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Material type and roughness influence structure of inter-tidal communities on coastal defenses

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10 **Material type and roughness influence structure of intertidal communities on coastal**
11 **defences**

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22 **Abstract**

23 On a global scale, urbanisation has resulted in substantial proportions of the coast being
24 replaced by artificial structures such as marinas, breakwaters or seawalls. There is broad
25 consensus that coastal defence structures are poor surrogates of the natural habitats they
26 replace. Here we investigate the effect of the type and roughness of materials used for the
27 construction of artificial structures on the biota by comparing abundances and distribution
28 of key intertidal taxa between natural shores and coastal defences. Lower abundance of
29 gastropods and barnacles were found on artificial coastal defence structures (regardless of
30 the material type). At small–spatial scales, there was a significant effect of roughness which
31 increased the abundances of key taxa. Results suggest that choice of materials used for the
32 construction of coastal defence structures *per se* has little effect on community structure,
33 but that enhanced roughness could make coastal defences better surrogates of natural
34 habitats by supporting assemblages that are more similar to those found on natural shores.

35 **Keywords:** artificial structures, intertidal assemblages, marine biodiversity, urbanisation,
36 macroalgae

37 **Introduction**

38 The extent of natural coastal habitats converted for urban use, including the construction of
39 coastal defence structures such as seawalls, breakwaters or groynes, is increasing globally
40 (Goodsell 2009; Firth *et al.* 2013). This trend is likely to continue, given predictions for sea
41 level rise and increased storminess (Thompson *et al.* 2002; Wong *et al.* 2014). There is thus
42 a clear interest in understanding the environmental consequences of these artificial habitats
43 (Moschella *et al.* 2005), with several studies highlighting the importance of understanding
44 the underlying ecological processes (Moreira *et al.* 2006; Munari 2013) when planning
45 developments along shores (Chapman & Bulleri 2003).

46 Construction of artificial structures provides additional hard substrata for epibenthic
47 organisms. These structures, however, can have a strong effect on the structure and
48 functioning of flora and fauna assemblages in adjacent hard- or soft-bottom habitats (e.g.
49 Martin *et al.* 2005; Martins *et al.* 2009; Bertasi *et al.* 2007). Moreover, although epibiotic
50 communities on artificial structures can be qualitatively similar to those on natural rocky
51 shores, differences in the diversity, abundance, behaviour and/or phenology of epibiota on
52 breakwaters, seawalls or groynes have been reported by many authors (e.g. Chapman 2003;
53 Chapman & Bulleri 2003; Bulleri *et al.* 2004; Moschella *et al.* 2005; Moreira 2006;
54 Moreira *et al.* 2006; Martins *et al.* 2009; Firth *et al.* 2013). Collectively, these studies
55 suggest that artificial structures cannot generally be considered surrogates of the natural
56 habitats they replace.

57 Some studies consider that artificial structures built with locally quarried materials are
58 likely to have minimal effect on intertidal assemblages, and therefore predict that the

59 epibiotic communities on those structures would be similar to those colonizing nearby
60 natural rocky habitats (see Thompson *et al.* 2002; Branch *et al.* 2008). However, there is
61 evidence that this is not always true and differences have been found between assemblages
62 on natural habitats and artificial structures made of locally quarried rock (see Bulleri &
63 Chapman 2010, for review). Moreover, current literature on the effects of coastal
64 urbanisation includes ambiguous results, revealing both positive and negative effects on the
65 maintenance of local populations. For instance, the outcomes of investigations on the
66 effects of coastal urbanisation on the distribution of limpets have been variable. Some
67 authors (Moreira *et al.* 2006; Díaz–Agras *et al.* 2010) found no differences in the
68 abundance or frequency of occurrence of limpets inhabiting artificial substrata and rocky
69 shores, while other authors reported greater numbers of limpets on either natural (e.g.
70 Bulleri & Chapman 2004; Bulleri *et al.* 2004) or artificial structures (Guerra–García *et al.*
71 2004).

72 Modification of artificial structures to make them better surrogates of natural habitats is a
73 form of mitigation that is receiving increasing attention (Moreira *et al.* 2007; Chapman and
74 Blockey 2009; Martins *et al.* 2010; Firth *et al.* 2013). Some attempts to reduce their
75 ecological impacts have been addressed by adding elements (e.g. wetland vegetation) or
76 features of habitat (e.g. rock-pools) that are absent from urban structures (Zedler & Leach
77 1998; Bulleri & Chapman 2010). Natural rocky shores differ from artificial structures in a
78 number of important features (Chapman and Blockey 2009; Firth *et al.* 2013) namely
79 differences in material composition and structural roughness, and there is now a substantial
80 body of work highlighting the important role of substratum heterogeneity in structuring
81 intertidal communities (Thompson *et al.* 1996; Pinn *et al.* 2008; Griffin *et al.* 2009; Skov *et*

82 *al.* 2011; Gartner *et al.* 2013). Artificial structures generally fail to provide the array and
83 diversity of habitat heterogeneity found on most natural shores (Chapman 2006; Firth *et al.*
84 2013; Browne & Chapman 2014). For instance, seawalls generally lack microhabitats such
85 as rock pools that retain water during low tide allowing the establishment specialist species
86 (Chapman & Blockley 2009; Firth *et al.* 2013; Browne & Chapman 2014). Likewise,
87 seawalls or groynes have steep inclinations, which reduce the areal extent of the intertidal
88 zone compared to the generally gentler slope of natural habitats (Moreira *et al.* 2007;
89 Bulleri & Chapman 2010). Therefore, we hypothesize that artificial structures with rougher
90 surfaces, i.e., more similar to natural habitats, will benefit intertidal species, at least those
91 small-sized which can easily find refuge from the harsh intertidal conditions.

