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**Patchiness in habitat distribution can enhance biological diversity of  
coastal engineering structures**

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34

35 **Abstract**

36 1. Urbanization of coastal habitats is increasing worldwide. However, most man-  
37 made structures are poor surrogates for the habitats they replace and can  
38 strongly impact the diversity and functioning of coastal habitats.

39 2. The value of coastal engineering can be enhanced by the provision of  
40 microhabitats that facilitate colonization by marine life. One step forward is  
41 moved in this research by combining species coexistence theory, resource  
42 patchiness, and applied ecology in order to find ways that maximize the  
43 biological diversity of coastal defence structures.

44 3. Featureless areas of a seawall were modified by the addition of microhabitats  
45 (resource) that were distributed in different configurations of patchiness.

46 4. Gastropod diversity peaked at intermediate levels of microhabitat patchiness.  
47 This appeared to be driven by different patterns of resource use among species.  
48 Gastropods dispersed longer distances on unmodified seawalls than on natural  
49 rocky shores but when microhabitats were added dispersal decreased. The  
50 ability to find microhabitats differed among species.

51 5. Our results confirm that patchiness in microhabitat distribution affects  
52 biodiversity. The extent of microhabitat patchiness could potentially be tailored  
53 by coastal engineers to meet specific conservation priorities: increasing diversity  
54 vs. increasing number of individuals.

55

56 **Keywords:** benthos, coastal, ecosystem services, biodiversity, intertidal,

57 invertebrates, urban development

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## 60 **1 INTRODUCTION**

61 Coastal urbanization, the process whereby stretches of natural shoreline are  
62 modified or replaced by the addition of man-made coastal structures, is  
63 increasing worldwide (Firth, Knights, et al., 2016). Coastal urbanization is  
64 associated with a variety of negative impacts on the ecology of coastal habitats  
65 via changes in important physical, chemical and biological processes, which can  
66 strongly impact the structure and functioning of coastal habitats (Bishop et al.,  
67 2017; Heery et al., 2017; Nordstrom, 2014).

68

69 Generally, coastal defence structures are considered as poor surrogates for the  
70 natural shores they replace (Bulleri & Chapman, 2010; Chapman, 2003;  
71 Chapman & Bulleri, 2003; Coombes, La Marca, Naylor, & Thompson, 2015; Evans  
72 et al., 2015; Firth, Knights, et al., 2016; Moschella et al., 2005); when compared to  
73 natural habitats, coastal defence structures often support assemblages that are  
74 less diverse (Cacabelos et al., 2016a,b; Chapman, 2003, 2006; Chapman & Bulleri,  
75 2003; Connell & Glasby, 1999; Evans et al., 2015; Firth et al., 2015; Firth,  
76 Mieszkowska, Thompson, & Hawkins, 2013; Moschella et al., 2005; Pister, 2009;  
77 Vaselli, Bulleri, & Benedetti-Cecchi, 2008). This effect has been attributed to the  
78 lack of topographic complexity that characterizes many of such structures (e.g.  
79 seawalls, pontoons, groynes) and which is important for many marine organisms  
80 (Aguilera, Broitman, & Thiel, 2014; Chapman, 2003; Metaxas & Scheibling, 1993;  
81 Moschella et al., 2005).

82

83 Recently, efforts to enhance the diversity on coastal defence structures showed  
84 that structures such as seawalls and breakwaters could be modified in an  
85 attempt to increase the biodiversity they support. This has included the addition  
86 of simple topographic features such as pits, grooves, cracks or water-retaining  
87 structures (Browne & Chapman, 2014; Chapman & Blockley, 2009; Coombes et  
88 al, 2015; Dafforn, Glasby, et al., 2015; Dafforn, Mayer-Pinto, Morris, & Waltham,  
89 2015; Evans et al., 2015; Firth, Browne, Knights, Hawkins, & Nash, 2016; Firth,  
90 Mieszkowska, et al., 2013; Firth, Schofield, White, Skov, & Hawkins, 2014; Firth,  
91 Thompson, et al., 2013, 2014; Martins, Thompson, Neto, Hawkins, & Jenkins,  
92 2010; Morris, Chapman, Firth, & Coleman, 2017; Morris et al., 2018; Strain et al.,  
93 2018 for a review). In order to further increase their ecological value, we need to  
94 understand how modifications made to coastal defence structures might affect  
95 species coexistence with potential long-lasting effects (Martins, Jenkins, Neto,  
96 Hawkins, & Thompson, 2016).

