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## **Spatial patterns and response to wave exposure of shallow water algal assemblages across the Canarian Archipelago: A multi-scaled approach**

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1 **Spatial patterns and response to wave exposure of shallow water**  
2 **algal assemblages across the Canarian Archipelago: a multiscaled**  
3 **approach**

4  
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8  
9 Running Head: Organization of shallow water algae

10  
11 **ABSTRACT:** We conducted a mensurative survey to investigate spatial variability and the  
12 effect of wave exposure at a range of spatial scales including islands (100s of kilometres  
13 apart), locations within islands (10s of kilometres apart), and sites within locations (100s of  
14 meters apart), on the composition, abundance and distribution of shallow water algal  
15 assemblages across subtidal hard bottoms of the Canarian Archipelago (eastern Atlantic). A  
16 multi-scaled hierarchical sampling design provided the framework for quantifying the  
17 variation among samples due to each spatial scale and level of wave exposure. Haphazardly  
18 placed 50 x 50 cm quadrats were deployed in shallow rocky-reefs to assess community  
19 structure and dominance. Non-parametric multivariate techniques, as well as univariate tests,  
20 provided evidence to collectively suggest that shallow water algal assemblages differed  
21 between protected (leeward) and exposed (windward) shores, with a consistency of its effects  
22 across islands, while different spatial scales were also involved in the variability and  
23 patchiness of these assemblages. In this sense, differences were clearly taxon and/or group-

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24 specific. In general, the presence and abundance of frondose furoid species was greater at  
25 exposed shores compared to protected shores, whereas turf-algae dominated protected shores  
26 at each island. Dissimilarities between islands for the overall algal assemblage generally  
27 increased with the distance between islands. In particular, the presence and abundance of  
28 furoid species was larger in the eastern islands, while in contrast turf and bush-like algae  
29 increased in the western islands. The large-scale gradient of the oceanographic conditions in  
30 an east-to-west direction across the Canarian Archipelago provided a parsimonious  
31 explanation for this observation, yet some inconsistencies were observed in the overall  
32 regional pattern.

33

34 **KEY WORDS:** Algae • Phyto-benthic assemblages • Hierarchical design • Spatial variability •  
35 Wave exposure • PERMANOVA • Canary Islands

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37

## **INTRODUCTION**

38 Differences in environmental conditions play an important role in landscape heterogeneity at  
39 different scales, from local patchiness to variation along biogeographic gradients (Levin 1992,  
40 Tilman & Kareiva 1997, Fraschetti et al. 2001, Garrabou et al. 2002, Fraschetti et al. 2005).  
41 Consequently, linkages across multiple scales are increasingly being considered by ecologists  
42 (Brown 1995, Fraschetti et al. 2005). The use of macroecology to reconcile biogeography and  
43 ecology has focused mainly on terrestrial systems (Boero 1999), with scarce application of  
44 these concepts to marine habitats (Fraschetti et al. 2001); most studies have focused on a  
45 narrow range of spatial scales in a limited number of habitats (Fraschetti et al. 2005). In this  
46 sense, linkages between local geography and ecological features have seldom been considered  
47 for the composition, distribution and structure of subtidal assemblages on rocky reefs.

48 The main biological engineers of temperate rocky-reefs are macroalgae (Steneck et al. 2002,  
49 Graham 2004). The existence of algae is influenced by pre-recruitment processes (Hoffmann  
50 & Ugarte 1985, Andrew & Veijo 1998, Coleman 2003), environmental conditions (e.g. wave  
51 exposure) (Santelices 1990, Coleman 2003, Taylor & Schiel 2003), post-recruitment biotic  
52 processes (Underwood & Jernakoff 1981, Jernakoff 1983, Benedetti-Cecchi & Cinelli 1994),  
53 and physical stress and disturbance (Kennelly 1987, Kendrick 1991). The role played by  
54 different processes operating at different scales in the composition, distribution and structure  
55 of algal assemblages is a growing field of interest, and remains largely untested in the  
56 majority of coastal areas (Fraschetti et al. 2005). In this context, hierarchical spatially  
57 structured sampling programs provide a means of partitioning and quantifying the magnitude  
58 of variation at different spatial scales (Underwood & Chapman 1996, Underwood 1997,  
59 Menconi et al. 1999, Benedetti-Cecchi 2001, Benedetti-Cecchi et al. 2003, Anderson & Millar  
60 2004, Dethier & Schoch 2005, Fraschetti et al. 2005).

61 The Canary Islands lie between 100 and 600 km offshore from the north-west coast of Africa  
62 (~28°N) and comprise seven major islands, as well as a group of small islets (Chinijo  
63 Archipelago) (Fig. 1). Nearshore waters of north-western Africa are characterized by almost  
64 year-round wind-driven upwelling that brings cold, nutrient-rich sub-surface waters to the  
65 surface, extending as a 50–70 km band along shore (Davenport et al. 2002). Consequently, the  
66 Canarian Archipelago lies in the transition between the oligotrophic open ocean and the  
67 northwest African upwelling (so-called Northwest African Coastal Transition Zone  
68 [NACTZ]). Large spatial variation in sea surface temperature (SST) occurs across an east–  
69 west gradient perpendicular to the African coast (Davenport et al. 2002), with an average  
70 difference of 2°C between the eastern and western islands (Barton et al. 1998, Davenport et al.  
71 2002). As a result, marine assemblages at widely separated islands (100s of km) are subjected  
72 to different oceanographic conditions and regimes of 'bottom-up' effects (*sensu* Menge 2000),

73 that produce qualitative and quantitative differences between the eastern and western islands,  
74 as has been observed for demersal fish (Tuya et al. 2004a). At the same time, persistent trade  
75 winds induce strong turbulence (swell and wind) at exposed north and northeast facing shores,  
76 while south and southwest facing shores are more sheltered.

77 Islands have provided valuable systems to test hypotheses about the effect of environmental  
78 heterogeneity on the spatial patterns of natural subtidal assemblages (Benedetti-Cecchi et al.  
79 2003, Lindegarth & Gamfeldt 2005, Micheli et al. 2005). We took advantage of the natural  
80 conditions across the Canarian Archipelago to assess the role played by environmental factors  
81 in determining the composition, structure and organization of shallow water algal  
82 assemblages on rocky reefs. In this sense, we conducted a mensurative, multi-scaled,  
83 observational experiment (*sensu* Underwood 1997, Anderson & Millar 2004, Fraschetti et al.  
84 2005) to study the effects of: (i) the degree of wave exposure and spatial variability associated  
85 with a hierarchy of spatial scales ranging from (ii) islands (100s of kilometres apart), to (iii)  
86 locations within islands (10s of kilometres apart), and (iv) sites within locations (100s of  
87 meters apart) on the composition, abundance and distribution of shallow water algal  
88 assemblages at a regional context (< 1000 km). More specifically, we tested the hypothesis  
89 that the role of wave exposure is significant in determining the structure and organization of  
90 shallow water algal assemblages, and assessed the consistency of this pattern across the  
91 islands constituting the Canarian Archipelago. Since frondose furoid algae may be considered  
92 as temperate-water elements of the shallow subtidal zone (Lüning 1990, Steneck et al. 2002),  
93 whereas turf and bush-like algae are more common in tropical waters (Lüning 1990), we  
94 additionally hypothesized that the presence and abundance of furoid algae should be larger in  
95 the eastern islands, while in contrast turf and bush-like algae should increase in the western  
96 islands. Algae can be expected to be more susceptible to disturbance by wave action and/or  
97 have lower capabilities to recover after disturbance when other factors make the environment

98 stressful. As a result, we predicted that the effects of wave exposure would interact with  
99 variability among islands, and that the different algal taxa and/or algal groups would show  
100 different patterns in this regard.

101

102

## MATERIALS AND METHODS

103 **Area of study and sampling design.** The study was carried out on basaltic rocky bottoms  
104 between 2 to 8 m of depth at the Canarian Archipelago (28° N, eastern Atlantic Ocean),  
105 during March 2005. In this region, the long-spined black sea urchin, *Diadema antillarum*  
106 (Philippi), plays a key role on the structure of subtidal rocky reefs (Tuya et al., 2004a),  
107 transforming areas previously covered by erect algae to unvegetated substrates. In general,  
108 water turbulence inhibits considerably the presence of *D. antillarum* within the first meters of  
109 the subtidal across the eastern Atlantic (Alves et al. 2001). As a result, the distribution of  
110 benthic communities along the bathymetric axis shows usually a clear vertical zonation  
111 pattern. Within the shallowest zone, extensive stands of algal assemblages dominate the  
112 community with a scarce presence of *D. antillarum* (densities typically range between 0 to 1  
113 ind m<sup>-2</sup>). Intensive grazing by *D. antillarum* produces clear interfaces between these shallow  
114 water algal stands and deeper areas devoid of vegetation (densities usually range between 2 to  
115 12 ind m<sup>-2</sup>, Tuya et al. 2004a). The contribution of other herbivorous fauna to the organization  
116 of subtidal reefs is negligible compared to *D. antillarum* (Tuya et al. 2004b). For example,  
117 echinoid species such as *Paracentrotus lividus* or *Arbacia lixula* are found at low densities  
118 across all the Canary Islands, in contrast to the nearby Mediterranean Sea.