92 The ecological impacts of coastal infrastructure in shallow coastal waters may vary
93 accordingly with the nature of the surrounding habitat (Bulleri & Chapman 2010). Most of
94 the research to date has considered coastal defences that lie behind soft sedimentary
95 shorelines that are at risk from erosion (Gacia *et al.* 2007), thus providing additional hard
96 surface for colonization by benthic organisms where it was previously absent (Chapman &
97 Bulleri 2003; Moschella *et al.* 2005). This study was conducted in the Azores, an oceanic
98 archipelago where volcanic rubble and steep cliffs constitute the most common marine
99 habitats. In the Azores, most artificial structures are used to protect nearby towns from high
100 sea levels during winter storms. In contrast to many other locations worldwide, coastal
101 defences in the Azores are typically built on top of former natural stretches of rocky coasts,
102 thus showing similarities in physical nature (i.e., hard substrate) to adjacent natural
103 environments. Therefore, unlike areas where artificial structures are deployed on soft-
104 bottom areas, we hypothesize that assemblages on most of the Azorean artificial structures

105 will be of similar composition to those found on adjacent natural environments. However,
106 given the well known effect of substratum type in structuring intertidal assemblages (e.g.
107 Connell & Glasby 1999; Glasby 1999), the first objective in this study was exactly to
108 compare patterns of distribution and abundance of intertidal organisms on natural rocky
109 shores with that of coastal defence structures (boulders and blocks) made of either basalt
110 (locally quarried rock) or concrete (a non–natural substratum, and probably the most
111 common material used in coastal urbanisation). We are interested in testing if using rocks
112 that were locally quarried would somehow minimise the impacts of coastal urbanisation. In
113 addition to this, we also investigated how natural small-scale variability in substratum
114 topography (within artificial structures made of basalt) influences the structure of intertidal
115 assemblages. We predict that areas of the substratum with rougher topography will support
116 assemblages that differ from those found in areas of the substratum with smoother
117 topography.

118 This information will help to understand the effects of hard defence structures, and may be
119 potentially provide information that can be used to mitigate the ecological impacts of
120 coastal urbanisation (e.g. Martin *et al.* 2005; Moschella *et al.* 2005; Martins *et al.* 2010).

121 **Material and Methods**

122 The study was conducted on São Miguel Island (Azores, Fig. 1), where maximum tidal
123 range is approximately 2 m and the coast is exposed to medium to high levels of wave
124 action. In general, three zones can be recognized in the São Miguel Island rocky intertidal,
125 following classical zonation schemes (Stephenson & Stephenson 1972): the low–shore is
126 characterized by a covering of coarsely branched, coralline and turf–forming species of

127 macroalgae; the mid–shore is dominated by the barnacle *Chthamalus stellatus*, whereas the
128 gastropod littorinids *Tectarius striatus* and *Melarhaphé neritoides* usually inhabit in the
129 upper–shore (Martins *et al.* 2008b).

130 To characterize the intertidal assemblage community composition and abundance, sampling
131 was carried out on natural rocky shores of basaltic nature (hereafter referred to as Natural
132 shore), and artificial coastal defence structures built of either basalt (hereafter Basalt
133 artificial structures) or concrete (hereafter Concrete artificial structures) located along the
134 coastline of São Miguel (176 km perimeter, length 65 km, width 8–15 km) (Fig. 1). Only
135 the seaward sides of natural and artificial habitats were sampled to standardize for wave
136 exposure. Five locations representative of the three habitat types (Natural shore, Basalt
137 artificial structures and Concrete artificial structures) were randomly selected (Fig. 1). All
138 locations were separated by tens of kilometers and similarly exposed to incoming oceanic
139 swell. Within each location, five replicate quadrats (25x25 cm) were randomly placed at
140 least 2 m apart on emergent substrata at low–, mid– and upper–shore levels, visually
141 determined by the presence of macroalgae, barnacles and littorinid respectively. The
142 assemblage structure was hence assessed at each level. Percentage cover of sessile
143 organisms (e.g. macroalgae, barnacles) and bare rock (a measure of unoccupied space)
144 were obtained following the methodology described in Dethier *et al.* (1993), in which the
145 abundance of organisms within each of the 25 5x5 cm sub–quadrats (that add up a sampling
146 quadrat) was assigned a score ranging between 0 (absent) and 4 (100% cover of the sub–
147 quadrat). Total percentage cover is then estimated by summing the scores of all sub–
148 quadrats (see Dethier *et al.* 1993 for further details). Macroalgae were identified and
149 grouped into distinct morpho–functional groups (FGs), based on species’s morphology and

150 the way they compete for resources (Steneck & Dethier 1994; Arenas *et al.* 2006; Veiga *et*
151 *al.* 2013). The selected FGs were: Ephemerals (considering first colonizers, including
152 diatomaceous biofilms, microalgae and filamentous algae such as *Chaetomorpha*,
153 *Cladophora*), Foliose (e.g. *Porphyra*, *Ulva rigida*), Coarsely branched (e.g. *Caulacanthus*
154 *ustulatus*), Coenocytic (*Codium adhaerens*), Articulated calcareous (e.g. *Corallina*
155 *elongata*), Leathery (e.g. *Fucus spiralis*), Calcified crustose (e.g. *Lithophyllum*), and Non-
156 calcified crustose (e.g. *Nemoderma*). Taxa present within quadrats but not reaching a score
157 of 1 were given a nominal value of 0.5%. Motile invertebrates were identified up to species
158 level, counted and expressed as number of individuals per quadrat. All surveys were made
159 between the 24th June and 4th August 2013, during low-water spring tides.