97

98 Much research, both theoretical and empirical, has focused on the mechanisms  
99 that determine diversity and local species coexistence such as resource  
100 partitioning (e.g. Schoener, 1974), predator-mediated effects (e.g. Leibold, 1996)  
101 and interference competition (e.g. Richards, Nisbet, Wilson, & Possingham, 2000;  
102 Vance, 1985). An important consideration is that spatial variability in the  
103 distribution of resources can promote coexistence by exploiting differences in  
104 foraging traits of competing species. This has been elegantly demonstrated by  
105 Chase, Wilson, and Richards (2001) who showed that coexistence (and hence  
106 species richness) in freshwater snails was driven by the interplay between  
107 differences in foraging trade-offs (ability to find a resource vs. ability to exploit

108 it) and patchiness in resource (patches of food) distribution. They found that  
109 diversity was greatest at intermediate levels of resource patchiness. These  
110 authors discussed findings in light of a digger-grazer model developed for  
111 marine snails (Schmitt, 1996; Wilson, Osenberg, Schmitt, & Nisbet, 1999) under  
112 which two competing species can coexist due to complementary foraging  
113 strategies: one species (coined as digger) excels at harvesting food in each patch,  
114 whereas the other species (coined as grazer) maximizes the area over which  
115 food is consumed. It was not possible for a species to simultaneously do both.  
116 Wilson et al (1999) also provided compelling evidence that the digger-grazer  
117 model may be much more widely applicable, including ecosystems such as the  
118 rocky intertidal.

119

120 In the north-eastern Atlantic, rocky shore snails (e.g. *Phorcus* spp., *Littorina* spp.,  
121 *Patella* spp.) overlap considerably in spatial distribution and can all be found  
122 together on open rock. These grazer gastropods differ markedly in their feeding  
123 mode according to the morphology of their radula and feeding mechanism. For  
124 instance, docoglossan patellid limpets can penetrate hard substrates,  
125 taenioglossan littorinids can only penetrate softer substrates and rhipidoglossan  
126 trochids can only superficially brush the substrate surface (Hawkins et al., 1989).  
127 The way they use their radula to feed on algae has been likened to 'shovels',  
128 'rakes' and 'brooms', respectively (Steneck & Watling, 1982). Moreover, these  
129 species differ remarkably in the way they move. Patellid limpets are known for  
130 their homing behaviour, the consistent return of individuals to a specific location  
131 on the substratum when not feeding or searching for food (Lord, 2008; Santana,  
132 1993; Shanks, 2002; Steneck, 1982). In contrast, trochids and littorinids show

133 little site fidelity and gradually disperse away to locate new patches with  
134 resources (Chapman, 1995; Norton, Hawkins, Manley, Williams, & Watson,  
135 1990). They must either move faster between patches or convert more  
136 efficiently the resources to population growth (Richards et al., 2000) than  
137 species exhibiting homing behaviour.

138

139 For many intertidal snails, however, food is not the only important resource  
140 (Rochette & Dill, 2000). Intertidal microhabitats such as rockpools, pits and  
141 grooves also play an important role, at least during some stage of their life-cycle  
142 (Firth & Crowe, 2010), by dampening environmental extremes during low water  
143 (Fairweather, 1988; Gray & Hodgson, 1998) and/or providing protection from  
144 predation (Bertness, Garrity, & Levings, 1981; Garrity, 1984). In fact, most  
145 enhancements done to coastal defence structures (see above) are effective  
146 because they provide a refuge for environmental stressors or the risk of  
147 predation (Browne & Chapman, 2011, 2014; Chapman & Blockley, 2009;  
148 Coombes et al., 2015; Evans et al., 2015, 2017; Firth, Browne, et al., 2016; Firth,  
149 Knights, et al., 2016; Firth, Mieszkowska, et al., 2013; Firth, Schofield, et al., 2014;  
150 Firth, Thompson, et al., 2013, 2014; Loke, Ladle, Bouma, & Todd, 2015; Martins  
151 et al., 2010, 2016; reviews in Dafforn, Glasby, et al., 2015; Dafforn, Mayer-Pinto,  
152 et al., 2015; Firth, Knights, et al., 2016; Strain et al., 2018). However, the  
153 magnitude of the effects varied among considered functional groups and habitat  
154 settings (Strain et al., 2018). For instance, Martins et al. (2016) showed that the  
155 response of three intertidal snails to the addition of pits to a topographically  
156 simple seawall varied according to pit size and number: littorinids (*Tectarius*  
157 *striatus* and *Melarhaphe neritoides*) tended to aggregate on small microhabitats,