119 Responses of algae to environmental variability are best tested with a functional group  
120 approach instead of using specific species (Steneck & Dethier 1994). Fleshy, canopy-forming,  
121 algae were categorized into three morphological groups, by taking into account the algal form  
122 groups reported in the literature (Steneck & Dethier 1994, Garrabou et al. 2002, Fowler-

123 Walker & Connell 2002, McClanahan et al. 2003), especially those from the nearby  
124 Mediterranean (Ruitton et al. 2000), as well as our own experience. Turf algae (hereafter TA)  
125 consist of small cushion-shaped and filamentous species, usually < 5 cm in height, such as  
126 *Codium* spp., *Colpomenia sinuosa*, *Dasycladus vermicularis* and, principally, *Lobophora*  
127 *variegata*. Bush-like algae (hereafter BA) are sheet-shaped, jointed non-crustose calcareous  
128 and thick leathery-shaped species (e.g. *Asparagopsis* spp., *Corallina elongata*, *Dyctiota* spp.,  
129 *Padina pavonica*, *Stypocaulon scoparium*, *Stypopodium zonale*, *Taonia atomaria*, *Zonaria*  
130 *turnefortii*, etc.), from 1 to 15 cm in height, which constitute either large algal cushions or  
131 thin sheets with mixtures of algal species. Corticated, large, canopy-forming brown  
132 macrophytes (hereafter BM) are erect, frondose, coarsely-branched fucoid species (the genera  
133 *Cystoseira* and *Sargassum*), usually > 15 cm in height, and in general forming low diversity  
134 algal stands. Understory algae were excluded from the surveys as their coverage is hard to  
135 determinate, and a meticulous investigation of the whole substratum is too time-consuming.  
136 However, crustose coralline algae (e.g. the genera *Lithothamnion*, *Lithophyllum*,  
137 *Neogoniolithon*, *Titanoderma*, etc) were counted when not overgrown by other algae.

138 Our sampling design tested the effect of the degree of wave exposure to the dominant, trade  
139 wind-induced NE-swells (categorized as high *versus* low exposure = exposed or windward  
140 *versus* protected or leeward shores, see Lindegarth & Gamfeldt 2005 for a discussion on this  
141 topic) at each of the seven islands constituting the Canary Islands, as well as a group of small  
142 islets, the “Chiniyo Archipelago”, to the north of Lanzarote Island (Fig. 1). We selected a total  
143 of 32 locations across the Canarian Archipelago as spatial replicates of the 16 defined  
144 treatments (2 levels of degree of wave exposure x 8 islands), with 2 locations separated by 10s  
145 of kilometres per treatment (Fig. 1). Exposed locations directly received the prevailing swells  
146 and winds from the northeast, whereas protected locations lay to the south on the opposite  
147 side of each island (Fig. 1). Swells from the south are significantly rarer (Martín Ruiz 2001).

148 Additionally, we surveyed two randomly-selected sites separated by 10s of meters within each  
149 location. As a result, a hierarchical, structured, sampling design (*sensu* Underwood 1997,  
150 Frascchetti et al. 2005) provided the framework for quantifying the variation among samples  
151 due to each spatial scale and both levels of wave exposure at a regional scale (< 1000 km).

152 **Sampling and data analysis.** At each site, a SCUBA-diver quantified *in situ* the percent  
153 cover of algae in four 50 x 50 cm quadrats (0.25 m<sup>2</sup>), following point-quadrat procedures with  
154 a grid of 121 points per quadrat. Quadrats, several meters apart, were haphazardly laid out.  
155 This is a rapid, non-destructive, technique to assess community structure and dominance of  
156 sessile biota (Fowler-Walker & Connell 2002, McClanahan et al. 2003). Final values for each  
157 taxon were expressed as percentages. Taxa presented in less than a 4% cover were omitted.  
158 Unidentified filamentous turf consisted principally of red algae belonging to the families  
159 Ceramiaceae and Rhodomelaceae.

160 Hypotheses were tested using multivariate and univariate procedures. To test for differences  
161 in the algal community caused by the two levels of wave exposure across the hierarchy of  
162 spatial scales, we selected non-parametric approaches (Anderson 2001, Anderson & Millar  
163 2004) and applied a mixed analysis technique by combining the semi-parametric, distance  
164 based, Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson 2004),  
165 and non-metric multidimensional scaling (MDS) ordination (PRIMER software; Clarke &  
166 Warwick 1994). In both cases, data were transformed to square root and analyses were based  
167 on Bray-Curtis dissimilarities. The PERMANOVA incorporated the following factors: (1)  
168 'Wave Exposure' (fixed factor with two levels: protected *versus* exposed) (2) 'Island' (fixed  
169 factor with eight levels corresponding to the seven islands plus Chinijo Archipelago, and  
170 orthogonal to the previous factor), (3) 'Locations' (random factor with two levels, nested  
171 within the interaction term between 'Islands' and 'Wave exposure') and (4) 'Sites' (random  
172 factor with two levels, nested within the interaction term between 'Locations', 'Islands' and



173 'Wave exposure'). PERMANOVA was used to partition variability and provide measures of  
174 multivariate variability at different scales in the structured design in a manner analogous to  
175 univariate partitioning using ANOVA (Anderson & Millar 2004, Fraschetti et al. 2005). We  
176 applied this technique to the overall community dataset, as well as to each of the three defined  
177 morphological groups of algae. When appropriate, pairwise *a posteriori* comparisons were  
178 executed using permutations (Anderson 2004).

179 To visualize multivariate patterns, non-metric multidimensional scaling (MDS) ordinations  
180 were carried out. The MDS was applied for three different scenarios, gradually increasing the  
181 complexity of the analysis. Firstly, we analyzed the algal community structure by considering  
182 only the 16 established treatments (8 islands x 2 levels of wave exposure) by pooling the  
183 overall data within each treatment. In the second step, we included replicated locations within  
184 each treatment; and in the third step, we included replicated sites within locations for each  
185 treatment. Stress values are a measure of goodness of fit of data points in the MDS, and stress  
186 equals zero when data are perfectly represented (Clarke & Warwick 1994). If the stress levels  
187 are greater than 0.2, plots are considered difficult to interpret. Since an acceptable stress value  
188 (< 0.14) was only obtained for the first scenario, we used only this analysis.

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

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

198 When the factor 'Islands' was significant for some of the ANOVAs, pairwise *a posteriori*  
199 SNK tests were used. Before analysis, the Cochran's test was used to check for homogeneity  
200 of variances. Although no transformation rendered homogeneous variances in the majority of  
201 cases (Cochran's test,  $p < 0.01$ ), the ANOVA was carried out as it is robust to heterogeneity  
202 of variances, particularly for large balanced experiments (Underwood 1997). The significance  
203 level was thus set at the 0.01 level instead of 0.05 (Underwood 1997).  
204 Finally, we assessed the geographical affinities in the composition and structure of algal  
205 assemblages across the Canarian Archipelago by means of a correlation analysis between the  
206 average pairwise dissimilarities matrix among islands for the entire dataset and a pairwise  
207 matrix containing the minimum lineal distances (in km) between each pair of islands. We  
208 used the pairwise average dissimilarities matrix output from both the SIMPER procedure and  
209 the PERMANOVA.

210

211

## RESULTS

212 A total of 39 algal taxa were observed in the 256 quadrats conducted at the 32 study locations  
213 (Appendix 1). The prominent taxa within the TA were, in decreasing order, *Lobophora*  
214 *variegata* (40.6% frequency of occurrence in the 256 quadrats), unidentified filamentous turf  
215 (38.6%) and *Jania* spp. (32.4%). The BA group was mainly dominated by *Dyctiota*  
216 *dichotoma* (68.7%), *Padina pavonica* (31.6%) and *Asparagopsis* spp. (21.9%). Finally, the  
217 BM group was represented by *Cystoseira* spp. (21.9%) and *Sargassum* spp. (11.3%).

218

### Multivariate analysis

219 Multivariate techniques revealed large and significant differences in the composition and  
220 structure of the algal community for the different factors. Firstly, the multivariate ANOVA  
221 performed on the entire algal dataset (Table 1) detected significant variability at the three  
222 spatial scales considered by our study: differences among islands, differences between

223 locations within each island and level of wave exposure, and differences between sites within  
224 locations within each island and level of wave exposure ( $p < 0.001$ , Table 1). Significant  
225 variability attributable to differences in the degree of wave exposure was found ( $p = 0.01$ ,  
226 Table 1); its effect was otherwise consistent across the islands (Table 1, 'I x WE',  $p > 0.05$ ).  
227 Secondly, the two-dimensional MDS (Fig. 2, stress value = 0.09) revealed a separation of the  
228 treatments along the ordination diagram, with the eastern islands (Chinijo, Lanzarote,  
229 Fuerteventura and Gran Canaria) falling in the left side of the plot with the exception of  
230 exposed locations in Lanzarote (LZ-E in Fig. 2); whereas the western islands (Tenerife,  
231 Gomera, La Palma and El Hierro) were positioned in the right side of the plot. Several islands  
232 (Fuerteventura, Gran Canaria, Tenerife and Gomera) had similar assemblages in both  
233 protected and exposed locations, while the rest of the islands showed a clearer separation  
234 between protected and exposed locations in the ordination space (Fig. 2). *A posteriori*  
235 permutational tests among islands revealed a total of 10 significant differences of the overall  
236 28 possible comparisons ( $p$ -Monte Carlo  $< 0.01$ ) with 8 significant differences including El  
237 Hierro or La Palma islands. This result was indicative of the different composition, abundance  
238 and structure of the algal assemblages of these two islands compared to the rest of the islands.  
239 Moreover, the MDS plot also revealed this difference (Fig. 2), with the majority of locations  
240 within El Hierro and La Palma positioned at the top of the plot.

241 Alternatively, we found group-specific results when we analyzed the output of the  
242 PERMANOVA for each algal group (Table 1). Coverage of the BM group was significantly  
243 greater at exposed shores compared to protected shores ( $p < 0.01$ , Table 1) across islands  
244 (Table 2, 'I x WE',  $p > 0.05$ ); while TA cover differed among islands ( $p < 0.01$ , Table 1),  
245 which was corroborated by some significant pairwise comparisons (Table 1). In all cases, we  
246 detected substantial variability at the medium (differences between locations) and small  
247 (differences between sites) spatial scales ( $p < 0.01$ , Table 1).

