

1 Running Head: Effects of matrix and environmental variability

2 MACROFAUNAL RESPONSES TO STRUCTURAL COMPLEXITY ARE MEDIATED  
3 BY ENVIRONMENTAL VARIABILITY AND SURROUNDING HABITATS

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17

**ABSTRACT**

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Investigating the context that surrounds each habitat is crucial to understand local responses of assemblages of species to habitats. Here, I tested whether responses of benthic macro-invertebrates to the structural complexity of experimental habitats were mediated by the characteristics of their surrounding habitats (i.e. rockpools or emergent-rock surfaces). Each type of surrounding habitat provided particular biotic (e.g. algal growth) and abiotic (e.g. temperature, water movement, etc.) conditions that were expected to affect benthic assemblages. The results show that: 1) composition of entire assemblages was affected by the matrix and type of habitat; 2) effects of the matrix on the number of species varied depending on the different types of habitats; 3) abundant species showed specific responses to type of habitat, independently of the matrix; and that 4) relationships between numbers of species and two major environmental variables (i.e. micro-algal biomass and sediment) varied depending on the type of habitats and the surrounding matrix. Generally, these findings demonstrate that understanding the consequences of the spatial structure of these habitats is essential to advance our knowledge on patterns of abundance and distributions of functionally important species and ultimately the structure of intertidal assemblages.

34

## INTRODUCTION

35           Ecologists have long been interested in species' associations with their habitats with  
36 the aim of understanding spatial variability in abundances of species (e.g. MacArthur and  
37 MacArthur 1961; MacArthur 1964; Pianka 1966). Habitats with different physical structure  
38 generally offer different resources (i.e. food, shelter, etc.) that are, in turn, exploited by  
39 different species (e.g. Downes et al. 2000). Local variation in the physical structure of  
40 habitats does not, however, completely explain the distribution and abundance of species at  
41 coarser scales, because the colonization of habitats is often greatly influenced by processes  
42 operating at regional scales (e.g. MacArthur and Wilson 1967). Generally, the realization that  
43 habitats may have different degrees of isolation depending on the nature of the surrounding  
44 matrix has prompted a whole body of work investigating the role of the matrix in which  
45 habitats are embedded (i.e. landscape context, Mazerolle and Villard 1999) and how it  
46 mediates the level of connectivity with neighbouring habitats (i.e. "connectivity is the degree  
47 to which the landscape facilitates or impedes movement among resource patches"; Taylor et  
48 al. 1993). The extent to which connectivity is altered depends on scale and the organisms'  
49 perception of changes in spatial patterns (e.g. Kotliar and Wiens 1990; Wiens 2002), the  
50 spatial configuration of patches (e.g. Roberts and Poore 2006), the surrounding matrix (e.g.  
51 Crowe 1996; Ricketts 2001; Debinski 2006; Tanner 2006) and dispersal among patches (e.g.  
52 Ewers and Didham 2006).

53           Most organisms are more likely to interact with organisms in neighbouring habitats  
54 than with more distant ones (Tilman 1994). Such interactions with surrounding habitats are  
55 particularly important for sessile organisms (e.g. corals, Karlson and Cornell 2002; terrestrial  
56 plants, Pacala and Silander 1990; macroalgae, Goodsell and Connell 2008; bryozoans,  
57 terHorst and Dudgeon 2009). The magnitude of interactions with surrounding habitats across

58 habitat boundaries is also dependent on the quality of these surrounding habitats (Fagan et al.  
59 1999; Ries and Sisk 2004). Dispersal and resource-use is strongly influenced by the spatial  
60 structure of neighbouring habitats, which determines the structure and dynamics of natural  
61 assemblages (Tilman 1994; Loreau and Mouquet 1999; Ricketts 2001). Empirical studies on  
62 patterns of diversity and distribution of species in naturally isolated patches of habitat have  
63 shown that the nature of the surrounding matrix determines the effective level of isolation of  
64 natural patches of habitat (Ricketts 2001). Furthermore, the extent to which the surrounding  
65 landscape, i.e. the matrix (Ricketts 2001; Murphy and Lovett-Doust 2004), may function as a  
66 barrier to movement of animals between patches of habitats may depend on the extent and  
67 type of habitat it contains (e.g. Goodsell and Connell 2008; Johnson et al. 1992). Investigating  
68 the matrix that surrounds each habitat is therefore crucial to understand local responses of  
69 assemblages of species to habitats.

70         Historically, most studies of the roles of matrix have been done in terrestrial systems,  
71 although there is growing evidence that matrix habitats are also a fundamental component of  
72 connectivity (i.e. dispersal) within marine systems (e.g. Tanner 2006; Goodsell and Connell  
73 2008; Hovel and Fonseca 2005). In marine systems, connectivity between patches of habitat  
74 is generally thought to be great due to many marine species having planktonic larval stages  
75 (Scheltema 1974). Consequently, most research on the effects of the type of the surrounding  
76 matrix has been focused on differences in connectivity and colonization of patches. For  
77 example, the matrix and structure of seagrass patches are important determinants of spatial  
78 patterns and variability of fish assemblages (Gullstrom et al. 2008) and marine crustaceans  
79 (Skilleter et al. 2005). Nevertheless, experimental manipulations to test hypotheses about the  
80 effects of spatial arrangement and composition of habitats remain scarce (but see Tanner  
81 2006; Goodsell and Connell 2008; Hovel and Lipcius 2001; Macreadie et al. 2009). It is

82 difficult to separate the effects of the matrix from those of changes in the habitats themselves  
83 (Macreadie et al. 2009; Macreadie et al. 2010). For example, finding differences among  
84 assemblages in seagrass patches near and far from mangroves could not be solely attributed to  
85 the effects of the matrix (i.e. mangroves). The seagrass patches – the focal habitat – could  
86 also be altered by their proximity to mangroves, which ultimately could explain the  
87 differences in assemblages. It is, therefore, essential to separate these effects to understand  
88 better how the matrix affects species' responses to different types of habitats.

