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

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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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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.

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**INTRODUCTION**

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

The effects of habitat area and isolation on population dynamics were formalized with the development of metapopulation (Hanski & 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 (Kelaher

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 be 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 37º44'34''N, Longitude 25º38'31''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 cm$^2$ 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 metacommunties 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 ± 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 ±

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 ($1.9 \pm 0.2$) compared to patches away from the reef ($1.4 \pm 0.2$). 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 metacommunty-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.

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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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415                      Figure 1.

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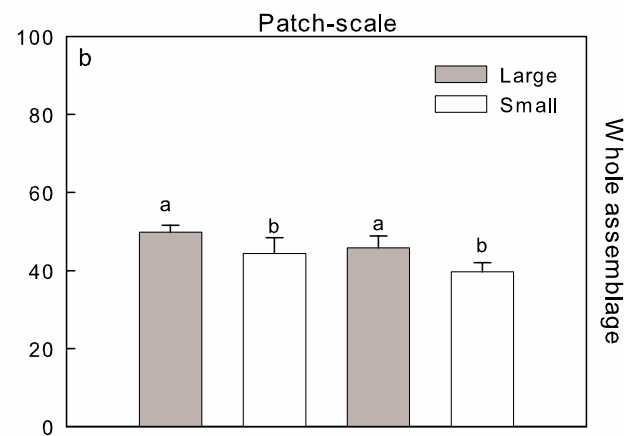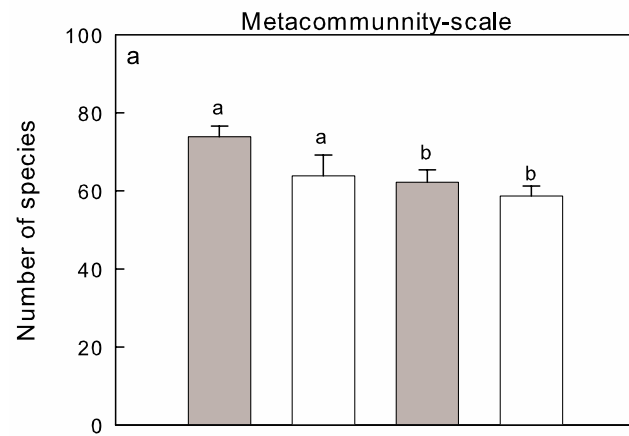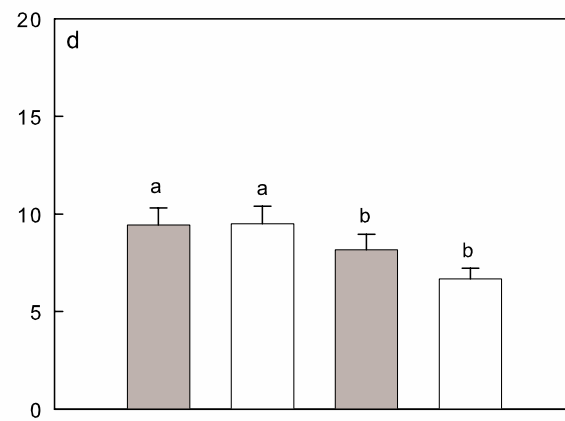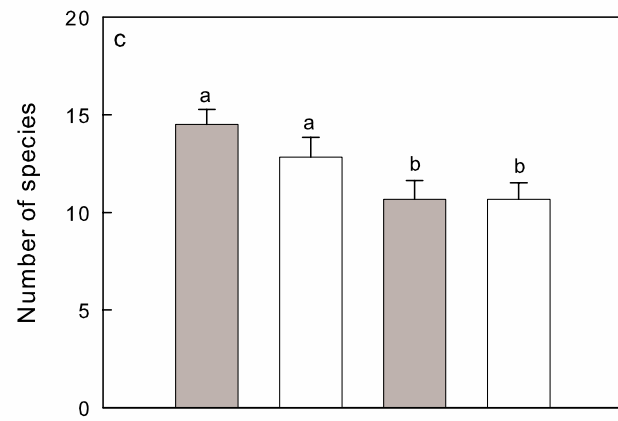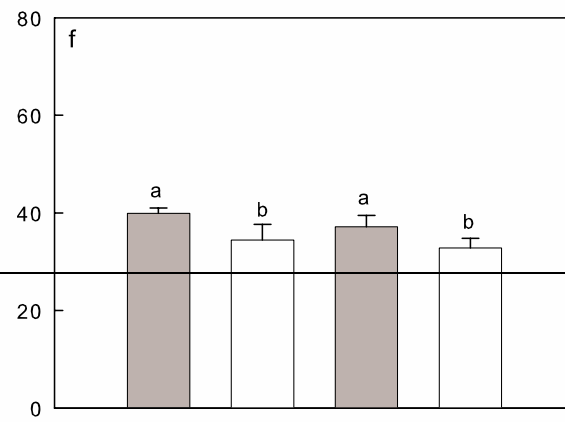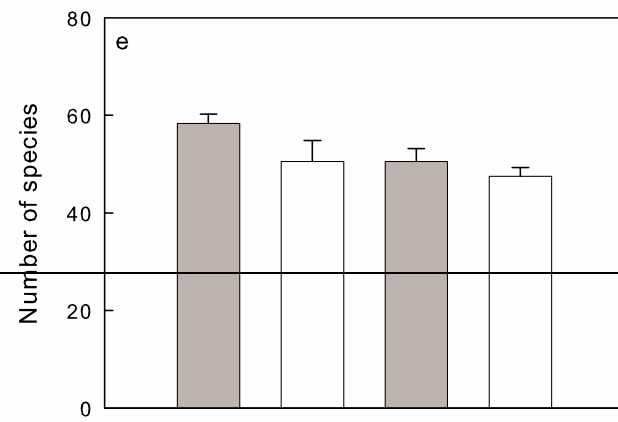
419                  **Supplementary online material**