160 A complementary small-scale study investigated the role of substratum roughness in
161 determining patterns of species distribution on coastal defence structures by comparing the
162 abundance of organisms in blocks with smooth and rough surfaces visually selected *a*
163 *priori* on a basalt seawall at two sites selected 10's of meters apart. Five replicate plots on
164 smooth *vs.* rough blocks were sampled. In this case, only mid- and upper-shore was
165 sampled in this survey, since low-shore roughness was hidden by dense macroalgal
166 dominance. A pin-microrelief method (Vázquez *et al.* 2009) was adapted to measure
167 substratum random roughness (RR) in the sampled plots. Differences in substratum surface
168 height were recorded in 15 cm transects with spacing between readings of 2.5 mm, and RR
169 index was calculated as the standard error among heights (Allmaras *et al.* 1966). This
170 survey was made between August 12th and September 12th 2014, during low-water spring
171 tides. Sampling of the biota was done as described above.

172 Data analysis

173 Multivariate analysis.

174 Differences in the structure of assemblages were investigated for each tidal height using a
175 two-way permutational analysis of variance (PERMANOVA) with habitat (Ha, fixed, with
176 three levels: Natural shores, Basalt artificial structures and Concrete artificial structures)
177 and location (Lo, random, nested in habitat, with five levels) as factors. PERMANOVA
178 analyses were run on Bray Curtis similarity matrix of both untransformed and presence–
179 absence transformed complete epibenthic assemblage (i.e. including percentage cover of
180 macroalgae/barnacles and abundance of gastropods). Pair-wise tests were used to compare
181 the effects within significant factors.

182 Univariate analysis.

183 The numbers of macroalgal FGs as well as the relative abundance of taxa were compared
184 among habitats following the same procedure as described before but using, in this case,
185 traditional analysis of variance. Prior to analyses, Cochran's test was used to detect
186 heterogeneity of variances and data were transformed where appropriate (Underwood
187 1997). When homogeneity of data was not achieved after transformation, analyses were run
188 on the untransformed data but using a more conservative significance level ($P < 0.01$)
189 (Underwood 1997).

190 The role of roughness in determining small-scale patterns of species distribution in hard–
191 defence structures, namely the abundance of gastropods and the percentage cover of
192 barnacles, was also investigated using an approach similar to that described above, but
193 including roughness (Ro, fixed, two levels: Smooth and Rough) and site (Si, random, two
194 levels) as factors.

195 Multivariate analyses were run using PRIMER 6 statistical package with the
196 PERMANOVA+ add-on (PRIMER-E, Plymouth Marine Laboratory, UK), whereas
197 univariate analysis were run using GMAV5 (University of Sydney).

198 **Results**

199 Multivariate analysis.

200 Assemblage structure (both on the untransformed, Table 1a, and presence-absence data,
201 Table 1b) did not differ significantly among habitats (i.e., Natural shore, Concrete and
202 Basalt artificial structures) on the lower-shore. On the mid-shore, assemblage structure
203 differed significantly between Natural and Basalt when considering abundance data (Table
204 1a), but not when considering only compositional data (Table 1b). Significant differences
205 on the assemblage structure were detected between Natural shores and both artificial
206 habitats (Concrete and Basalt artificial structures) on the upper-shore, when considering
207 abundance (Table 1a) but not presence-absence (Table 1b) data.

208 Univariate analysis.

209 The numbers of macroalgal FGs were generally similar among habitats at all tidal levels,
210 although differences were found among locations ($P < 0.001$, Table 2, Fig. 2).

211 At low-shore level, the abundance of macroalgal FG showed no differences among habitats,
212 although differences were found among locations ($P < 0.001$, Table 3, Fig. 3).

213 At mid-shore level, only coarsely branched algae were significantly more abundant on
214 Natural shores than on artificial reefs (means of 6.0% on Natural vs. 0.8% on Basalt and
215 0.7% on Concrete artificial structures; Table 3, Fig. 3). The abundance of the remaining

216 functional groups (coenocytic, foliose, articulated calcareous, leathery and calcified and
217 non-calcified crusts) did not vary significantly among natural shores and basalt and
218 concrete artificial habitats, although differences were always found among locations (Table
219 3, Fig. 3). The number of both *M. neritoides* and *T. striatus* was significantly greater on
220 natural shores than in artificial structures (Table 4, Fig. 4). Mean numbers of littorinids
221 from 0.08 to 1.6 ind. 0.06 m⁻² were observed on coastal defences, while densities between
222 10.9 and 12.8 ind. 0.06 m⁻² were observed on natural shores (Fig. 4). The abundance of
223 *Patella* spp. did not significantly differ between habitats (Fig. 4, Table 4), while the cover
224 of *C. stellatus*, was significantly greater on Natural shores compared to Basalt artificial
225 structures (28.3 vs. 5.5 % respectively, Fig. 4, Table 4).