89         Here, I investigated the responses of benthic assemblages to structural complexity  
90 under different surrounding habitats. In particular, I tested the hypothesis that assemblages  
91 should vary according to the matrix in which patches of habitats are embedded (Hypothesis  
92 1). Alternatively, not all types of habitats may be affected in the same way by their matrix.  
93 This model would be supported if there were an interaction between effects of type of habitat  
94 and context (Hypothesis 2). I tested these predictions by deploying two types of experimental  
95 habitats in two different matrices: rockpools and emergent-rock surfaces (i.e. open rock).  
96 These two different matrices have consequences for assemblages colonizing experimental  
97 habitats because it affects biotic (e.g. algal growth) and abiotic (e.g. temperature, water  
98 movement, etc.) factors: rockpools are completely submerged during the tidal cycle and are  
99 often covered by loosely compacted turfs (Akioka et al. 1999; Hull 1999; Worthington and  
100 Fairweather 1989), whilst emergent-rock surfaces are exposed to air during low tides and thus  
101 subject to desiccation. For example, the structure of biogenic habitats is affected by their  
102 position in the shore (e.g. length and packedness of coralline turfs; Akioka et al. 1999), which,  
103 in turn, might determine how organisms use these habitats (Worthington and Fairweather  
104 1989). Such variability in the nature of the surrounding habitats is determinant for benthic

105 assemblages colonizing biogenic habitats since it affects colonization or movement of  
106 organisms in focal patches of habitat (e.g. Cole 2009).

## 107 **METHODS**

### 108 **Experimental design**

109 This study was done on intertidal rock-platforms at the Cape Banks Special Scientific  
110 Research Area, Botany Bay (NSW, Australia) from November 2009 to February 2010. I  
111 surveyed areas 100's of metres apart with similar orientation and exposure to waves on gently  
112 sloping low-shore rock platforms or large boulders, 0.3 to 0.6 m above mean low water. In  
113 these areas, I selected rockpool and emergent-rock locations that had patches of *Corallina*  
114 *officinalis* L. Rockpools were of similar size and depth; small (area < 1 m<sup>2</sup>) and/or deep  
115 rockpools (depth > 0.5 m) were not included since these characteristics can have major effects  
116 on the assemblages of macro-algae (Martins et al. 2007; Underwood and Skilleter 1996).  
117 Emergent-rock surfaces were selected in areas that were completely emerged during low  
118 tides. In total, there were 10 separate locations: 5 rockpools and 5 emergent-rock areas.  
119 Thus, the factor *location* was necessarily nested in the type of matrix. Note that it would not  
120 be feasible to find enough individual rockpools of appropriate dimensions to accommodate  
121 each experimental habitat (see details below) separately. To control for possible confounding  
122 effects of shading and wave-action, all locations were approximately horizontally oriented  
123 and subject to moderate wave action. Care was taken to ensure that rockpool and emergent-  
124 rock locations were large enough to accommodate all experimental units while keeping  
125 distances between experimental units similar to those outside rockpools (i.e. > 50 cm apart).

126 Experimental habitats were independently attached and interspersed amongst algal  
127 turfs in rockpool or emergent-rock, using stainless steel screws and rubber washers.

128 Experimental habitats are uniform and have same general history (e.g. they are the same age),  
129 which reduces the variability among experimental units (Underwood and Chapman 2006).  
130 This is a central aspect of this study as it removes the confounding effect of variability in  
131 natural coralline turfs between rockpools and on emergent rock, which would have  
132 confounded the experiment because of structure of these turfs determines assemblages that  
133 colonize these habitats (Kelaher et al. 2001). Thus, using experimental habitats, the  
134 variability between assemblages in rockpools or on emergent-rock should be attributable to  
135 environmental variables or resources associated with these surrounding habitats, rather than  
136 any differences in structure of the focal patches of habitat.

### 137 **Experimental habitats**

138 Two types of artificial turf (Grassman Pty Ltd., NSW, Australia) were selected (Types  
139 A and C in Matias et al. 2010) to the construct experimental habitats. These turfs were  
140 chosen because of their differences in length ( $A < C$ ) and also in density of fronds ( $A > C$ ),  
141 although they provide comparable amounts of surface of fronds to be colonized (i.e. 26.5 (A)  
142 and 25.9 (C)  $\text{cm}^2$ ). These characteristics maximized the structural differences needed to test  
143 hypotheses about different types of habitats (Matias et al. 2010, 2011). The variation between  
144 types of habitat falls within the dimensions of naturally occurring coralline turfs on rocky  
145 reefs (Akioka et al. 1999). Benthic assemblages in experimental habitats would therefore be  
146 affected by the combined effect of density and length of fronds. A previous study using these  
147 artificial habitats determined that these two types of habitats are colonized by significantly  
148 different numbers of species ( $C > A$ ). Hereafter, for clarity, I refer to the types of fronds as  
149 *short* (i.e. A) or *long* (i.e. C).

