

**Post-settlement dispersal ability determines structure of marine benthic metacommunities**

Martins, Gustavo M.; Matias, Miguel ; Moniz, Isadora; Ruis, Carlos ; Sanderson, Josephine ; Neto, Ana Isabel; Jenkins, Stuart

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1 **Post-settlement dispersal ability determines structure of marine benthic metacommunities**

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3 **Running head:** Dispersal determines metacommunity structure

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6 Gustavo M. Martins^{1,2*}, Miguel G. Matias^{3,4}, Isadora Moniz², Carlos Rius¹, Josephine Sanderson¹, Ana I. Neto¹, Stuart R. Jenkins⁵

7
8 ¹ CE3C - Centre for Ecology, Evolution and Environmental Changes/Azorean Biodiversity Group, Universidade dos Açores, 9501-801 Ponta
9 Delgada, Azores, Portugal

10 ² Centro Interdisciplinar de Investigação Marinha e Ambiental (CIIMAR/CIMAR), Universidade do Porto, 4050-123 Porto, Portugal

11 ³ InBio/CIBIO, University of Évora, Largo dos Colegiais, 7000 Évora, Portugal

12 ⁴ Department of Biogeography and Global Change, National Museum of Natural Sciences, CSIC, 28006, Madrid, Spain

13 ⁵ School of Ocean Sciences, Bangor University, Menai Bridge, LL59 5AB Anglesey, UK

14
15
16 * gustavo.om.martins@uac.pt

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22 **Abstract**

23 Changes in natural habitats and the community response to such changes have important impacts on the distribution of diversity. Theoretical
24 advances have highlighted the importance of including dispersal traits to predict responses to habitat loss but there is a lack of empirical
25 evidence. We investigated the effect of metacommunity size (by manipulating the number of habitat patches) and isolation (by manipulating
26 proximity to reefs) in structuring marine macrofaunal communities. The overall response of macrofauna to changes in habitat size and proximity
27 to reefs varied according to the species' ability to disperse after settlement. Whilst the richness of species with sessile adult stages responded to
28 proximity to reefs in which metacommunities were deployed, species with motile adult stages responded to metacommunity size. Results were
29 similar at both the patch- and metacommunity scales. A subsequent experiment showed that colonisation had an impact on the macrofaunal
30 responses to reef proximity, which persisted throughout the community assembly process. The inclusion of simple functional traits (i.e. post-
31 settlement dispersal) allows a better understanding of species responses to the spatial configuration of habitats at multiple ecological scales,
32 which may be key for predicting the consequences of habitat loss.

33

34 **Keywords:** Biological traits, Community assembly, Experimental habitats, Habitat Size, Isolation, Scale.

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41 **INTRODUCTION**

42 There is widespread evidence linking spatial variation in the structure of natural habitats with patterns of distribution of species diversity
43 (e.g. MacArthur & Wilson 1963, Rosenzweig 1995). The development of the field of spatial ecology has highlighted the importance of spatial
44 dynamics, connectivity and dispersal for the structure of populations and communities (MacArthur & Wilson 1963, Rosenzweig 1995). This has
45 led to a shift in focus from purely description of pattern, toward empirical and modelling approaches to understand the mechanistic basis of
46 community change as a consequence of habitat modification (Holyoak 2000, Matias et al. 2010ab).

47 The effects of habitat area and isolation on population dynamics were formalized with the development of metapopulation (Hanski &
48 Gilpin 1991, Hanski 1994) and metacommunity (Leibold et al. 2004) theories, which resulted in a greater understanding of the role of

49 coexistence mechanisms and dispersal and improved our ability to predict distributional patterns in spatially structured landscapes (Hanski
50 1999). Theory predicts that when habitat patches are destroyed, species may be able to persist if different populations are linked by dispersal
51 (Hanski & Gilpin 1991, Hanski 1994). The ability to disperse and colonise new patches is therefore a key trait in determining patterns of species
52 diversity at different scales (Cadotte 2006).

53 It has been hypothesised that species' vulnerability to habitat loss and/or fragmentation, can be determined by species-specific life-
54 histories (Öckinger et al. 2010) or functional traits such as body size, dispersal ability, trophic level, diet breadth, among others (see Ewers &
55 Didham 2006 for reviews). Previous studies measuring the effect of dispersal on metacommunity structure have often used indirect measures
56 (e.g. body-size), although recent studies have shown that dispersal mode or ability are better predictors of spatial patterns in macroinvertebrate
57 metacommunities (LeCraw et al. 2014). In order to make better predictions of the response of species to changes in habitats, further work is
58 required to determine how particular traits determine the ability of species to disperse and colonise habitat patches in interconnected
59 communities.

60 Despite these advances, there is still a disconnect between theoretical and empirical studies (see Logue et al. 2011). As suggested by
61 Logue et al. (2011), theoretical predictions should be tested empirically across a range of habitats and species to make a better link between
62 spatial dynamics, dispersal rate and mobility. One particular issue is that defining relevant spatial scales can be problematic (Srivastava 1999,
63 Munguia 2004). This issue has been raised by empirical work done both in marine (Munguia & Miller 2008) and terrestrial (Miller & Kneitel
64 2005) systems, where the possibility of very high long-distance dispersal for some species means that identifying regionally closed systems,

65 assumed in most metacommunity theory, (e.g. Leibold et al. 2004) is challenging. It is likely that most metacommunities are not completely
66 closed, at least at the scale that regional processes (such as dispersal and habitat heterogeneity) are thought to operate. In discussing
67 metapopulations (the archetype for metacommunities), Hanski and Gilpin (1991) defined three scales: local, metapopulation and geographic; the
68 geographic scale encompassing distances greater than those over which an individual moves over its lifetime. Recognising this caveat in the
69 theoretical background of metacommunities, Cadotte and Fukami (2005) explicitly tested the effects of dispersal at two different scales: among
70 local communities and among metacommunities. They found that dispersal at the two scales had distinct effects on diversity stressing the need
71 to consider the effects of dispersal occurring at multiple scales rather than only at a regional scale. The above suggests that the metacommunity
72 concept may be best applied in a less rigid manner than considered by most theory and that the effects of variability in dispersal (among species,
73 rate or scale) must be further explored.

74 Here, we investigated the response of marine invertebrates to experimental manipulations of habitat patches made of artificial turfs.
75 These turfs are quickly colonised by a range of organisms and have proved to be a tractable model system to investigate the community response
76 to the structure and spatial configuration of habitat patches (Matias et al. 2007), including responses to changes in structural complexity (Kelaheer
77 2003), habitat area and heterogeneity (Matias et al. 2010b), isolation (Virnsten & Curran 1986) and environmental context (Matias 2013). We
78 investigated the effects of metacommunity size on benthic assemblages colonising artificial turfs (i.e. patches) by manipulating the number of
79 patches within groups of patches (analogous to metacommunity size *sensu* Leibold et al. 2004) and proximity to reefs within which
80 metacommunities were embedded as a surrogate for isolation. We predicted that, generally, greater numbers of species would be found in large

81 metacommunities and that proximity to reefs would affect the numbers and identity of species present. We further predicted that the response of
82 species to metacommunity size and proximity to reefs would depend on the post-settlement ability of species to disperse (e.g. whether species
83 were motile or sessile after initial larval colonisation). While many of the benthic invertebrate species colonising artificial turfs have a
84 planktonic larval phase and therefore the possibility of very high long-distance dispersal over regional scales, we focused on the implications of
85 dispersal following settlement and specifically the difference between species which are motile or sessile as adults. Sessile species are not able,
86 or unlikely capable, of further dispersal, whilst motile species are able to redistribute themselves at local scales. As such, we predicted that the
87 numbers of species with sessile adult stages would remain relatively constant among habitats differing in size (provided that the sampled areas is
88 kept constant) as a simple response to habitat area, whilst species with motile adult stages, which have the ability to redistribute themselves after
89 colonisation, would show variable patterns of distribution among habitats differing in size. Moreover, a greater number of sessile individuals,
90 and hence species, would be expected to be found in habitats close to reefs (greater larval pressure close to reefs owing to the fact that it was the
91 main source of larvae; mass effects), while motile species, whilst also influenced by the larval pressure during the colonization stage, again,
92 would potentially have the ability to redistribute themselves after colonization. The latter, perhaps, may even be able to continuously exchange
93 individuals between the reef and the nearby habitat patches.