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

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

424            \*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.
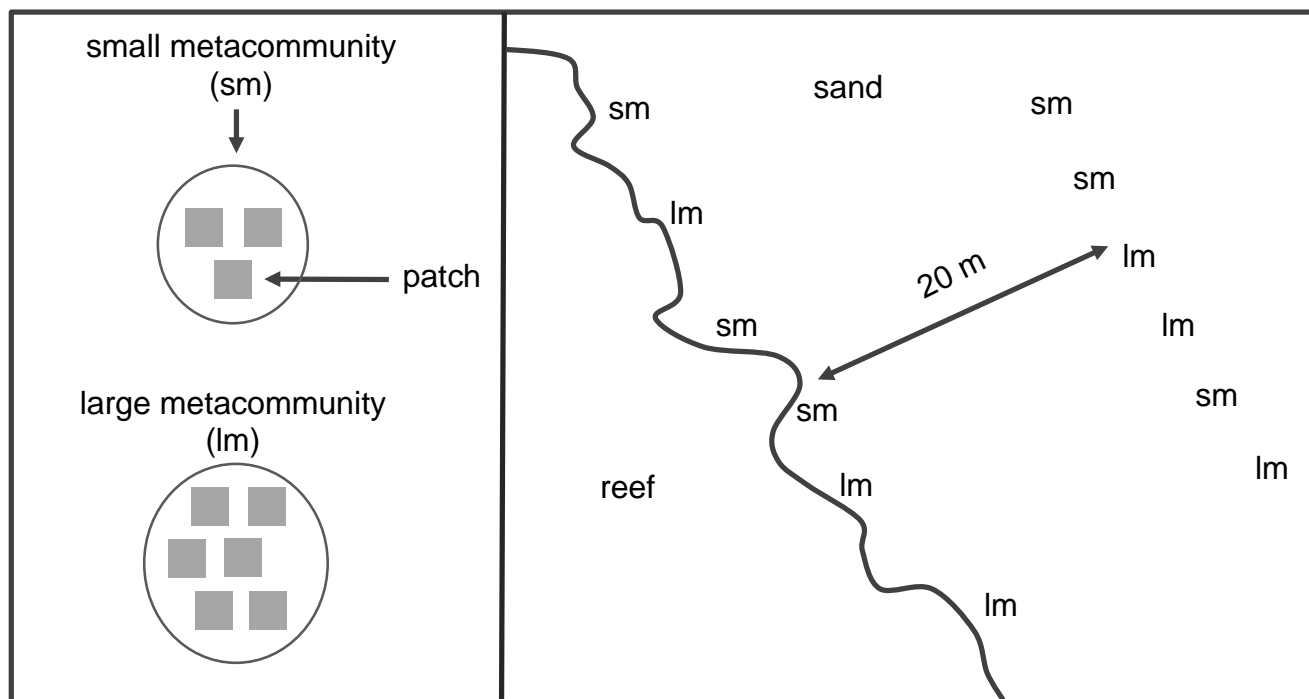
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429     Fig. S2. Schematic representation of experimental design.