150 Experimental habitats were made of squares of artificial turf (10 x 10 cm<sup>2</sup>) that were  
151 attached to a base of wire mesh using cable-ties. Previous work has shown that experimental  
152 habitats of this size are appropriate to test hypotheses about different types of habitats (Matias  
153 et al. 2007; Matias et al. 2010). Numerous invertebrates rapidly colonize artificial turfs after  
154 just 14 days of deployment (Olabarria 2002; Kelaher 2005). Fifty days after deployment,  
155 there are significant differences between assemblages colonizing habitats with different  
156 structural diversity (Matias et al. 2007). After 4 months, diversity and abundance of  
157 invertebrates in artificial turfs are not different from those in natural turfs (i.e. *Corallina* sp;  
158 Kelaher 2003a), which suggests that they are consistent with the natural assemblages. From  
159 this, I considered 4 months as appropriate for testing hypotheses about the effects of matrix  
160 and structure of habitats.

161 After 4 months, I carefully placed a plastic bag over the experimental habitat before  
162 removing the screws. This procedure ensured that all epiphytes and fauna associated with  
163 each sample were completely recovered. I cut two sub-samples (2 x 2 cm<sup>2</sup>) from the middle  
164 of each artificial turf and placed them in separate labelled plastic bags for chlorophyll  
165 extraction (see next section); all samples were immediately frozen at -80°C. I washed the  
166 remainder of each artificial turf in a 500 µm sieve and all invertebrates were sorted and  
167 counted under a binocular microscope at 16 x magnification. All molluscs were identified to  
168 the finest possible taxonomic resolution, either species or morphospecies i.e. as surrogate for  
169 taxonomic species when taxonomic classification is immediately available (e.g. Underwood  
170 and Chapman 2006).

171 **Estimating micro-algal biomass and sediment**



172 I quantified micro-algal biomass and accumulated sediment on experimental habitats  
173 to investigate how the variability in environmental variables is related to the variability  
174 among assemblages (Kelaheer et al. 2001). These environmental variables are important  
175 because many of the marine gastropods colonizing these habitats feed on micro-algae,  
176 diatoms and detritus (Beesley et al. 1998). Also, it has been shown experimentally that  
177 sediment particles are structural components of coralline turfs and some species of gastropods  
178 show preference for turfs with greater amounts of sediment (Olabarria and Chapman 2001).  
179 To measure the variability of each of the environmental variables and how they related to the  
180 variability of assemblages, I estimated micro-algal biomass and the amount of sediment in  
181 each experimental habitat. Micro-algal biomass was estimated using the concentration of  
182 chlorophyll-*a* as a proxy (Thompson et al. 1999; Murphy et al. 2005).

183 Preliminary trials were done to determine commonly used inorganic solvents (acetone,  
184 methanol and dimethyl-formamide (DMF); Thompson et al. 1999; Murphy et al. 2005) would  
185 degrade the synthetic turfs and modify spectrophotometric readings. Results showed that  
186 extractions using DMF had no measurable differences in spectrophotometer readings when  
187 compared with blanks (i.e. with no artificial turfs) and were therefore appropriate for this  
188 study. Micro-algal biomass was estimated from chlorophyll-*a* ( $\text{mg l}^{-1}$ ) overnight extraction in  
189 dimethyl-formamide (DMF) from each of two sub-samples that had been previously frozen.  
190 The concentration of chlorophyll-*a* in the solvent was calculated using the following equation  
191 (Porra et al. 1989; Murphy et al. 2005):

$$192 \text{ chlorophyll-}a = 12(A_{664} - A_{750}) - 3.11(A_{647} - A_{750}) \quad (1)$$

193 where A is the absorbance at the indicated wavelength.

194 The amount of sediment in each experimental habitat was estimated by collecting  
195 sediment particles using a 63 mm sieve. Sediment samples were then dried in an oven for 48  
196 h at 80°C and weighted. The relationships between numbers of species and each of the two  
197 environmental variables were examined by correlations (n = 15 in each correlation).

## 198 **Analyses of data**

199 Predictions about whether or not assemblages colonizing habitats with different  
200 structure were different depending on their surrounding habitats were tested using  
201 PERMANOVA (Anderson 2001) on Bray-Curtis dissimilarities calculated on Log(X+1)  
202 transformed abundances of species; Type was a fixed factor (2 levels: short vs long); Matrix  
203 was a fixed factor (2 levels: rockpool or emergent-rock). As explained in the previous  
204 section, the experimental habitats that were attached in either rockpool or on emergent-rock  
205 were in no way paired, so they were independent from each other. From this, Location was a  
206 random factor nested in Matrix. All multivariate analyses were done using PRIMER 6.0 and  
207 PERMANOVA+ (PRIMER-E Ltd, Plymouth).

208 Predictions about numbers of species in different types of habitats and matrices were  
209 tested using ANOVA with Type, Matrix and Location as in previous analyses. When  
210 appropriate, data were transformed following a Cochran's test for homogeneity of variances  
211 (Underwood 1997). Additional ANOVAs comparing the densities of the most abundant  
212 species to test whether these responded consistently to different types of habitats and  
213 matrices. *Post-hoc* comparisons of means were done using Student-Newman-Keuls (SNK)  
214 tests. All univariate tests were done using WinGMAV 5.0 (EICC, The University of Sydney).

## 215 **RESULTS**

### 216 **Diversity and structure of assemblages**

217 I collected 7,288 individuals belonging to 58 morphospecies (hereafter species), 44 of  
218 which were found in rockpools, whereas only 38 species were found in open rock. The four  
219 most abundant species (>85% individuals) were the bivalve *Lasaea australis* (Lamarck, 1818)  
220 and the gastropods *Amphithalamus incidata* (Frauenfeld, 1867), *Austrocochlea porcata*  
221 (Adams, 1851) and *Eatoniella atropurpurea* (Frauenfeld, 1867). The remainder of species  
222 had relatively smaller abundances; 19 of these species were represented by a single one.