248 SIMPER analysis indicated that the average similarity among protected locations (38.46%)  
249 was greater than the average similarity among exposed locations (28.80%), suggesting a  
250 greater heterogeneity of exposed algal assemblages. Eight taxa contributed extensively to the  
251 differences between both levels of wave exposure accounting for the 57.97% of the overall  
252 dissimilarity (Appendix 2). In general, these taxa, as well as the fucoids *Cystoseira*  
253 *mauritanica* and *Sargassum* spp., accounted for dissimilarities among islands, although the  
254 relative importance of each taxon varied for each pair of comparisons (Appendix 2).  
255 Average dissimilarities between pairs of islands were significantly correlated with lineal  
256 distances in km between them ( $r_s = 0.49$ ,  $0.001 < p < 0.01$  using the output from the SIMPER  
257 procedure;  $r_s = 0.36$ ,  $0.01 < p < 0.05$  using the output from the PERMANOVA).

258

#### 259 **Univariate analyses**

260 Mean percentage covers across the study area (islands, locations within islands, and sites  
261 within locations) for three defined algal groups: TA, BA and BM are shown in Figures 3, 4  
262 and 5, respectively. Results from the ANOVAs performed on the three groups are presented  
263 in Table 2. Although the ANOVAs indicated a significant effect of the variability between  
264 sites separated by 10s of m within locations only for the BM, we detected substantial spatial  
265 heterogeneity at the medium spatial scale (differences between locations separated by 10s of  
266 km within each island and level of wave exposure) for the three morphological groups ( $p <$   
267  $0.01$ , Table 2). This large variability prevented the detection of significant differences caused  
268 by some of the two main effects in the three ANOVAs. However, the power of the ANOVAs  
269 was sufficient to reject some null hypotheses. In this sense, the BM group was significantly  
270 more abundant on exposed shores ( $p < 0.01$ , Table 2; Fig. 5), whereas the TA group was more  
271 abundant on protected shores ( $p < 0.01$ , Table 2; Fig. 3). In both cases, the effect of the 'wave  
272 exposure' was consistent across the islands (Table 2, 'I x WE',  $p > 0.05$ ). Significant

273 differences caused by the different islands were not detected for BM ( $p > 0.01$ , Table 2),  
274 although visual inspection of the results (Fig. 5) suggests the existence of differences. In  
275 contrast, significant differences caused by 'Islands' were detected for TA ( $p < 0.01$ , Table 2)  
276 and BA ( $p = 0.01$ , Table 2), and can be seen in Figs 3 & 4. *A posteriori* SNK tests (Table 2)  
277 indicated the TA group dominated the western islands, whereas BA dominated the central and  
278 eastern islands with the exception of Chinijo Archipelago.

279 Results from the ANOVAs performed on the prominent algal taxa are presented in Table 3.  
280 Again, the analyses indicated substantial variability at the medium and low spatial scales  
281 (differences between locations 10s of kilometres apart within each island and level of wave  
282 exposure, and between sites 10s of meters apart within locations, respectively). Due to the  
283 variability between locations within each treatment, detection of significant differences  
284 among islands and between levels of wave exposure was only found for *Lobophora variegata*,  
285 *Jania* spp., and the unidentified filamentous turf (Figs 6, 7 & 8, respectively). *Lobophora*  
286 *variegata* (Fig. 6) monopolized the rocky bottoms of both El Hierro and La Palma with mean  
287 percent coverages up to 90% per location, and it was significantly more abundant in these  
288 islands than all other islands ( $p < 0.01$ , SNK tests, Table 3). *Jania* spp. (Fig. 7) appeared to be  
289 more abundant in the eastern islands ( $p < 0.01$ , SNK tests, Table 3). Finally, the unidentified  
290 filamentous turf (Fig. 8) was significantly more abundant in Gomera and Tenerife than the  
291 rest of the islands ( $p < 0.01$ , SNK tests, Table 3).

292

293

## DISCUSSION

294 The presence of multiple islands along an oceanographic gradient with shores exposed to  
295 different hydrographic conditions provided an ideal opportunity to test hypotheses about the  
296 separate and combined effects of geographical and physical processes on the whole subtidal  
297 shallow water algal assemblages. Collectively, the findings of this study showed that subtidal

298 algal assemblages differ consistently between protected and exposed shores across surveyed  
299 islands. Additionally, clear differences between islands situated at the opposite sides of the  
300 Canary Archipelago were observed.

301 The analysis of pattern in distribution and abundance of marine organisms has direct  
302 relevance to the identification of underlying causal processes (Benedetti-Cecchi et al. 2003  
303 and references therein, Fraschetti et al. 2005). Biotic processes and behaviour are usually  
304 implicated in the maintenance of small-to-medium scale spatial patchiness (e.g. differences  
305 between sites and locations separated by 100s of meters to 10s km), whereas oceanographic  
306 conditions and climate largely dictate regional, large-scale patterns operating at 100s of km  
307 (Underwood & Chapman 1996, Menconi et al. 1999). Our results support, in part, these  
308 conclusions. In particular, certain important group-specific differences within islands can be  
309 attributable to differences in levels of wave exposure, while significant differences at a  
310 regional scale (differences among islands 100s of kilometres apart) were found for some  
311 groups and taxa.

312

### 313 **Variability associated with differences in the level of wave exposure**

314 The combined indirect and direct hydrodynamic effects of wave action on nearshore biota are  
315 often grouped under the term 'wave exposure' (Taylor & Schiel 2003). Distinct patterns arose  
316 when the results of our study on the effect of 'wave exposure' were interpreted at a  
317 morphological group level. In general, the presence and abundance of species within the BM  
318 group (frondose furoid species) was clearly greater at exposed locations (mean coverage for  
319 all exposed locations =  $22.00 \pm 5.61$ , mean  $\pm$  SE) compared to protected locations (mean  
320 coverage for all protected locations =  $1.56 \pm 1.07$ , mean  $\pm$  SE). Subtidal furoid plants tend to  
321 be better adapted to exposed or semi-exposed conditions compared with other algal species in  
322 the Canary Islands (Medina & Haroun 1993, Haroun et al. 2003).

323 However, the ecological mechanisms underlying this difference are unknown. Variation in  
324 hydrographic conditions at the scales considered by our sampling design probably influence  
325 algal assemblages through the temporal variability and intensity of swells and storms, and the  
326 release of propagules from the water column (Micheli et al. 2005). Usually, water motion (i)  
327 enhances nutrient uptake by reducing or breaking the boundary layer, (ii) removes epiphytes  
328 and waste products, and (iii) allow algal stands to use light more efficiently by stirring their  
329 fronds, ensuring that no frond is either always shaded or always in the sun (Diez et al. 2003  
330 and references therein). These mechanical advantages are accompanied by a continued  
331 mechanical stress that only morphologically adapted species can resist. Algae in these  
332 disturbed environments are characterized by a flexible thallus and an efficient attachment  
333 mechanism, such as the basal disc of certain species belonging to the genera *Cystoseira* and  
334 *Sargassum*.

335 Alternatively, this pattern could be related to anthropogenic perturbations. There is an  
336 increasing trend for long-term, and perhaps permanent, loss of canopy-forming algae to occur  
337 along human-impacted coasts (Russell & Connell 2005 and references therein). The loss of  
338 canopy-forming algae typically results in the immediate colonisation and spatial dominance of  
339 turf algae (Russell & Connell 2005). In this context, Benedetti-Cecchi et al. (2001) found that  
340 frondose, coarsely-branched algae were virtually absent from urban areas in the  
341 Mediterranean, with replacement by turf-forming algae. These authors argued that this group  
342 of furoid algae (e.g. the genus *Cystoseira*) is highly sensitive to human disturbances. In the  
343 Canarian Archipelago, the most important urban areas associated with the tourist industry are  
344 located in the protected southern shores of each island (Martin-Ruiz 2001). As a result, the  
345 large number of sewage discharges, and subsequently the nutrient enrichment, along these  
346 human-perturbed areas could be involved in the lack of BM in the protected locations of our  
347 study. It is possible that a combination of wave action and anthropogenic disturbance is

348 important in this variability within each island. However, lack of historical data on these  
349 assemblages and of direct quantification of the intensity and distribution of disturbances on  
350 the islands make it impossible to conclusively link these observed patterns to human impacts.  
351 The pattern detected for the BM group clearly contrast with that observed for TA, and in  
352 particular, for the patterns observed for the unidentified filamentous turf group. As a general  
353 pattern, TA dominated protected locations within each island with the exception of La Palma.  
354 For example, the unidentified filamentous turf group was twice as abundant in protected  
355 locations (coverage for all protected locations =  $20.84 \pm 5.70$ , mean  $\pm$  SE) than exposed  
356 locations (coverage for all exposed locations =  $10.37 \pm 4.03$ , mean  $\pm$  SE) for the overall study.  
357 Consequently, our observations reinforce the findings of other investigations that have  
358 highlighted the important role that wave exposure plays in shaping shallow marine benthic  
359 communities in temperate waters (Blanchette et al. 1999, Benedetti-Cecchi et al. 2003, Taylor  
360 & Schiel 2003, Lindegarth & Gamfeldt 2005, Micheli et al. 2005).

361

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

363 In all cases analyzed by means of the multivariate ANOVAs, sampled locations within each  
364 island and level of wave exposure, as well as sites within locations, were quantitatively  
365 different. Considerable heterogeneity at these spatial scales highlights the complex nature of  
366 these assemblages; small-scale variability is a general property of benthic assemblages in  
367 marine coastal habitats (Underwood & Chapman 1996, Menconi et al. 1999, Benedetti-Cecchi  
368 2001, Fowler-Walker & Connell 2002, Benedetti-Cecchi et al. 2003, Coleman 2003,  
369 Frascetti et al. 2005). Differences among locations within each island and level of wave  
370 exposure were often as large as differences among islands or level of wave exposure.  
371 Variability at the location level probably obscured differences in cover between levels of  
372 wave exposure and islands for some algal groups and taxa. We can only speculate on the



373 underlying causes of this variation, which are likely to involve complex interactions among  
374 several physical (e.g. availability of resources, habitat attributes) and biological processes  
375 (e.g. competition, predation). Clearly, different explanations can be proposed for different  
376 taxa according to their life-history strategies and biology.