94 Considering the above, it would be logical to also predict that spatial patterns of sessile species would tend to be more similar, in the
95 longer-term, to those established during early stages of patch colonization (e.g. larval recruitment of patches), while for motile species, spatial
96 patterns would tend to become increasingly different from those established during the early stages of colonization owing to their ability to

97 disperse (move) among habitat patches after settlement. That is, the process of patch colonization would be of greater importance in determining
98 longer-term patterns of species distribution for sessile species compared to motile species. The latter was tested using a complementary
99 experiment investigating the role of species' colonisation (early stages of community assembly) in determining the results observed over the
100 longer-term (2-month period; the above experiment). We predicted that if early stages of species colonisation played an important role in
101 determining community structure relative to post-colonisation processes (i.e. biotic interactions, dispersal), the response of species to distance
102 from the reef during the very early stages of community assembly (3 days) would be similar to patterns observed during the 2-month
103 experiment. In contrast, if post-colonisation processes were relatively more important for community structure, patterns established during early
104 stages of species colonisation would be modified and results from both experiments would differ.

105

106 **MATERIALS AND METHODS**

107 **Study locations**

108 We chose two different locations about 500 m apart at São Roque (São Miguel, Azores: Latitude 37°44'34''N, Longitude 25°38'31''W).
109 At each of the two locations, the rocky reef, composed of natural basaltic rocks, extends subtidally from the intertidal zone for 50 - 100 m
110 offshore and is then replaced by sandy-bottom substrates. The transition zone between the reef and sand occurs at approximately 10 - 14 m depth
111 at each of the two locations. Rocky reefs in the area support a rich flora dominated by turf-forming species (e.g. *Corallina* spp.) sustaining a
112 diverse assemblage of macrofauna numerically dominated by gastropods (~25%) and amphipods (~15%) (Martins et al. 2016). The sandy-

113 bottom supports a relatively depauperate assemblage of macrofauna numerically dominated by the polychaetes *Exogone naidina* and *Spio* aff.
114 *filicornis* and the bivalve *Ervilia castanea* (Martins et al. 2013). All the experiments described below were replicated in each of these locations.

115

116 **Experiment 1: Metacommunity size and proximity to reef**

117 Patches of 50 cm² of artificial turfs (40 mm long and sparse synthetic grass supplied by Maxmat, Ponta Delgada) were attached to the
118 end of 50 cm metal rods (one patch per rod) that were driven into the sand leaving the artificial turfs at about 10 cm from the sea-bottom (see
119 Fig. S1 in the supplement). Metacommunities of different sizes were created by deploying groups of either 3 or 6 patches. Within each
120 metacommunity, patches were deployed about 10 cm from each other. We varied the proximity to the reef within which metacommunities were
121 embedded by deploying patches at two different distances from the reef: close (< 2 m) and away (25 m). Based on previous studies, macrofaunal
122 assemblages adjacent to reefs are considerably different from those > 15 m away (Virnstein & Curran 1986, Martins et al. 2013). Sandy habitats
123 are locally dominated by polychaetes (Martins et al. 2013), which were mostly absent from our experimental patches. Only a small fraction
124 (~7%) of species was found both in experimental patches and the adjacent sandy bottom, suggesting that assemblages colonising experimental
125 patches originated mostly from the nearby algal-dominated reefs or directly from the water column. Overall, our approach of using patches of
126 turf surrounded by an inhospitable habitat is similar to that used by Munguia & Miller (2008) who used individual pen shells, as ‘islands’ of hard
127 substrate habitat within seagrass beds grouped in metacommunities.

128 In each of the two locations, three replicate metacommunities were deployed corresponding to each combination of metacommunity size
129 and proximity to the reef (totalling 12 metacommunities and 54 individual patches per location, see Fig. S2 in the supplement). Experimental
130 patches were deployed in early June 2012 and retrieved approximately 2 months after. This 2-month period is consistent with previous studies
131 using these experimental habitat patches (e.g Kelaher 2002, Matias et al. 2007, 2010b). Moreover, preliminary observations conducted in the
132 same locations as those in our experiment showed that numbers of species tended to stabilize after 2 weeks of patch deployment (see Fig. S3 in
133 the supplement), which may indicate post-colonisation processes affecting the accumulation of species. From these considerations, the 2-month
134 period was considered appropriate to allow the initial establishment of assemblages and to encapsulate post-settlement processes affecting
135 assemblage structure (e.g. inter-patch dispersal by motile species). Upon collection, 3 individual patches from each replicate metacommunity
136 were carefully removed from the rods and enclosed in plastic zip-closed bags while still underwater. Note that the number of patches sampled
137 was always the same (3) for both the small and large metacommunity treatments so that the sampled area was consistent and is not a
138 confounding factor. In the laboratory, samples were sieved (< 2 hours from collection) using a 0.5 mm sieve. The material retained was stored in
139 alcohol in labelled plastic jars until further inspection.

140

141 **Experiment 2: Short-term colonisation**

142 An additional experiment was established to allow assessment of short-term colonisation patterns. In each of the two locations described
143 above, 5 replicate habitat patches were deployed (~5 m apart) both close (< 2m) and away (25m) from the reef. Unlike in Experiment 1, habitat

144 patches were not grouped in metacommunities. Habitat patches were sampled (as described above) after a period of colonisation of only 3 days.
145 Because recruitment can show significant variability at small temporal scales this experiment was repeated three times between June-August
146 2012.

147

148 **Taxonomic resolution and dispersal traits**

149 Sorted individuals were identified to species or morphospecies (hereafter species). We classified all species according to dispersal ability
150 as adults into either motile or sessile as in Munguia (2004). Sessile species were species with sessile (permanently attached) adult stages (e.g.
151 spirobid polychaetes, bryozoans), plus species that generally have little active locomotion as adults (e.g. bivalves). The latter are species that are
152 unlikely to migrate among habitat patches after settlement. Motile species were those with an active means of locomotion (e.g. swimming,
153 crawling) in the adult stage and that are therefore expected to be able to move freely among patches (e.g. amphipods, gastropods). Although
154 initially we suspected that there could be a difference between crawlers and swimmers, preliminary analyses showed their response was similar
155 and these were thus lumped together as a single group. One assumption made in this distinction between sessile and motile species was that
156 sessile species once arriving (as larvae) and recruiting to a single habitat patch are no longer able or likely to disperse to the surrounding patches.
157 They are unlikely to produce free-swimming larvae within the 2-month period of the experiment. Motile species, in contrast, may disperse
158 among patches during their entire life-cycle.

159

160 **Data analysis**

161 We conducted a permutational ANOVA (PERMANOVA based on Euclidean distances, Anderson 2001) to test for differences in the
162 numbers of species using a 3-way fully factorial design: *Size* (fixed; small [3 patches] and large [6 patches]); *Proximity to reef* (fixed; close and
163 away) and *Location* (random).