223 Entire assemblages varied depending on interaction between Type and Location  
224 (PERMANOVA: Type x Location (Matrix) interaction, Table 1a, Fig. 1). Differences  
225 between assemblages colonizing different types of turfs were consistent in rockpool or  
226 emergent-rock (Pair-wise comparisons, Table 1b). In contrast, dissimilarity between  
227 assemblages in rockpool or on emergent-rock were consistently greater in habitats with long  
228 turfs (Table 1c). Generally, dissimilarity between assemblages in habitats with short versus  
229 long turfs was consistent across different locations, but the magnitude of such differences  
230 varied (Table 1d).

231 The number of species varied with matrix, although these differences depended on the  
232 type of habitat (ANOVA: Type x Matrix interaction, Table 2a, Fig. 2). With regards to the  
233 comparisons between each Matrix within each level of the factor Type, there were  
234 significantly greater numbers of species in short turfs, whilst on emergent-rock, there were  
235 significantly greater numbers of species in long turfs (SNK tests, Table 2b, Fig. 2). With  
236 regards to the comparisons between each Types within each level of the factor Matrix, the  
237 numbers of species in longer turfs were greater when these were on emergent rock; in  
238 contrast, there were no differences in numbers of species in short turfs depending on the  
239 matrix (SNK tests, Table 2b). These results suggest that effects of type of habitats were, in

240 fact, dependent on their surroundings thus supporting hypothesis 2 (i.e. not all types of  
241 habitats were affected in the same way by their matrix).

242 The most abundant species generally responded to the type of habitat and not the  
243 matrix (Table 3, Fig. 3). There were larger densities of the bivalve *L. australis*, gastropods *E.*  
244 *atropurpurea* and *A. porcata* in habitats with shorter turfs (SNK at  $P < 0.05$ , Table 3). *A.*  
245 *incidatus* also occurred in greater numbers in habitats with shorter turfs, and in significantly  
246 greater densities in location 3 (Table 3).

### 247 Environmental variables

248 There was considerable variability in dry weight of sediment across different  
249 locations, although dry weight of sediment per patch was consistently greater in shorter turfs  
250 (Table 4). The dry weight of sediment per patch varied between 74g (location 5) and 125g  
251 (location 2). In contrast, the concentration of chlorophyll-*a* was not affected by type or  
252 matrix of habitats, even though there was a Type x Location (Matrix) interaction (Table 4).  
253 The concentration of chlorophyll-*a* per patch was relatively consistent across several locations  
254 (53-74  $\mu\text{g.ml}^{-1}$ ), although, in location 4 there was a relatively high average value of 131  
255  $\mu\text{g.ml}^{-1}$ . No significant differences or pattern was found in the rank order of means of  
256 concentration of chlorophyll-*a*.

257 The strength of the relationship between numbers of species and sediment varied  
258 depending on Type and Matrix (Fig. 4). On emergent-rock, the relationship between  
259 sediment and numbers of species was different depending on the type of turfs (short:  $r = 0.19$ ,  
260  $F_{1,15} = 0.5$ ,  $P > 0.4$ ; long:  $r = 0.81$ ,  $F_{1,15} = 27.2$ ,  $P < 0.001$ ). In rockpools, there were no  
261 significant relationships between amounts of sediment and numbers of species in either type  
262 of turfs (short:  $r = 0.003$ ,  $F_{1,15} = 0.0$ ,  $P > 0.9$ ; long:  $r = 0.45$ ,  $F_{1,15} = 3.6$ ,  $P > 0.08$ ). Most

263 patches with shorter turfs had approximately 40g of sediment, suggesting a maximal amount  
264 of sediment that turfs can retain. Similarly, the relationship between chlorophyll-*a* and  
265 numbers of species depended on the matrix and the type of turfs. In rockpools, there was no  
266 significant relationship in either type of turfs (short:  $r = 0.38$ ,  $F_{1,15} = 2.47$ ,  $P > 0.1$ ; long:  $r =$   
267  $0.07$ ,  $F_{1,15} = 0.06$ ,  $P > 0.8$ ) whilst on emergent-rock there was a significant relationship in  
268 long-turfs ( $r = -0.55$ ,  $F_{1,15} = 6.16$ ,  $P < 0.03$ ) but in short-turfs ( $r = -0.36$ ,  $F_{1,15} = 2.04$ ,  $P >$   
269  $0.1$ ).

## 270 DISCUSSION

271 This study demonstrated that: 1) the composition of assemblages was affected by the  
272 matrix (i.e. rockpools or emergent-rock) and type of habitat, but this varied in magnitude  
273 among random locations; 2) the effects of the matrix on the number of species varied between  
274 the different types of habitats; 3) abundant species showed specific responses to type of  
275 habitat, independently of the matrix; 4) relationships between numbers of species and two  
276 major environmental variables varied depending on the type of habitats and the matrix.  
277 Generally, findings demonstrate that responses to different types of habitats are dependent on  
278 the surrounding habitat, even though several common species did not show any particular  
279 response to different matrices. The challenge for investigating biotic responses to structure of  
280 natural habitats is therefore to determine whether the context in which these habitats occur  
281 modifies the physical structure (e.g. Driscoll and Donovan 2004), the resources (e.g. Van  
282 Elven et al. 2004); or the potential pool of species colonizing habitats (e.g. Lawton 1999).