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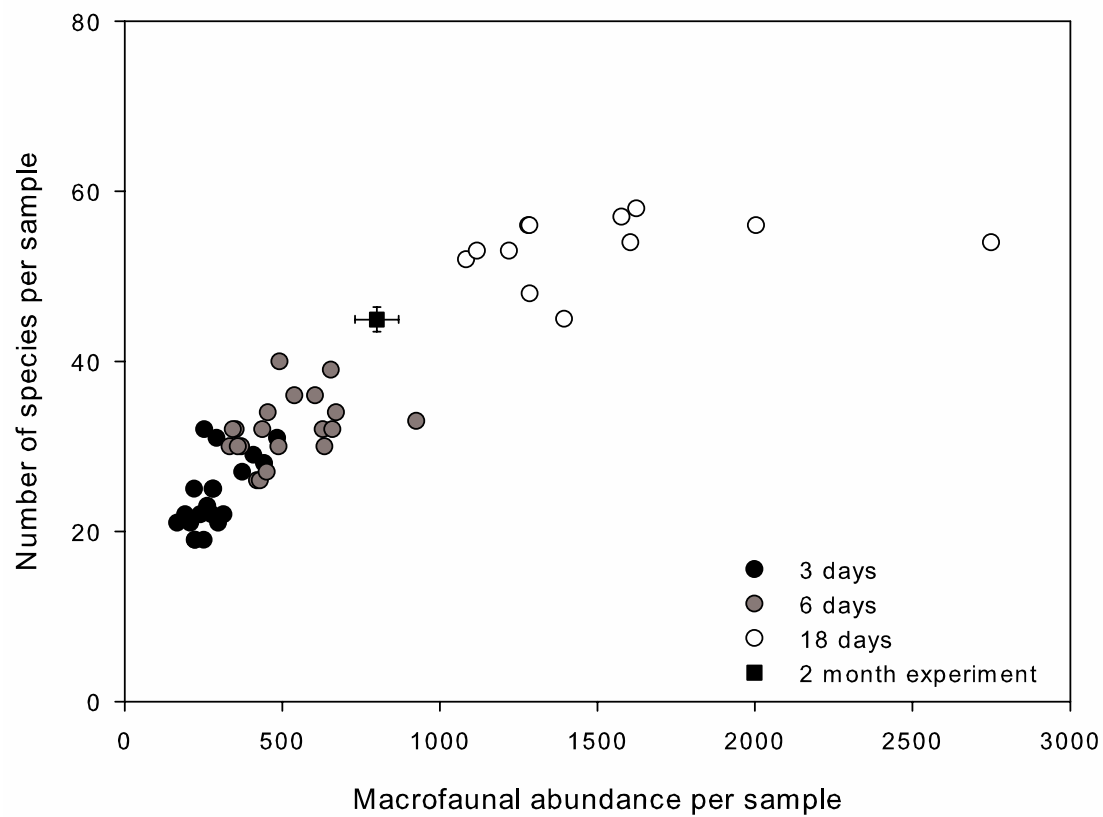
432  Fig. S3. Numbers of species and total abundance in experimental patches after 3, 6 and 18

433  days of deployment and averaged (± 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 |
| | | | *Euphrosine foliosa* | Motile |
| | | Sedentaria | Sedentaria sp1 | Sessile |
| | | | Spirorbid sp1 | Sessile |
| | | | Spirorbid sp2 | Sessile |
| | | | Spirorbid sp3 | Sessile |