164 Multivariate analyses were used to examine the effects of size and proximity to the reef on the structure of macrofaunal assemblages.
165 Analyses were run using permutational ANOVA as described above. These were run on two different similarity matrices: Bray-Curtis on
166 untransformed data and Jaccard. Both indices explore differences in species composition. However, when calculated on untransformed data,
167 Bray-Curtis gives more weight to changes in species abundances, whereas Jaccard does not take into account the species relative abundances
168 and is based on changes in species identities alone. The combined use of these two measures of similarity allow assessment of the importance of
169 changes in species abundances relative to changes in composition (e.g. Anderson 2005). Similarity of percentages (SIMPER) was used to
170 identify the taxa contributing to differences within significant terms.

171 For all the above, analyses were run at two scales: patch- and metacommunity-scales. At the patch-scale, numbers of species were
172 averaged from the three patches within each replicate metacommunity. At the metacommunity-scale, numbers of species was the total number of
173 species found in each metacommunity (combining the 3 sampled patches per metacommunity).

174 The short-term colonisation experiment was analysed using permutational ANOVA with: *Time* (random; three random dates chosen
175 between June-August 2013); *Proximity to reef* (fixed; close and away) and *Location* with two levels (random).

176 All analyses were performed using PRIMER 6 with PERMANOVA+ (PRIMER-E, Plymouth) using 999 permutations.

177

178 **RESULTS**

179 **Experiment 1: Metacommunity size and proximity to reef**

180 A total of 145 taxa were identified from 57,558 individuals of which 123 were classified as motile and 22 as sessile (see Table S1 in
181 supplement). Amphipods (65% of total number individuals), motile polychaetes (5%) and gastropods (4%) were the dominant motile taxa.
182 Bivalves (8%), bryozoans (3%) and sessile polychaetes (2%) were the dominant sessile taxa. Most sessile (73%) and motile (82%) species were
183 found both close and away from the reef. Species absent from the patches far from the reef were all rare or uncommon (*c.a.* 6 individuals per
184 patch) in patches close to reef, whereas < 2% of species were exclusive to the areas away from the reef.

185 For the whole assemblage (both sessile and motile), the numbers of species varied depending on the scale (metacommunity- versus
186 patch-scale) at which richness was measured. Macrofaunal richness responded significantly to proximity to the reef only at the metacommunity-
187 scale ($F_{1,19} = 5.06$, $P = 0.036$; Fig. 1a, see Table S2 in the supplement), with greater numbers of species colonising close to the reef (mean
188 richness \pm SE, close to reef: 68.8 ± 3.2 , far from reef: 60.4 ± 2.0). When considering the response of richness to metacommunity size, the
189 number of species tended to be greater in large metacommunities both at the patch- (large: 47.8 ± 1.8 , small: 42.0 ± 2.3 ; $F_{1,19} = 3.77$, $P = 0.064$)
190 and metacommunity-scale (large: 68.0 ± 2.7 , small: 61.3 ± 2.9 ; $F_{1,19} = 3.26$, $P = 0.09$) (Fig. 1b).

191 When we analysed the data according to the dispersal traits, we found that there were significantly greater numbers of sessile species
192 closer to the reef at both the patch- (27% more species; $F_{1,19} = 8.73$, $P = 0.006$) and metacommunity- (28% more species; $F_{1,19} = 11.88$, $P =$
193 0.003) scales (Fig. 1c,d). For motile species, proximity to the reef had no significant effect at the patch-scale ($F_{1,19} = 0.91$, $P = 0.328$). At the
194 metacommunity-scale, the number of species tended to greater (11%) in patches close to reef ($F_{1,19} = 3.42$, $P = 0.08$).

195 Size had no effect on the numbers of sessile species at both the patch- ($F_{1,19} = 1.08$, $P = 0.328$) and metacommunity-scale ($F_{1,19} = 0.92$, P
196 $= 0.334$, Fig. 1c,d). Numbers of motile species were generally greater in larger habitats at both the patch-scale (large: 38.6 ± 1.3 , small: $33.6 \pm$
197 1.8 ; $F_{1,19} = 4.59$, $P = 0.048$) and metacommunity-scale (large: 54 ± 2.0 , small: 49.0 ± 2.2 ; $F_{1,19} = 3.42$, $P = 0.084$)(Fig. 1e,f).

198 For the whole assemblage, the output of multivariate analyses was generally similar at the two scales (patch- and metacommunity-
199 scales). A significant interaction was found between metacommunity size and location (as well as between proximity to the reef and location)
200 for both the Bray-Curtis and Jaccard similarity indices (see Table S3 in the supplement). Post hoc comparisons of these interaction terms showed
201 consistent effect of both metacommunity size and proximity to reef (i.e. effects were seen at both locations) (Table 1).

202 When analysing data according to dispersal traits, we found that sessile assemblages did not respond to metacommunity size, but
203 generally differed or tended to differ according to proximity to the reef (Jaccard, $P < 0.01$; Bray-Curtis, $P = 0.07$) (Table 1). SIMPER analysis
204 (see Table S4 in the supplement) revealed that most sessile taxa occurred more often in habitats close to the reefs. Motile assemblages responded
205 significantly to size and proximity to the reef (Table 1). The latter was, however, only significant when considering species abundances (Bray-
206 Curtis), but not when relying only on changes in species identities (Jaccard). SIMPER analyses (Table S4) revealed that motile taxa were on

207 average more abundant in large metacommunities. When considering the effect of proximity to the reef, most taxa were generally more
208 abundant in metacommunities far from the reef.

209

210 **Experiment 2: Short-term colonisation**

211 A total of 103 taxa (89 motile and 14 sessile) were identified from 4,289 individuals. Motile assemblages were dominated by amphipods
212 (58%), gastropods (18%) and decapods (4%). Sessile assemblages were dominated by bryozoans (6%) and bivalves (5%). Most motile (71%)
213 and a large number of the sessile (54%) species were found both far and away from reef.

214 For the whole assemblage (sessile and motile included) there was no effect of proximity to reef on numbers of species ($F_{1,2} = 0.93$, $P =$
215 0.377). When we considered dispersal traits, however, we found significantly ($F_{1,53} = 4.30$, $P = 0.039$) greater numbers of sessile species in
216 patches close to the reef (1.9 ± 0.2) compared to patches away from the reef (1.4 ± 0.2). In contrast, the numbers of motile species did not vary
217 with proximity to the reef ($F_{1,53} = 0.84$, $P = 0.396$)(see Fig. S4 and Table S5 in the supplement).

218 Multivariate analysis showed that, proximity to the reef generally did not determine the structure of whole assemblages (Bray-Curtis:
219 $F_{1,53} = 191$, $P = 0.126$) although it appeared to have some effect on species identities (Jaccard: $F_{1,53} = 1.46$ $P = 0.083$). When analysing data
220 according to the dispersal traits, again there were significant differences in the structure of assemblages of sessile species with proximity to reef
221 (Bray-Curtis: $F_{1,53} = 4.09$, $P = 0.003$; Jaccard: $F_{1,53} = 2.48$, $P = 0.046$)(see table S6 in the supplement for ANOVAs). SIMPER analyses (see
222 Table S7 in the supplement) showed that 5 out of the 8 sessile taxa accounting for 90% of the differences between habitat patches deployed at

223 different distances from the reef were more frequent (found in a greater number of patches) in patches close to the reefs. In contrast to sessile
224 assemblages, proximity to reefs had no significant effect in the assemblage structure of motile species (Bray-Curtis: Location x Time x
225 Proximity to reef $F_{2,51} = 1.34$, $P = 1.39$; Proximity to reef $F_{1,2} = 2.04$, $P = 0.167$; Jaccard: $F_{1,53} = 2.44$, $P = 0.110$).