283 The relationships between structure of habitat and patterns of diversity of benthic  
284 invertebrates have been previously studied using coralline turfs naturally occurring on rock  
285 platforms (e.g. Akioka et al. 1999; Kelaher et al. 2001) or in artificial turfs (Kelaher 2003a, b;

286 Matias et al. 2010). There have, however, been fewer studies that have investigated coralline  
287 turfs in rock pools (but see Hull 1999; Bussell et al. 2007). Rockpools are extremely variable  
288 (e.g. in size, depth and shade) which possibly explains why there is great variability in  
289 composition of faunal assemblages colonizing algae in rockpools (Huggett and Griffiths  
290 1986; Metaxas and Scheibling 1994; Hicks 1980; Hull 1999). The results of the current study  
291 showed, in contrast, that assemblages colonising habitats in rockpools were considerably less  
292 variable than those on emergent-rock surfaces. This discrepancy might be because several  
293 natural species of macro-algae may change growth form as a result of physical characteristics  
294 of rockpools (e.g. coralline turfs have different morphologies in rockpools and non-rockpools  
295 surfaces; Akioka et al. 1999), which ultimately modifies the type of habitat provided for  
296 invertebrate species (Metaxas and Scheibling 1994). In the present study, however,  
297 experimental habitats had the same structure and period of colonization across different  
298 matrices, which removed potential differences in habitat structure and therefore any  
299 difference between the different matrices must be attributed to differences other than  
300 differences in habitat structure.

301         An alternative explanation is that habitats under different contexts provide different  
302 resources so that the assemblages colonizing such habitats are also different (e.g. Andren  
303 1994; Steffan-Dewenter et al. 2002; Collinge et al. 2003; Skilleter et al. 2005). The  
304 colonization of similar experimental habitats embedded in different matrices has been  
305 previously studied (e.g. sand vs seagrass, Tanner 2006), although quantifications of resources  
306 in different matrices remain scarce. In artificial seagrass beds, the diversity and biomass of  
307 macro-algal epiphytes – an important resource associated with faunal assemblages – differ  
308 depending on the context in which artificial patches are embedded (i.e. varying proximity to  
309 rocky reefs, Van Elven et al. 2004). The present results showed that two environmental

310 variables shown to be important for many marine gastropods (i.e. microalgal biomass and  
311 accumulated sediment; Beesley et al. 1998, Kelaher et al. 2001, Olabarria and Chapman  
312 2001) were greatly influenced by the location on the shore, which was probably better  
313 explained by differences in wave-exposure to ocean swell between locations (Underwood  
314 1984). This was expected since different wave-exposure is known to affect the accumulation  
315 of sediment (Prathep et al. 2003; e.g. Motta et al. 2003) and micro-algal growth (e.g.  
316 Thompson et al. 2005) in intertidal habitats. Furthermore, the variance of these  
317 environmental variables was only correlated with the numbers of species in particular  
318 combinations of habitat and matrix (i.e. long turfs on emergent-rock), which indicates that the  
319 importance of environmental variables may not be the same across all habitats in this system.  
320 Thus, these results are further evidence of the importance of determining the appropriate  
321 scales at which benthic assemblages respond to habitat structure and other environmental  
322 variables (e.g. food availability). Future studies could investigate these responses at finer  
323 spatial scales to further advance our understanding of the patterns of distribution of benthic  
324 assemblages in relation to environmental variability.

325         Another potential source of variability between assemblages in different habitats might  
326 be attributed to changes in biotic interaction (e.g. predation, Hughes and Grabowski 2006;  
327 inter-specific competition, Spooner and Vaughn 2006; Matias et al. 2012) depending on the  
328 matrix in which habitats were deployed. Generally, habitats with longer turfs had greater  
329 numbers of species. In rockpools, however, there were no differences in numbers of species  
330 between types of habitats. Common species *Lasaea australis* and *Amphithalamus incidatus*  
331 did not occur in similar numbers inside or outside of rockpools; other common species  
332 *Austrocochlea porcata* and *Eatoniella atropurpurea*, occurred in similar numbers in either  
333 matrix (Fig. 3). These observations might be explained by previous evidence that competition

334 between species of gastropods might be dependent on the quality of the habitat (e.g. “habitat  
335 suitability”, Firth and Crowe 2010) possibly due to differential competitive ability of species  
336 depending on the habitat in which they are found (Keough et al. 1997). Furthermore, several  
337 species of gastropods show habitat-associated survival as a result of variability in structural  
338 components of the habitat (e.g. amount of sediment, Olabarria and Chapman 2001). Future  
339 research on these assemblages should investigate whether the structure of patches of habitat  
340 affect competitive interactions.

341         These results may have additional implications for our understanding of the  
342 distribution and abundance of species in intertidal rocky shores. Many common grazers in  
343 intertidal rocky shores (e.g. gastropods *Austrocochlea porcata*, *Bembicium nanum*, *Nerita*  
344 *atramentosa*, and limpet *Patelloida* sp.) recruit in large numbers to coralline turfs – artificial  
345 or natural – and then disperse to the surrounding emergent-rock. Experiments in different  
346 regions (e.g. Australia, Chile and Ireland; Kelaher et al. 2004) showed that assemblages in  
347 coralline habitats may vary depending on the pool of species of each region, which is possibly  
348 explained by different matrices in which coralline habitats were embedded in those different  
349 regions. On many Australian shores, coralline turfs occur predominantly in low-shore areas;  
350 on rocky shores in other parts of the world, coralline turfs occur almost exclusively in  
351 rockpools (e.g. UK, Bussell et al. 2007), with low-shore areas often dominated by other  
352 macro-algal beds (e.g. fucoids). Understanding the consequences of the spatial structure of  
353 these habitats complements our knowledge on patterns of abundance and distributions of  
354 functionally important species and ultimately the structure of intertidal assemblages.