226 Regarding the upper-shore, significant differences were detected among habitats when
227 considering the percent cover of ephemerals, more abundant on Basalt artificial structures
228 (0.14%) than in Concrete artificial structures (0.04%, Table 3, Fig. 3). Articulated
229 calcareous and calcified crusts showed differences among locations ($P < 0.001$, Table 3,
230 Fig. 3), but not among habitats. The abundance of *T. striatus* significantly differed between
231 habitats (Fig. 4, Table 4), with numbers of 11.8 ind. 0.06 m⁻² in natural shores and 1.5 in
232 artificial structures. The numbers of the remaining faunal species were similar among
233 habitats, although differences were found among locations ($P < 0.05$, Table 4, Fig. 4).

234 Small-scale effect of substratum roughness.

235 There were significant differences in substratum roughness between the *a priori* selected
236 smooth vs. rough surfaces, with values of 0.18 ± 0.02 mm (mean \pm SE, $n = 20$) and $0.05 \pm$

237 0.01 respectively (ANOVA, Mid-shore: $F(1,17)$ (pooled) = 16.13, $P < 0.001$; Upper-shore:
238 $F(1,17)$ (pooled) = 16.22, $P < 0.001$).

239 At mid-shore level, significant differences were found in the mean abundance of *M.*
240 *neritoides* and *C. stellatus* between rough and smooth blocks although these effects were
241 site-dependent. *M. neritoides* was significantly more abundant on rough blocks (mean
242 values of 10.4 in rough vs. 0.10 ind. 0.06 m^{-2} in smooth surfaces) at site 1, while *C.*
243 *stellatus* was significantly more abundant on smooth blocks on both sites (mean cover of
244 39.4% in smooth vs. 6.8% in rough blocks; Fig. 5, Table 5). The littorinid *T. striatus* was
245 significantly more abundant on rough surfaces at both the mid- and the upper-shore (mean
246 number of 12.3 in rough vs. 0.2 ind. 0.06 m^{-2} in smooth surfaces on mid- and 16.7 vs. 1.0
247 ind. 0.06 m^{-2} on upper-shore levels; Fig 5, Table 5).

248 **Discussion**

249 As we hypothesized, qualitatively similar assemblages of animals and plants were found on
250 both the coastal defence structures and natural habitats. There were, however, relevant
251 effects of urbanisation on the abundance of some intertidal organisms. For instance, the two
252 littorinid species and the cirripid barnacle were substantially (and significantly) less
253 abundant on the artificial structures. Moreover, this effect was generally similar on defence
254 structures made of either concrete or basalt suggesting that they were not directly
255 influenced by the material type of the substratum *per se*. Results from the small-scale study
256 showed that these species were highly influenced by small-scale variation in roughness.
257 The lower abundance of littorinids found on artificial structures may thus be related to the
258 general lack of microtopographic features that are important as habitat for these molluscs.

259 This is in accordance with the wider literature showing that littorinids generally tend to
260 aggregate around small-scale features of the substratum (Chapman 1995; Jones &
261 Boulding 1999; Silva *et al.* 2014). Both the physical characteristics of the habitats
262 (roughness; e.g. Gray and Hodgson 2004) and also the presence of *C. stellatus*, could
263 provide refuges for this fauna. As observed by other authors (Silva *et al.* 2014), small
264 gastropods were observed inhabiting the tests of dead barnacles, acting therefore as
265 biogenic microhabitats (Aguilera *et al.* 2014), altering the complexity of the substratum and
266 providing shelter and protection from physiological stress to intertidal organisms
267 (Underwood *et al.* 1983; Jernakoff 1985). Roughness has been also considered an important
268 variable on barnacle settlement (e.g. Chabot & Bourget 1988; Skinner & Coutinho 2005).
269 Barnacles had lower abundance on artificial structures (as observed e.g. by Aguilera *et al.*
270 2014), but in our case, within the artificial structures the effect of roughness contrasted that
271 found for littorinids (i.e., lower abundance on smooth surfaces). Although we did not
272 expect biotic or abiotic factors to differ between sites within the artificial shore, e.g.
273 chemical cues generated by barnacle adults could be influencing our results, since barnacles
274 are known to respond positively to the presence of conspecifics (Skinner & Coutinho
275 2005), and we could not separate such effects from those related to roughness.

276 Due to their key role in intertidal assemblages, changes in limpet abundance among habitats
277 may indirectly influence the distribution of other organisms (Hawkins *et al.* 1992). In the
278 present study, and in contrast with Bulleri & Chapman (2004) or Bulleri *et al.* (2004),
279 although natural habitats supported greater densities of limpets than basalt at low-shore
280 levels, no differences were found on the mid-shore, where limpets are usually more
281 abundant (Martins *et al.* 2010). In this and other systems (e.g. Oliva & Castilla 1986,

282 Branch & Moreno 1994, Moreno 2001) , substantial harvesting of limpets, a traditionally
283 important source of income for many families (Ferraz *et al.* 2001; Martins *et al.* 2008a)
284 may have masked natural patterns of distribution.