226

227 **DISCUSSION**

228 Our study illustrates that, as expected, macrofaunal assemblages as a whole responded to differences in habitat configuration
229 (metacommunity size and proximity to reef). More importantly, however, we found that the overall response of macrofauna varied according to
230 species post-settlement dispersal abilities. For instance, results showed that assemblages of sessile and sedentary invertebrates were *ca.* 30%
231 more diverse, and significantly so, in metacommunities deployed close to reefs, whereas motile invertebrates displayed no such pattern. Also
232 post-settlement dispersal ability determined responses to metacommunity size: motile assemblages were more diverse (at both the patch- and
233 metacommunity-scales) in larger metacommunities, while sessile assemblages did not respond to metacommunity size.

234 Making the distinction between species that are able to actively disperse as adults and species that are not proved useful in contributing
235 to a greater understanding of the responses observed to variation in habitat configuration and may provide insights about the underlying
236 mechanisms. For instance, a greater number of species in larger habitats probably indicates that a greater number of individual patches sample
237 more of the species pool and that species once arriving to a single patch can, afterwards, disperse to other patches within a metacommunity.
238 Thus on average (and not only at the metacommunity-scale), all patches within a metacommunity have more species. Post-settlement species

239 dispersal among patches within metacommunities is, however, less likely in the case of sessile species and in accordance, there were no effects
240 of size (at both the patch- and metacommunity-scales). The distinct response of sessile and motile taxa to changes in metacommunity size
241 highlights the importance of recognizing post-settlement dispersal among habitat patches in mediating the response of species to habitat loss.
242 Such considerations may prove particularly important, for instance, when considering the effects of variations in the spatial configuration of
243 networks of marine protected areas on particularly important species (Shanks et al. 2003). In this regard, it would be important to investigate if
244 the results from our small-scale experiment can be scaled-up to larger spatial scales (i.e. reefs, coasts, islands). It should be noted, however, that
245 processes affecting the distribution of larval recruitment may be relatively more important at explaining such larger-scale distributions (among
246 MPAs) than the post-settlement ability of species to disperse among habitat patches (addressed in this study), which likely is more important at
247 smaller spatial scales, although this may still be important in distinguish some species (e.g. cryptic reef fish vs benthonic fish).

248 Distinction between sessile and motile species also proved useful in understanding the responses of macrofauna to experimental changes
249 in proximity to reef (or source of colonists). Our prediction was that distance to a nearby reef plays an important role in structuring communities
250 (e.g. Chase & Ryberg 2004) with habitats further away from the reef supporting lower numbers of species. In accordance, assemblages of
251 invertebrates with sessile adult stages were significantly influenced by the proximity to the reef with habitat patches deployed away from the
252 reef supporting less diverse assemblages. Assemblages of invertebrates with motile adult stages, however, did not respond as predicted (and in
253 fact showed greater abundances in habitats away from the reef). Here it seems that distance from a source of colonists was not the driver of
254 community composition. Given the perceived and documented importance of habitat isolation for many organisms, including species with high

255 levels of motility (reviewed by Cadotte 2006), it may be tentatively suggested that larval dispersal ability of the motile invertebrates during the
256 colonisation stage was larger than the level of ‘isolation’ of patches deployed away from the reefs and that for some reason (e.g. higher rates of
257 predation by reef fish, ‘oasis’ effect), the abundance of individuals is reduced close to the reef. It is interesting to note that this pattern of greater
258 abundance of individuals recorded in patches further away from reefs was also shown by Virnstein and Curran (1986) for some amphipods.

259 While results were generally similar regardless of scale (patch- or metacommunity-scale), there were a few exceptions, most notably, the
260 fact that when considering the assemblage as a whole, significant effects of proximity to reefs were found only at the metacommunity-scale. A
261 possible explanation for this result might be attributed to the fact that probabilities of sampling rare species depend on the scale at which one
262 measures species diversity (i.e. patch vs. metacommunity). It has been shown that differences between different habitat types might be driven
263 simply by the presence or absence of rare species, with common species being present across all habitat types (Matias et al. 2010a). In our study,
264 rare species often colonized a single patch within the metacommunity and, thus, their contribution to species diversity is reduced when diversity
265 is measured at patch-scale (i.e. numbers of species were averaged from the three patches within each metacommunity). In contrast,
266 metacommunities were colonised by multiple rare species (i.e. the sum of rare species in each of the three patches) that all contribute to species
267 diversity at the metacommunity-scale. For this reason, the contribution of rare species is greater at the metacommunity-scale when compared to
268 the patch-scale, providing a better “sample” of benthic organisms, since there were clearly fewer rare species away from the reef. These results
269 show that the scale at which we measured diversity is inevitably linked to the degree to which the same measure of diversity is able to capture
270 the effects of isolation.

271 Although post-colonisation processes for community assembly may clearly be important (e.g. Chase et al. 2010), our complementary
272 experiment investigating the short-term effects of habitat proximity to the reef on early patterns of species colonisation showed that patterns
273 were consistent with those observed during the main experiment (no effect of proximity to reef on species with motile adult stages, greater
274 richness of species with sessile adult stages close to the reef). Such consistent responses found between the two experiments imply a rather
275 influential role of larval dispersal or colonisation over post-colonisation processes for community assembly in terms of patch isolation
276 (proximity to reef). Note that the overall numbers of species colonising the individual patches in this short-term experiment (3 days) was
277 relatively small for species with sessile adult stages (see Fig. S4b). The small number of sessile species colonising habitat patches may affect our
278 ability to extrapolate these results to a wider assemblage of sessile species (as found in the main experiment), which also suggests that species
279 dispersal ability clearly affects the way species colonise new patches. While species with sessile adult stages are dependent on larval recruitment
280 from plankton (i.e. which is influenced by species reproductive seasonality), species with motile adult stages appear to be able to arrive and
281 colonise new habitat patches both via larval recruitment from plankton and via dispersal of adult individuals. Although we have not tested the
282 short-term colonisation effect on species response to changes in metacommunity size, this result may suggest that proximity to reef and
283 metacommunity size differently affect the distribution of species according to life-cycle stage; proximity to reef may be relatively more
284 important in determining the ability of larvae colonising experimental patches, whereas metacommunity size may be relatively more important
285 in determining post-settlement dispersal of adults (for motile species).

286 Interpretation of the output from analyses was in some cases based on trends ($P < 0.1$) rather than strictly statistically significant ($P <$
287 0.05) responses (i.e. see response of species richness in the whole assemblage to metacommunity size). We believe that lack of statistical
288 significance in some cases was likely driven by the overall low number of replicates used ($n = 3$). Such low number of replicates results from the
289 fact that (i) sorting, identifying and enumerating macrofauna is a laborious task and (ii) we adopted a hierarchical framework in which individual
290 habitat patches were grouped as metacommunities. In our case, we sampled three individual habitat patches per replicate metacommunity, which
291 tripled the number of samples. We believe that even though this approach reduced statistical power to detect significant effects, it was also
292 important as it allows one to distinguish scale-dependent effects.

293 As human populations grow, the natural environment is under increasing pressure leading to the modification and destruction of habitats;
294 such impacts are recognized as one of the greatest threats to biodiversity (Pimm & Raven 2000). Most common approaches used to predict
295 species loss as a function of the amount of habitat (e.g. Rozenweig 1995) assume implicitly that the mechanisms causing species loss are
296 equivalent among species and their ecological context (Matias et al. 2014). Our results clearly show that species do not all respond in the same
297 way and that part of that variability can be partially explained by the ability and scale at which species disperse (see also Johnson et al. 2001,
298 Munguia & Miller 2008). Inclusion of traits when modelling responses to habitat loss is a promising avenue to disentangle the contrasting results
299 in the literature (Ewers & Didham 2006). This study follows a variety of studies calling for the inclusion of further complexity in field-
300 experiments (Kareiva 1990), which might come in the form of better knowledge of species functional traits or through testing responses at
301 multiple ecological scales. Unless this is achieved, it will be hard to advance our understanding of the consequences of habitat loss.

