

4-13-2006

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

Fernando Tuya
Edith Cowan University

Ricardo J. Haroun
University of Las Palmas de Gran Canaria,

Follow this and additional works at: https://ro.ecu.edu.au/snsc_papers



Part of the [Aquaculture and Fisheries Commons](#)

This article was originally published : Marine ecology. Progress series v.311 2006 p. 15-28 ISSN 0171-8630 Original article available [here](#)

This Journal Article is posted at Research Online.
https://ro.ecu.edu.au/snsc_papers/5

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

4
5 **Fernando Tuya¹, Ricardo J. Haroun**

6 **BIOGES, Department of Biology, Campus Tafira, University of Las Palmas de G.C., E-**
7 **35017, Las Palmas, Canary Islands, Spain**

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-

¹ E-mail: ftuya@yahoo.es

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 • Phytobenthic assemblages • Hierarchical design • Spatial variability •
35 Wave exposure • PERMANOVA • Canary Islands

36

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⁻²). 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⁻², 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 *tournefortii*, 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 “Chinijo 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 m²), 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 ± 5.61 , mean \pm SE) compared to protected locations (mean
320 coverage for all protected locations = 1.56 ± 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 ± 5.70 , mean \pm SE) than exposed
356 locations (coverage for all exposed locations = 10.37 ± 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

432 *Acknowledgements.* We thank I. Blanch for help with the underwater collection of data. Dr T.
433 Dempster significantly improved previous drafts with his English editing, while comments by
434 three anonymous reviewers significantly improved the manuscript. Financial support was
435 provided by the EU INTERREG-IIIB initiative in the frameworks of the MARMAC and
436 PARMAR projects.

437

438

LITERATURE CITED

439 Alves FMA, Chicharo LM, Serrao E, Abreu AD (2001) Algal cover and sea urchin spatial
440 distribution at Madeira Island (NE Atlantic). *Sci Mar* 65:383-392

441

442 Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance in
443 ecology. *Aust Ecol* 26: 32-46

444

445 Anderson MJ (2004) PERMANOVA_2factor: a FORTRAN computer program for
446 permutational multivariate analysis of variance (for any two-factor ANOVA design) using
447 permutation tests. Department of Statistics, University of Auckland, New Zealand

448

449 Anderson MJ, Millar RB (2004) Spatial variation and effects of habitat on temperate reef
450 assemblages in north eastern New Zealand. *J Exp Mar Biol Ecol* 305: 191-221

451

452 Andrew NL, Veijo RM (1998) Ecological limits to invasion of *Sargassum muticum* in
453 northern Spain. *Aquat Bot* 60: 251-263

454

455 Barton ED, Arístegui J, Tett P, Cantón M, García-Braun J, Hernández-León S, Nykjaer J,
456 Almedia C, Almunia J, Ballesteros S, Basterretxea G, Escánez J, García-Weill L, Hernández-
457 Guerra A, López-Laatzén F, Molina R, Montero MF, Navarro-Perez E, Rodríguez JM, van
458 Lening K, Velez H, Wild K (1998) The transition zone of the Canary Current upwelling
459 region. *Prog Oceanog* 41: 455-504

460

461 Benedetti-Cecchi L, Cinelli F (1994) Recovery of patches in an assemblage of geniculate
462 coralline algae: variability at different successional stages. *Mar Ecol Prog Ser* 110: 9-18

463

464 Benedetti-Cecchi L. (2001) Variability in abundance of algae and invertebrates at different
465 spatial scales on rocky sea shores. *Mar Ecol Prog Ser* 215: 79-92

466

467 Benedetti-Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoidi L, Relini G, Cinelli F
468 (2001) Predicting the consequences of anthropogenic disturbances: large-scale effects of loss
469 of canopy algae on rocky shores. *Mar Ecol Prog Ser* 214: 137-150

470

471 Benedetti–Cecchi L, Maggi E, Bertocci I, Vaselli S, Micheli F, Osio GC, Cinelli F (2003)
472 Variation in rocky shore assemblages in the northwestern Mediterranean: contrasts between
473 islands and the mainland. *J Exp Mar Biol Ecol* 293: 193-215
474
475 Blanchette CA, Thornber C, Gaines S (1999) Effects of wave exposure on intertidal fucoid
476 algae. *Proceedings of the California Islands Symposium* 5: 347-355
477
478 Bode A, Barquero S, Varela M, Braun JG, De Armas D (2001) Pelagic bacteria and
479 phytoplankton in oceanic waters near the Canary Islands in summer. *Mar Ecol Prog Ser* 209:
480 1-17
481
482 Boero F (1999) Macroecology returns. *J Evol Biol* 12: 999-1001
483
484 Brown JH (1995) *Macroecology*. University of Chicago Press, Chicago, USA
485
486 Clarke KR, Warwick RM (1994) *Change in Marine Communities: An Approach to Statistical*
487 *Analysis and Interpretation*. Natural Environment Research Council, United Kingdom
488
489 Coleman MA (2003) The role of recruitment in structuring patterns of small-scale spatial
490 variability in intertidal and subtidal algal turfs. *J Exp Mar Biol Ecol*: 131-145
491
492 Davenport R, Never S, Helmke P, Perez-Moreno J, Llinás O (2002) Primary productivity in
493 the northern Canary Islands region as inferred from Seawifs imagery. *Deep Sea Research II*
494 49: 3481-3496
495