377

### 378 **Variability at the large spatial scale: differences among islands**

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

384 What are the underlying mechanisms that could account for differences among islands?

385 Generally, differences in patterns of water circulation, availability of resources and type of  
386 substratum affecting recruitment, growth and mortality of algae have been proposed as  
387 explanations of variability at large spatial scales (from 10s to 100s of kilometres) (Santelices  
388 1990, Menconi et al. 1999). The large-scale gradient in oceanographic conditions, such as  
389 SST and nutrients, in an east-to-west direction across the Canarian Archipelago (Barton et al.  
390 1998, Bode et al. 2001, Davenport et al. 2002) provides a parsimonious explanation for this  
391 observation. Variation in oceanographic conditions usually results in differences in local  
392 productivity potential, which, in turn, can result in a visible and predictable change in the  
393 algal community (Steneck & Dethier 1994). In this context, our results agree with those of  
394 Schils and Coppejans (2003), who attributed differences in the composition, abundance and  
395 structure of subtidal algal communities in the Socotra Archipelago, Indian Ocean, to  
396 differences in SSTs and bottom-up resources caused by upwelling. The drawback of this  
397 approach is that islands may differ in other respects than differences in bottom-up availability

398 of resources. Hence, caution is necessary in ascribing differences in the observed algal  
399 assemblages; causality can only be determined through experimental manipulation (Dulvy et  
400 al. 2004).

401 We hypothesized that the presence and abundance of furoid species should be larger in the  
402 eastern islands, where SSTs are about 2°C lower than the western islands, while in contrast  
403 the TA and BA groups should increase in the western islands. Our results generally support  
404 this pattern. For example, the furoid alga *Cystoseira mauritanica* was only recorded at  
405 Chinijo Archipelago; whereas turf algae, and specially *Lobophora variegata*, were most  
406 abundant in the westernmost islands (El Hierro and La Palma). This result is consistent with  
407 the composition and structure of populations of the genus *Cystoseira* across subtidal and  
408 intertidal habitats of the Canarian Archipelago (Medina et al. 1995, Haroun 1997).  
409 Nevertheless, we found some inconsistencies in this general pattern. For example, no furoid  
410 species (BM) were observed in Fuerteventura Island, while this algal group was relatively  
411 abundant in the westernmost island (El Hierro). The origin of the potential mechanisms  
412 explaining the 'temperate vs. tropical' differences in the algal assemblages are unknown,  
413 though differences in the availability of 'bottom-up' resources apparently play an important  
414 role explaining such differences. More work is desirable to empirically assess the reasons of  
415 this pattern.

416 Consequently, generalization of patterns and the establishment of a regional framework for  
417 the composition, abundance and distribution of shallow water algal assemblages along the  
418 overall Canarian Archipelago is complicated. Many environmental factors covary across large  
419 spatial gradients (Harley et al. 2003); making temperate rocky reef assemblages highly  
420 variable and dynamic at a regional scale (Micheli 2005). Within-island variability also  
421 obscures the hypothesized regional pattern. As a result, increasing the spatial replication at the  
422 smallest spatial scales (replicated quadrats within sites, and sites within locations) would

423 probably help to decrease the 'noise' associated with other sources of environmental  
424 variability. To understand the generality of patterns in algal assemblages is difficult using a  
425 hierarchy of spatial scales covering < 1000 km (Fowler-Walker & Connell 2002). We  
426 therefore suggest increasing the spatial scale of observation (> 1000 km) to encompass a  
427 wider area of study along the warm-temperate waters of eastern Atlantic in the northern  
428 hemisphere. Probably, this approach could provide evidence of the existence of simple  
429 underlying rules (*sensu* Fowler-Walker & Connell 2002, Fraschetti et al. 2005) in the  
430 organization of shallow water algal assemblages.

431

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437

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Table 1: 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 by PERMANOVA. p-values were obtained using 4999 random permutations. CH: Chinijo, LZ: Lanzarote, FV: Fuerteventura, GC: Gran Canaria, TF: Tenerife, GO: Gomera, LP: La Palma, EH: El Hierro

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)
Islands = 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
Wave exposure = 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 x 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 x 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 x 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		
Pairwise <i>a posteriori</i> comparisons								EH > GO; EH > TF; EH >GC; EH > CH LP > GO; LP > TF; LP > CH GC > GO; FV > GO; FV > TF					

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 three algal morphological groups. Acronyms for islands as in Table 1. \*:  $p < 0.01$

Source of variation	DF	Brown Macrophytes		Turf Algae		Bush-like Algae	
		MS	F	MS	F	MS	F
Islands = I	7	0.0777	1.58	0.2448	5.48*	0.3256	4.02 (p = 0.01)
Wave Exposure = WE	1	0.5036	10.22*	0.4399	9.85*	0.0002	0.00
Locations (I x WE)	16	0.0493	8.15*	0.0447	5.38*	0.0811	18.36*
Sites (Locations (I x WE))	32	0.0060	1.79*	0.0083	1.51	0.0044	1.02
I x WE	7	0.0490	0.99	0.0620	1.39	0.0750	0.92
Residual	192	0.0034		0.0055		0.0043	
SNK tests				<u>LP EH GC &gt; CH &gt; FV GO TF LZ</u> <u>LZ FV GC TF &gt; GO CH LP EH</u>			



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. \*: p < 0.01

Source of variation	DF	<i>Lobophora variegata</i>		Unidentified filamentous turf		<i>Dyctiota</i>		<i>Stypocaulon</i>		<i>Asparagopsis</i> spp.		<i>Jania</i> spp.	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Islands = I	7	40.1578	23.88*	16.8451	4.80*	13.1876	3.63	0.0385	1.29	4.2593	3.42	4.9245	6.02*
Wave Exposure = WE	1	3.1696	1.88	51.8169	14.77*	0.7873	0.22	0.0078	0.26	0.1253	0.10	1.6889	2.06
Locations (I x WE)	16	1.6819	5.30*	3.5074	4.52*	3.6322	15.84*	0.0298	22.05*	1.2458	1.27	0.8180	3.77*
Sites (Locations (I x WE))	32	0.3174	1.25	0.7758	2.26*	0.2293	0.86	0.0014	1.16	0.9833	4.51*	0.2167	1.29
I x WE	7	3.0250	1.80	1.5045	0.43	1.6675	0.46	0.0240	0.81	3.1134	2.50	0.9106	1.11
Residual	192	0.2546		0.3435		0.2680		0.0012		0.2178		0.1679	
SNK tests		<u>EH LP &gt; GC &gt; CH FV LZ TF GO</u>			<u>GO TF &gt; FV &gt; GC LP CH LZ EH</u>				<u>FV GC &gt; CH LZ &gt; LP TF EH GO</u>				

Table 3 (continued): 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. \*:  $p < 0.01$

Source of variation	DF	<i>Padina pavonica</i>		<i>Cystoseira abies-marina</i>		<i>Cystoseira mauritanica</i>		<i>Sargassum</i> spp.	
		MS	F	MS	F	MS	F	MS	F
Islands = I	7	3.3948	1.27	0.1150	0.95	0.0164	1.62	0.0325	2.11
Wave Exposure = WE	1	2.6661	1.00	0.3494	2.90	0.0038	0.38	0.0627	4.07
Locations (I x WE)	16	2.6696	28.64*	0.1206	31.14*	0.0101	7.95*	0.0154	4.91*
Sites (Locations (I x WE))	32	0.0932	1.11	0.0039	2.03*	0.0013	0.98	0.0031	2.27*
I x WE	7	1.1227	0.42	0.1150	0.95	0.0038	0.38	0.0243	1.58
Residual	192	0.0839		0.0019		0.0013		0.0014	



## Legends

Figure 1: Map of study locations within islands. Black circles: locations protected from the NE-swell. Grey squares: locations exposed to the NE-swell

Figure 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. Black circles are locations within the western islands; grey circles are locations within the eastern islands

Figure 3: Turf-algae. Mean percentage cover across the study area. Black bars are protected locations (L1 and L2) and white bars are exposed locations (L1 and L2). Error bars represent SE of means

Figure 4: Bush-like algae. Mean percentage cover across the study area. Black bars are protected locations (L1 and L2) and white bars are exposed locations (L1 and L2). Error bars represent SE of means

Figure 5: Brown macrophytes. Mean percentage cover across the study area. Black bars are sites within protected locations (e.g. S1L1 denotes site 1 within location 1) and white bars are sites within exposed locations. Error bars represent SE of means

Figure 6: *Lobophora variegata*. Mean percentage cover across the study area. Black bars are protected locations (L1 and L2) and white bars are exposed locations (L1 and L2). Error bars represent SE of means

Figure 7: *Jania* spp. Mean percentage cover across the study area. Black bars are protected locations (L1 and L2) and white bars are exposed locations (L1 and L2). Error bars represent SE of means