158 limpets (*Patella candei*) tended to aggregate in areas with large microhabitats,  
159 whilst all species tended to be more abundant with increasing microhabitat  
160 density. Moreover, the contrasting response of limpets and littorinids to  
161 microhabitat size had community-wide cascading effects, leading, in the longer-  
162 term, to the establishment of very distinct assemblages. Martins et al. (2016) also  
163 noted that whilst many individual littorinids were often found aggregating in a  
164 single pit, limpets were generally found alone (one individual limpet per pit).  
165 This pattern suggests that inter- and intra-specific competition (for pits) is  
166 higher for limpets than among littorinids.

167

168 In the present study we build on previous findings (Martins et al., 2010, 2016) to  
169 test if spatial variability (patchiness) in the distribution of microhabitats (pits)  
170 can affect snail behaviour and be used as a means to enhance diversity in coastal  
171 defence structures.

172 We hypothesize that (1) intertidal gastropods have distinct displacement  
173 behaviours on seawalls and natural rocky shores, (2) patterns of gastropod  
174 dispersal and microhabitat use differs among species; specifically, littorinids (*M.*  
175 *neritoides* and *T. striatus*) disperse further and utilise experimental pits more  
176 quickly than limpets, and finally (3) richness in gastropod snails will be  
177 enhanced at intermediate levels of microhabitat patchiness, reflecting the  
178 divergent patterns of motility, intra- and inter-specific competition among these  
179 species.

180

## 181 **2 METHODS**

### 182 **2.1 Study sites and gastropod assemblages**



183 The Azores archipelago is volcanic by origin and the coast is mainly composed of  
184 boulder shores interspersed between rocky platforms. The tides are semidiurnal  
185 and the tidal range small (< 2 m). The experimental study was done on a natural  
186 rocky shore platform and the adjacent steep seawall consisting of large regular-  
187 sized basalt blocks, comprising a stretch of the coast of 200 m with south-  
188 southwest orientation at São Roque (São Miguel Island). The basalt blocks had a  
189 smooth surface and lacked the microtopographic complexity of the surrounding  
190 natural rocky shore (see Martins et al., 2010). The assemblage of grazer  
191 gastropods from mid to upper shore levels comprised the limpet *Patella candei*  
192 and the littorinids *Tectarius striatus* and *Melarhappe neritoides* (Martins,  
193 Thompson, Hawkins, Neto, & Jenkins, 2008), both in natural shores and seawall.  
194 These are, for the most part, the only macroinvertebrate grazing gastropods  
195 present in the intertidal throughout the archipelago. Other species (e.g. *Littorina*  
196 *saxatilis*) are rare on Azorean coasts.

197

## 198 **2.2 Dispersion behaviour on seawalls vs. natural rocky shores**

199 Since patterns of dispersion on seawalls have been shown to differ from those  
200 observed on natural rocky shores (Bulleri, Chapman, & Underwood, 2004), it  
201 was important to test, prior to the main experiment, if the same occurred in the  
202 study system and focal species. To compare the movement of gastropods in each  
203 habitat (seawall and natural rocky shore), the distance travelled per unit time on  
204 both habitats was investigated during the summer of 2014. On the seawall and  
205 on an adjacent natural rocky shore (a platform shore with the same orientation  
206 100 m apart), random sites metres apart were selected at similar intertidal level  
207 and animals were individually labelled. We calculated the distance travelled over

208 different periods of time (1 and 14 days) by measuring the distance between the  
209 animals and two fixed marks. The distance travelled over the different periods of  
210 time was calculated by co-ordinate geometry, using paired measures at the  
211 beginning and at the end of the period of time (Underwood 1977). As many  
212 individuals were lost, we repeated the procedure described several times to  
213 obtain enough replicates. For the purpose of analyses (see below), data from  
214 each time period were pooled together.