496 Dethier MN, Grahan ES, Cohen S, Tear LM (1993) Visual versus random-point percent cover
497 estimations: “objective” is not always better. *Mar Ecol Prog Ser* 96: 93-100
498

499 Dethier MN, Schoch GC (2005). The consequences of scale: assessing the distribution of
500 benthic populations in a complex estuarine fjord. *Estuar Coast Shelf Sci* 62: 253- 270
501

502 Diez I, Santolaria A, Gorostiaga JM (2003) The relationship of environmental factors to the
503 structure and distribution of subtidal seaweed vegetation of the western Basque coast (N
504 Spain). *Estuar Coast Shelf Sci* 56: 1041-1054
505

506 Dulvy NK, Freckleton RP, Polunin NVC (2004) Coral reef cascades and the indirect effects
507 of predator removal by exploitation. *Ecology Letters* 7: 410-416
508

509 Fowler-Walker MJ, Connell SD (2002) Opposing states of subtidal habitat across temperate
510 Australia: consistency and predictability in kelp canopy-benthic associations. *Mar Ecol Prog*
511 *Ser* 240: 49-56
512

513 Frascchetti S, Bianchi CN, Terlizzi A, Fanelli G, Morri C, Boero F (2001) Spatial variability
514 and human disturbances in shallow subtidal hard substrate assemblages: a regional approach.
515 *Mar Ecol Prog Ser* 212: 1-12
516

517 Frascchetti S, Terlizzi A, Benedetti-Cecchi L (2005) Patterns of distribution of marine
518 assemblages from rocky shores: evidence of relevant scales of variation. *Mar Ecol Prog Ser*
519 296: 13-29
520

521 Garrabou J, Ballesteros E, Zabala M (2002) Structure and dynamics of North-western
522 Mediterranean rocky benthic communities along a depth gradient. *Estuar Coast Shelf Sci* 55:
523 493-508
524

525 Graham MH (2004) Effects of local deforestation of the diversity and structure of southern
526 California giant kelp forest food webs. *Ecosystems* 7: 341-357
527

528 Harley CDG, Smith KF, Moore VL (2003) Environmental variability and biogeography: the
529 relationship between bathymetric distribution and geographical range size in marine algae and
530 gastropods. *Global Ecology and Biogeography* 12: 499-506
531

532 Haroun RJ, Afonso-Carrillo A (1997) Flora marina de Canarias y su biodiversidad In: Pérez de
533 Paz P (ed) *Ecosistemas Insulares Canarios. Usos y aprovechamientos en el territorio*. Consejería
534 de Política Territorial, Gobierno de Canarias, p 163-168
535

536 Haroun R, Gil-Rodríguez MC, Wildpret de la Torre W (2003) *Plantas marinas de Canarias*.
537 Canseco Press, Talavera, Spain
538

539 Hoffman AJ, Ugarte R (1985) The arrival of propagules of marine macroalgae in the intertidal
540 zone. *J Exp Mar Biol Ecol* 92: 83-95
541

542 Jernakoff P (1983) Factors affecting the recruitment of algae in a midshore region dominated
543 by barnacles. *J Exp Mar Biol Ecol* 67: 17-32
544

545 Kendrick GA (1991) Recruitment of coralline crusts and filamentous turf algae in the
546 Galapagos Archipelago: effect of simulated scour, erosion and accretion. J Exp Mar Biol Ecol
547 147: 47-63
548

549 Kennelly SJ (1987) Physical disturbance in an Australian kelp community: 1. Temporal
550 effects. Mar Ecol Prog Ser 40: 145-153
551

552 Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73: 1943-1967

553 Lindegarth M, Gamfeldt L (2005) Comparing categorical and continuous ecological analyses:
554 effects of “wave exposure” on rocky shores. Ecology 86: 1346-1357
555

556 Lüning K (1990) Seaweeds: their environment, biogeography, and ecophysiology. Wiley,
557 New York
558

559 Martín Ruiz JF (2001) Geografía de Canarias. Sociedad y medio natural. Ediciones del
560 Cabildo de Gran Canaria
561

562 McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Jones IV SH (2003)
563 Interaction between nutrients and herbivory in controlling algal communities and coral
564 condition on Glover’s Reef, Belize. Mar Ecol Prog Ser 261: 135-147
565

566 Medina M, Haroun RJ (1993) Preliminary study on the dynamics of *Cystoseira abies-marina*
567 populations on Tenerife (Canary Islands). Courier Forsch: 109-112
568

569 Medina M, Haroun RJ, Wildpret W (1995) Phytosociological study of the *Cystoseira abies-*
570 *marina* community in the Canarian Archipelago. Bull Museu Mun Funchal 4: 433-439
571

572 Menconi M, Benedetti-Cecchi L, Cinelli F (1999) Spatial and temporal variability in the
573 distribution of algae and invertebrates on rocky shores in the northwest Mediterranean. J Exp
574 Mar Biol Ecol 233: 1-23
575

576 Menge BA (2000) Top-down and bottom-up community regulation in marine rocky intertidal
577 habitats. J Exp Mar Biol Ecol 250: 257-289
578

579 Micheli F, Benedetti-Cecchi L, Gambaccini S, Bertocci I, Borsini C, Chato Osio G, Romano
580 F (2005) Cascading human impacts, marine protected areas, and the structure of
581 Mediterranean reef assemblages. Ecological Monographs 75: 81-102
582

