

Post-settlement dispersal ability determines structure of marine benthic metacommunities

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

KEY WORDS: Biological traits · Community assembly · Experimental habitats · Habitat size · Isolation · Scale

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INTRODUCTION

Widespread evidence links 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 pure descriptions 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. 2010a,b).

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 coexistence mechanisms and dispersal and improved our ability to predict distributional patterns

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

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

Despite these advances, there is still a disconnect between theoretical and empirical studies (see Logue et al. 2011). As suggested by Logue et al. (2011), theoretical predictions should be tested empirically across a range of habitats and species to make a better link between spatial dynamics, dispersal rate and mobility. One particular issue is that defining relevant spatial scales can be problematic (Srivastava 1999, Munguia 2004). This issue has been raised by empirical work done both in marine (Munguia & Miller 2008) and terrestrial (Miller & Kneitel 2005) systems, where the possibility of very high long-distance dispersal for some species means that identifying regionally closed systems, assumed in most metacommunity theory (e.g. Leibold et al. 2004), is challenging. It is likely that most metacommunities are not completely closed, at least at the scale that regional processes (such as dispersal and habitat heterogeneity) are thought to operate. In discussing metapopulations (the archetype for metacommunities), Hanski & Gilpin (1991) defined 3 scales: local, metapopulation and geographic, where the geographic scale encompasses distances greater than those over which an individual moves over its lifetime. Recognizing this caveat in the theoretical background of metacommunities, Cadotte & Fukami (2005) explicitly tested the effects of dispersal at 2 different scales: among local communities and among meta-

communities. They found that dispersal at the 2 scales had distinct effects on diversity, stressing the need to consider the effects of dispersal occurring at multiple scales rather than only at a regional scale. The above suggests that the metacommunity 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, rate or scale) must be further explored.

Here, we investigated the response of marine invertebrates to experimental manipulations of habitat patches made of artificial turfs. These turfs are quickly colonised by a range of organisms and are a tractable model system to investigate the community response to the structure and spatial configuration of habitat patches (Matias et al. 2007), including responses to changes in structural complexity (Kelaheer 2003), habitat area and heterogeneity (Matias et al. 2010b), isolation (Virnstein & Curran 1986) and environmental context (Matias 2013). We investigated the effects of metacommunity size on benthic assemblages colonising artificial turfs (i.e. patches) by manipulating the number of patches within groups of patches (analogous to metacommunity size *sensu* Leibold et al. 2004) and proximity to reefs within which metacommunities were embedded as a surrogate for isolation. We predicted that, generally, greater numbers of species would be found in large metacommunities and that proximity to reefs would affect the numbers and identity of species present. We further predicted that the response of species to metacommunity size and proximity to reefs would depend on the post-settlement ability of species to disperse (e.g. whether species were motile or sessile after initial larval colonisation). While many of the benthic invertebrate species colonising artificial turfs have a planktonic larval phase and therefore the possibility of very high long-distance dispersal over regional scales, we focussed on the implications of dispersal following settlement and specifically the difference between species which are motile or sessile as adults. Sessile species are not able, or unlikely capable, of further dispersal, whilst motile species are able to redistribute themselves at local scales. As such, we predicted that the numbers of species with sessile adult stages would remain relatively constant among habitats differing in size (provided that the sampled area is kept constant) as a simple response to habitat area, whilst species with motile adult stages, which have the ability to redistribute themselves after colonisation, would show variable patterns of distribution among habitats differing in size. Moreover, a greater number of sessile individuals,

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 main source of larvae; mass effects), while motile species, whilst also influenced by the larval pressure during the colonisation stage, again, would potentially have the ability to redistribute themselves after colonisation. The latter, perhaps, may even be able to continuously exchange individuals between the reef and the nearby habitat patches.