285 Generally, no differences were found in the number of macroalgal functional groups among
286 habitats. However, a lower number of functional groups tended to be found on the upper–
287 shore on natural shores. These macroalgae vary in consistent ways along physical gradients,
288 including, e.g., wave exposure and desiccation (Menge 2000). Wave splash operates
289 vertically, allowing organisms to extend upwards (Ballesteros & Romero 1988; Hobday
290 1995). In the case of artificial structures, the steep slope may break waves violently against
291 the artificial structures (Allsop *et al.* 2005), encompassing long–term exposure to waves
292 (wetting gradient, Chappuis *et al.* 2014). This could directly affect the vertical distribution
293 of some functional groups, such as calcified and non–calcified crustose algae. Only on the
294 mid– and upper–shore was the epibenthic assemblage composition of coastal defences
295 different from natural habitats. Unlike results from Bulleri & Chapman (2004) who found
296 compositional differences (differences in species identities) in assemblages on seawalls and
297 adjacent rocky shores, we did not find such compositional differences. In our study system,
298 differences found between natural shores and artificial structures were largely restricted to
299 changes in species abundances (not identity).

300 Conclusion

301 Information about patterns of distribution of species in natural and artificial habitats is
302 essential in order to understand the ecological impacts of coastal infrastructures (Bulleri &
303 Chapman 2010). Some studies have suggest that artificial structures provide habitat for

304 epibiotic communities that are qualitatively similar to those found inhabiting nearby natural
305 reefs (e.g. Branch *et al.* 2008) but quantitative studies (e.g. Moschella *et al.* 2005; Firth *et*
306 *al.* 2014), have shown artificial structures have significantly lower abundance of
307 gastropods, barnacles and coarsely branched algae, indicating some lack of similarity with
308 natural rocky shores. Our study indicates that roughness, rather than substratum type *per se*,
309 can play a key role in determining the distribution of barnacles and littorinids. Our results
310 indicate that selection of materials with rougher surfaces (i.e. enhanced roughness) when
311 building hard-defence structures may be an effective way to make them more similar to
312 natural substrata, enabling them to support taxa abundance more similar to those found on
313 natural shores.

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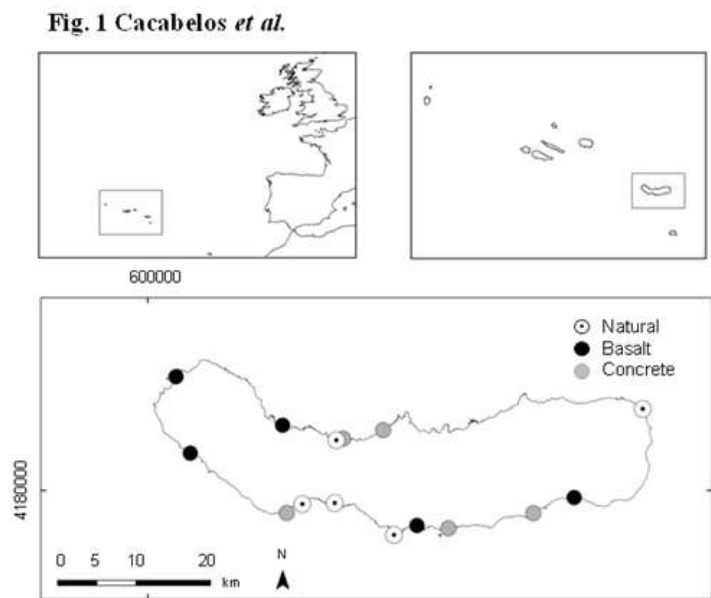
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530 **Figures**

531 **Fig. 1** Sampling locations on Natural shores and Basalt and Concrete artificial structures
532 around São Miguel (Azores).



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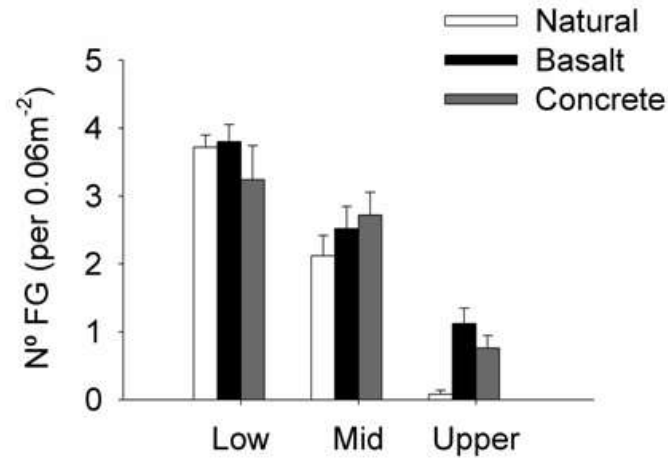
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543 **Fig. 2** Macroalgal morpho-functional groups (mean number + SE, $n = 25$) on Natural
544 shores and Basalt and Concrete artificial structures at different intertidal levels.

