the entire algal dataset (Table 1) detected significant variability at the 3 spatial scales considered in our study: differences between islands, differences between locations within each island and level of wave exposure, and differences between sites at the same location within each island and level of wave exposure ($p < 0.001$, Table 1). Significant variability attributable to differences in the degree of wave exposure was found ($p = 0.01$, Table 1); the effect of wave exposure was otherwise consistent across the islands (Table 1, 'I \times WE', $p > 0.05$). Secondly, the 2-dimensional MDS (Fig. 2, stress value = 0.09) revealed a separation of the treatments along the ordination diagram, with the eastern islands (Chinijo,

Table 1. PERMANOVA analysis of the effects of islands (fixed), wave exposure (fixed and orthogonal), locations (random and nested within islands and both levels of wave exposure), and sites (random and nested within locations, islands and levels of wave exposure) on the multivariate algal assemblages. p-values were obtained using 4999 random permutations (perm). I: islands, WE: wave exposure, Lo: location, CH: Chinijo, LZ: Lanzarote, FV: Fuerteventura, GC: Gran Canaria, TF: Tenerife, GO: Gomera, LP: La Palma, EH: El Hierro. Pairwise *a posteriori* comparisons for turf algae: EH>GO; EH>TF; EH>GC; EH>CH; LP>GO; LP>TF; LP>CH; GC>GO; FV>GO; FV>TF

Source of variation	df	Overall algal dataset			Brown macrophytes			Turf algae			Bush-like algae		
		MS	F	p(perm)	MS	F	p(perm)	MS	F	p(perm)	MS	F	p(perm)
I	7	33008.85	3.9300	0.0002	8821.11	1.4240	0.1900	29818.99	3.3717	0.0010	17632.73	1.5323	0.0230
WE	1	25228.32	3.0061	0.0124	48821.18	7.8814	0.0010	20309.00	2.2964	0.0480	16408.93	1.4260	0.1810
Locations (I × WE)	16	8392.32	6.5029	0.0002	6194.44	2.8576	0.0010	8843.78	2.6911	0.0010	11507.23	3.1114	0.0010
Sites (Lo (I × WE))	32	1290.55	2.6304	0.0002	2167.68	2.5944	0.0010	3286.32	1.2498	0.0190	3698.43	1.3257	0.0010
I × WE	7	8119.42	0.9675	0.5264	6473.99	1.0451	0.4220	9805.97	1.1088	0.3290	13786.41	1.9181	0.2020
Residual	192	490.6209			835.52			2629.50			2789.77		

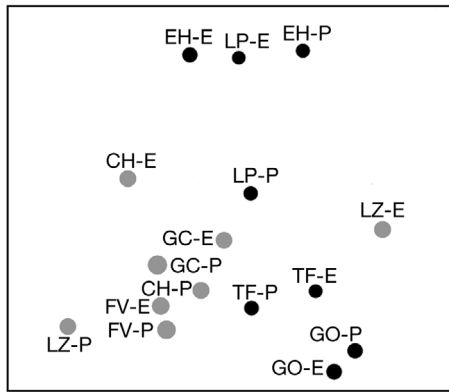


Fig. 2. MDS plot comparing the composition and structure of shallow water algal assemblages for each island and level of wave exposure. P: protected, E: Exposed, CH: Chinijo, LZ: Lanzarote, FV: Fuerteventura, GC: Gran Canaria, TF: Tenerife, GO: Gomera, LP: La Palma, EH: El Hierro. ●: western islands; ●: eastern islands

Lanzarote, Fuerteventura and Gran Canaria) falling in the left side of the plot, with the exception of exposed locations in Lanzarote (LZ-E in Fig. 2); whereas the western islands (Tenerife, Gomera, La Palma and El Hierro) were positioned in the right side of the plot.

Several islands (Fuerteventura, Gran Canaria, Tenerife and Gomera) had similar assemblages in both protected and exposed locations, while the rest of the islands showed a clearer distinction between protected and exposed locations in the ordination space (Fig. 2). *A posteriori* permutational tests among islands revealed a total of 10 significant differences for the 28 possible comparisons (p for Monte Carlo < 0.01), with 8 significant differences including El Hierro or La Palma. This result was indicative of the different composition, abundance and structure of the algal assemblages of these 2 islands compared to the rest of the islands. Moreover, the MDS plot also revealed this difference (Fig. 2), with the majority of locations on El Hierro and La Palma positioned at the top of the plot.

However, we found group-specific results when we analyzed the results of the PERMANOVA for each algal group (Table 1). Coverage of the BM group was significantly greater on exposed shores than on protected shores (p < 0.01, Table 1) for all islands (Table 2, Island × wave exposure ('I × WE'), p > 0.05); while TA cover differed among islands (p < 0.01, Table 1), a finding which was corroborated by some significant pairwise comparisons (Table 1). In all cases, we detected substantial variability at the medium (differ-

Table 2. Analysis of the effects of islands (fixed), wave exposure (fixed and orthogonal), locations (random and nested within islands and both levels of wave exposure), and sites (random and nested within locations, islands and levels of wave exposure) on the mean percent coverage of the 3 algal morphological groups. I: islands, WE: wave exposure, *p < 0.01. Acronyms for islands as in Table 1. *A posteriori* SNK tests for turf algae: LP EH GC>CH>FV GO TF LZ; for bush-like algae: LZ FV GC TF>GO CH LP EH