Considering the above, it would be logical to also predict that spatial patterns of sessile species would tend to be more similar, in the longer term, to those established during early stages of patch colonisation (e.g. larval recruitment of patches), while for motile species, spatial patterns would tend to become increasingly different from those established during the early stages of colonisation owing to their ability to disperse (move) among habitat patches after settlement. That is, the process of patch colonisation would be of greater importance in determining longer-term patterns of species distribution for sessile species compared to motile species. The latter was tested using a complementary experiment investigating the role of species' colonisation (early stages of community assembly) in determining the results observed over the longer term (2 mo period; the above experiment). We predicted that if early stages of species colonisation played an important role in determining community structure relative to post-colonisation processes (i.e. biotic interactions, dispersal), the response of species to distance from the reef during the very early stages of community assembly (3 d) would be similar to patterns observed during the 2 mo experiment. In contrast, if post-colonisation processes were relatively more important for community structure, patterns established during early stages of species colonisation would be modified and results from both experiments would differ.

MATERIALS AND METHODS

Study locations

We chose 2 different locations about 500 m apart at São Roque (São Miguel, Azores: 37° 44' 34" N, 25° 38' 31" W). At each of the 2 locations, the rocky reef, composed of natural basaltic rocks, extends subtidally from the intertidal zone for 50 to 100 m offshore and is then replaced by sandy-bottom substrates. The transition zone between the reef and sand occurs at approximately 10 to 14 m depth at

each of the 2 locations. Rocky reefs in the area support a rich flora dominated by turf-forming species (e.g. *Corallina* spp.) sustaining a diverse assemblage of macrofauna numerically dominated by gastropods (~25%) and amphipods (~15%) (Martins et al. 2016). The sandy bottom supports a relatively depauperate assemblage of macrofauna numerically dominated by the polychaetes *Exogone naidina* and *Spio* aff. *fili-cornis* and the bivalve *Ervillea castanea* (Martins et al. 2013). All experiments described below were replicated in each of these locations.

Expt 1: metacommunity size and proximity to reef

Patches of 50 cm² of artificial turfs (40 mm long and sparse synthetic grass; supplied by Maxmat) were attached to the end of 50 cm metal rods (1 patch rod⁻¹) that were driven into the sand leaving the artificial turfs at about 10 cm from the sea bottom (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m569p015_supp.pdf). Metacommunities of different sizes were created by deploying groups of either 3 or 6 patches. Within each metacommunity, patches were deployed about 10 cm from each other. We varied the proximity to the reef within which metacommunities were embedded by deploying patches at 2 different distances from the reef: close (<2 m) and far away (25 m). Based on previous studies, macrofaunal assemblages adjacent to reefs are considerably different from those >15 m away (Virnstein & Curran 1986, Martins et al. 2013). Sandy habitats are locally dominated by polychaetes (Martins et al. 2013), which were mostly absent from our experimental patches. Only a small fraction (~7%) of species was found both in experimental patches and the adjacent sandy bottom, suggesting that assemblages colonising experimental patches originated mostly from the nearby algal-dominated reefs or directly from the water column. Overall, our approach of using patches of turf surrounded by an inhospitable habitat is similar to that reported by Munguia & Miller (2008), who used individual pen shells as 'islands' of hard substrate habitat within seagrass beds grouped in metacommunities.

In each of the 2 locations, 3 replicate metacommunities were deployed, corresponding to each combination of metacommunity size and proximity to the reef (totalling 12 metacommunities and 54 individual patches per location, see Fig. S2 in the Supplement). Experimental patches were deployed in early June 2012 and retrieved after approximately 2 mo. This 2 mo period is consistent with previous studies using

these experimental habitat patches (e.g. Kelaher 2002, Matias et al. 2007, 2010b). Moreover, preliminary observations conducted in the same locations as those in our experiment showed that numbers of species tended to stabilize after 2 wk of patch deployment (see Fig. S3 in the Supplement), which may indicate post-colonisation processes affecting the accumulation of species. From these considerations, the 2 mo period was deemed appropriate to allow the initial establishment of assemblages and to encapsulate post-settlement processes affecting assemblage structure (e.g. inter-patch dispersal by motile species). Upon collection, 3 individual patches from each replicate metacommunity were carefully removed from the rods and enclosed in plastic zip-lock bags while still underwater. The number of patches sampled was always the same (3) for both the small and large metacommunity treatments so that the sampled area was consistent and is not a confounding factor. In the laboratory, samples were sieved (<2 h after collection) using a 0.5 mm sieve. The material retained was stored in alcohol in labelled plastic jars until further inspection.