215

216 The distances travelled by gastropods on the seawalls and the natural rocky  
217 shore were compared using a two-way permutational ANOVA (PERMANOVA,  
218 Anderson, 2005) with the factors 'Habitat' and 'Species' fixed and orthogonal to  
219 each other. The analyses were done separately for 1 and 14 days after the start  
220 of the experiment. Permutational ANOVA was used instead of traditional ANOVA  
221 because analyses were unbalanced (e.g. different numbers of animals per  
222 species). Prior to analyses, heterogeneity of variances was checked using  
223 PERMDISP and transformations were applied where necessary. Pair-wise  
224 comparisons were made when differences were found. All analyses were run on  
225 Euclidean distances with 999 permutations using the software PRIMER 6+  
226 (Clarke & Gorley, 2006).

227

### 228 **2.3 Microhabitat patchiness**

229 In December 2013, two sites 50 m long, belonging to the same continuous  
230 seawall, located 100 m apart and similarly exposed to oceanic swell, were  
231 selected for experimental manipulation. To test the effect of patchiness on  
232 gastropod diversity, 20 plots (25 x 25cm) were haphazard marked at mid-shore

233 level (approximately 1.50-1.90 m above lowest astronomical tide) of each site,  
234 where barnacles, limpets and littorinids are present, and randomly assigned to  
235 four treatments (n = 5): control (no pits added), low, intermediate and high  
236 levels of microhabitat patchiness (Figure 1). Comparison of controls and  
237 treatments were used to confirm that all the three species, *M. neritoides*, *T.*  
238 *striatus* and *P. candei*, responded positively to the experimental addition of pits,  
239 (see Martins et al., 2016). To ensure that the sizes of experimental pits were  
240 suitable for the majority of the individuals, the total number and size of pits was  
241 established *a priori* according to previous observational and experimental  
242 studies in the area (Martins et al., 2010, 2016). As pits can be key features for the  
243 recruitment and survival of many species, especially for the case of juvenile  
244 stages (e.g. recent recruited and immature limpets < 1cm), and the effect of pit  
245 density and size for small limpets was limited by the density of pits, whatever  
246 their size (Martins et al., 2010), here we opted for drilling pits 12 mm diameter,  
247 10 mm depth. Levels of patchiness were achieved by drilling 16 pits within the  
248 plot areas at varying arrangements following the design of Chase et al. (2001): a  
249 unique group of 16 adjacent pits (low patchiness), two groups of 8 adjacent pits  
250 in opposite corners of the plot (intermediate patchiness) and four groups of 4  
251 adjacent pits, each on a different corner of the plot (high patchiness) (Figure 1).

252

253 Martins et al. (2016) found that patterns of pit use on rocky shores differed  
254 slightly between the short (3 months to 1 year) and the long-term (7 years),  
255 probably reflecting the adjustment of animal densities to intra- and inter-specific  
256 competition. To allow plenty of time for individuals to relocate, experimental

257 plots were only sampled in June 2016, 30 months after experimental setup, when  
258 all gastropods within experimental plots were identified and counted.

259

260 The effects of microhabitat patchiness on the diversity (species richness and  
261 Shannon index of diversity) and abundance of gastropods was investigated using  
262 a two-way mixed model ANOVA with the following factors: 'Site' (random with  
263 two levels) and 'Treatment' (fixed with 3 levels: low, intermediate and high),  
264 orthogonal between them. Prior to analyses, data were inspected for  
265 heterogeneity of variances using Cochran's test, and transformations were  
266 applied where necessary. *Post-hoc* pooling was done at  $p > 0.25$ , by pooling MS  
267 terms and using the resultant term as the denominator for the *F. A posteriori*  
268 comparisons were made using the SNK test when differences were found.

269 Pearson correlation coefficient was calculated among all gastropod species  
270 across treatments to evaluate potential biotic interactions among these species.

271

#### 272 **2.4 Dispersion behaviour across microhabitat patchiness**

273 We compared the dispersal of gastropods across levels of patchiness in the winter  
274 of 2016-2017 at one of the experimental sites. Prior to the start of the experiment,  
275 plots were defaunated. Afterwards, *M. neritoides*, *T. striatus* and *P. candei* were  
276 collected from the surrounding area within the seawall, marked with coloured nail  
277 varnish and translocated to the centre of each experimental plot (5 individuals per  
278 species per plot). In the case of *P. candei*, more sensitive to manipulation, the use  
279 of smaller animals allowed us to easily dislodge them off the rock. Moreover,  
280 animals were carefully removed and immediately translocated to the  
281 experimental plots. Adherence of animals was checked about 30 minutes