Source of variation	df	Brown macrophytes		Turf algae		Bush-like algae	
		MS	F	MS	F	MS	F
I	7	0.0777	1.58	0.2448	5.48*	0.3256	4.02 (p = 0.01)
WE	1	0.5036	10.22*	0.4399	9.85*	0.0002	0.00
Locations (I × WE)	16	0.0493	8.15*	0.0447	5.38*	0.0811	18.36*
Sites (Locations (I × WE))	32	0.0060	1.79*	0.0083	1.51	0.0044	1.02
I × WE	7	0.0490	0.99	0.0620	1.39	0.0750	0.92
Residual	192	0.0034		0.0055		0.0043	

ences between locations) and small (differences between sites) spatial scales ($p < 0.01$, Table 1).

SIMPER analysis indicated that the average similarity among protected locations (38.46%) was greater than the average similarity among exposed locations (28.80%), suggesting a greater heterogeneity of exposed algal assemblages. Eight taxa contributed extensively to the differences between both levels of wave exposure, accounting for 57.97% of the overall dissimilarity (Appendix 2, available at www.int-res.com/articles/suppl/m311p015_app.pdf). In general, these taxa, as well as the fucoids *Cystoseira mauritanica* and *Sargassum* spp., accounted for dissimilarities among islands, although the relative importance of each taxon varied for each pair of comparisons (Appendix 2).

Average dissimilarities between pairs of islands were significantly correlated with the lineal distances in km between them ($r_s = 0.49$, $0.001 < p < 0.01$ using the results from the SIMPER procedure; $r_s = 0.36$, $0.01 < p < 0.05$ using the results from the PERMANOVA).

Univariate analyses

Mean percentage covers across the study area (islands, locations within islands, and sites within locations) for 3 defined algal groups: TA, BA and BM are shown in Figs. 3, 4 & 5, respectively. Results from the ANOVAs performed on the 3 groups are presented in Table 2. Although the ANOVAs indicated a significant effect of the variability between sites, 10s of m apart, within locations for the BM only, we detected substantial spatial heterogeneity at the medium spatial scale (differences between locations, 10s of km apart, within each island and level of wave exposure) for the 3 morphological groups ($p < 0.01$, Table 2). This considerable variability prevented the detection of significant differences caused by some of the 2 main effects in the 3 ANOVAs. However, the power of the ANOVAs was sufficient to reject some null hypotheses. In this sense, the BM group was significantly more abundant on exposed shores ($p < 0.01$, Table 2, Fig. 5), whereas the TA group was more abundant on protected shores ($p < 0.01$, Table 2, Fig. 3). In both cases, the effect of the

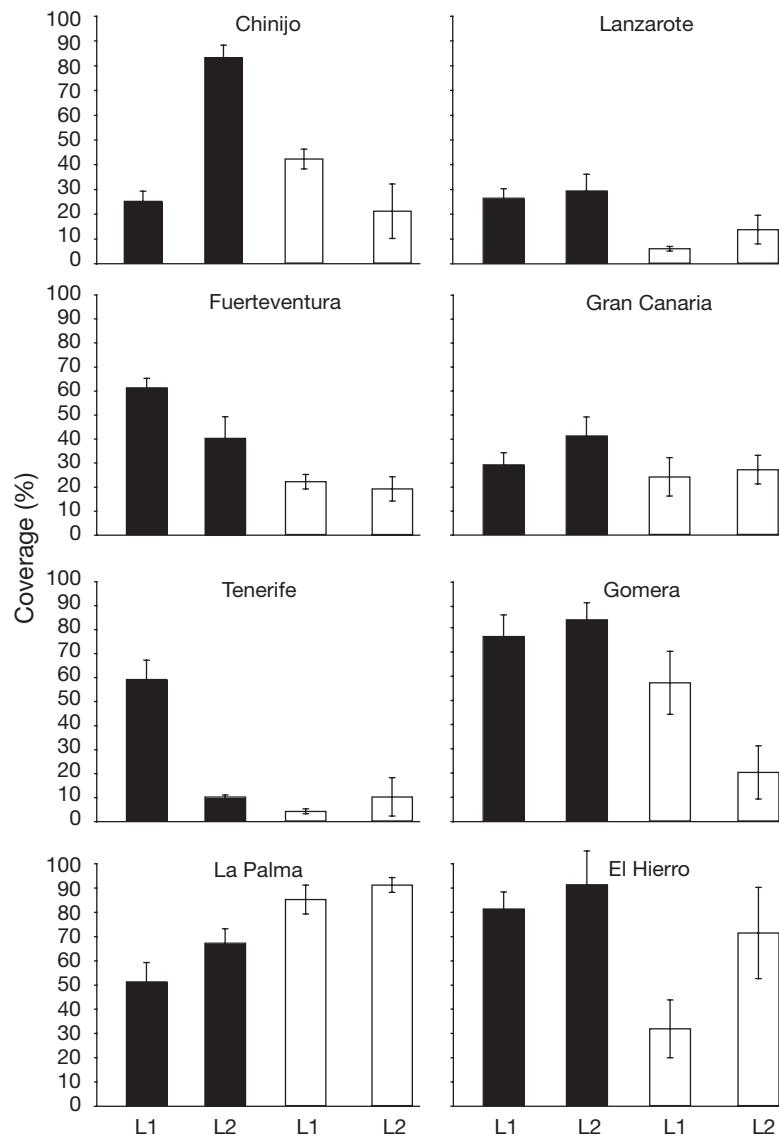


Fig. 3. Turf algae. Mean percentage cover across the study area. Black bars: protected locations (L1 and L2), white bars: exposed locations (L1 and L2). Error bars are mean \pm SE