302

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376 Table 1. Summary of PERMANOVA tests comparing responses to size and proximity to reefs in whole assemblages, sessile species or motile
377 species. Responses were calculated at the patch- (i.e. average abundances) or at the metacommunity-scale (i.e. sum of abundances across all
378 patches). Analyses were performed using two different dissimilarity measures: Bray-Curtis and Jaccard. Levels of significance: 0.05 (*), 0.01
379 (**), 0.001 (***). See Table S3 in the supplement for full tables.

		Metacommunity-scale		Patch-scale	
		Bray-Curtis	Jaccard	Bray-Curtis	Jaccard
Size	Whole assemblage	*	**	*	**
	Sessile assemblage				
	Motile assemblage	*	**	**	**
Proximity to reef	Whole assemblage	***	*	***	*
	Sessile assemblage		**		**
	Motile assemblage	***		***	

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390 **Figure Captions**

391 Figure 1. Mean (+ SE) numbers of species in metacommunities differing in size and proximity to reefs for (a,b) the assemblage as a whole, (c,d)
392 the sessile component of the assemblage, and (e,f) the motile component of the assemblage. Analyses were done at two scales: metacommunity-
393 (left panels) and patch- (right panels) scales. In each separate panel, different letters indicate significant differences between means (with
394 significance set at $P < 0.05$; Table S2).

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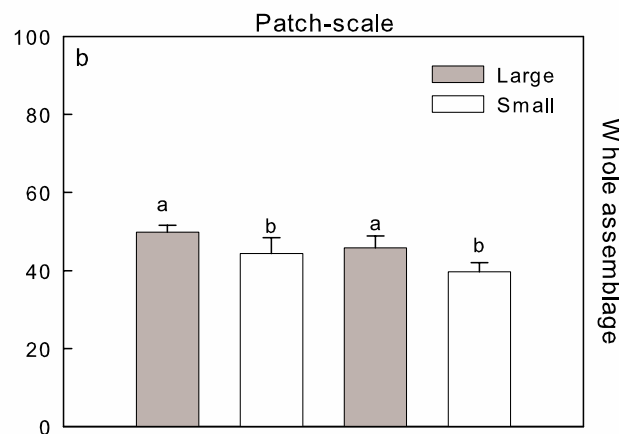
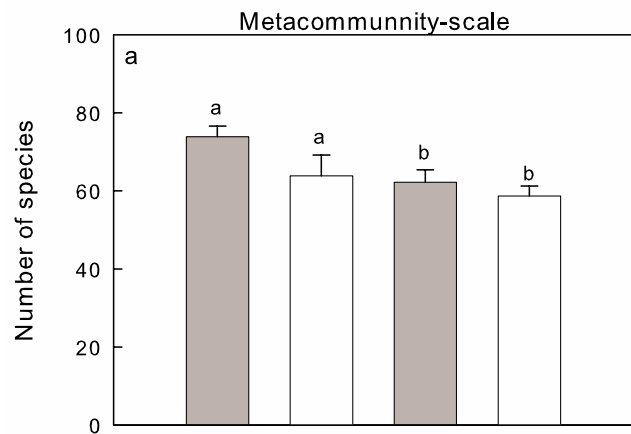
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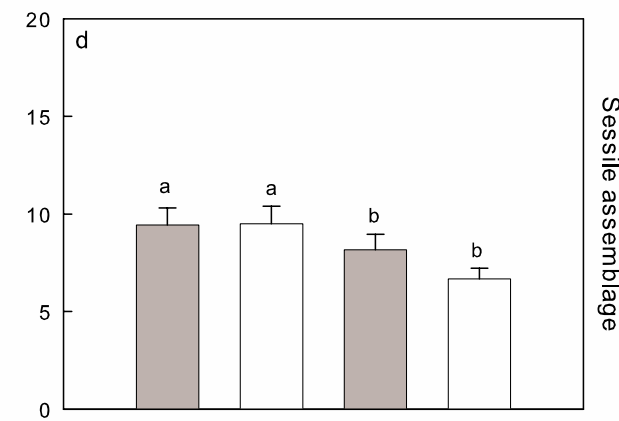
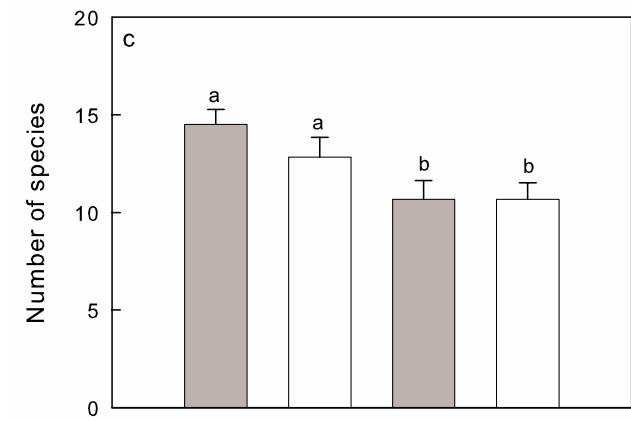
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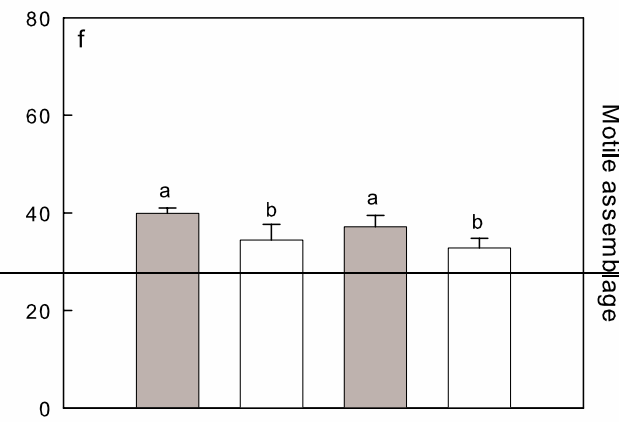
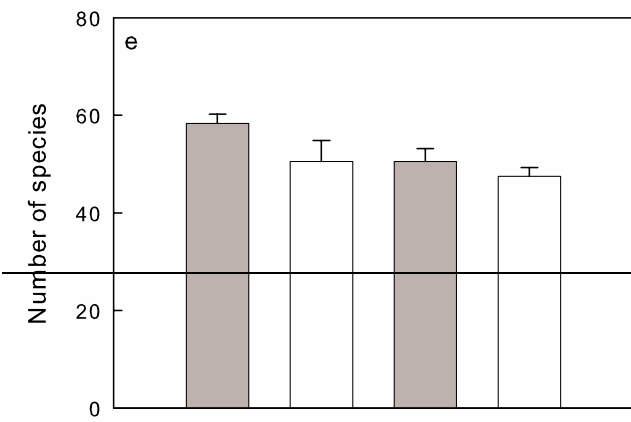




Whole assemblage



Sessile assemblage



Motile assemblage

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Figure 1.