282 afterwards. In most cases limpets reattached alone, but if not these were replaced.  
283 The number of animals transplanted into each plot was within the range of  
284 densities observed on several natural shores of the island (mean values of  
285  $12.8 \pm 5.0$ ,  $11.7 \pm 3.4$  and  $4.1 \pm 0.6$  individuals per  $625 \text{ cm}^2$  were observed for *M.*  
286 *neritoides*, *T. striatus* and *P. candei* respectively, during summer 2013 (n=25,  
287 Cacabelos et al., 2016a). In January 2014 we observed even higher densities on  
288 local natural shores ( $103.6 \pm 13.0$  *M. neritoides* individuals per  $625 \text{ cm}^2$ ,  $24.8 \pm 5.4$   
289 *T. striatus* and  $5.3 \pm 0.9$  *P. candei* (n=30) and therefore intra-species competition  
290 was not expected to occur. After 24h, we measured the distance travelled by each  
291 marked individual from the centre of each plot and recorded whether it was inside  
292 or outside a pit. To account for the number of animals which were lost, we  
293 repeated the procedure described two more times (total of 3 runs for *P. candei* and  
294 2 for littorinids).

295

296 To test the hypothesis that dispersal of gastropod species differed among levels  
297 of patchiness, for each individual we calculated its dispersal from the centre of  
298 the patch against the mean dispersal observed on controls (no pits) using the Ln  
299 ( $d_{\text{treatment}}/d_{\text{control}}$ ), d = distance travelled from the centre of the plot. This was  
300 done to standardize the distances travelled among species and against a  
301 situation where no microhabitats were available (controls). Negative values  
302 indicate that animals dispersed less than in controls, while positive values  
303 indicate that animals dispersed more than in controls. Data were analysed using  
304 a 2-way factorial permutational ANOVA with the following factors: 'Species' (3  
305 levels) and 'Treatment' (3 levels: low, intermediate and high), both fixed. Pair-  
306 wise comparisons were made when differences were found. Again,

307 permutational ANOVA was chosen due to the unbalanced dataset (for further  
308 details see above). For analysis, data from the different runs were pooled  
309 together.

310

### 311 **3 RESULTS**

#### 312 **3.1 Dispersion behaviour on seawall vs. natural rocky shore**

313 In the shorter-term (1 day), distances travelled by *Tectarius striatus* were always  
314 significantly greater than those travelled by *Melarhappe neritoides* and *Patella*  
315 *candei* (mean  $\pm$  SE, *T. striatus*:  $12.0 \pm 2.2$  cm, *M. neritoides*:  $3.9 \pm 0.9$  and *P. candei*:  
316  $1.8 \pm 0.5$  cm), but there were no differences in dispersal between habitats  
317 (natural rocky shore or seawall (Figure 2, Table S1). However, in the longer-term  
318 (14 days) there was a significant interaction between habitat and species (Table  
319 S1). Pair-wise comparisons showed that, on average, limpets dispersed very little  
320 regardless of habitat but that littorinids dispersed significantly greater distances  
321 on the seawall than on the natural rocky shore (Figure 2, Table S1). Pair-wise  
322 comparisons also showed that while on natural shores *M. neritoides* dispersed  
323 little (similar to *P. candei*), on the seawall *M. neritoides* dispersed much more  
324 (similar to *T. striatus*) (Table S1).

325

#### 326 **3.2 Suitability of experimental microhabitat addition**

327 The addition of experimental pits to the seawall proved a successful means to  
328 enhance the diversity and abundance of gastropods per unit area (Table 1):  
329 compared to controls, experimentally enhanced plots supported, on average, an  
330 abundance of individuals and a species richness that was 1 order of magnitude  
331 greater.

332

### 333 **3.3 Microhabitat patchiness**

334 When considering the effects of the different spatial arrangements of  
335 experimental pits, both the species richness and the Shannon diversity generally  
336 peaked at intermediate levels of patchiness (Figure 3). In fact, mean species  
337 richness at intermediate patchiness was significantly greater than found on high  
338 patchiness (Figure 3; see also Table S2 in supporting information for ANOVA  
339 tables). Shannon diversity was also significantly greater at intermediate  
340 patchiness compared to low and high patchiness (Figure 3, Table S2). For both  
341 richness and Shannon diversity, results were spatially consistent in both sites  
342 examined (Table S2).