355

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532

## FIGURE CAPTIONS

533 **Figure 1.** Multivariate nMDS ordination of Bray-Curtis distances between assemblages  
534 colonizing different type of habitats and matrix. Each symbol represents a centroid calculated  
535 for each combination of Type, Matrix and Location (using the averaged abundances of each  
536 species across replicates;  $n = 3$ ). Different symbols and colours indicate different type of  
537 habitats and matrix: turfs with long fronds in rockpools (●), emergent-rock (■); turfs with  
538 short fronds inside rockpools (○) and emergent-rock (□); Data were  $\text{Log}(X+1)$  transformed.

539 **Figure 2.** Diversity of assemblages in different type of habitats and matrix. Mean ( $\pm$ SE,  $n =$   
540 15) numbers of species in different type of habitats and matrix; white bars indicate rockpools;  
541 shaded bars indicate emergent-rock surfaces.

542 **Figure 3.** Densities of most abundant species in different type of habitats and matrix. Mean  
543 ( $\pm$ SE,  $n = 15$ ) densities of most abundant species *Lasaea australis*, *Austrocochlea porcata*,  
544 *Amphithalamus Incidata*, and *Eatoniella atropurpurea* in different types of habitats and  
545 matrix; 'white bars' indicate rockpools; shaded bars indicate emergent-rock surfaces.

546 **Figure 4.** Relationships between numbers of species and environmental variables (sediment  
547 or chlorophyll-*a*). Environmental variables were measured in different types of habitats (i.e.  
548 short vs long) under different matrix [i.e. rockpools: a) and b); emergent-rock: c) and d)].  
549 Different symbols indicate the types of habitats (short: white circles; long: black circles).  
550 Solid lines indicate regression lines for significant correlations; coefficients of correlation and  
551 significance values in *Results* section.

552 **Table 1.** (a) PERMANOVA and pair-wise comparisons of assemblages in different type of  
 553 habitats (2 levels: long vs short); matrix (2 levels: rockpool (RP) vs emergent-rock (ER))  
 554 using Bray-Curtis distances calculated on Log(X+1) transformed abundances; Location is a  
 555 random factor nested in Matrix. Pair-wise significance tests were done for significant  
 556 comparisons (b, c and d). Multivariate patterns (nMDS) are in Fig. 1. Numbers in the bottom  
 557 part of the table indicate average Bray-Curtis dissimilarity between levels of each significant  
 558 comparison. Levels of significance: \* =  $P < 0.05$ , \*\* =  $P < 0.01$  and \*\*\* =  $P < 0.001$ .

559	Source	DF	MS	Pseudo- <i>F</i>
560	Type = T	1	12297.0	6.7**
561	Matrix = M	1	7276.7	3.1**
562	Location (M) = L(M)	8	2353.5	2.1***
563	T x M	1	7351.1	4.0*
564	T x L(M)	8	1848.4	1.6**
565	Residual	40	1145.0	

566 Pair-wise comparisons:

567 Average Bray-Curtis dissimilarity between groups T x M

568	(a) Short vs Long		(b) RP vs ER	
569	RP	63**	Short	47
570	ER	60*	Long	74**

571 (c) Average Bray-Curtis dissimilarity between groups T x L(M)

572	Location	1	2	3	4	5
573	RP	60	63	41	65	64
574	ER	67	62	48	62	72

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576

577 **Table 2.** (a) ANOVA of numbers of species in different types of habitats (2 levels: long vs  
 578 short) and matrix (2 levels: rockpool (RP) vs emergent-rock (ER)); Location was a random  
 579 factor nested in Matrix. SNKs for the comparisons (b) Type (Matrix) and (c) Matrix (Type).  
 580 Means, standard errors and SNK tests are also indicated in Fig. 2. Levels of significance: \* =  
 581  $P < 0.05$ , \*\* =  $P < 0.01$  and \*\*\* =  $P < 0.001$ .

582	(a) Source	DF	MS	<i>F</i>
583	Type = T	1	1.4 <sup>†</sup>	0.2
584	Matrix = M	1	50.4	5.9*
585	Location (M) = L(M)	8	8.5 <sup>†</sup>	1.2
586	T x M	1	98.8 <sup>†</sup>	13.5***
587	T x L(M)	8	9.8	
588	Residual	40	6.8	
589	Transform: none			
590	SNK:			
591	(b) Matrix (Type):	Short	Long	
592		RP = ER	RP < ER	
593	(c) Type (Matrix)	RP	ER	
594		Short > Long	Short < Long	
595	†Tested against pooled Residual + T x L(M)			

596 **Table 3.** ANOVA of most abundant species: bivalve *Lasaea australis* (a), and gastropods *Austrocochlea porcata* (b), *Amphithalamus incidatus* (c), and  
 597 *Eatoniella atropurpurea* (d) in different types of habitats (2 levels: long vs short) and matrix (2 levels: rockpool (RP) vs emergent-rock (ER)); and  
 598 Location was a random factor nested in Matrix; means and standard errors are in Fig. 3. Levels of significance: \* =  $P < 0.05$ , \*\* =  $P < 0.01$  and \*\*\* =  $P <$   
 599 0.001.