583 Ruitton S, Francour P, Boudouresque CF (2000) Relationships between algae, benthic
584 herbivorous invertebrates and fishes in rocky sublittoral communities of a temperate sea
585 (Mediterranean). Estuar Coast Shelf Sci 50: 217-230
586

587 Russell BD, Connell SD (2005) A novel interaction between nutrients and grazers alters
588 relative dominance of marine habitats. Mar Ecol Prog Ser 289: 5-11
589

590 Santelices B (1990) Patterns of reproduction, dispersal and recruitment in seaweeds.
591 Oceanogr Mar Biol Annu Rev 28: 177-276
592

593 Schils T, Coppejans E (2003) Spatial variation in subtidal plant communities around the
594 Socorra Archipelago and their biogeographic affinities within the Indian Ocean. *Mar Ecol*
595 *Prog Ser* 251: 103-114
596

597 Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-
598 dominated communities. *Oikos* 69: 476-498
599

600 Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA, Tegner MT
601 (2002) Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental*
602 *Conservation* 29: 436-459
603

604 Taylor DI, Schiel DR (2003) Wave-related mortality in zygotes of habitat-forming algae from
605 different exposures in southern New Zealand: the importance of “stickability”. *J Exp Mar*
606 *Biol Ecol* 290: 229-245
607

608 Tilman D, Kareiva P (1997) *Spatial ecology: the role of space in population dynamics and*
609 *interspecific interactions*. Princeton University Press, Princeton, NJ
610

611 Tuya F, Boyra A, Sánchez-Jerez P, Haroun RJ, Barberá C (2004a) Relationships between
612 rocky-reef fish assemblages, the sea urchin *Diadema antillarum* and macroalgae throughout
613 the Canarian Archipelago. *Mar Ecol Prog Ser* 278: 157-169
614

615 Tuya F, Boyra A, Sánchez-Jerez P, Haroun RJ, Barberá C (2004b) Can alone one single
616 species determine the structure of a rocky benthic community: the case of the black long-
617 spined sea urchin *Diadema antillarum* in the eastern Atlantic. *Hydrobiologia* 519:211-21

618

619 Underwood AJ (1997) Experiments in Ecology: their logical design and interpretation
620 using Analysis of Variance. Cambridge University Press, Cambridge

621

622 Underwood AJ, Jernakoff P (1981) Interactions between algae and grazing gastropods
623 in the structure of a low shore algal community. *Oecologia* 48: 221-254

624

625 Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution on
626 intertidal invertebrates. *Oecologia* 107: 212-224

627

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 > CH > FV GO TF LZ</u> <u>LZ FV GC TF > 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 > GC > CH FV LZ TF GO</u>			<u>GO TF > FV > GC LP CH LZ EH</u>				<u>FV GC > CH LZ > 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