343

344 Statistical analyses failed to detect any significant variation in mean abundance  
345 of the different species among levels of patchiness, probably because there was  
346 much (and significant) spatial variability between sites for both *P. candei* and *M.*  
347 *neritoides* (see Table S3). However, when the numbers of all individuals per  
348 treatment were pooled together, the pattern varied substantially and we  
349 observed differences among species (Figure 4): the numbers of *T. striatus*  
350 increased with patchiness, whereas the numbers of both *P. candei* and *M.*  
351 *neritoides* peaked at intermediate levels of patchiness.

352

353 A negative correlation was found between the numbers of limpets and both  
354 species of littorinids (*P. candei* \* *T. striatus*,  $r = -0.34$ ; *P. candei* \* *M. neritoides*,  $r =$   
355  $-0.18$ ), whereas a positive correlation was found between the numbers of  
356 littorinids (*T. striatus* \* *M. neritoides*,  $r = +0.44$ ).

357

### 358 **3.4 Dispersion behaviour across microhabitat patchiness**

359 All species tended to disperse less in areas enhanced with experimental pits  
360 (Figure 5a). There were also significant differences in dispersal both among  
361 species and among treatments. Inspection of a posteriori comparisons showed  
362 that *P. candei* and *M. neritoides* dispersed significantly less than *T. striatus* (Table  
363 S4). Patterns of dispersion also varied across levels of patchiness, with all  
364 animals dispersing significantly less in areas with low patchiness (Figure 5a).  
365 Inspection of the experimental plots after 24h showed that the proportion of  
366 individuals (data pooled over replicates) found inside pits decreased with  
367 increasing patchiness (Figure 5b).

368

## 369 **DISCUSSION**

370 The main outcome of this study was that diversity, both in terms of richness and  
371 Shannon diversity, was greater at intermediate levels of microhabitat patchiness.  
372 This is in accordance with Chase et al. (2001) who found that the diversity of  
373 freshwater snails was also greatest at intermediate levels of resource patchiness.  
374 In their study, this pattern was driven by the interplay between differences in  
375 foraging trade-offs, coexisting due to complementary foraging strategies  
376 (Schmitt, 1996; Wilson et al., 1999), and patchiness in resource distribution, and  
377 thus highlight the importance of variability in species traits. Previous studies in  
378 natural systems demonstrated how the responses of species assemblages to  
379 microhabitats can vary among taxa (Bateman and Bishop, 2017). Here, too, we  
380 showed that not only the dispersal of intertidal gastropods varied among  
381 species, especially between littorinids and limpets which have contrasting



382 foraging behaviours (different abilities to find and exploit resources), but also  
383 between habitats (natural rocky platform and seawall) and between levels of  
384 habitat patchiness on a seawall.

385

386 A mechanism to explain the biotic response to microhabitat manipulation can be  
387 deduced from the observation that littorinids (but not limpets) dispersed over  
388 larger distances in seawalls compared with natural rocky habitats, a result also  
389 shown for the limpet *Cellana tramoserica* on seawalls in New South Wales  
390 (Bulleri et al., 2004). This greater mobility on artificial substrates suggests that  
391 gastropods move more because they may lack appropriate microhabitats (e.g.  
392 pits) in which to shelter. This hypothesis is further supported in our study by the  
393 result that all species also dispersed less in areas of the seawall enhanced with  
394 pits. In addition, complementary information, e.g. related to the age of the  
395 animals, could be incorporated when predicting patterns of movement of  
396 gastropods (Crowe, 1996). The three species also exhibited distinct short-term  
397 patterns of dispersal in relation microhabitat patchiness. Although not  
398 experimentally tested, we found evidence that at least limpets and littorinids  
399 may be competing for these microhabitats on the seawall. As such, the  
400 differential ability to disperse may be important in alleviating competition  
401 among these species, which could, in the longer term, result in the distinct  
402 patterns of abundance observed among treatments and hence, diversity. Our  
403 results thus suggest that the manipulation of microhabitat patchiness may be an  
404 effective way to exploit differences in species dispersal, and presumably foraging  
405 behaviour, and which may in fact have wider implications for the structure of  
406 remainder of the community (Martins et al., 2014; O'Connor & Crowe, 2005).