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Supplementary online material

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421

Post-settlement dispersal ability determines structure of marine benthic metacommunities

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Gustavo M. Martins*, Miguel G. Matias, Isadora Moniz, Carlos Rius, Josephine Sanderson, Ana I. Neto, Stuart R. Jenkins

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*Corresponding author: gustavo.om.martins@uac.pt

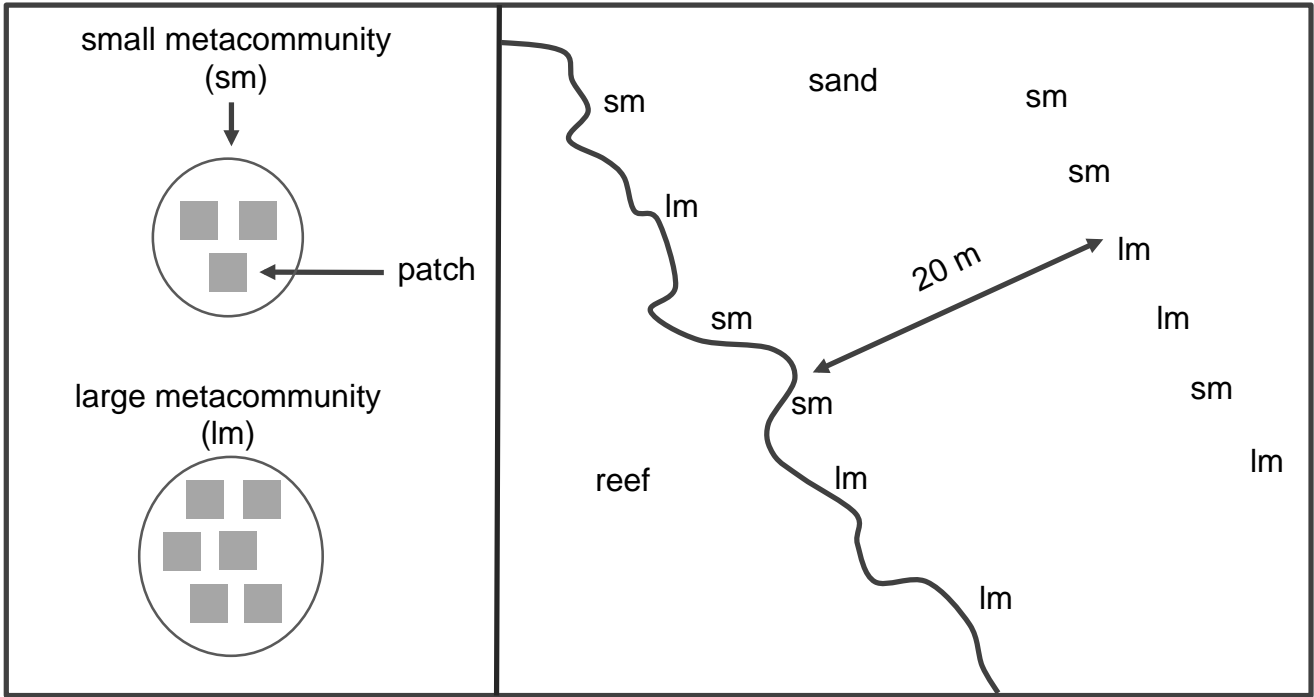
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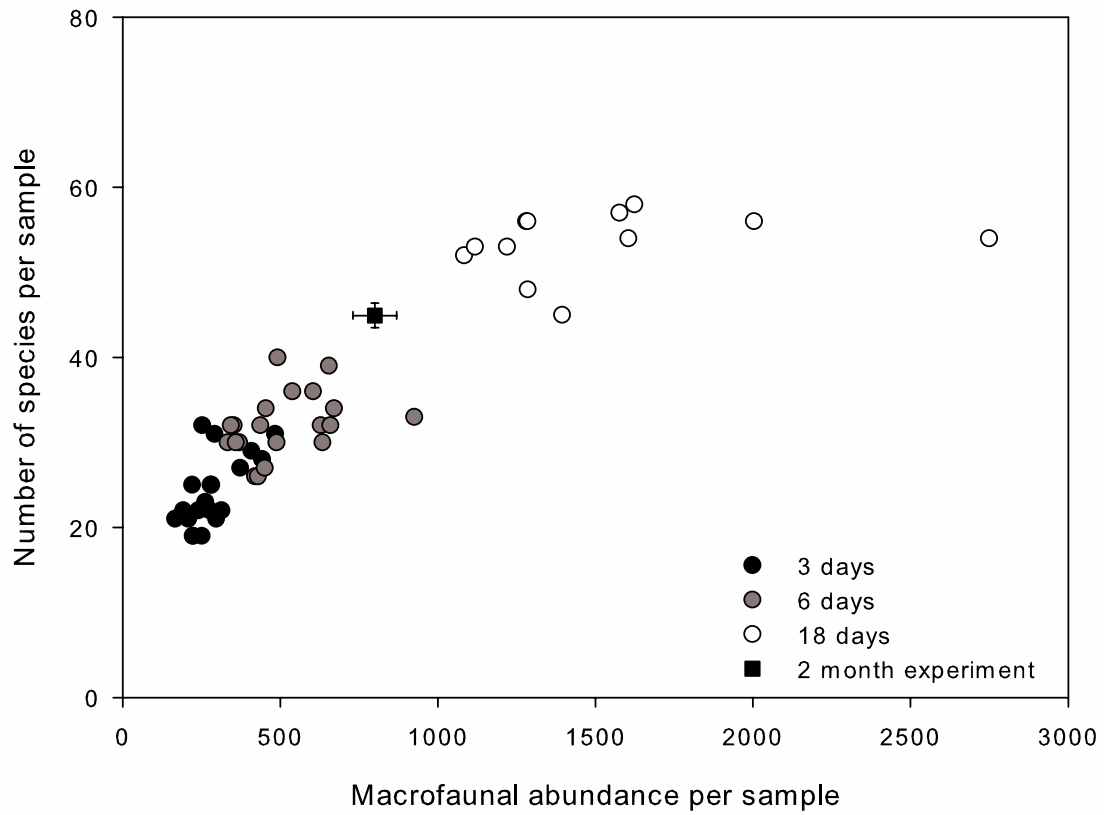


427 Fig. S1. Photographs of experimental patches and metacommunities (groups of patches) deployed in an inhospitable soft-bottom subtidal habitat.



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429 Fig. S2. Schematic representation of experimental design.



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432 Fig. S3. Numbers of species and total abundance in experimental patches after 3, 6 and 18

433 days of deployment and averaged (\pm SE) over our main experiment (2 months).

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437 Table S1. List of taxa (species or morpho-species) identified present in the experimental
 438 turfs.

Phylum	Class	Subclass/Order	Taxa	Post-settlement dispersal
Annelida	Clitellata	Oligochaeta	Oligochaeta sp1	Motile
			Oligochaeta sp2	Motile
			Oligochaeta sp3	Motile
			Oligochaeta sp4	Motile
			Oligochaeta sp5	Motile
			Oligochaeta sp6	Motile
Annelida	Polychaeta	Errantia	Errantia sp1	Motile
			Errantia sp2	Motile
			Errantia sp3	Motile
			Errantia sp4	Motile
			Errantia sp5	Motile
			Errantia sp6	Motile
			Errantia sp7	Motile
			Errantia sp8	Motile
			Errantia sp9	Motile
			Errantia sp10	Motile
			Errantia sp11	Motile
			Errantia sp12	Motile
			Errantia sp13	Motile
			Errantia sp14	Motile
		<i>Euphrosine foliosa</i>	Motile	
	Sedentaria	Sedentaria sp1	Sessile	
		Spirorbid sp1	Sessile	
		Spirorbid sp2	Sessile	
		Spirorbid sp3	Sessile	