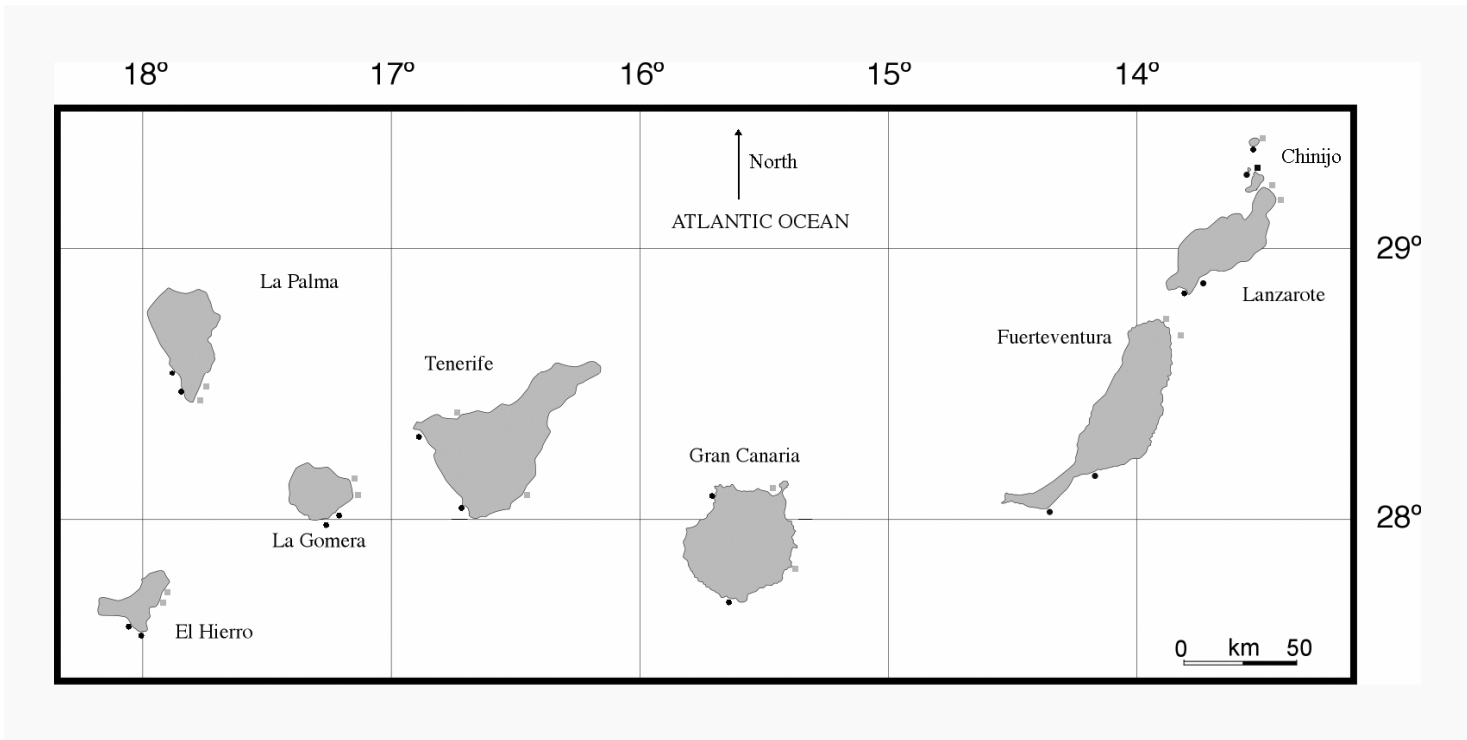


Fig.1

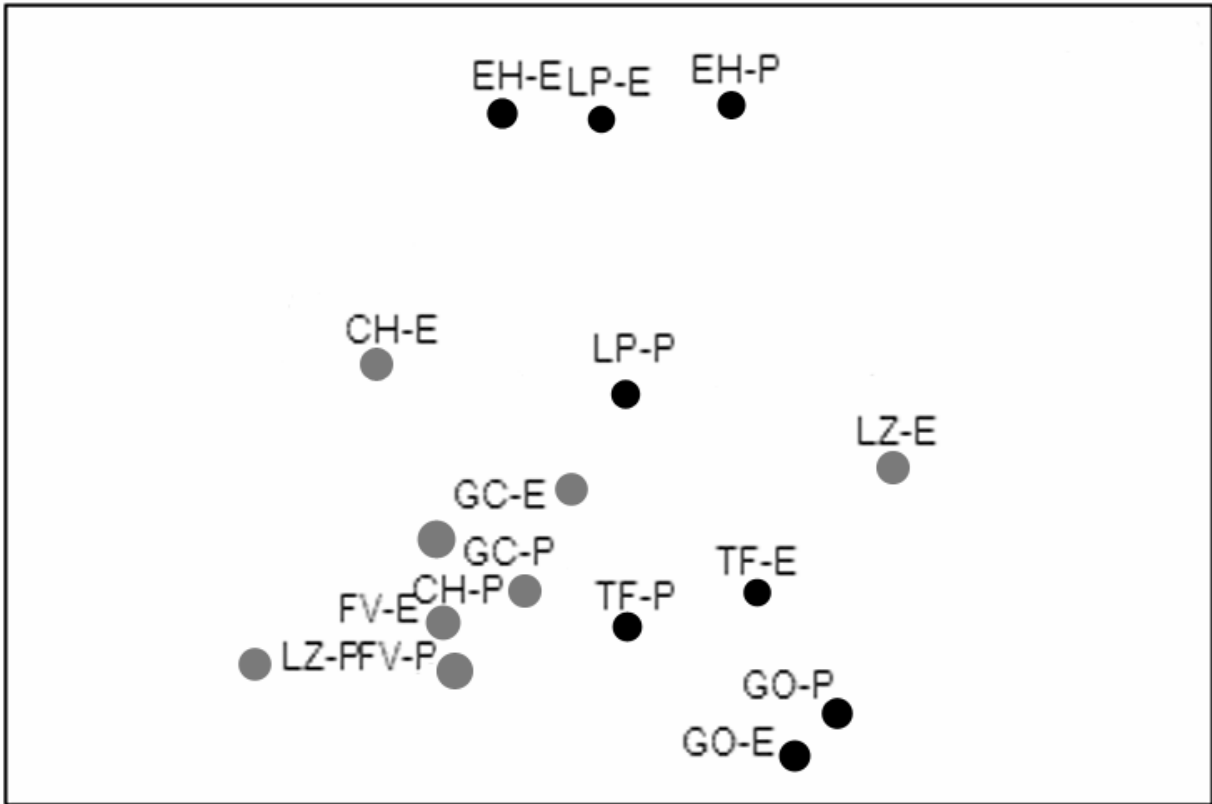


Fig. 2

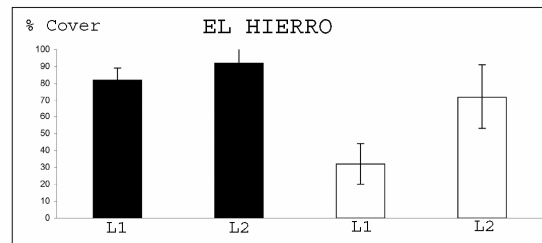
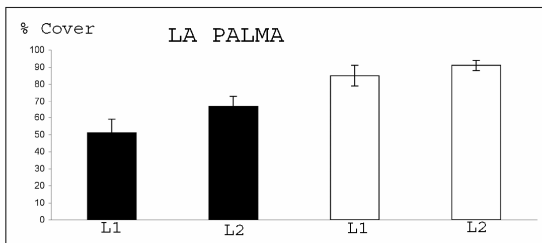
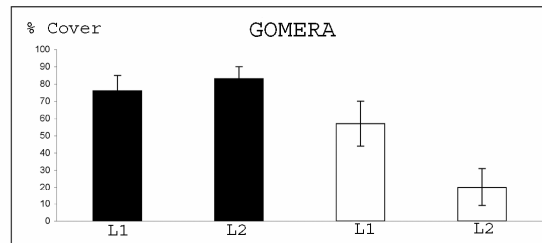
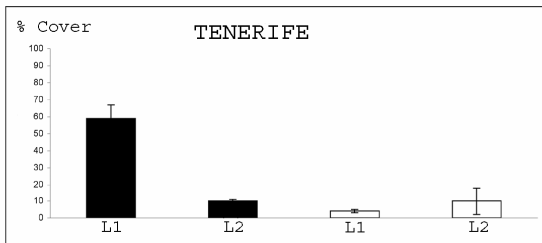
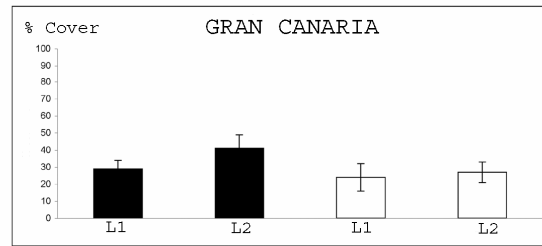
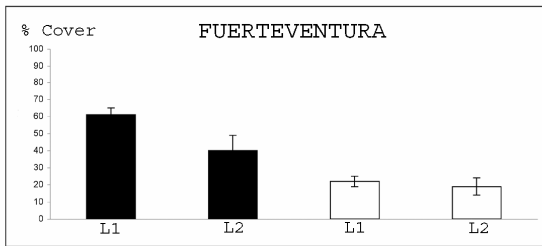
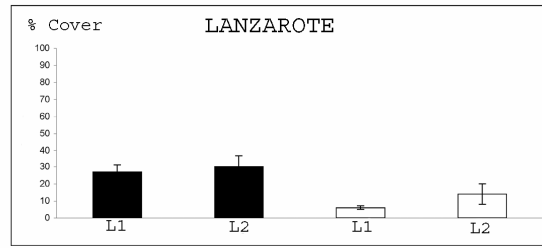