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

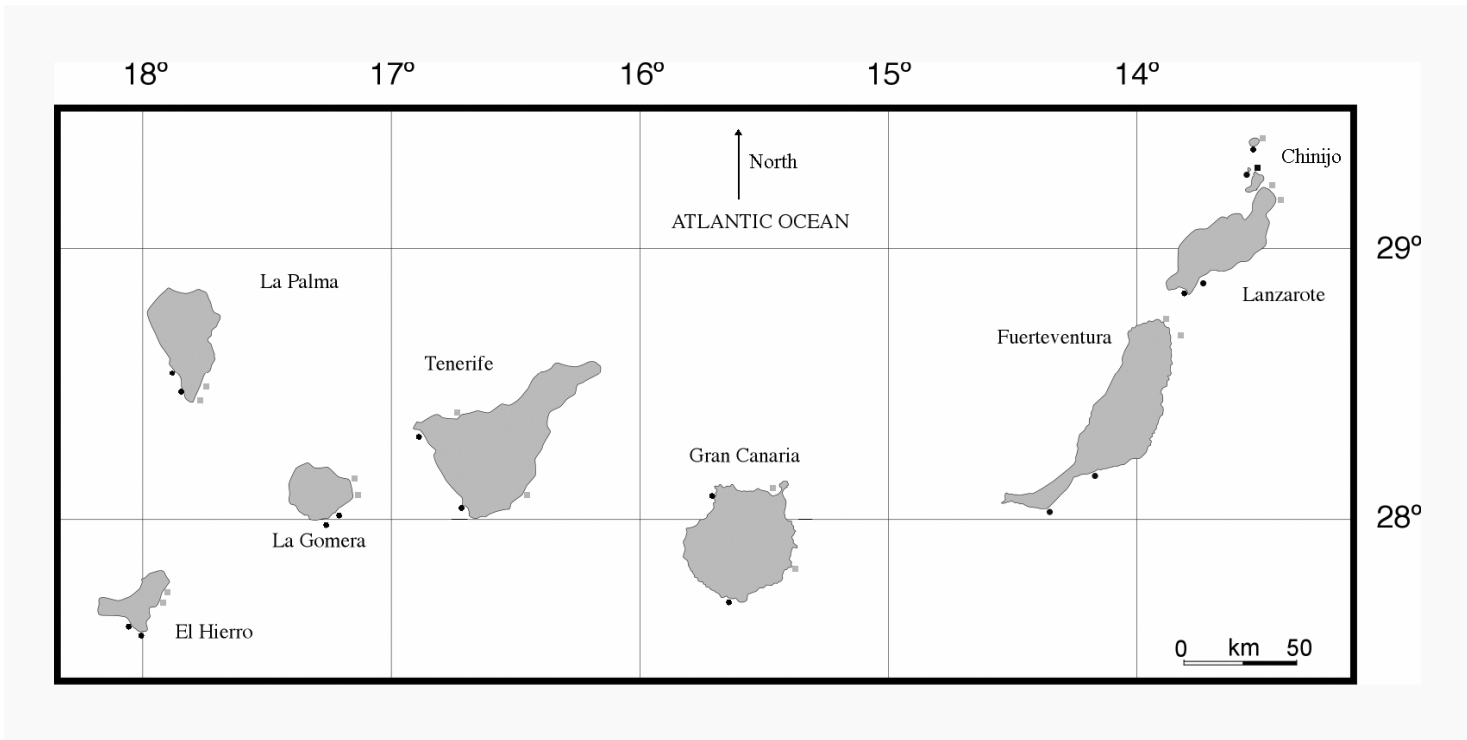


Fig.1

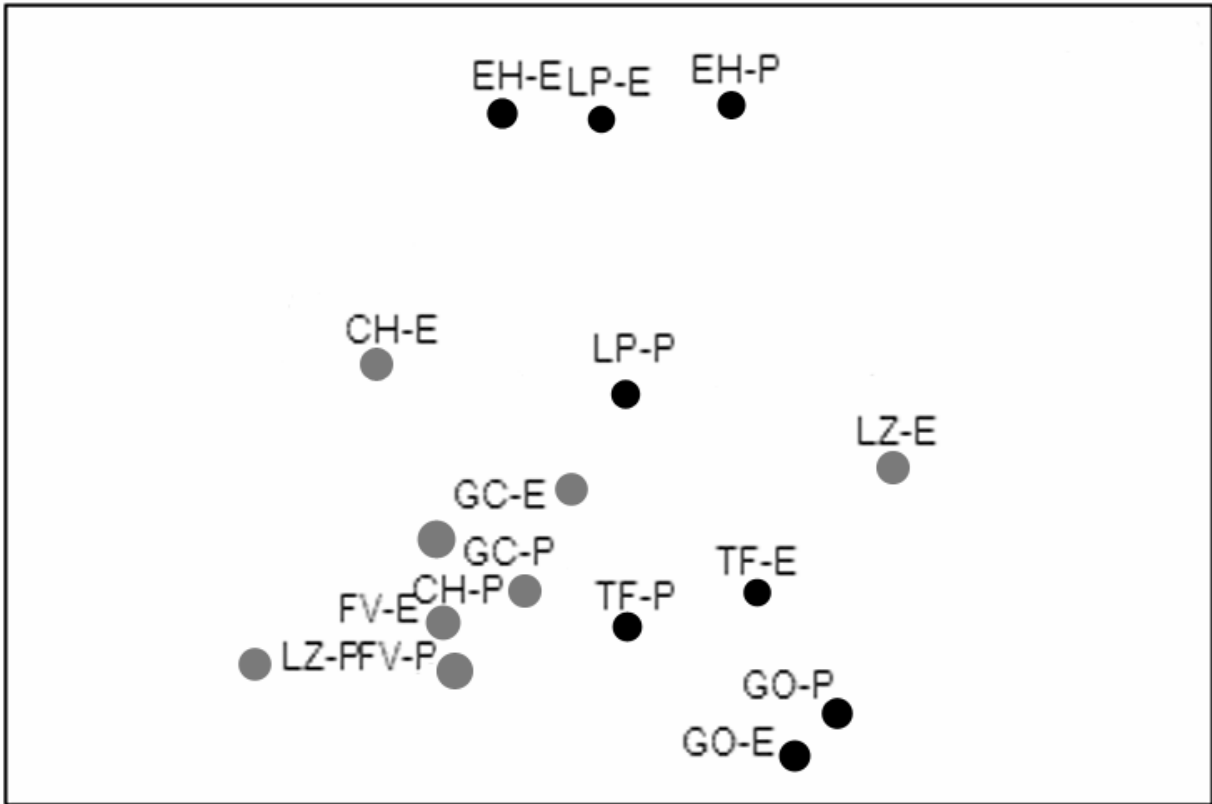


Fig. 2

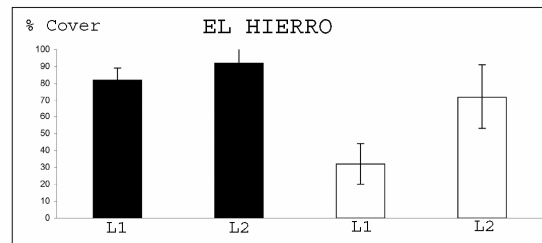
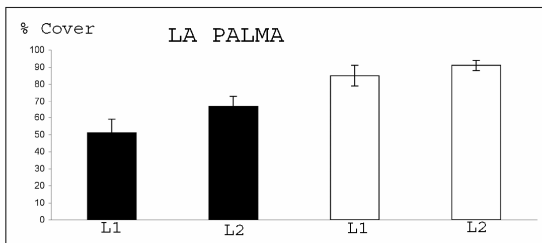
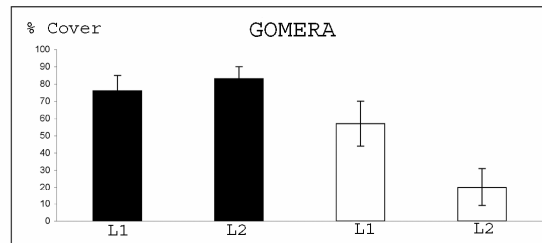
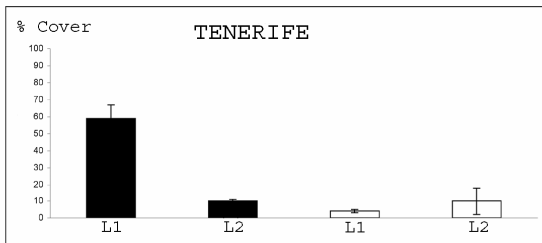
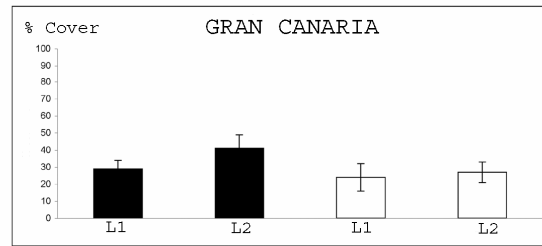
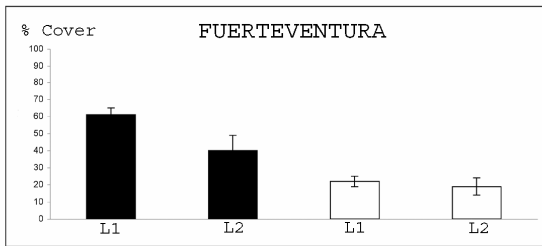
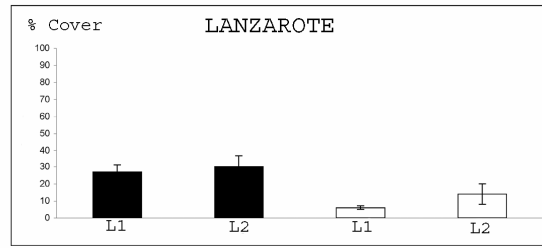
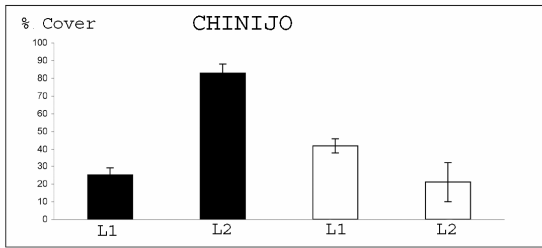