'wave exposure' was consistent across the islands (Table 2, 'I \times WE', $p > 0.05$). Significant differences caused by the different islands were not detected for BM ($p > 0.01$, Table 2), although visual inspection of the results (Fig. 5) suggests the existence of differences. In contrast, significant differences caused by 'Islands' were detected for TA ($p < 0.01$, Table 2) and BA ($p = 0.01$, Table 2), and can be seen in Figs. 3 & 4. *A posteriori* SNK tests (Table 2) indicated that the TA group dominated the western islands, whereas BA dominated the central and eastern islands, with the exception of Chinijo Archipelago.

Results from the ANOVAs performed on the prominent algal taxa are presented in Table 3. Again, the

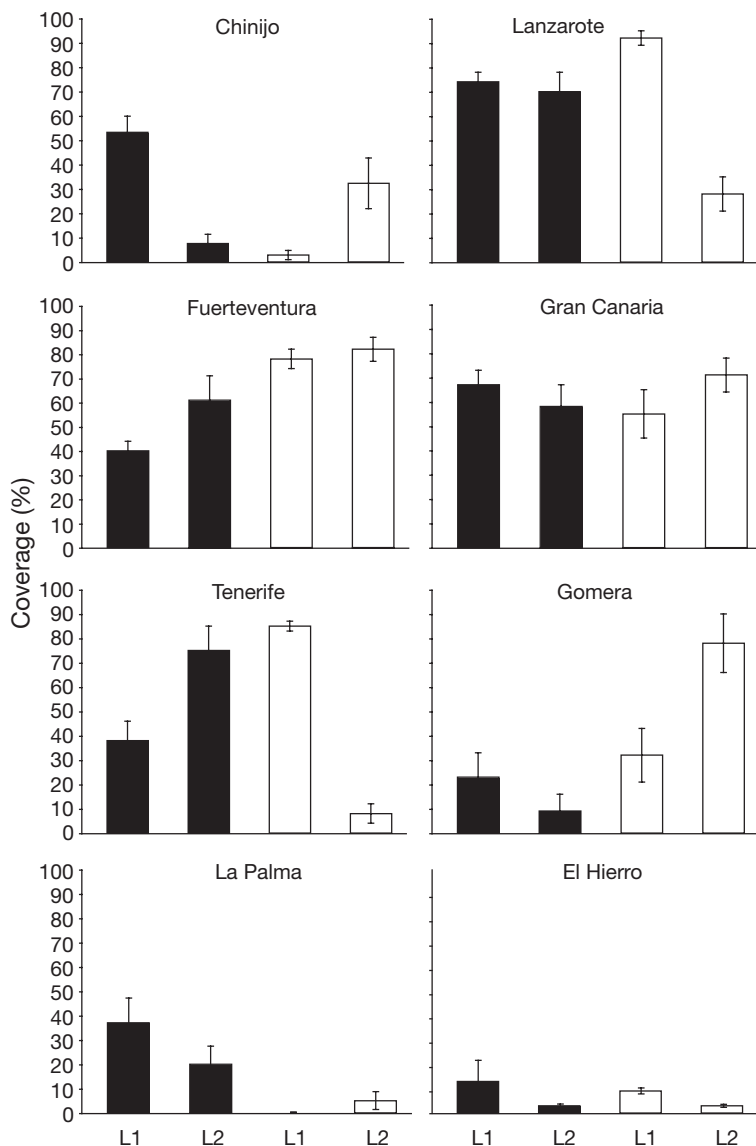


Fig. 4. Bush-like algae. Mean percentage cover across the study area. Black bars: protected locations (L1 and L2), white bars: exposed locations (L1 and L2). Error bars are mean \pm SE

analyses indicated substantial variability at the medium and low spatial scales (differences between locations 10s of km apart within each island and level of wave exposure, and between sites 10s of m apart within locations, respectively). Due to the variability between locations within each treatment, significant differences were only found between islands and between levels of wave exposure for *Lobophora variegata*, *Jania* spp., and the unidentified filamentous turf (Figs. 6, 7 & 8, respectively). *L. variegata* (Fig. 6) monopolized the rocky bottoms of both El Hierro and La Palma with mean percent coverages of up to 90% per location, and was significantly more abundant in these islands than in all other islands ($p < 0.01$,

SNK tests, Table 3). *Jania* spp. (Fig. 7) appeared to be more abundant in the eastern islands ($p < 0.01$, SNK tests, Table 3). Finally, the unidentified filamentous turf (Fig. 8) was significantly more abundant in Gomera and Tenerife than in the rest of the islands ($p < 0.01$, SNK tests, Table 3).