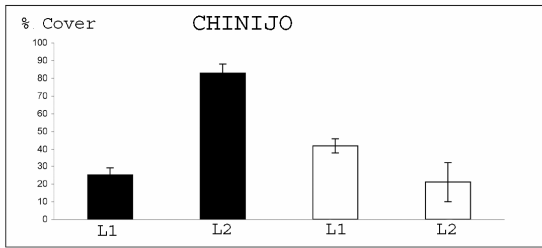


Figure 3

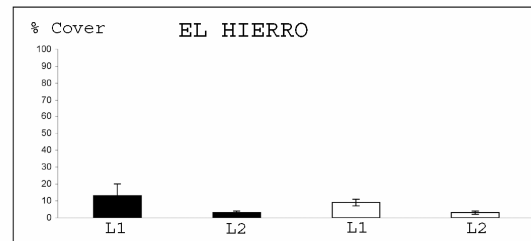
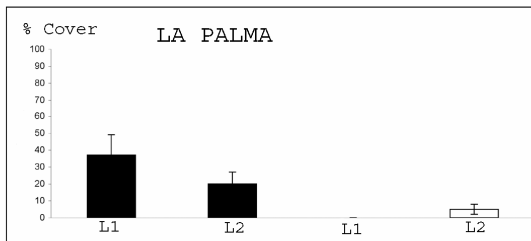
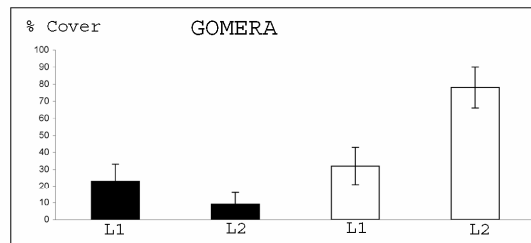
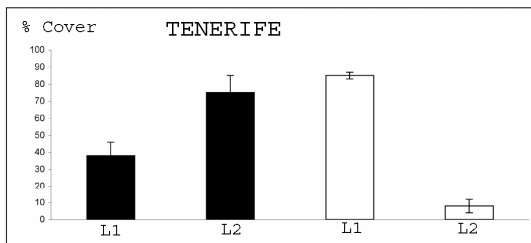
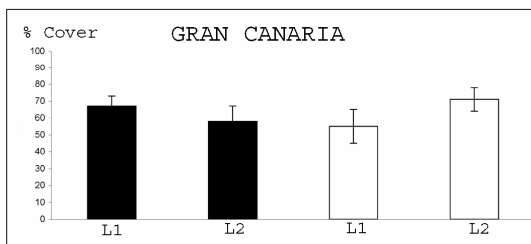
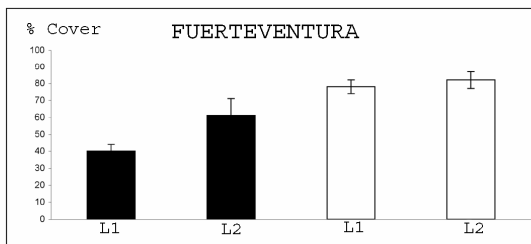
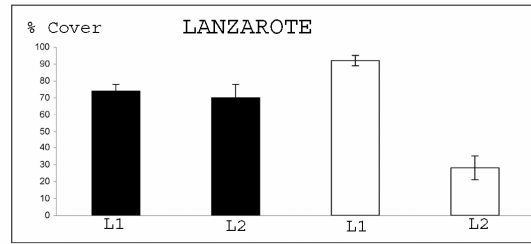
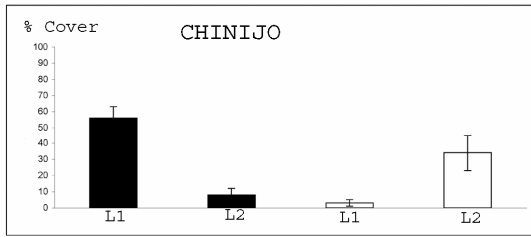