| Phylum | Class | Order | Species | Motility |
|---|---|---|---|---|
| Arthropoda | Arachnida | Sarcoptiformes | Acarii sp1 | Motile |
| | | | Acarii sp2 | Motile |
| | | | Acarii sp3 | Motile |
| Arthropoda | Malacostraca | Amphipoda | *Abludomelita obtusata* | Motile |
| | | | Amphipoda sp1 | Motile |
| | | | Amphipoda sp2 | Motile |
| | | | Amphipoda sp3 | Motile |
| | | | Amphipoda sp4 | Motile |
| | | | Amphipoda sp5 | Motile |
| | | | Amphipoda sp6 | Motile |
| | | | Amphipoda sp7 | Motile |
| | | | *Amphitoe rubricata* | Motile |
| | | | *Aora gracilis* | Motile |
| | | | *Apherusa jurinei* | Motile |
| | | | *Caprella acanthifera* | Motile |
| | | | *Caprella linearis* | Motile |
| | | | *Dexamine spinosa* | Motile |
| | | | *Ericthonius difformis* | Motile |
| | | | *Ericthonius punctatus* | Motile |
| | | | *Gammarella fucicola* | Motile |
| | | | *Jassa falcata* | Motile |
| | | | *Maera grossimana* | Motile |
| | | | *Phtisica marina* | Motile |
| | | | Pseudoprotellaphasma | Motile |
| | | | Thalassosmittiaatlantica | Motile |
| | | Cumacea | *Diastylis* sp. | Motile |
| | | Decapoda | Decapoda sp1 | Motile |
| | | | Decapoda sp2 | Motile |
| | | | Decapoda sp3 | Motile |
| | | | Decapoda sp4 | Motile |

| | | | | |
|---|---|---|---|---|
| | | | Decapoda sp5 | Motile |
| | | | Decapoda sp6 | Motile |
| | | | Decapoda sp7 | Motile |
| | | | *Macropodi*a sp. | Motile |
| | | | Pagurus sp1 | Motile |
| | | | Pagurus sp2 | Motile |
| | | Isopoda | *Anthura gracilis* | Motile |
| | | | *Dynamene bidentata* | Motile |
| | | | *Gnathia maxillaris* | Motile |
| | | | *Janiropsis breviremis* | Motile |
| | | Tanaidacea | *Leptochelia caldera* | Motile |
| | | | *Paratanais martinsi* | Motile |
| | | | *Tanais grimaldii* | Motile |
| | Maxillopoda | Copepoda | Copepoda sp1 | Motile |
| | | | Copepoda sp2 | Motile |
| | | | Copepoda sp3 | Motile |
| | | | Copepoda sp4 | Motile |
| | | | Copepoda sp5 | Motile |
| | Pycnogonida | Pantopoda | *Achelia echinata* | 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 |
| | | | *Chlamis* sp1 | Sessile |
| | | | *Chlamis* sp2 | Sessile |
| | | | *Ervilia castanea* | Sessile |
| | | | *Limaria hians* | Sessile |
| | | | *Papillicardium papillosum* | Sessile |
| | Gastropoda | | *Alvania angioyi* | Motile |
| | | | *Alvania cancellata* | Motile |
| | | | *Bittium nanum* | Motile |
| | | | *Caecum wayae* | Motile |
| | | | Gastropoda sp1 | Motile |
| | | | Gastropoda sp2 | Motile |
| | | | *Gibbula magus* | Motile |
| | | | *Jaeropsis brevicornis* | Motile |
| | | | *Jujubinus pseudogravinae* | Motile |
| | | | *Lamellaria perspicua* | Motile |
| | | | *Manzonia unifasciata* | Motile |
| | | | *Microprotopus maculatus* | Motile |
| | | | *Nassarius cf cuvierii* | Motile |
| | | | *Nassarius cf recidivus* | Motile |
| | | | Nudibranchia sp1 | Motile |

| | | | | |
|---|---|---|---|---|
| | | | Nudibranchia sp2 | Motile |
| | | | Nudibranchia sp3 | Motile |
| | | | Nudibranchia sp4 | Motile |
| | | | Nudibranchia sp5 | Motile |
| | | | *Odostomia cf bernardi* | Motile |
| | | | *Omalogyra atomus* | Motile |
| | | | *Philine* sp. | Motile |
| | | | Raphitoma sp1 | Motile |
| | | | Raphitoma sp2 | Motile |
| | | | Raphitoma sp3 | Motile |
| | | | *Retusa truncatula* | Motile |
| | | | *Rissoela* sp1 | Motile |
| | | | *Setia subvaricosa* | Motile |
| | | | *Solariella azorensis* | Motile |
| | | | *Tricolia pullus azorica* | Motile |
| | | | *Tricolia* sp1 | Motile |
| | | | *Trophonopsis muricatus* | Motile |
| Platyhelminthes | Rhabditophora | Tricladida | Planaria sp1 | Motile |
| Porifera | | | *Grantia* 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.