Arthropoda	Arachnida	Sarcoptiformes	Acarii sp1	Motile
			Acarii sp2	Motile
			Acarii sp3	Motile
Arthropoda	Malacostraca	Amphipoda	<i>Abludomelita obtusata</i>	Motile
			Amphipoda sp1	Motile
			Amphipoda sp2	Motile
			Amphipoda sp3	Motile
			Amphipoda sp4	Motile
			Amphipoda sp5	Motile
			Amphipoda sp6	Motile
			Amphipoda sp7	Motile
			<i>Amphitoe rubricata</i>	Motile
			<i>Aora gracilis</i>	Motile
			<i>Apherusa jurinei</i>	Motile
			<i>Caprella acanthifera</i>	Motile
			<i>Caprella linearis</i>	Motile
			<i>Dexamine spinosa</i>	Motile
			<i>Erichthonius difformis</i>	Motile
			<i>Erichthonius punctatus</i>	Motile
			<i>Gammarella fucicola</i>	Motile
			<i>Jassa falcata</i>	Motile
			<i>Maera grossimana</i>	Motile
			<i>Phtisica marina</i>	Motile
			Pseudoprotellaphasma	Motile
			Thalassosmittiaatlantica	Motile
		Cumacea	<i>Diastylis</i> sp.	Motile
		Decapoda	Decapoda sp1	Motile
			Decapoda sp2	Motile
			Decapoda sp3	Motile
			Decapoda sp4	Motile

			Decapoda sp5	Motile
			Decapoda sp6	Motile
			Decapoda sp7	Motile
			<i>Macropodia</i> sp.	Motile
			Pagurus sp1	Motile
			Pagurus sp2	Motile
		Isopoda	<i>Anthura gracilis</i>	Motile
			<i>Dynamene bidentata</i>	Motile
			<i>Gnathia maxillaris</i>	Motile
			<i>Janiropsis breviremis</i>	Motile
		Tanaidacea	<i>Leptochelia caldera</i>	Motile
			<i>Paratanais martinsi</i>	Motile
			<i>Tanais grimaldii</i>	Motile
	Maxillopoda	Copepoda	Copepoda sp1	Motile
			Copepoda sp2	Motile
			Copepoda sp3	Motile
			Copepoda sp4	Motile
			Copepoda sp5	Motile
	Pycnogonida	Pantopoda	<i>Achelia echinata</i>	Motile
			Pycnogonida sp1	Motile
Bryozoa	Stenolaemata		Bryozoa sp1	Sessile
			Bryozoa sp2	Sessile
			Bryozoa sp3	Sessile
			Bryozoa sp4	Sessile
			Bryozoa sp5	Sessile
			Bryozoa sp6	Sessile
			Bryozoa sp7	Sessile
			Bryozoa sp8	Sessile
Chordata	Actinopterygii	Gobiesocidae	Diplecogaster sp1	Motile
			Diplecogaster sp2	Motile

			Diplecogaster sp3	Motile	
Echinodermata	Echinoidea	Echinoida	Echinoida sp1	Motile	
			Echinoida sp2	Motile	
			Echinoida sp3	Motile	
	Ophiuroidea	Ophiurida	Ophiurida sp1	Motile	
			Ophiurida sp2	Motile	
			Ophiurida sp3	Motile	
			Ophiurida sp4	Motile	
	Mollusca	Bivalvia		Bivalve sp1	Sessile
			Bivalve sp2	Sessile	
			<i>Chlamis</i> sp1	Sessile	
			<i>Chlamis</i> sp2	Sessile	
			<i>Ervilia castanea</i>	Sessile	
			<i>Limaria hians</i>	Sessile	
			<i>Papillicardium papillosum</i>	Sessile	
Gastropoda				<i>Alvania angioyi</i>	Motile
				<i>Alvania cancellata</i>	Motile
				<i>Bittium nanum</i>	Motile
			<i>Caecum wayae</i>	Motile	
			Gastropoda sp1	Motile	
			Gastropoda sp2	Motile	
			<i>Gibbula magus</i>	Motile	
			<i>Jaeropsis brevicornis</i>	Motile	
			<i>Jujubinus pseudogravinae</i>	Motile	
			<i>Lamellaria perspicua</i>	Motile	
		<i>Manzonia unifasciata</i>	Motile		
		<i>Microtopus maculatus</i>	Motile		
		<i>Nassarius cf cuvierii</i>	Motile		
	<i>Nassarius cf recidivus</i>	Motile			
	Nudibranchia sp1	Motile			

			Nudibranchia sp2	Motile
			Nudibranchia sp3	Motile
			Nudibranchia sp4	Motile
			Nudibranchia sp5	Motile
			<i>Odostomia cf bernardi</i>	Motile
			<i>Omalogyra atomus</i>	Motile
			<i>Philine</i> sp.	Motile
			Raphitoma sp1	Motile
			Raphitoma sp2	Motile
			Raphitoma sp3	Motile
			<i>Retusa truncatula</i>	Motile
			<i>Rissoela</i> sp1	Motile
			<i>Setia subvaricosa</i>	Motile
			<i>Solariella azorensis</i>	Motile
			<i>Tricolia pullus azorica</i>	Motile
			<i>Tricolia</i> sp1	Motile
			<i>Trophonopsis muricatus</i>	Motile
Platyhelminthes	Rhabditophora	Tricladida	Planaria sp1	Motile
Porifera			<i>Grantia</i> sp.	Sessile
			Porifera sp1	Sessile
			Porifera sp2	Sessile
Retaria			Foraminifera sp1	Motile
			Foraminifera sp2	Motile
			Foraminifera sp3	Motile
Sipuncula	Sipunculidea	Sipunculiformes	Sipuncula sp1	Motile
			Sipuncula sp2	Motile
			Sipuncula sp3	Motile
			Sipuncula sp4	Motile
			Sipuncula sp5	Motile
			Sipuncula sp6	Motile

439 Table S2. Permutational ANOVA testing the response of species richness to size and proximity to reef when considering the (a) whole
 440 assemblage, (b) the sessile assemblage and (c) the motile assemblage. Responses were calculated at the patch- (averaged among patches within
 441 metacommunities) or at the metacommunity-scale (total number of species within each metacommunity). Analyses were performed using
 442 PERMANOVA based on Euclidean distances.

Source	df	Patch-scale						Metacommunity-scale					
		(a) Whole		(b) Sessile		(c) Motile		(a) Whole		(b) Sessile		(c) Motile	
		<i>F</i>	P	<i>F</i>	P	<i>F</i>	P	<i>F</i>	P	<i>F</i>	P	<i>F</i>	P
Location = L	1	<0.01	0.965	6.94	0.020	0.54	0.504	<0.01	0.957	2.35	0.137	0.29	0.598
Proximity to reef = P	1	2.08	0.183	8.73	0.006	0.91	0.328	5.06	0.036	11.88	0.003	3.42	0.081
Size = S	1	3.77	0.064	1.08	0.328	4.59	0.048	3.26	0.09	0.92	0.334	3.42	0.084
L × P	1	Pooled		Pooled		Pooled		Pooled		Pooled		Pooled	
L × S	1	Pooled		Pooled		Pooled		Pooled		Pooled		Pooled	
P × S	1	0.01	0.915	1.25	0.28	0.06	0.787	0.75	0.394	0.92	0.366	0.68	0.415
L × P × S	1	Pooled		Pooled		Pooled		Pooled		Pooled		Pooled	
Res	16												

443 Pooling was done when $P > 0.25$ (Underwood 1997).

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449 Table S3. Permutational ANOVA testing the response of assemblage structure to size and proximity to reef (as in Table C1). Analyses were
 450 performed using PERMANOVA based on Bray-Curtis and Jaccard similarities.