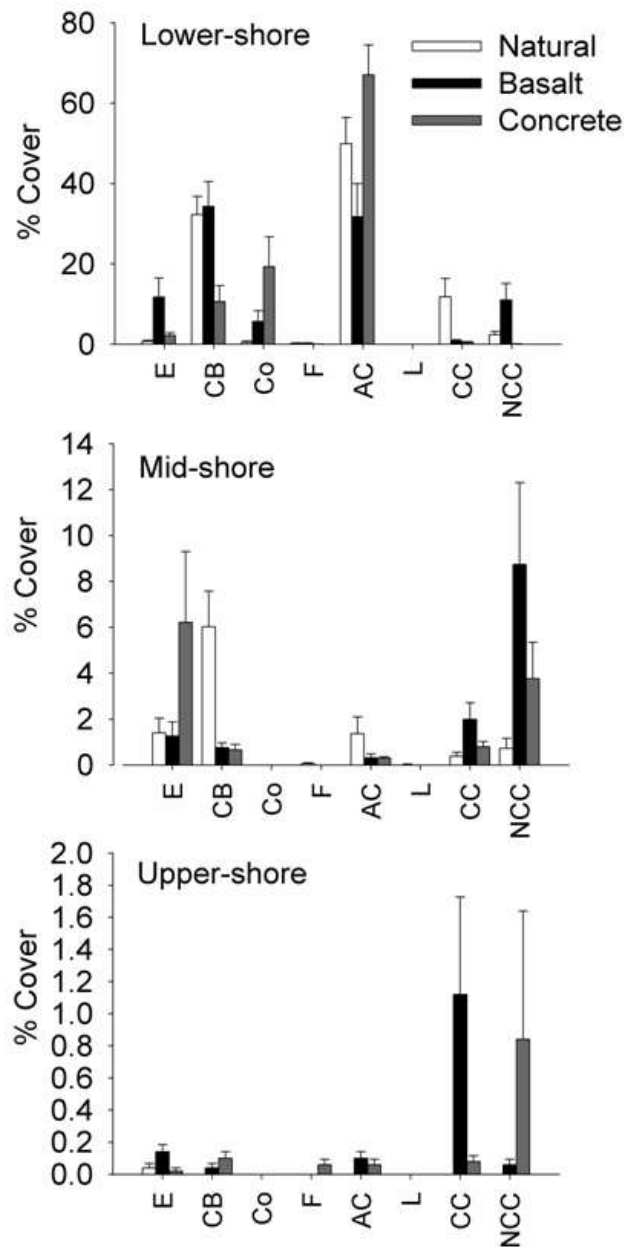
Fig. 2. Cacabelos et al.



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559 **Fig. 3** Covers of macroalgal morpho-functional groups (mean + SE, $n = 25$) associated
 560 with Natural shores and Basalt and Concrete artificial structures at different intertidal levels
 561 (E, Ephemeral Algae; CB, Coarsely branched; Co, Coenocytic; F, Foliose; AC, Articulated
 562 calcareous; L, Leathery; CC, Calcified crustose, NCC, Non-calcified crustose).

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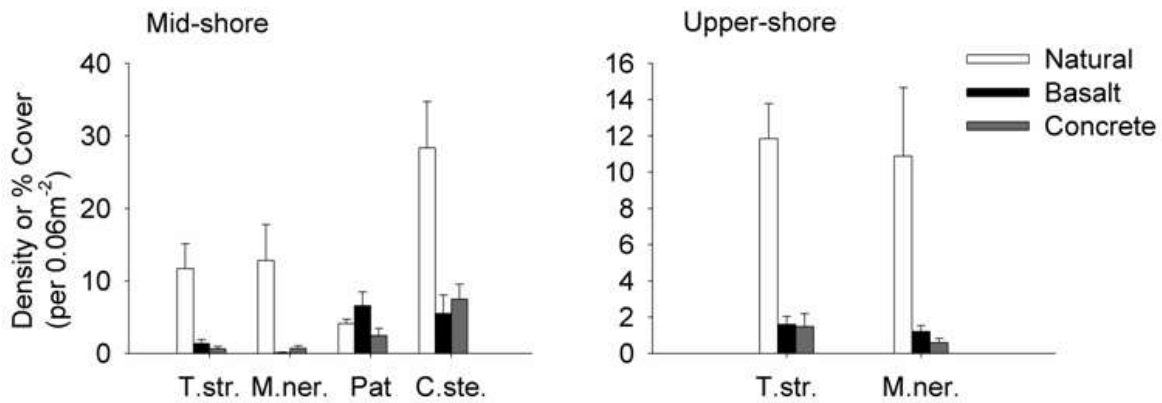


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565 **Fig. 4** Gastropod (mean number + SE, $n = 25$) and barnacle (percent cover + SE)
 566 abundance associated with Natural shores and Basalt and Concrete artificial structures at
 567 mid- and upper-shore (molluscs: T.str, *T. striatus*; M.ner., *M. neritoides*; Pat, *Patella* spp.;
 568 barnacle *C. stellatus*, *C.ste.*).