Figure 4

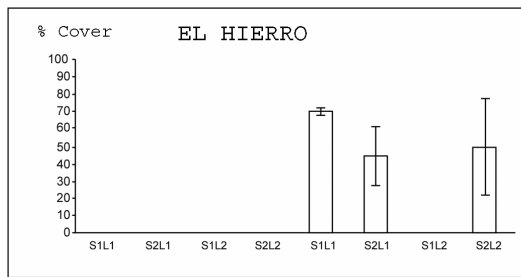
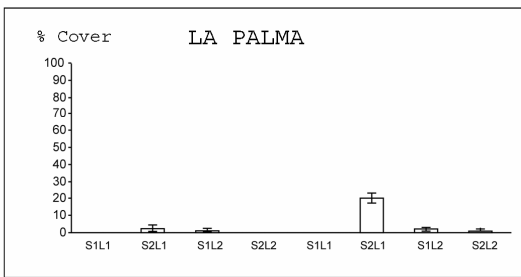
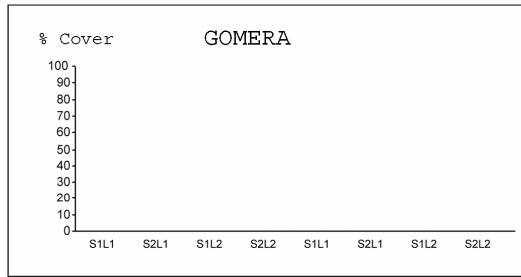
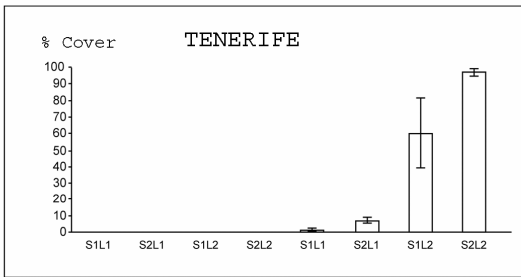
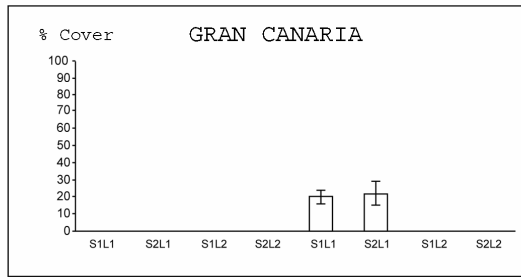
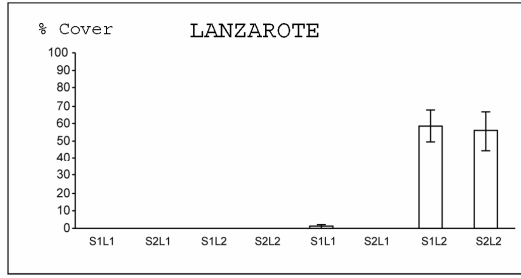
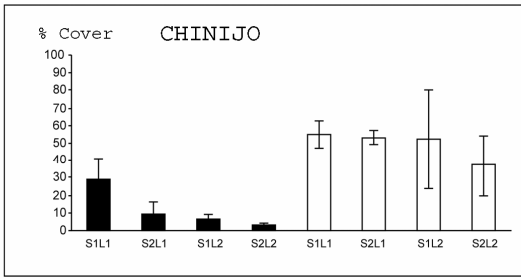