Figure 3

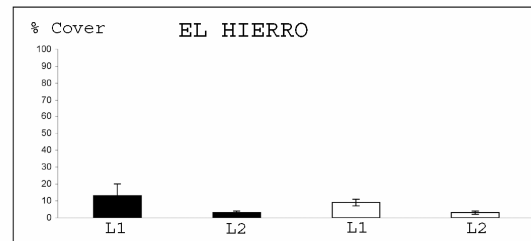
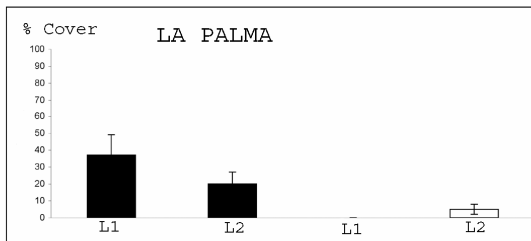
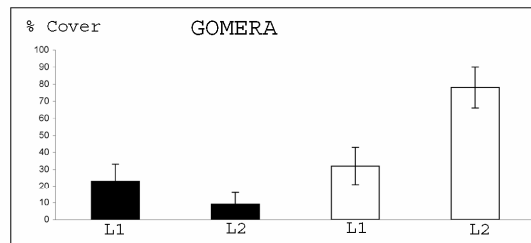
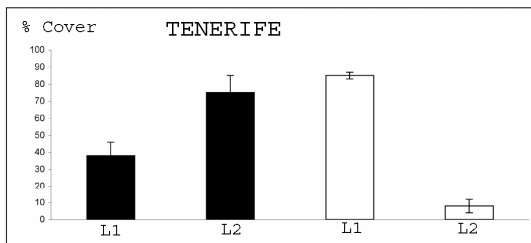
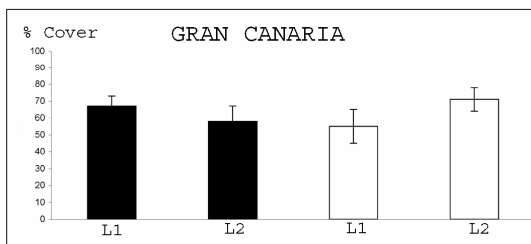
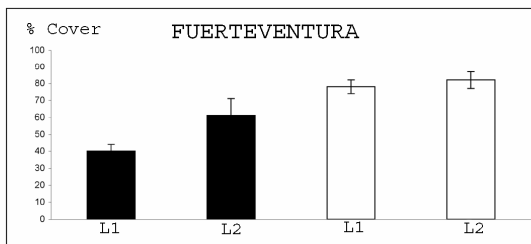
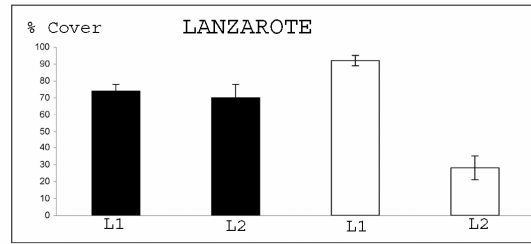
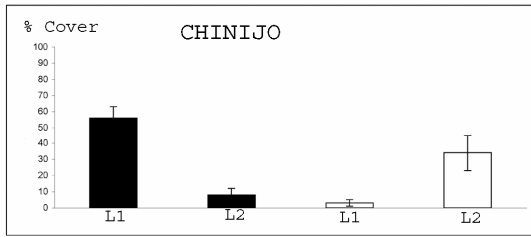


Figure 4

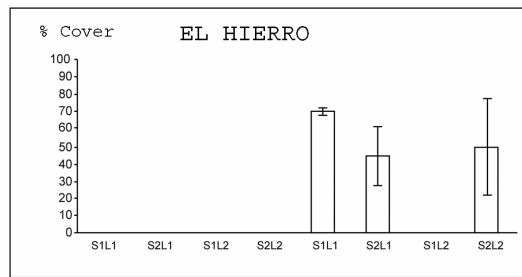
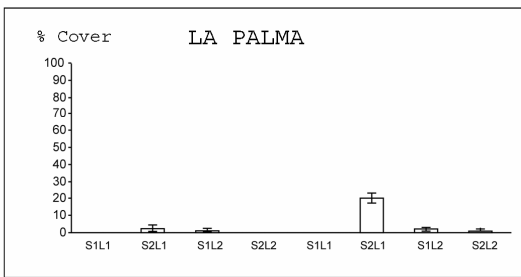
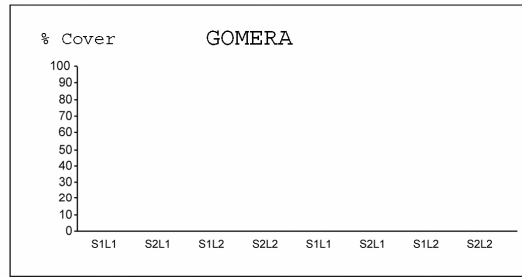
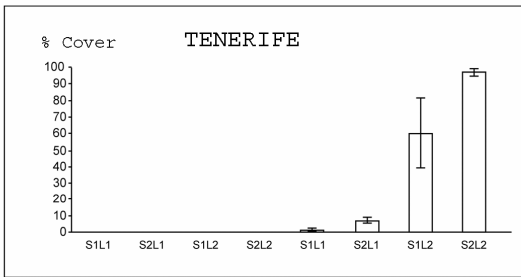
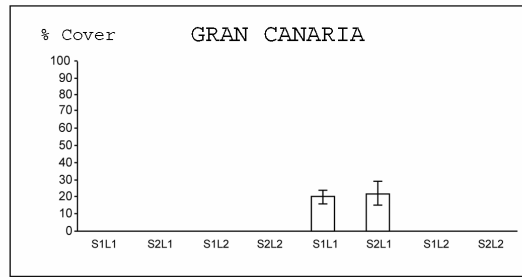
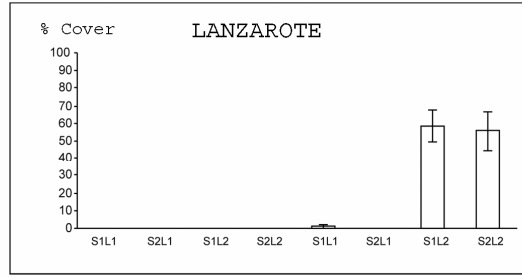
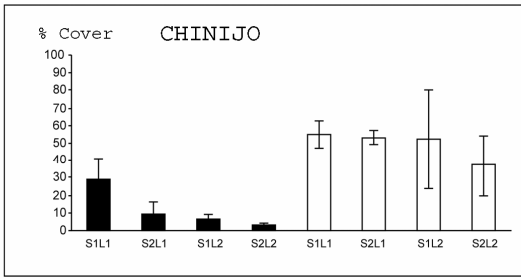


Figure 5

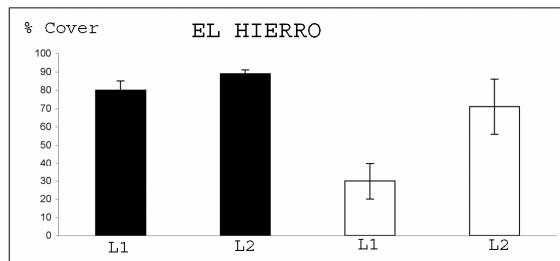
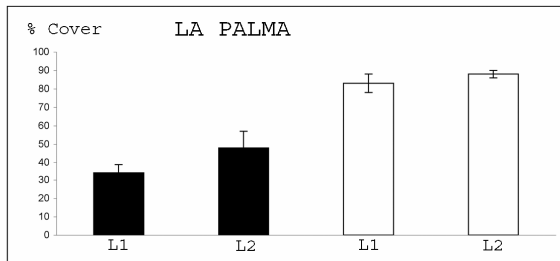
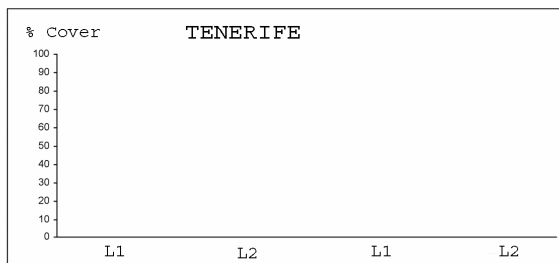
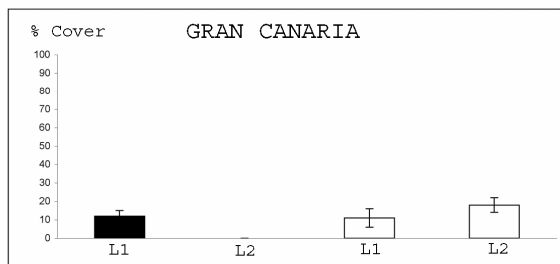
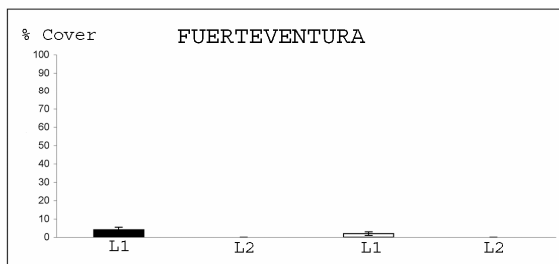
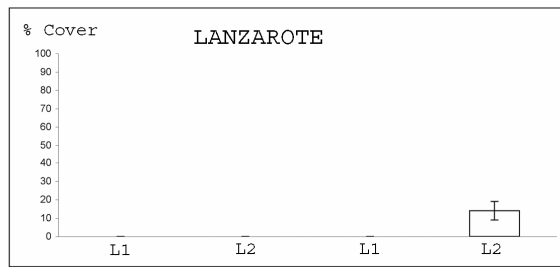
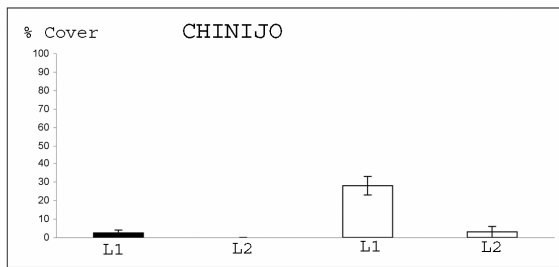