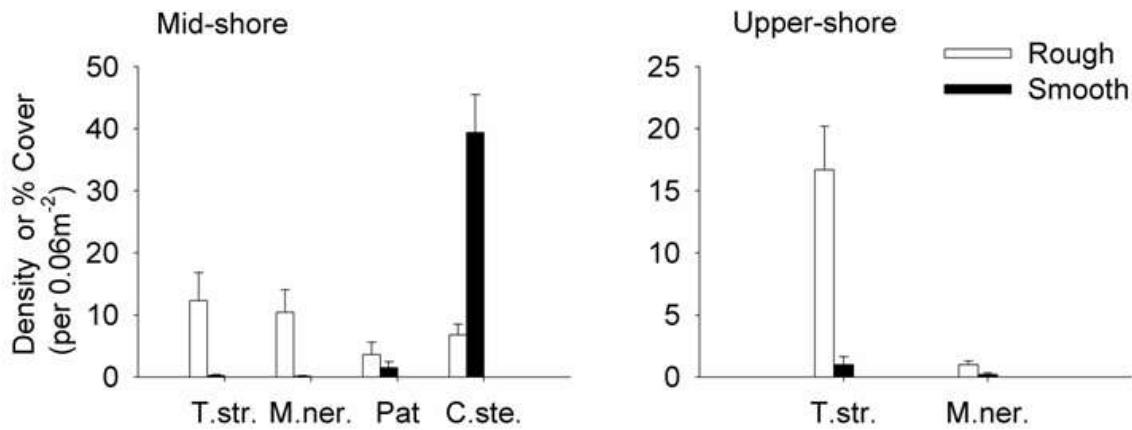
Fig. 4. Cacabelos et al.



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584 **Fig. 5** Gastropod (mean number + SE, $n = 10$) and barnacle (percent cover + SE)
 585 abundance associated with rough and smooth surfaces at mid- and upper-shore (molluscs:
 586 T.str, *T. striatus*; M.ner., *M. neritoides*; Pat, *Patella* spp.; barnacle *C. stellatus*, C.ste.).

Fig. 5. Cacabelos et al.



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601 **Table 1** Two-way PERMANOVA comparing a) untransformed and b) presence/absence
 602 transformed assemblage structure data (including numbers of gastropods and percentage
 603 cover of macroalgal functional groups and *C. stellatus*) among habitats (N Natural shore, B
 604 Basalt artificial structure, C Concrete artificial structure) and locations (five per habitat, see
 605 in Fig. 1) at different intertidal levels.*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

		Low-shore			Mid-shore		Upper-shore	
	Source	df	MS	<i>Pseudo-F</i>	MS	<i>Pseudo-F</i>	MS	<i>Pseudo-F</i>
	Habitat	2	13146.0	1.59	13478.0	1.74*	21666.0	4.15**
a)	Location(Habitat)	12	8291.0	12.47***	7730.1	4.03***	5218.8	4.62***
	Residual	60	665.2		1917.8		1130.4	
	Total	74						
	Pair-wise comparisons					N diff. B*		N diff. B** N diff. C**
	Habitat	2	9033.2	1.70	9687.7	1.77	8696.0	1.92
b)	Location(Habitat)	12	5321.2	6.74***	5480.6	5.25***	4525.9	4.95***
	Residual	60	789.9		1044.4		913.9	
	Total	74						

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620 **Table 2** Two-way ANOVA comparing the numbers of macroalgal morpho-functional
 621 groups among habitats (Natural shore, Basalt artificial structure, Concrete artificial
 622 structure) and locations at different intertidal levels.*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Source	df	Low-shore		Mid-shore		Upper-shore	
		MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Habitat	2	2.29	0.49	0.03	0.07	0.90	3.25
Location(Habitat)	12	4.63	4.96***	0.37	4.24***	0.28	5.16***
Residual	60	0.93				0.05	
Total	74						
Cochran's test		ns, 0.1786		ns, 0.2303		ns, 0.232	
Transformation		None		X ^{0.1}		Sqrt(X+1)	

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641 **Table 3** Two-way ANOVA comparing the cover of macroalgal morpho-functional groups
 642 among Habitats (Natural shores N, Basalt artificial structure B and Concrete artificial
 643 structure C) at different intertidal levels. E, Ephemerals; CB, Coarsely branched; Co,
 644 Coenocytic; F, Foliose; AC, Articulated calcareous; L, Leathery; CC, Calcified crustose,
 645 NCC, Non-calcified crustose.*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$. Natural (N).

		Low-shore		Mid-shore		Upper-shore		
		df	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
	Habitat	2	0.56	0.50	0.39	0.45	0.10	4.77*
	Location(Habitat)	12	1.12	7.03***	0.85	4.04***	0.02	0.76
	Residual	60	0.16		0.19		0.03	
	Total	74						
	Cochran's test		ns, 0.1856		ns, 0.1425		ns, 0.1765	
E	Transformation		X ^{0.1}		X ^{0.1}		None	
	Pair-wise comparisons							B diff. C*
	Habitat	2	4320.10	2.93	8.11	7.82**	0.06	2.11
	Location(Habitat)	12	1473.90	3.27***	1.03	2.40*	0.03	1.64
	Residual	60	450.28				0.02	
	Total	74						
	Cochran's test		ns, 0.2037		ns, 0.2391		$P < 0.05$, 0.2727	
CB	Transformation		None		Ln(X+1)		None	
	Pair-wise comparisons				N diff. B*			N diff. C*
	Habitat	2	2380.3	0.84				
	Location(Habitat)	12	2846.7	44.67***				
	Residual	60	63.7					
	Total	74						
	Cochran's test		$P < 0.01$, 0.5898					
Co	Transformation		None					
	Habitat	2	0.24	0.40	0.03	1		
	Location(Habitat)	12	0.61	4.45***	0.03	6**		
	Residual	60	0.14		0.01			
	Total	74						
	Cochran's test		$P < 0.01$, 0.6341		$P < 0.01$, 1.000			
F	Transformation		None		None			
	Habitat	2	7816.6	1.16	0.44	0.67	0.06	0.79
AC	Location(Habitat)	12	6719.6	21.72***	0.66	4.61***	0.08	9.86***