			(a)		(b)		(c)		(d)	
Source	DF	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	
Type = T	1	67.8 <sup>†</sup>	69.5***	14.7	6.7*	4.3 <sup>†</sup>	5.2*	25.0	21.7**	
Matrix = M	1	0.5	0.3	4.8	1.5	3.2	2.4	1.1	1.3	
Location (M) = L(M)	8	1.6 <sup>†</sup>	1.7	3.2	3.1**	1.3 <sup>†</sup>	1.6	0.8	1.3	
T x M	1	1.2	1.2	1.1	0.5	2.2 <sup>†</sup>	2.6	0.3	0.3	
T x L(M)	8	1.3 <sup>†</sup>		2.2	2.1	0.5		1.2	1.8	
Residual	40	0.9		1.0		0.8		0.6		
Transform:		Ln(X+1)		Ln(X+1)		Ln(X+1)		Ln(X+1)		
SNK:		Short > Long		Short > Long		Short > Long		Short > Long		
†Tested against pooled Residual + T x L(M)										

611 **Table 4.** ANOVA of (a) weight of sediment and (b) concentration of chlorophyll-a in different type  
 612 of habitats (2 levels: long vs short) and matrix (2 levels: rockpool (RP) vs emergent-rock (ER));  
 613 Location was a random factor nested in Matrix. Levels of significance: \* =  $P < 0.05$ , \*\* =  $P < 0.01$   
 614 and \*\*\* =  $P < 0.001$ .

	(a)			(b)		
Source	DF	MS	<i>F</i>	MS	<i>F</i>	
Type = T	1	0.5 <sup>†</sup>	9.2**	15206.4	3.7	
Matrix = M	1	0.4	1.3	427.6	0.1	
Location (M) = L(M)	8	0.3 <sup>†</sup>	5.3***	7442.4	13.2***	
T x M	1	0.0 <sup>†</sup>	0.0	0.8	0.0	
T x L(M)	8	0.1		4124.3	7.3***	
Residual	40	0.1		562.2		
Transform:		Ln(X+1)		none		
SNK:		Short > Long				

625 <sup>†</sup>Tested against pooled Residual + T x L(M)

626

Figure 1

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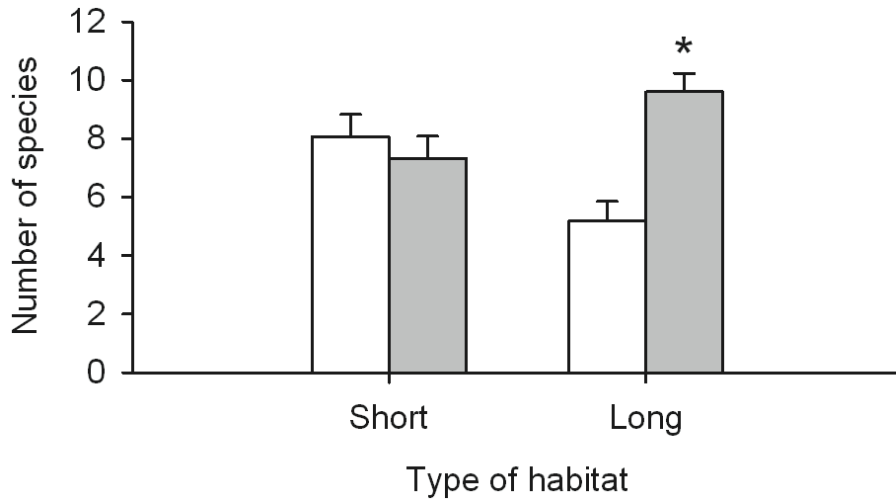
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631 **Figure 1.** Multivariate nMDS ordination of Bray-Curtis distances between assemblages colonizing  
632 different type of habitats and matrix. Each symbol represents a centroid calculated for each  
633 combination of Type, Matrix and Location (using the averaged abundances of each species across  
634 replicates;  $n = 3$ ). Different symbols and colours indicate different type of habitats and matrix: turfs  
635 with long fronds in rockpools (●), emergent-rock (■); turfs with short fronds inside rockpools (○)  
636 and emergent-rock (□); Data were  $\text{Log}(X+1)$  transformed.

637

**Figure 2**

638



639

640 **Figure 2.** Diversity of assemblages in different type of habitats and matrix. Mean ( $\pm$ SE,  $n = 15$ )

641 numbers of species in different type of habitats and matrix; white bars indicate rockpools; shaded

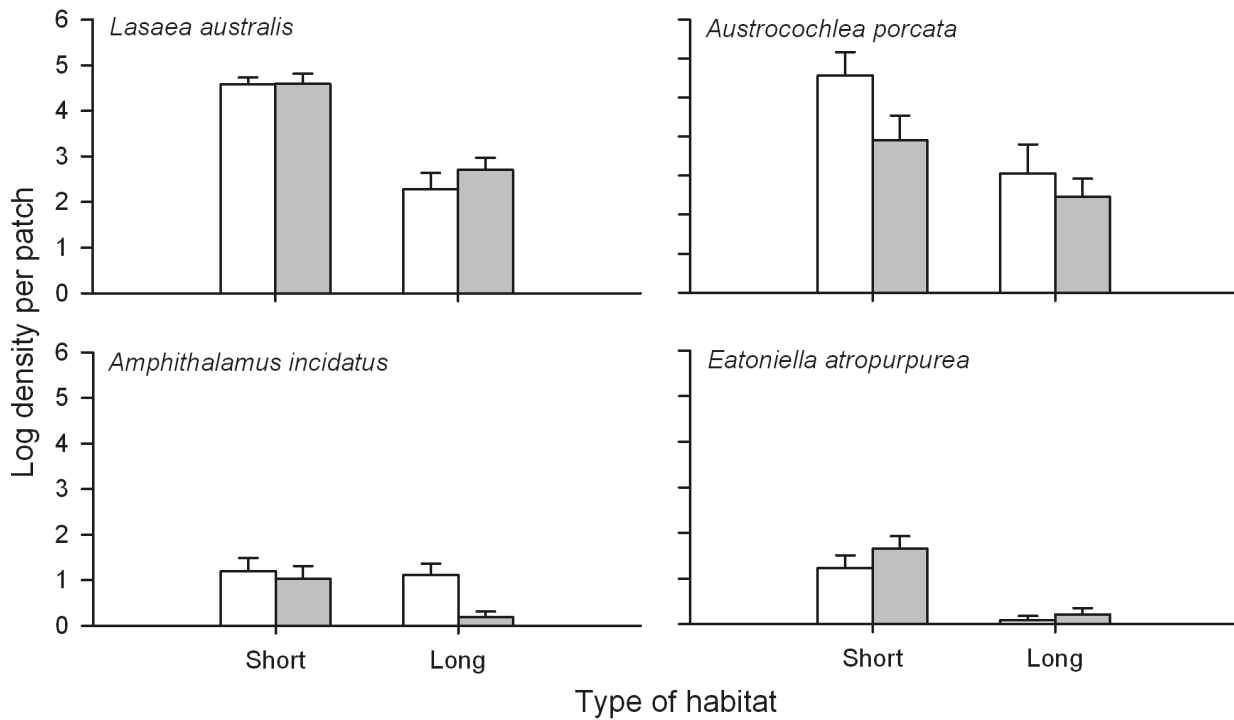
642 bars indicate emergent-rock surfaces.