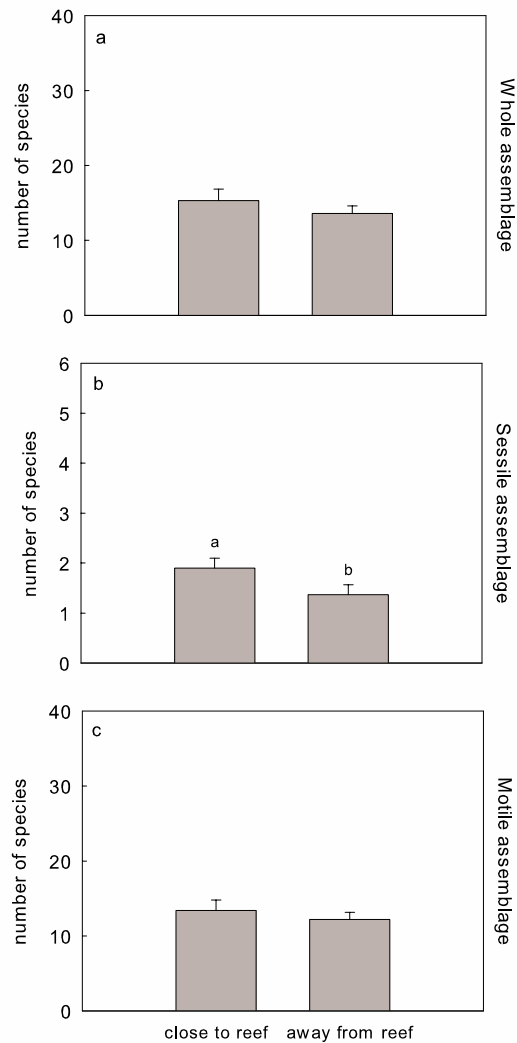
Source	df	Patch-scale						Metacommunity-scale					
		Bray -Curtis			Jaccard			Bray-Curtis			Jaccard		
		Whole	Sessile	Motile	Whole	Sessile	Motile	Whole	Sessile	Motile	Whole	Sessile	Motile
<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	<i>F</i>	
Location = L	1	14.07****	5.39****	16.40****	3.61****	5.70****	3.24****	14.07****	5.39****	16.40****	3.61****	5.75****	3.24****
Proximity to reef = P	1	2.52	1.18	2.23	2.00	1.25	2.21	2.53	1.19	2.23	2.00	1.25	2.21
Size = S	1	2.08*	0.96	2.56**	2.07**	0.91	2.30**	2.08*	0.96	2.56*	2.07**	1.21	2.30**
L x P	1	5.59****	1.89	8.22****	1.74*	3.62**	1.50	5.59****	1.89	8.22****	1.74*	3.65**	1.50
L x S	1	Pooled	1.42	Pooled	Pooled	1.31	Pooled	Pooled	1.42	Pooled	Pooled	Pooled	Pooled
P X S	1	0.27	0.17	0.37	0.87	0.29	0.98	0.27	0.17	0.37	0.87	0.20	0.98
L X P X S	1	1.52	Pooled	1.64	1.55	Pooled	1.61	1.52	Pooled	1.64	1.55	1.48	1.61

451 Pooling was done when $P > 0.25$ (Underwood 1997).

452

453 Table S4. SIMPER analysis comparing (a) occurrences (presence-absences) of sessile taxa in habitats differing in proximity to reefs (close and
 454 away), and (b) abundances (untransformed) of motile taxa in habitats differing in proximity to reef and size (large and small metacommunities).

Taxa	Proximity to reef effect				Size effect			
	Av. away	Av. close	Av. Diss.	% Cont.	Av. Large	Av. Small	Av. Diss.	% Cont.
(a) Sessile assemblages								
Sessile polychaetes	0.50	0.58	4.96	39				
Porifera	0.75	0.83	3.69	29				
Cnidarians	0.92	0.92	1.95	15				
Bryozoans	0.92	1.00	1.16	9				
(b) Motile assemblage								
Taxa	Av. away	Av. close	Av. Diss.	% Cont.	Av. Large	Av. Small	Av. Diss.	% Cont.
Amphipods	2486.9	658.1	44.48	80	1668.7	1474.8	36.11	76
Motile polychaetes	75.0	120.1	2.15	4	103.6	91.5	2.15	5
Gastropods	113.8	79.6	1.65	3	104.4	89.0	1.76	4
Oligochaetes	59.6	26.8	1.09	2	53.8	32.6	1.03	2
Cumaceans	56.3	24.9	0.96	2	42.4	38.9	0.97	2
Pycnogonids	-	-			42.9	29.3	0.98	2



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457 Figure S4. Mean (+SE) numbers of species found on experimental patches deployed close

458 and away from the reef after 3 days of colonisation. Data are (a) the total numbers of species

459 (b), numbers of sessile species only, and (c) numbers of motile species only. Note that this

460 experiment was repeated X times and that there were no differences between trials. Letters

461 indicate significant pairwise comparisons of means at $P < 0.05$.

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465 Table S5. Permutational ANOVA comparing the short-term response of species richness to
 466 proximity to reef (close and away) when considering the (a) whole assemblage, (b) the sessile
 467 assemblage and (c) the motile assemblage. Analyses were performed using PERMANOVA
 468 based on Euclidean distances.

Source	df	(a) Whole		(b) Sessile		(c) Motile	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Location = L	1	7.71	0.186	9.14	0.185	7.42	0.168
Time = T	2	2.23	0.475	2.59	0.348	2.15	0.415
Proximity to reef = P	1	0.93	0.377	4.30	0.039	0.84	0.396
L × T	2	3.35	0.044	1.06	0.335	3.14	0.060
L × P	1	Pooled		Pooled		Pooled	
T × P	2	1.63	0.200	Pooled		Pooled	
L × T × P	2	Pooled		Pooled		Pooled	
Res	48						

469

470 Table S6. PERMANOVA comparing the short-term response of assemblages to proximity to reef (close and away) when considering the (a)
 471 whole assemblage, (b) the sessile assemblage and (c) the motile assemblage. Analyses were two different dissimilarity measures: Bray-Curtis
 472 and Jaccard index.

		Bray-Curtis						Jaccard					
		(a) Whole		(b) Sessile		(c) Motile		(a) Whole		(b) Sessile		(c) Motile	
Source	df	<i>F</i>	P	<i>F</i>	P	<i>F</i>	P	<i>F</i>	P	<i>F</i>	P	<i>F</i>	P
Location = L	1	7.71	0.186	1.04	0.338	3.72	0.178	2.40	0.182	3.16	0.104	2.28	0.171
Time = T	2	2.23	0.475	0.44	0.851	2.20	0.171	1.12	0.391	0.88	0.486	1.13	0.397
Proximity to reef = P	1	0.93	0.377	4.09	0.003	2.04	0.167	1.46	0.083	2.48	0.046	1.41	0.11
L × T	2	3.35	0.044	2.97	0.011	3.17	0.001	2.36	0.001	1.61	0.104	2.44	0.001
L × P	1	Pooled		Pooled		Pooled		Pooled		Pooled		Pooled	
T × P	2	1.63	0.200	Pooled		Pooled		Pooled		Pooled		Pooled	
L × T × P	2	Pooled		Pooled		1.34	0.139	Pooled		Pooled		Pooled	
Res	48												

473 Table S7. SIMPER analysis comparing patterns of occurrence (presence-absence data) of
 474 sessile taxa in habitats differing in proximity to reefs (close and away).

Taxa	Av. Away	Av. Close	Av. Diss.	% Cont.
<i>Ervilia castanea</i>	0.73	0.87	17.58	31
Unidentified bryozoan sp1	0.13	0.37	10.62	19
<i>Gregariella semigranata</i>	0.17	0.13	8.01	14
<i>Papillicardium papillosum</i>	0.10	0.20	6.91	12
Unidentified bryozoan sp2	0.10	0.03	2.93	5
<i>Limaria hians</i>	0.03	0.03	2.43	4
Porifera	0.07	0.00	2.04	4
Unidentified bryozoan sp3	0.00	0.07	1.46	3

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