| | | Patch-scale | | | | | | Metacommunity-scale | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | (a) Whole | | (b) Sessile | | (c) Motile | | (a) Whole | | (b) Sessile | | (c) Motile | |
| Source | df | $F$ | P | $F$ | P | $F$ | P | $F$ | P | $F$ | P | $F$ | 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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Table S3. Permutational ANOVA testing the response of assemblage structure to size and proximity to reef (as in Table C1). Analyses were performed using PERMANOVA based on Bray-Curtis and Jaccard similarities.

| | | Patch-scale | | | | | | Metacommunity-scale | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Bray -Curtis | | | Jaccard | | | Bray-Curtis | | | Jaccard | | |
| | | Whole | Sessile | Motile | Whole | Sessile | Motile | Whole | Sessile | Motile | Whole | Sessile | Motile |
| Source | df | $F$ | $F$ | $F$ | $F$ | $F$ | $F$ | $F$ | $F$ | $F$ | $F$ | $F$ | $F$ |
| 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 |

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

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. | | | | | |
| (a) Sessile aassemblages | | | | | | | | | |
| 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 | Proximity to reef effect | | | | | Size effect | | | |
| 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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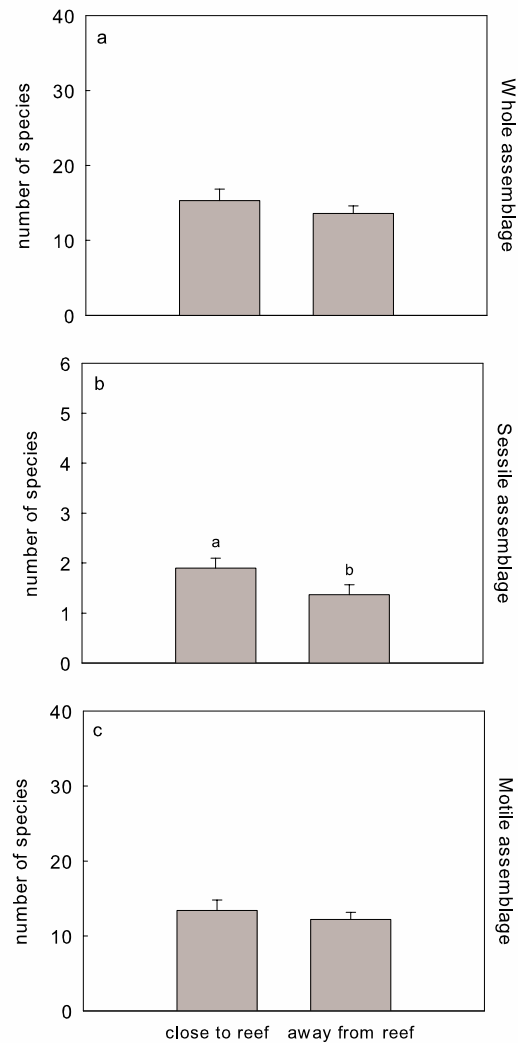
457 Figure S4. Mean (+SE) numbers of species found on experimental patches deployed close

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 | |
|---|---|---|---|---|---|---|---|
| | | $F$ | P | $F$ | P | $F$ | P |
| 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 | | | | | | |

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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 | $F$ | P | $F$ | P | $F$ | P | $F$ | P | $F$ | P | $F$ | 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. |
|---|---|---|---|---|
| *Ervilia castanea* | 0.73 | 0.87 | 17.58 | 31 |
| Unidentified bryozoan sp1 | 0.13 | 0.37 | 10.62 | 19 |
| *Gregariella semigranata* | 0.17 | 0.13 | 8.01 | 14 |
| *Papillicardium papillosum* | 0.10 | 0.20 | 6.91 | 12 |
| Unidentified bryozoan sp2 | 0.10 | 0.03 | 2.93 | 5 |
| *Limaria hians* | 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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