DISCUSSION

The presence of multiple islands along an oceanographic gradient with shores exposed to different hydrographic conditions provided an ideal opportunity to test hypotheses about the individual and combined effects of geographical and physical processes on entire subtidal shallow water algal assemblages. Collectively, the findings of this study showed that subtidal algal assemblages differ consistently between protected and exposed shores across the surveyed islands. Additionally, clear differences were observed between islands situated on opposite sides of the Canarian Archipelago.

The analysis of pattern in distribution and abundance of marine organisms has direct relevance to the identification of underlying causal processes (Benedetti-Cecchi et al. 2003 and references therein, Fraschetti et al. 2005). Biotic processes and behavior are usually implicated in the maintenance of small to medium scale spatial patchiness (e.g. differences between sites and locations separated by 100s of m to 10s of km), whereas oceanographic conditions and climate largely dictate regional, large-scale patterns operating over distances of 100s of km (Underwood & Chapman 1996, Menconi et al. 1999). Our

results support, in part, these conclusions. In particular, certain important group-specific differences within islands can be attributed to differences in levels of wave exposure, while significant differences at a regional scale (differences between islands 100s of km apart) were found for some groups and taxa.

Variability associated with differences in the level of wave exposure

The combined indirect and direct hydrodynamic effects of wave action on nearshore biota are often grouped under the term 'wave exposure' (Taylor &

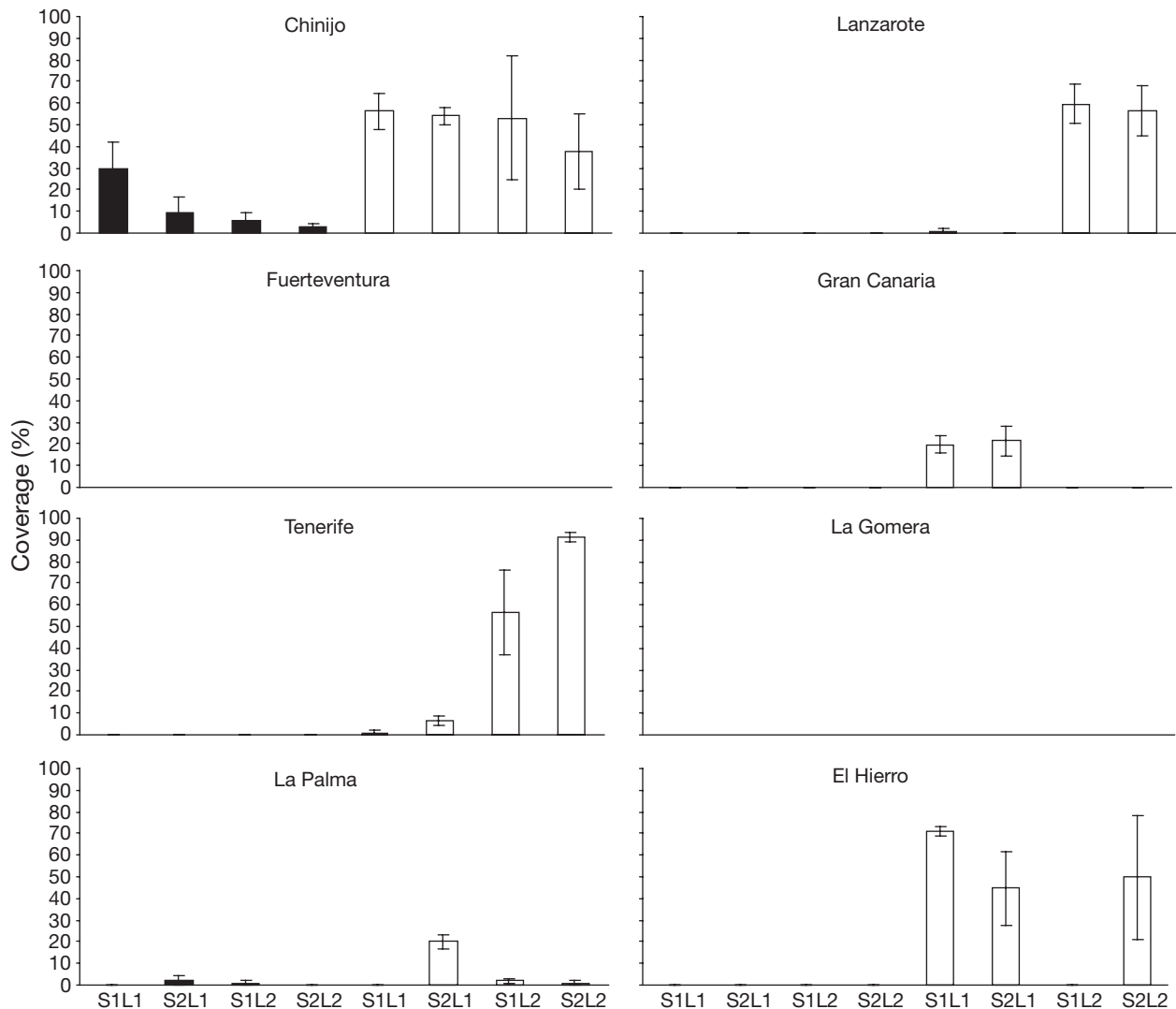


Fig. 5. Brown macrophytes. Mean percentage cover across the study area. Black bars: sites within protected locations (e.g. S1L1 denotes site 1 within location 1), white bars: sites within exposed locations. Error bars are mean \pm SE

Schiel 2003). Distinct patterns arose when the results of our study on the effect of 'wave exposure' were interpreted at a morphological group level. In general, the presence and abundance of species within the BM group (frondose furoid species) was clearly greater at exposed locations (mean coverage for all exposed locations = 22.00 ± 5.61 , mean \pm SE) compared to protected locations (mean coverage for all protected locations = 1.56 ± 1.07 , mean \pm SE). Subtidal furoid plants tend to be better adapted to exposed or semi-exposed conditions than other algal species in the Canary Islands (Medina & Haroun 1993, Haroun et al. 2003).