Figure 5

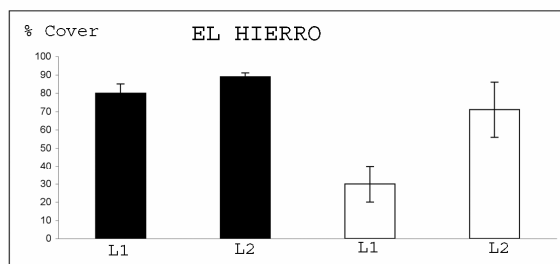
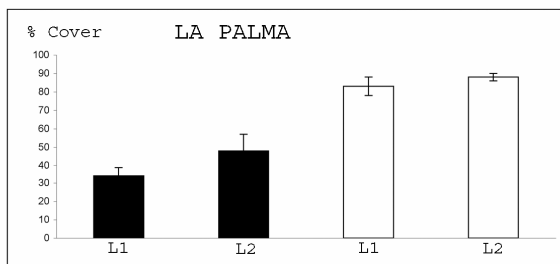
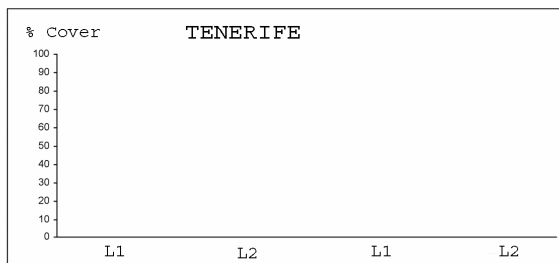
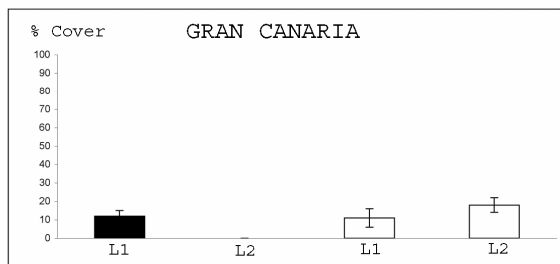
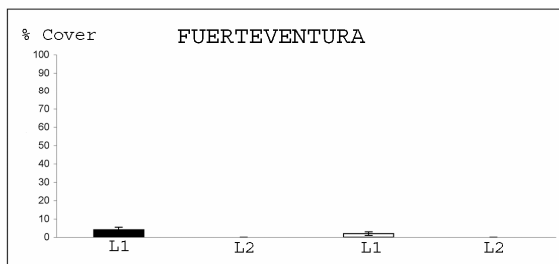
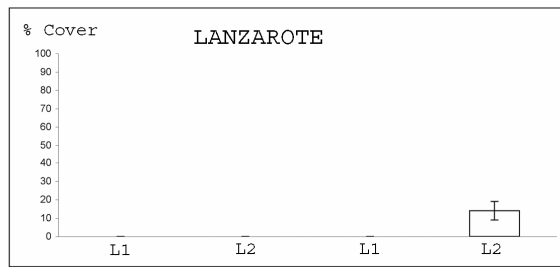
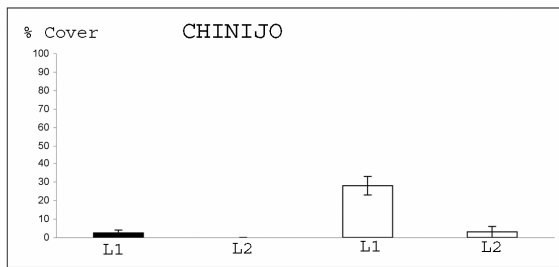


Figure 6

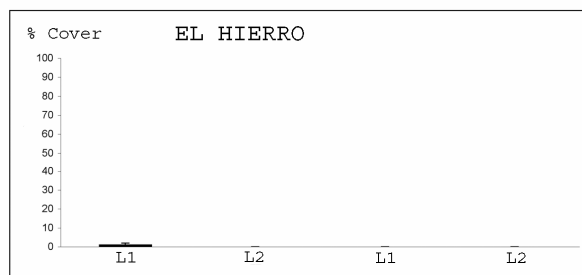
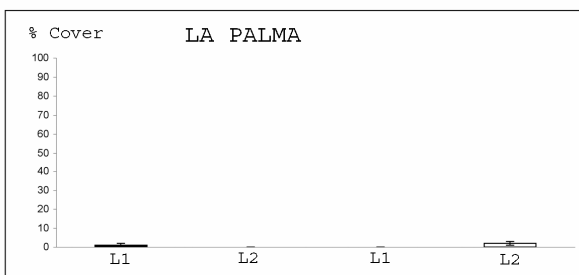
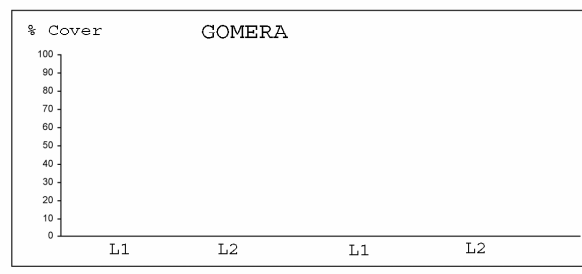
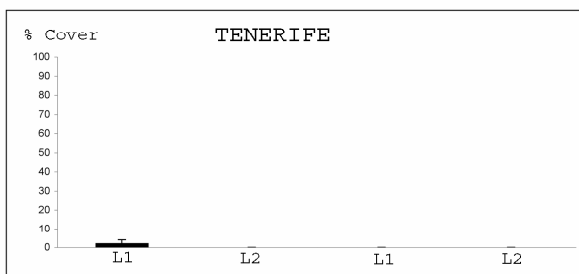
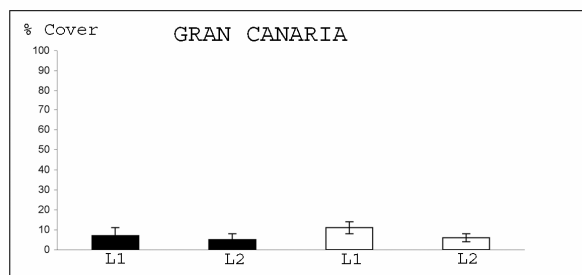
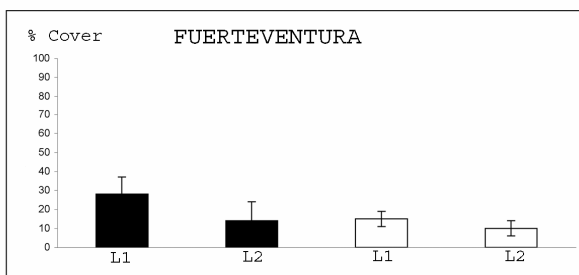
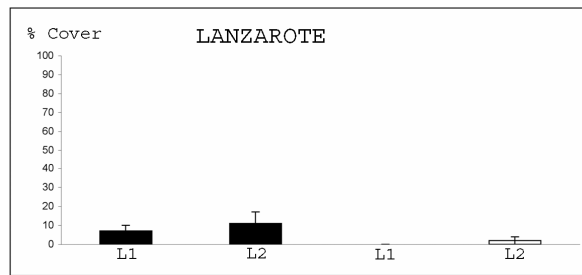
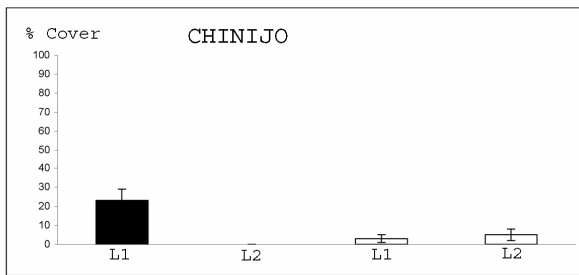