407

408 Understanding the mechanisms that drive species coexistence has been a central  
409 question in theoretical ecology, but it may have wider applied interest. The  
410 addition of microhabitats to an existing seawall without previously water  
411 retaining features was shown to be an effective way to enhance the local  
412 numbers and diversity of gastropods, confirming previous studies (Martins et al.,  
413 2010, 2016) and suggesting the potential use of such modifications as a means to  
414 enhance the diversity of intertidal biota on coastal defence structures (see Firth,  
415 Knights, et al., 2016 and references therein). Here we show that controlling the  
416 spatial patchiness of microhabitats is an effective way to enhance the local  
417 abundance or diversity of target species in artificial substrates. However, a  
418 frequent limitation of eco-engineering research is the investigation of large-scale  
419 effects or habitat modifications (but see Morris et al., 2017). Although our  
420 experiments have been replicated at sites within a single artificial structure, a  
421 next step would be to evaluate the effect size of such treatments at the scale of  
422 the entire structure, on different geographical areas and with different  
423 assemblages of organisms. Provided that results hold, this study suggests that  
424 managements strategies could potentially be tailored to meet specific  
425 conservation priorities and inform eco-engineering approaches to enhance  
426 biodiversity, namely increasing diversity vs. increasing number of individuals.

427

428 This work emphasizes the importance of field experiments as a powerful tool to  
429 establish causal relationships and adds to the toolkit of coastal engineers in the  
430 design of more ecologically friendly coastal structures, providing direct evidence  
431 of the suitability of low-cost engineering modifications to enhance artificial

432 ecosystems. Our study adds to the wider literature showing that coastal  
433 structures can be enhanced in different ways: (i) via the provision of different  
434 microhabitat types (e.g. pits, grooves, rockpools) (e.g. Browne & Chapman, 2014;  
435 Coombes et al., 2015; Firth, Schofield, et al., 2014; Firth, Thompson, et al., 2014),  
436 (ii) via the provision of microhabitat of different sizes (Martins et al., 2010,  
437 2016), or (iii) by controlling the level of patchiness in the provision of  
438 microhabitats (this study). Ultimately, the choice among these options should be  
439 dictated by the desired outcome (e.g. ecological, conservation of exploited  
440 species) and by the available intervention possibilities.

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668 **TABLES**

669 **Table 1.** Mean ( $\pm$  SE) numbers and richness of gastropods found on plots with  
670 experimental pits added (n = 30) and unmanipulated controls (n = 10).

	<i>P. candei</i>	<i>T. striatus</i>	<i>M. neritoides</i>	Richness
Treatment	2.27 $\pm$ 0.89	22.37 $\pm$ 4.44	2.43 $\pm$ 0.93	1.73 $\pm$ 0.17
Control	0.10 $\pm$ 0.10	0.40 $\pm$ 0.22	0.20 $\pm$ 0.13	0.60 $\pm$ 0.27

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690 **FIGURE CAPTIONS**

691 **Figure 1.** Different levels of patchiness obtained by drilling 16 pits (12 mm  
692 diameter, 10 mm depth) within the plot areas, achieving (a) low, (b)  
693 intermediate and (c) high patchiness. In Control plots (d), no pits are added.

694 **Figure 2.** Mean (+SE) dispersal of tagged individuals of *P. candei*, *T. striatus* and  
695 *M. neritoides* on seawalls and natural rocky shores after (a) 1 and (b) 14 days.  
696 Letters highlight significant differences among means as detected by *a posteriori*  
697 comparisons (see Table S1 for further details).

698 **Figure 3.** Mean (+SE) grazing gastropod (a) richness and (b) Shannon diversity  
699 in experimental enhanced areas of the seawall after 30 months at increasing  
700 levels of the patchiness in the spatial distribution of pits. Letters highlight  
701 significant differences among means as detected by *a posteriori* SNK tests (for  
702 further details see Table S2)

703 **Figure 4.** Total number of individuals of (a) *P. candei*, (b) *T. striatus* and (c) *M.*  
704 *neritoides* found after 30 months in experimentally enhanced areas of the  
705 seawall at increasing levels of microhabitat patchiness.

706 **Figure 5.** (a) Mean ( $\pm$ SE) dispersal relative to controls among gastropod species  
707 across all levels of microhabitat patchiness after 24h. Letters highlight significant  
708 differences among means as detected by pair wise comparisons (for further  
709 details see Table S4); (b) Proportion of relocated gastropods found inside pits  
710 after 24h.