However, the ecological mechanisms underlying this difference are unknown. Variation in hydrographic conditions at the scales considered by our sampling design probably influence algal assemblages through

the temporal variability and intensity of swells and storms, and the release of propagules from the water column (Micheli et al. 2005). Usually, water motion (1) enhances nutrient uptake by reducing or breaking the boundary layer, (2) removes epiphytes and waste products, and (3) allows algal stands to use light more efficiently by stirring their fronds, ensuring that no frond is either always shaded or always in the sun (Diez et al. 2003 and references therein). These mechanical advantages are accompanied by a continued mechanical stress that only morphologically adapted species can resist. Algae in these disturbed environments are characterized by a flexible thallus and an efficient attachment mechanism, such as the basal disc of certain species belonging to the genera *Cystoseira* and *Sargassum*.

Table 3. Analysis of the effects of islands (fixed), wave exposure (fixed and orthogonal), locations (random and nested within islands and both levels of wave exposure), and sites (random and nested within locations, islands and levels of wave exposure) on the mean percent of coverage of selected algal species. Acronyms for islands as in Table 1. I: islands, WE: wave exposure *p < 0.01. *A posteriori* SNK tests for *Lobophora variegata*: EH LP>GC>CH FV LZ TF GO; for unidentified filamentous turf: GO TF>FV>GC LP CH LZ EH; for *Jania* spp.: FV GC>CH LZ>LP TF EH GO

Source of variation	df	<i>Lobophora variegata</i>		Unidentified filamentous turf		<i>Dyctiota dichotoma</i>		<i>Stypocaulon scoparium</i>		<i>Asparagopsis</i> spp.	
		MS	F	MS	F	MS	F	MS	F	MS	F
I	7	40.1578	23.88*	16.8451	4.80*	13.1876	3.63	0.0385	1.29	4.2593	3.42
WE	1	3.1696	1.88	51.8169	14.77*	0.7873	0.22	0.0078	0.26	0.1253	0.10
Locations (I × WE)	16	1.6819	5.30*	3.5074	4.52*	3.6322	15.84*	0.0298	22.05*	1.2458	1.27
Sites (Locations (I × WE))	32	0.3174	1.25	0.7758	2.26*	0.2293	0.86	0.0014	1.16	0.9833	4.51*
I × WE	7	3.0250	1.80	1.5045	0.43	1.6675	0.46	0.0240	0.81	3.1134	2.50
Residual	192	0.2546		0.3435		0.2680		0.0012		0.2178	
		<i>Jania</i> spp.		<i>Padina pavonica</i>		<i>Cystoseira abies-marina</i>		<i>Cystoseira mauritanica</i>		<i>Sargassum</i> spp.	
I	7	4.9245	6.02*	3.3948	1.27	0.1150	0.95	0.0164	1.62	0.0325	2.11
WE	1	1.6889	2.06	2.6661	1.00	0.3494	2.90	0.0038	0.38	0.0627	4.07
Locations (I × WE)	16	0.8180	3.77*	2.6696	28.64*	0.1206	31.14*	0.0101	7.95*	0.0154	4.91*
Sites (Locations (I × WE))	32	0.2167	1.29	0.0932	1.11	0.0039	2.03*	0.0013	0.98	0.0031	2.27*
I × WE	7	0.9106	1.11	1.1227	0.42	0.1150	0.95	0.0038	0.38	0.0243	1.58
Residual	192	0.1679		0.0839		0.0019		0.0013		0.0014	

Alternatively, this pattern could be related to anthropogenic perturbations. There is an increasing trend towards long-term, and perhaps permanent, loss of canopy-forming algae along human-impacted coasts (Russell & Connell 2005 and references therein). The loss of canopy-forming algae typically results in the immediate colonisation and spatial dominance of turf algae (Russell & Connell 2005). In this context, Benedetti-Cecchi et al. (2001) found that frondose, coarsely-branched algae were virtually absent from urban areas in the Mediterranean, having been replaced by turf-forming algae. These authors argued that this group of furoid algae (e.g. the genus *Cystoseira*) is highly sensitive to human disturbances. In the Canarian Archipelago, the most important urban areas associated with the tourist industry are located on the protected southern shores of each island (Martin-Ruiz 2001). As a result, the large number of sewage discharges, and subsequently the nutrient enrichment, along these human-disturbed areas could be one reason for the lack of BM in the protected locations of our study. It is possible that a combination of wave action and anthropogenic disturbance is important in this variability within each island. However, the lack of historical data on these assemblages and of any direct quantification of the intensity and distribution of disturbances on the islands make it impossible to conclusively link these observed patterns to human impacts.