Figure 6



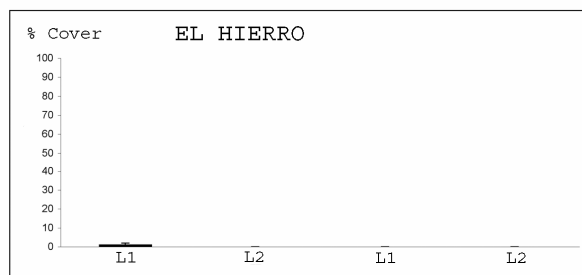
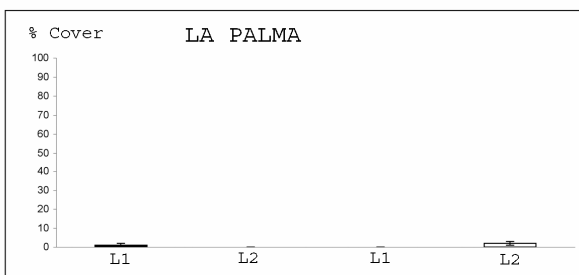
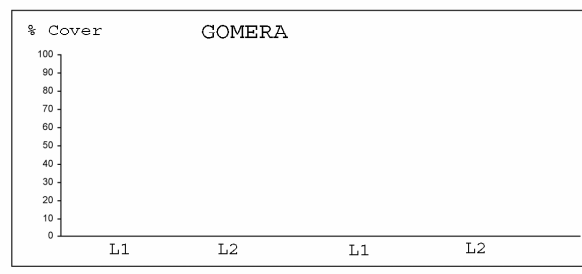
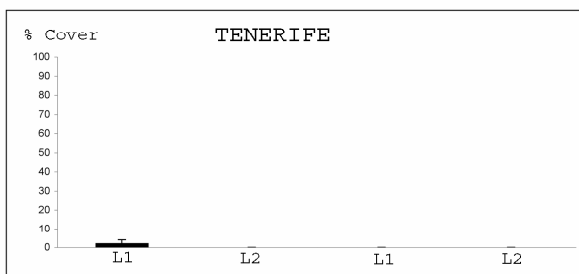
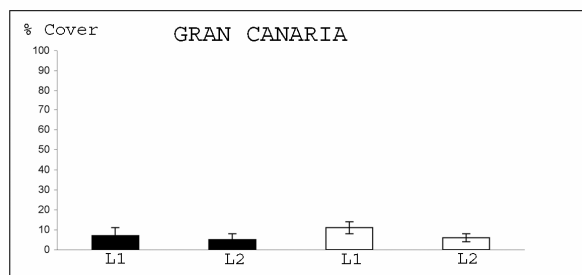
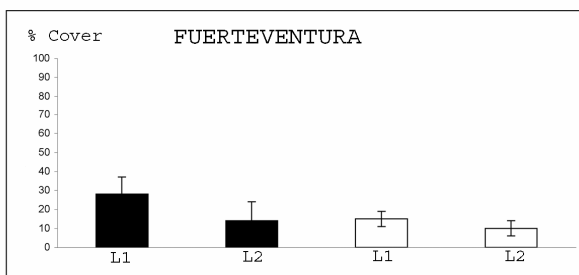
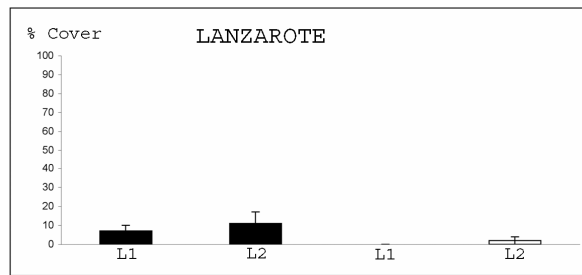
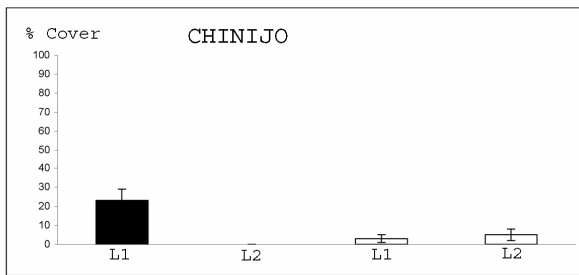


Figure 7

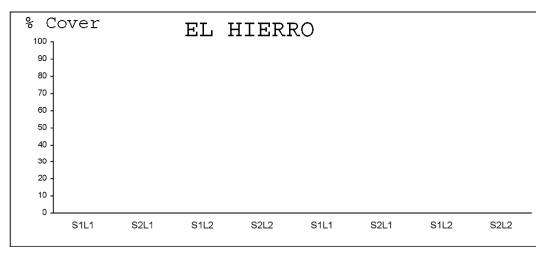
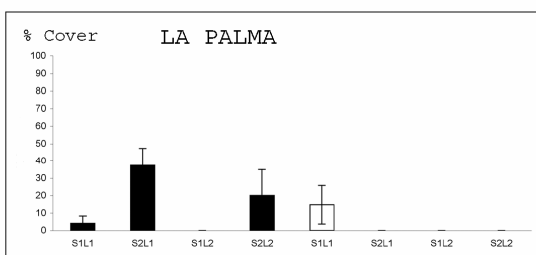
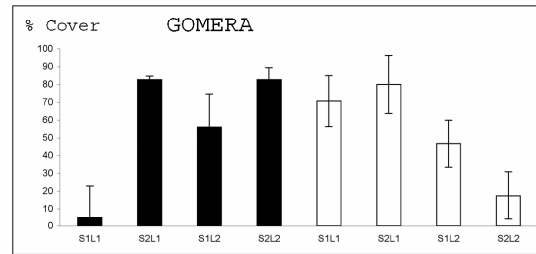
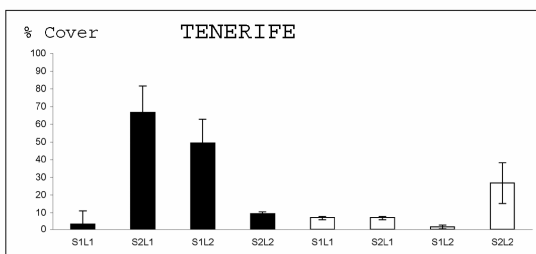
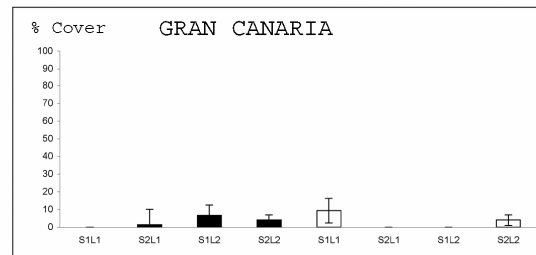
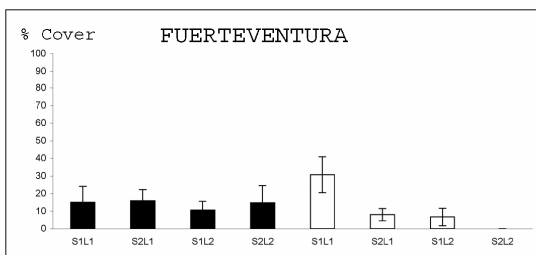
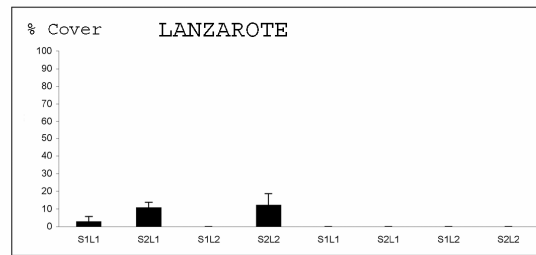
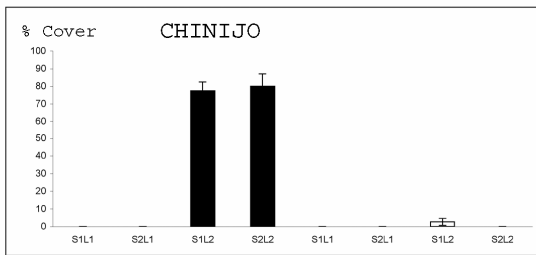


Figure 8

Supplementary material (Appendices 1 & 2)



## Appendix 2: Summary of the results from the SIMPER procedure

	Taxon	Contribution to dissimilarity (%)
<b>1. Protected <i>versus</i> Exposed locations</b>		
Average dissimilarity = 67.49		
	<i>Lobophora variegata</i>	12.03
	Unidentified Filamentous Turf	10.76
	<i>Dyctiota dichotoma</i>	7.29
	<i>Stypocaulon scoparium</i>	5.87
	<i>Asparagopsis</i> spp.	5.79
	<i>Padina pavonica</i>	5.61
	<i>Jania</i> spp.	5.49
	<i>Cystoseira abies-marina</i>	5.13
<b>2. Dissimilarities among islands</b>		
<b>2.1 Chinijo <i>versus</i> Lanzarote</b>		
Average dissimilarity = 70.99		
	Unidentified Filamentous Turf	9.01
	<i>Sargassum</i> spp.	8.84
	<i>Stypocaulon scoparium</i>	8.35
	<i>Cystoseira mauritanica</i>	7.34
	<i>Lobophora variegata</i>	6.85
	<i>Padina pavonica</i>	6.48
	<i>Cystoseira abies-marina</i>	6.28
	<i>Asparagopsis</i> spp.	6.00
<b>2.2 Chinijo <i>versus</i> Fuerteventura</b>		
Average dissimilarity = 62.97		
	Unidentified Filamentous Turf	11.42
	<i>Stypocaulon scoparium</i>	10.98
	<i>Sargassum</i> spp.	9.50
	<i>Padina pavonica</i>	8.31
	<i>Cystoseira mauritanica</i>	7.92
	<i>Jania</i> spp.	7.92
	<i>Dyctiota dichotoma</i>	6.42
	<i>Lobophora variegata</i>	6.21
<b>2.3 Chinijo <i>versus</i> Gran Canaria</b>		
Average dissimilarity = 56.92		
	Unidentified Filamentous Turf	10.50
	<i>Dyctiota dichotoma</i>	10.49
	<i>Sargassum</i> spp.	9.50
	<i>Cystoseira mauritanica</i>	8.32
	<i>Lobophora variegata</i>	8.11
	<i>Stypocaulon scoparium</i>	7.33
<b>2.4 Lanzarote <i>versus</i> Gran Canaria</b>		
Average dissimilarity = 58.14		
	<i>Stypocaulon scoparium</i>	9.79
	<i>Dyctiota dichotoma</i>	8.06
	<i>Lobophora variegata</i>	7.93
	<i>Cystoseira abies-marina</i>	7.92
	<i>Colpomenia sinuosa</i>	7.33