	Residual	60		309.3		0.14		0.12
	Total	74						
	Cochran's test			ns, 0.2397		ns, 0.1543		$P < 0.01$, 0.4286
	Transformation			None		$X^{0.1}$		None
	Habitat	2		13.52	1.02	17.67	2.15	9.76
	Location(Habitat)	12		13.23	98.5***	8.21	1.97*	6.50
	Residual	60		0.13		4.18		2.40
	Total	74						
	Cochran's test			ns, 0.2174		ns, 0.4581		$P < 0.01$, 0.9806
CC	Transformation			Sqrt(X+1)		None		None
	Habitat	2		1.84	1.98	2.09	2.14	5.49
	Location(Habitat)	12		0.93	6.17***	0.98	6.43***	5.89
	Residual	60		0.15		0.15		5.22
	Total	74						
	Cochran's test			ns, 0.1427		ns, 0.1923		$P < 0.01$, 0.9981
NCC	Transformation			$X^{0.1}$		$X^{0.1}$		None

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661 **Table 4** Two-way ANOVA comparing the numbers of faunal species (density of *T.*
662 *striatus*, *M. neritoides* and *Patella* spp. and percent cover of *C. stellatus*) among habitats
663 (Natural shores N, Basalt artificial structure B and Concrete artificial structure C) and
664 locations at different intertidal levels.*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

		Mid-shore			Upper-shore	
		df	MS	<i>F</i>	MS	<i>F</i>
<i>T. striatus</i>	Habitat	2	15.96	6.89**	25.43	18.42**
	Location(Habitat)	12	2.32	3.30**	31.38	3.60**
	Residual	60	0.70		0.38	
	Total	74				
	Cochran's test		ns, 0.1918		ns, 0.2141	
	Transformation		Ln(x+1)		Ln(x+1)	
	Pair-wise comparisons			N diff. B* N diff. C*		N diff. B** N diff. C***
<i>M. neritoides</i>	Habitat	2	2.28	3.84*	0.91	0.79
	Location(Habitat)	12	0.60	3.57**	1.15	7.11***
	Residual	60	0.17		0.16	
	Total	74				
	Cochran's test		ns, 0.1905		ns, 0.1377	
	Transformation		X ^{0.1}		X ^{0.1}	
	Pair-wise comparisons			N diff. B* B diff. C*		
<i>C. stellatus</i>	Habitat	2	17.25	4.66*	0.11	0.16
	Location(Habitat)	12	3.70	5.39***	0.70	4.97***
	Residual	60	0.69		0.14	
	Total	74				
	Cochran's test		ns, 0.2250		ns, 0.1122	
	Transformation		Ln(X+1)		X ^{0.1}	
	Pair-wise comparisons			N diff. B*		
		Mid-shore			Low-shore	
		df	MS	<i>F</i>	MS	<i>F</i>
<i>Patella</i> spp.	Habitat	2	3.07	0.94	0.05	0.17
	Location(Habitat)	12	3.28	4.52***	0.31	2.57*
	Residual	60	0.73		0.12	
	Total	74				
	Cochran's test		ns, 0.1873		ns, 0.1866	
	Transformation		Ln(X+1)		X ^{0.1}	

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667 **Table 5** Two-way ANOVA comparing the numbers of faunal species (density of *T.*
 668 *striatus*, *M. neritoides* and *Patella* spp. and percent cover of *C. stellatus*) between
 669 roughness (Smooth surface S, Rough surface R) and sites (Site 1, S1; Site 2, S2) at different
 670 intertidal levels.*** $P < 0.001$.

	Source	df	Mid-shore		Upper-shore	
			MS	<i>F</i>	MS	<i>F</i>
<i>T. striatus</i>	Roughness	1	17.02	18.35***	35.81	28.84***
	Site	1	0.84	0.91	0.27	0.22
	Pooled Data	17	0.93		1.24	
	Total	19				
	Cochran's test		ns, 0.5710		ns, 0.5099	
	Transformation		Ln(x+1)		sqrt(x+1)	
<i>M. neritoides</i>	Roughness	1	3.98	4.46		
	Site	1	0.25	1.67		
	Roughness x Site	1	0.89	6.05*		
			(S1, R>S***; S2, R=S)			
	Residual	16	0.15			
	Total	19				
	Cochran's test		ns, 0.4034			
	Transformation		X ^{0.1}			
<i>Patella</i> spp.	Roughness	1	22.05	0.84		
	Site	1	4.05	0.15		
	Pooled Data	17	26.40			
	Total	19				
	Cochran's test		ns, 0.4715			
	Transformation		None			
<i>C. stellatus</i>	Roughness	1	5313.80	6.69		
	Site	1	405.00	2.71		
	Roughness x Site	1	793.80	5.32*		
			(S1, R<S*; S2, R<S***)			
	Residual	16	149.20			
	Total	19				
	Cochran's test		ns, 0.4871			
	Transformation		None			

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