The pattern detected for the BM group clearly contrasts with that observed for TA, and in particular, for the patterns observed for the unidentified filamentous turf group. As a general pattern, TA dominated protected locations within each island, with the exception of La Palma. For example, the unidentified filamentous turf group was twice as abundant in protected locations (coverage for all protected locations = 20.84 ± 5.70 , mean \pm SE) as in exposed locations (coverage for all exposed locations = 10.37 ± 4.03 , mean \pm SE) for the overall study. Consequently, our observations reinforce the findings of other investigations that have highlighted the important role played by wave exposure in shaping shallow marine benthic communities in temperate waters (Blanchette et al. 1999, Benedetti-Cecchi et al. 2003, Taylor & Schiel 2003, Lindegarth & Gamfeldt 2005, Micheli et al. 2005).

Variability at the medium and small spatial scale: differences within islands

In all cases analyzed by means of the multivariate ANOVAs, sampled locations within each island and level of wave exposure, as well as sites within locations, were quantitatively different. Considerable heterogeneity at these spatial scales highlights the complex nature of these assemblages; small-scale vari-

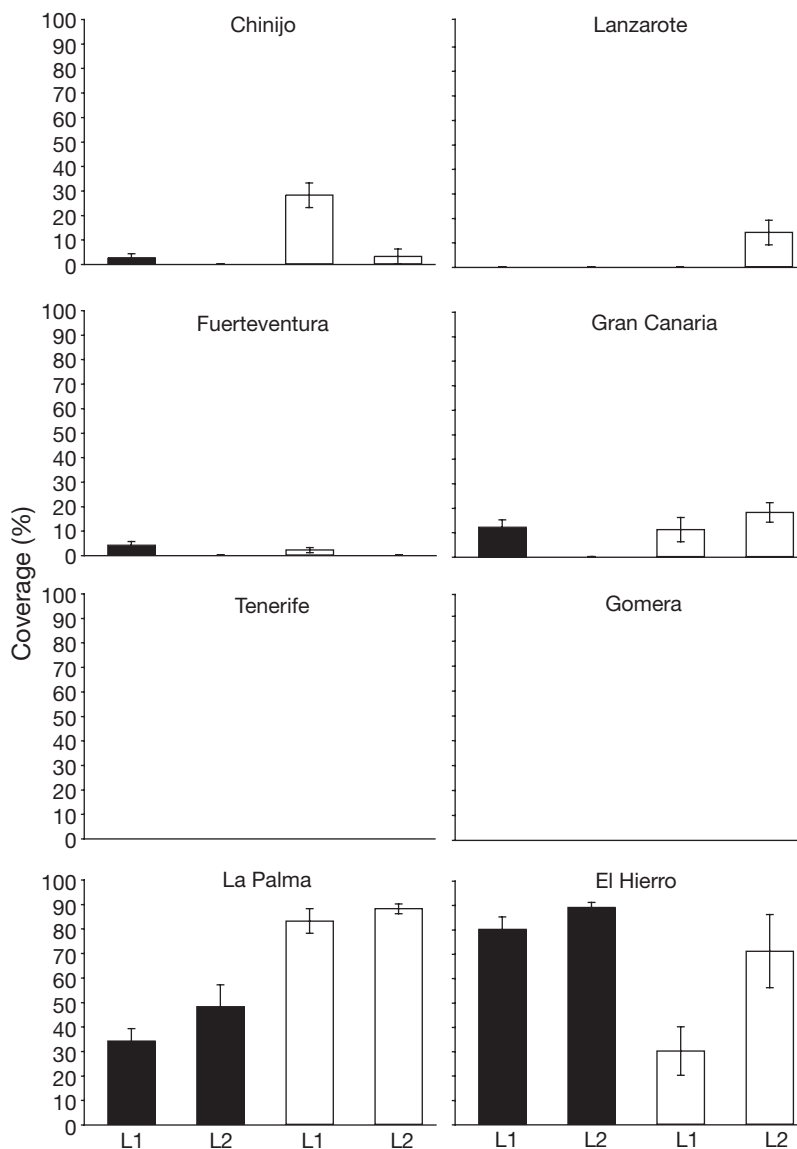


Fig. 6. *Lobophora variegata*. Mean percentage cover across the study area. Black bars: protected locations (L1 and L2), white bars: exposed locations (L1 and L2). Error bars are mean \pm SE

ability is a general property of benthic assemblages in marine coastal habitats (Underwood & Chapman 1996, Menconi et al. 1999, Benedetti-Cecchi 2001, Fowler-Walker & Connell 2002, Benedetti-Cecchi et al. 2003, Coleman 2003, Fraschetti et al. 2005). Differences between locations within each island and level of wave exposure were often as great as differences among islands or level of wave exposure. For some algal groups and taxa, variability at the location level probably obscured differences in cover between levels of wave exposure and islands. We can only speculate on the underlying causes of this variation, which are likely to involve complex interactions among several

physical (e.g. availability of resources, habitat attributes) and biological processes (e.g. competition, predation). Clearly, different explanations can be proposed for different taxa, according to their life-history strategies and biology.

Variability at the large spatial scale: differences between islands

Dissimilarities between islands for the overall subtidal algal community generally increased with the distance between islands. For example, El Hierro and La Palma, the westernmost islands, constituted a different assemblage 'block' from the rest of the islands. However, significant differences between islands were group, or more specifically, taxon-specific.