	<i>Asparagopsis</i> spp.	6.97
<hr/>		
2.5 Fuerteventura <i>versus</i> Gran Canaria		
Average dissimilarity = 50.20		
	<i>Dyctiota dichotoma</i>	9.54
	<i>Stypocaulon scoparium</i>	9.24
	<i>Lobophora variegata</i>	8.75
	<i>Padina pavonica</i>	7.59
	<i>Colpomenia sinuosa</i>	7.02
	Unidentified Filamentous Turf	6.82
	<i>Asparagopsis</i> spp.	6.50
<hr/>		
2.6 Chinijo <i>versus</i> Tenerife		
Average dissimilarity = 68.91		
	Unidentified Filamentous Turf	11.85
	<i>Cystoseira abies-marina</i>	9.30
	<i>Sargassum</i> spp.	9.21
	<i>Cystoseira mauritanica</i>	7.64
	<i>Dyctiota dichotoma</i>	7.52
	<i>Asparagopsis</i> spp.	7.47
<hr/>		
2.7 Lanzarote <i>versus</i> Tenerife		
Average dissimilarity = 64.10		
	<i>Cystoseira abies-marina</i>	12.05
	<i>Stypocaulon scoparium</i>	10.50
	Unidentified Filamentous Turf	8.77
	<i>Padina pavonica</i>	8.53
	<i>Asparagopsis</i> spp.	7.34
	<i>Dyctiota dichotoma</i>	6.88
<hr/>		
2.8 Fuerteventura <i>versus</i> Tenerife		
Average dissimilarity = 66.15		
	<i>Stypocaulon scoparium</i>	12.35
	<i>Jania</i> spp.	11.28
	<i>Cystoseira abies-marina</i>	9.24
	<i>Lophocladia trichoclados</i>	7.51
<hr/>		
2.9 Gran Canaria <i>versus</i> Tenerife		
Average dissimilarity = 53.45		
	<i>Cystoseira abies-marina</i>	11.21
	<i>Lobophora variegata</i>	10.12
	<i>Lophocladia trichoclados</i>	8.85
	<i>Colpomenia sinuosa</i>	8.20
	<i>Asparagopsis</i> spp.	8.05
	<i>Stypocaulon scoparium</i>	7.93
<hr/>		
2.10 Chinijo <i>versus</i> Gomera		
Average dissimilarity = 70.98		
	Unidentified Filamentous Turf	15.95
	<i>Sargassum</i> spp.	9.06
	<i>Cystoseira mauritanica</i>	7.51
	<i>Colpomenia sinuosa</i>	7.39
	<i>Asparagopsis</i> spp.	7.04
	<i>Lobophora variegata</i>	6.82
<hr/>		
2.11 Lanzarote <i>versus</i> Gomera		
Average dissimilarity = 79.81		
	Unidentified Filamentous Turf	14.70
	<i>Asparagopsis</i> spp.	10.48

	<i>Stypocaulon scoparium</i>	7.13
	<i>Cystoseira abies-marina</i>	7.11
	<i>Padina pavonica</i>	6.56
	<i>Dyctiota dichotoma</i>	5.89
<hr/>		
2.12 Fuerteventura <i>versus</i> Gomera		
Average dissimilarity = 74.98		
	Unidentified Filamentous Turf	11.36
	<i>Jania</i> spp.	11.24
	<i>Stypocaulon scoparium</i>	11.04
	<i>Padina pavonica</i>	8.27
	<i>Asparagopsis</i> spp.	8.01
	<i>Corallina elongata</i>	7.27
	<i>Dyctiota dichotoma</i>	6.38
<hr/>		
2.13 Gran Canaria <i>versus</i> Gomera		
Average dissimilarity = 65.89		
	Unidentified Filamentous Turf	13.76
	<i>Dyctiota dichotoma</i>	12.99
	<i>Lobophora variegata</i>	8.31
	<i>Colpomenia sinuosa</i>	7.17
	<i>Jania</i> spp.	6.99
	<i>Stypocaulon scoparium</i>	6.51
<hr/>		
2.14 Tenerife <i>versus</i> Gomera		
Average dissimilarity = 54.35		
	Unidentified Filamentous Turf	14.20
	<i>Cystoseira abies-marina</i>	13.36
	<i>Dyctiota dichotoma</i>	12.93
	<i>Asparagopsis</i> spp.	9.78
	<i>Lophocladia trichoclados</i>	9.52
	<i>Corallina elongata</i>	8.74
<hr/>		
2.15 Chinijo <i>versus</i> La Palma		
Average dissimilarity = 68.91		
	<i>Lobophora variegata</i>	18.41
	Unidentified Filamentous Turf	10.33
	<i>Sargassum</i> spp.	9.45
	<i>Cystoseira mauritanica</i>	7.81
	<i>Colpomenia sinuosa</i>	6.79
	<i>Asparagopsis</i> spp.	5.94
<hr/>		
2.16 Lanzarote <i>versus</i> La Palma		
Average dissimilarity = 77.32		
	<i>Lobophora variegata</i>	20.23
	<i>Stypocaulon scoparium</i>	7.46
	<i>Padina pavonica</i>	6.86
	<i>Cystoseira abies-marina</i>	6.04
	Unidentified Filamentous Turf	5.85
	<i>Dyctiota dichotoma</i>	5.81
<hr/>		
2.17 Fuerteventura <i>versus</i> La Palma		
Average dissimilarity = 78.21		
	<i>Lobophora variegata</i>	19.30
	<i>Stypocaulon scoparium</i>	10.70
	<i>Jania</i> spp.	9.57
	<i>Padina pavonica</i>	8.02
	<i>Dyctiota dichotoma</i>	7.16
	Unidentified Filamentous Turf	6.42
<hr/>		

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2.18 Gran Canaria *versus* La Palma  
Average dissimilarity = 64.76

<i>Lobophora variegata</i>	16.08
<i>Dyctiota dichotoma</i>	12.37
<i>Stypocaulon scoparium</i>	6.69
<i>Padina pavonica</i>	6.62
<i>Colpomenia sinuosa</i>	6.55
Unidentified Filamentous Turf	6.46

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2.19 Tenerife *versus* La Palma  
Average dissimilarity = 72.82

<i>Lobophora variegata</i>	24.69
<i>Dyctiota dichotoma</i>	9.34
<i>Cystoseira abies-marina</i>	9.27
Unidentified Filamentous Turf	8.83
<i>Lophocladia trichoclados</i>	7.45
<i>Asparagopsis</i> spp.	6.31

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2.20 Gomera *versus* La Palma  
Average dissimilarity = 71.91

<i>Lobophora variegata</i>	25.35
Unidentified Filamentous Turf	15.97
<i>Asparagopsis</i> spp.	11.11
<i>Corallina elongata</i>	7.51
<i>Cystoseira compressa</i>	5.10
<i>Dyctiota dichotoma</i>	4.66

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2.21 Chinijo *versus* El Hierro  
Average dissimilarity = 71.85

<i>Lobophora variegata</i>	19.40
<i>Sargassum</i> spp.	10.38
Unidentified Filamentous Turf	8.41
<i>Cystoseira mauritanica</i>	7.87
<i>Colpomenia sinuosa</i>	7.80
<i>Asparagopsis</i> spp.	6.17

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2.22 Lanzarote *versus* El Hierro  
Average dissimilarity = 83.98

<i>Lobophora variegata</i>	20.30
<i>Sargassum</i> spp.	7.39
<i>Stypocaulon scoparium</i>	7.25
<i>Dyctiota dichotoma</i>	6.14
<i>Padina pavonica</i>	6.10
<i>Lophocladia trichoclados</i>	5.87

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2.23 Fuerteventura *versus* El Hierro  
Average dissimilarity = 88.50

<i>Lobophora variegata</i>	18.54
<i>Stypocaulon scoparium</i>	9.95
<i>Jania</i> spp.	9.48
Unidentified Filamentous Turf	7.23
<i>Padina pavonica</i>	7.12
<i>Sargassum</i> spp.	6.65

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2.24 Gran Canaria *versus* El Hierro  
Average dissimilarity = 74.00

<i>Lobophora variegata</i>	15.45
<i>Dyctiota dichotoma</i>	13.07



	<i>Sargassum</i> spp.	7.57
	<i>Colpomenia sinuosa</i>	6.77
	Unidentified Filamentous Turf	6.34
	<i>Stypocaulon scoparium</i>	6.13
<hr/>		
2.25 Tenerife <i>versus</i> El Hierro		
Average dissimilarity = 81.89		
	<i>Lobophora variegata</i>	23.87
	Unidentified Filamentous Turf	10.78
	<i>Dyctiota dichotoma</i>	9.94
	<i>Cystoseira abies-marina</i>	8.74
	<i>Sargassum</i> spp.	7.67
	<i>Lophocladia trichoclados</i>	6.18
<hr/>		
2.26 Gomera <i>versus</i> El Hierro		
Average dissimilarity = 85.44		
	<i>Lobophora variegata</i>	23.20
	Unidentified Filamentous Turf	19.22
	<i>Asparagopsis</i> spp.	10.20
	<i>Sargassum</i> spp.	7.45
	<i>Corallina elongata</i>	6.01
	<i>Dyctiota dichotoma</i>	5.93
<hr/>		
2.27 La Palma <i>versus</i> El Hierro		
Average dissimilarity = 48.34		
	<i>Sargassum</i> spp.	13..3
	Unidentified Filamentous Turf	9.33
	<i>Cystoseira compresa</i>	9.14
	<i>Lobophora variegata</i>	8.02
	<i>Dyctiota dichotoma</i>	6.54
	<i>Stypopodium zonale</i>	5.32
<hr/>		