Figure 7

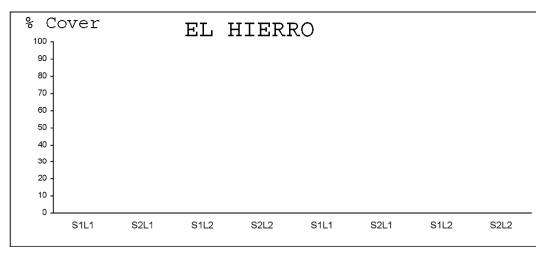
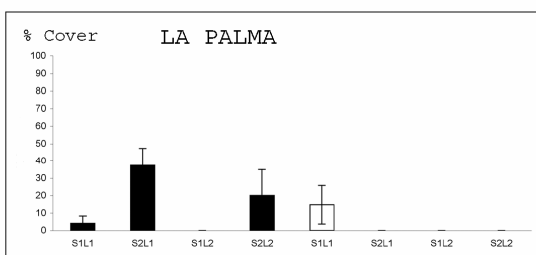
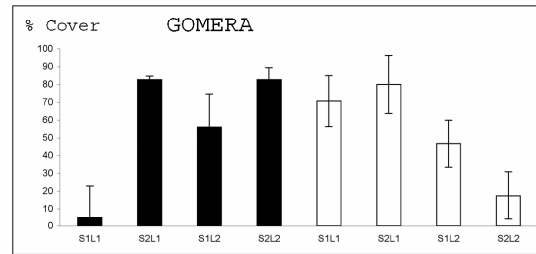
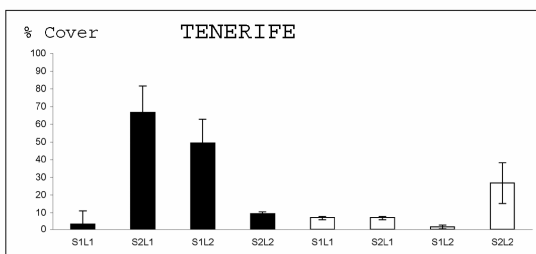
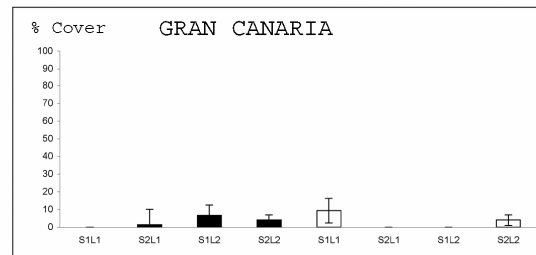
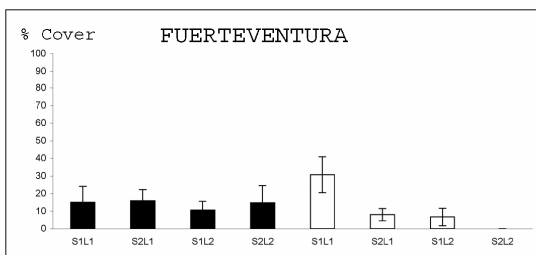
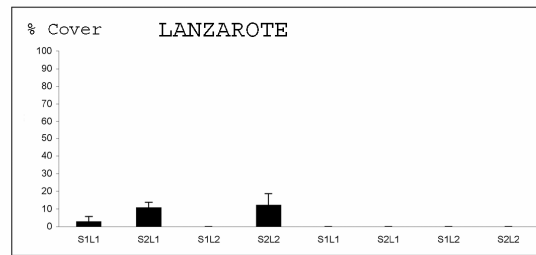
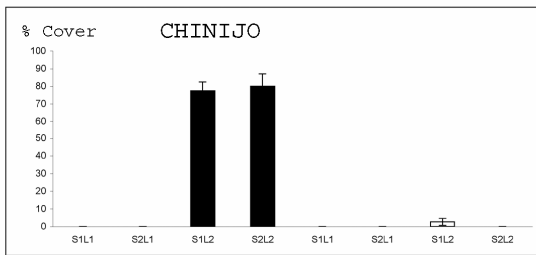


Figure 8

Supplementary material (Appendices 1 & 2)

Appendix 2: Summary of the results from the SIMPER procedure

	Taxon	Contribution to dissimilarity (%)
1. Protected <i>versus</i> Exposed locations		
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
2. Dissimilarities among islands		
2.1 Chinijo <i>versus</i> Lanzarote		
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
2.2 Chinijo <i>versus</i> Fuerteventura		
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
2.3 Chinijo <i>versus</i> Gran Canaria		
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
2.4 Lanzarote <i>versus</i> Gran Canaria		
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/>		

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

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

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

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

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

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

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>Stypodium zonale</i>	5.32
<hr/>		