643

**Figure 3**

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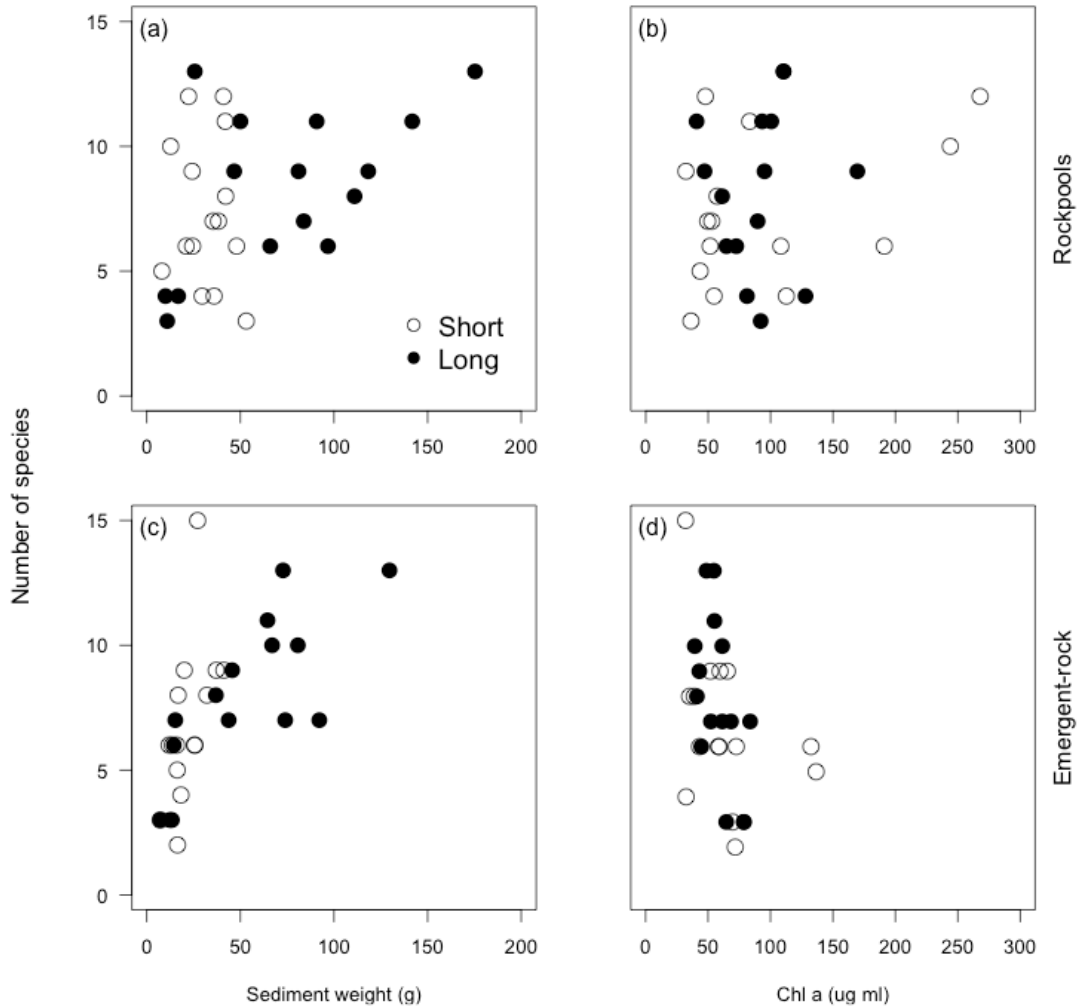
647 **Figure 3.** Densities of most abundant species in different type of habitats and matrix. Mean ( $\pm$ SE,  
 648  $n = 15$ ) densities of most abundant species *Lasaea australis*, *Austrocochlea porcata*,  
 649 *Amphithalamus Incidata*, and *Eatoniella atropurpurea* in different types of habitats and matrix;  
 650 'white bars' indicate rockpools; shaded bars indicate emergent-rock surfaces.

651

Figure 4

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653



654

655 Figure 4. Relationships between numbers of species and environmental variables (sediment or  
 656 chlorophyll-a). Environmental variables were measured in different types of habitats (i.e. short vs  
 657 long) under different matrix [i.e. rockpools: a) and b); emergent-rock: c) and d)]. Different symbols  
 658 indicate the types of habitats (short: white circles; long: black circles). The coefficients of  
 659 correlation and the significance values in *Results* section.