What are the underlying mechanisms that could account for differences between islands? Generally, differences in patterns of water circulation, availability of resources and type of substratum affecting recruitment, growth and mortality of algae have been proposed as explanations of variability at large spatial scales (from 10s to 100s of km) (Santelices 1990, Menconi et al. 1999). The large-scale gradient in oceanographic conditions, such as SST and nutrients, in an east-to-west direction across the Canarian Archipelago (Barton et al. 1998, Bode et al. 2001, Davenport et al. 2002) provides a possible explanation for this observation. Variation in oceanographic conditions usually results in differences in local productivity potential, which, in turn, can result in a visible and predictable change in the algal community (Steneck & Dethier 1994). In this context, our results agree with those of Schils and Coppejans (2003), who attributed differences in the composition, abundance and structure of subtidal algal communities in the Socotra Archipelago, Indian Ocean, to differences in SSTs and bottom-up resources caused by upwelling. The drawback of this approach is that islands may differ in other respects than differences in bottom-up availability of resources. Hence, caution is necessary in ascribing differences in the observed algal assemblages; causality can only be determined through experimental manipulation (Dulvy et al. 2004).

We hypothesized that the presence and abundance of fucoid species should be larger in the eastern

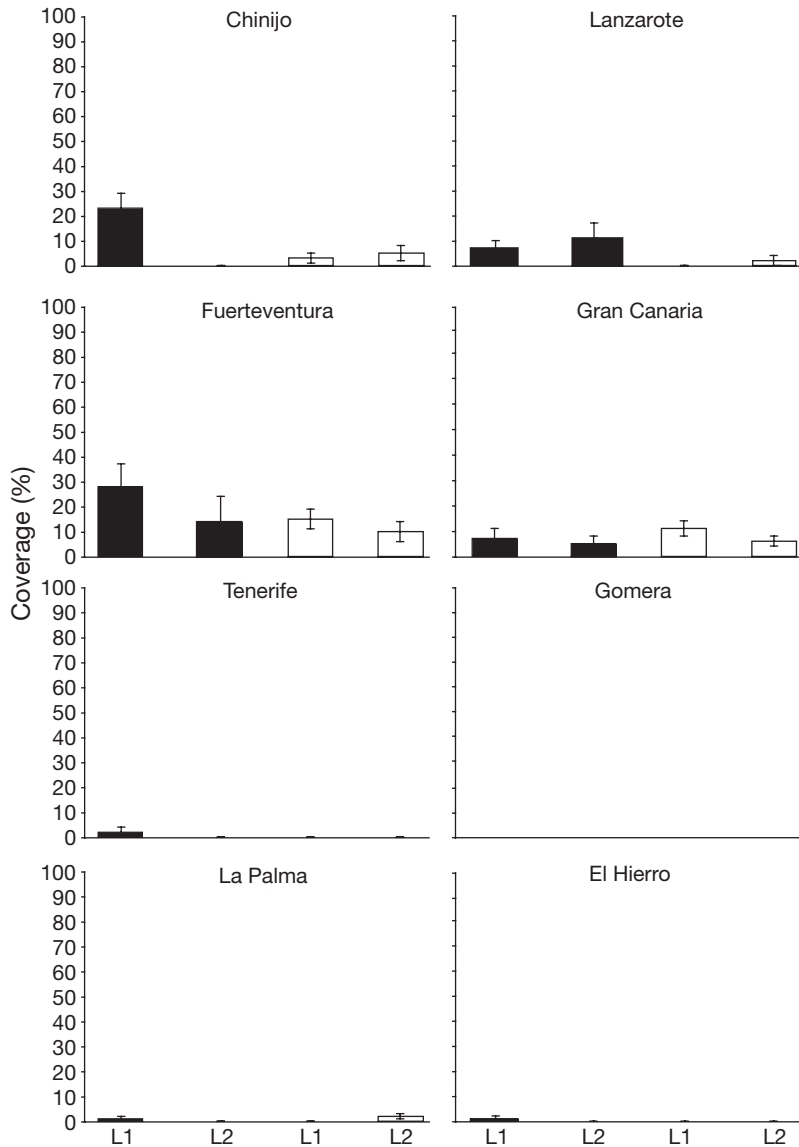


Fig. 7. *Jania* spp. Mean percentage cover across the study area. Black bars: protected locations (L1 and L2), white bars: exposed locations (L1 and L2). Error bars are mean \pm SE

islands, where SSTs are about 2°C lower than in the western islands, while the TA and BA groups should increase in the western islands. Our results generally support this pattern. For example, the furoid alga *Cystoseira mauritanica* was only recorded at Chinijo Archipelago; whereas turf algae, and particularly *Lobophora variegata*, were most abundant in the westernmost islands (El Hierro and La Palma). This result is consistent with the composition and structure of populations of the genus *Cystoseira* across subtidal and intertidal habitats of the Canary Archipelago (Medina et al. 1995, Haroun & Afonso-Carrillo 1997). Nevertheless, we found some inconsistencies in this

general pattern. For example, no furoid species (BM) were observed in Fuerteventura, while this algal group was relatively abundant in the westernmost island (El Hierro). The origin of the potential mechanisms explaining the 'temperate vs. tropical' differences in algal assemblages is unknown, though differences in the availability of 'bottom-up' resources apparently play an important role in explaining such differences. More work is desirable to empirically assess the reasons for this pattern.

Consequently, a generalization of patterns and the establishment of a regional framework for the composition, abundance and distribution of shallow water algal assemblages along the entire Canary Archipelago is complicated. Many environmental factors co-vary across large spatial gradients (Harley et al. 2003), making temperate rocky reef assemblages highly variable and dynamic at a regional scale (Micheli et al. 2005). Within-island variability also obscures the hypothesized regional pattern. As a result, increasing the spatial replication at the smallest spatial scales (replicated squares within sites, and sites within locations) would probably help to decrease the 'noise' associated with other sources of environmental variability. It is difficult to understand the generality of patterns in algal assemblages using a hierarchy of spatial scales covering <1000 km (Fowler-Walker & Connell 2002). We therefore suggest increasing the spatial scale of observation (>1000 km) to encompass a wider area of study along the warm-

temperate waters of the eastern Atlantic in the northern hemisphere. This approach would probably provide evidence of the existence of simple underlying rules (sensu Fowler-Walker & Connell 2002, Fraschetti et al. 2005) in the organization of shallow water algal assemblages.

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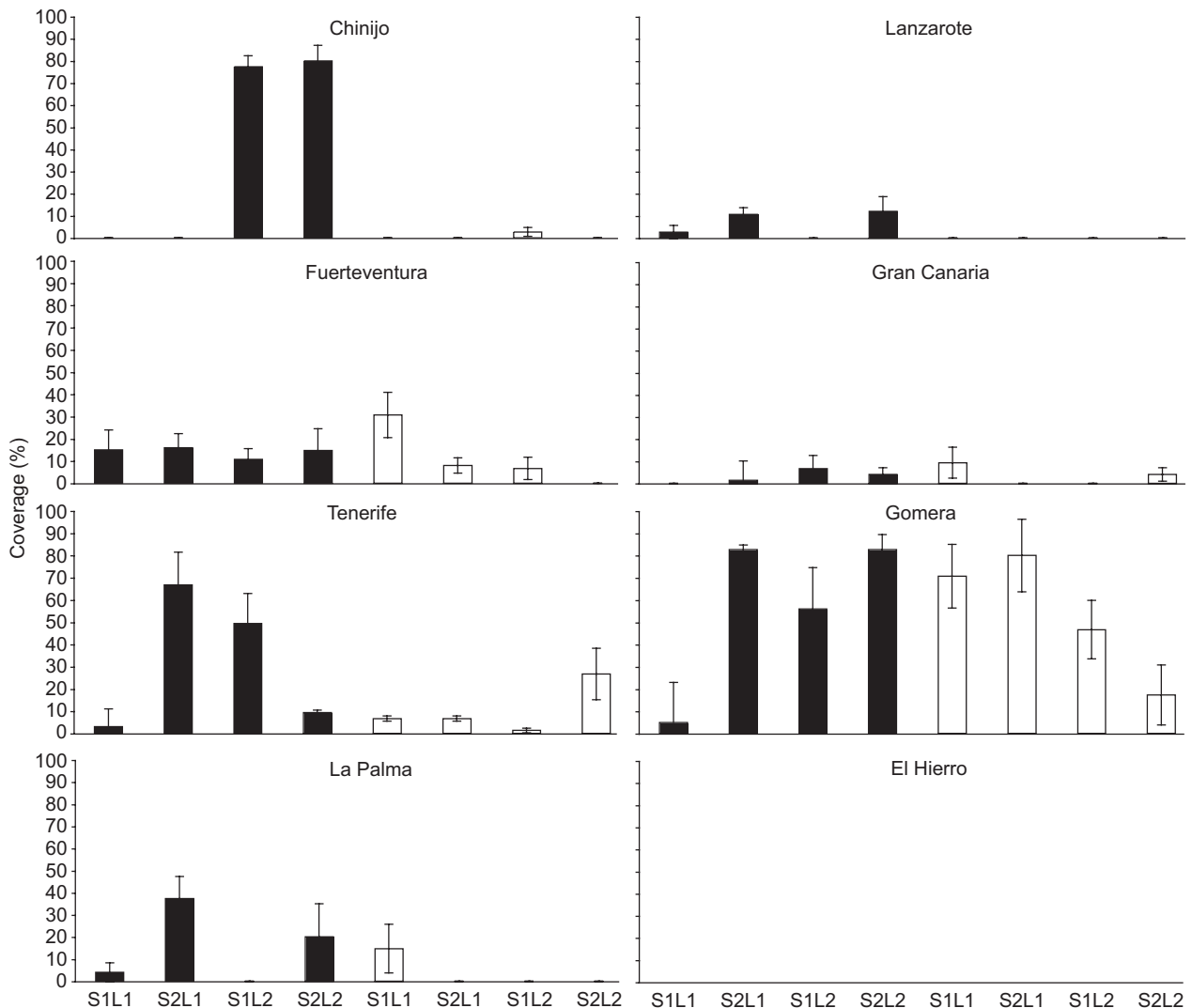


Fig. 8. Unidentified filamentous turf (red algae belonging to the families Ceramiaceae and Rhodomelaceae). Mean percentage cover across the study area. Black bars: sites within protected locations (e.g. S1L1 denotes site 1 within location 1), white bars: sites within exposed locations. Error bars are mean \pm SE

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