Expt 2: short-term colonisation

An additional experiment was established to assess short-term colonisation patterns. In each of the 2 locations described above, 5 replicate habitat patches were deployed (~5 m apart) both close to (<2 m) and far from (25 m) the reef. Unlike in Expt 1, habitat patches were not grouped in metacommunities. Habitat patches were sampled (as described above) after a period of colonisation of only 3 d. Because recruitment can show significant variability at small temporal scales, this experiment was repeated 3 times between June and August 2012.

Taxonomic resolution and dispersal traits

Sorted individuals were identified to species or morphospecies (hereafter species). We classified all species according to dispersal ability as adults into either motile or sessile as in Munguia (2004). Sessile species were species with sessile (permanently attached) adult stages (e.g. spirobid polychaetes, bryozoans), plus species that generally have little active locomotion as adults (e.g. bivalves). The latter are species that are unlikely to migrate among habitat patches after settlement. Motile species were those with an active means of locomotion (e.g. swimming,

crawling) in the adult stage and that are therefore expected to be able to move freely among patches (e.g. amphipods, gastropods). Although initially we suspected that there could be a difference between crawlers and swimmers, preliminary analyses showed their response was similar, so they were lumped together as a single group. One assumption made in this distinction between sessile and motile species was that upon arriving (as larvae) and recruiting to a single habitat patch, sessile species are no longer able or likely to disperse to the surrounding patches. They are unlikely to produce free-swimming larvae within the 2 mo period of the experiment. Motile species, in contrast, may disperse among patches during their entire life cycle.

Data analysis

We conducted a permutational ANOVA (PERMANOVA based on Euclidean distances, Anderson 2001) to test for differences in the 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 far away) and 'Location' (random).

Multivariate analyses were used to examine the effects of size and proximity to the reef on the structure of macrofaunal assemblages. Analyses were run using PERMANOVA as described above. These were run on 2 different similarity matrices: Bray-Curtis on untransformed data and Jaccard. Both indices explore differences in species composition. However, when calculated on untransformed data, Bray-Curtis gives more weight to changes in species abundances, whereas Jaccard does not take into account the relative abundances of species and is based on changes in species identities alone. The combined use of these 2 measures of similarity allow assessment of the importance of changes in species abundances relative to changes in composition (e.g. Anderson et al. 2005). Similarity of percentages (SIMPER) was used to identify the taxa contributing to differences within significant terms.

For all of the above, analyses were run at 2 scales: patch and metacommunity scales. At the patch scale, numbers of species were averaged from the 3 patches within each replicate metacommunity. At the metacommunity scale, numbers of species was the total number of species found in each metacommunity (combining the 3 sampled patches per metacommunity).

The short-term colonisation experiment was analysed using PERMANOVA with 'Time' (random; 3

random dates chosen between June and August 2012); 'Proximity to reef' (fixed; close and away) and 'Location' with 2 levels (random).

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

RESULTS

Expt 1: metacommunity size and proximity to reef

From 57 558 individuals collected, we identified a total of 145 taxa, of which 123 were classified as motile and 22 as sessile (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m569p015_supp.pdf). Amphipods (65% of the total number of individuals), motile polychaetes (5%) and gastropods (4%) were the dominant motile taxa. Bivalves (8%), bryozoans (3%) and sessile polychaetes (2%) were the dominant sessile taxa. Most sessile (73%) and motile (82%) species were found both close to and far from the reef. Species absent from the patches far from the reef were all rare or uncommon (ca. 6 ind. patch⁻¹) in patches close to reef, whereas <2% of species were exclusive to the areas far from the reef.

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

When we analysed the data according to the dispersal traits, we found significantly greater numbers of sessile species closer to the reef at both the patch scale (27% more species; $F_{1,19} = 8.73$, $p = 0.006$) and the metacommunity scale (28% more species; $F_{1,19} = 11.88$, $p = 0.003$; 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 metacommunity scale, the number of species tended to greater (11%) in patches close to reef ($F_{1,19} = 3.42$, $p = 0.08$).

Size had no effect on the numbers of sessile species at both scales (patch: $F_{1,19} = 1.08$, $p = 0.328$; metacommunity: $F_{1,19} = 0.92$, $p = 0.334$; Fig. 1c,d). Numbers of motile species were generally greater in larger habitats at both the patch scale (large: 38.6 ± 1.3 ; small:

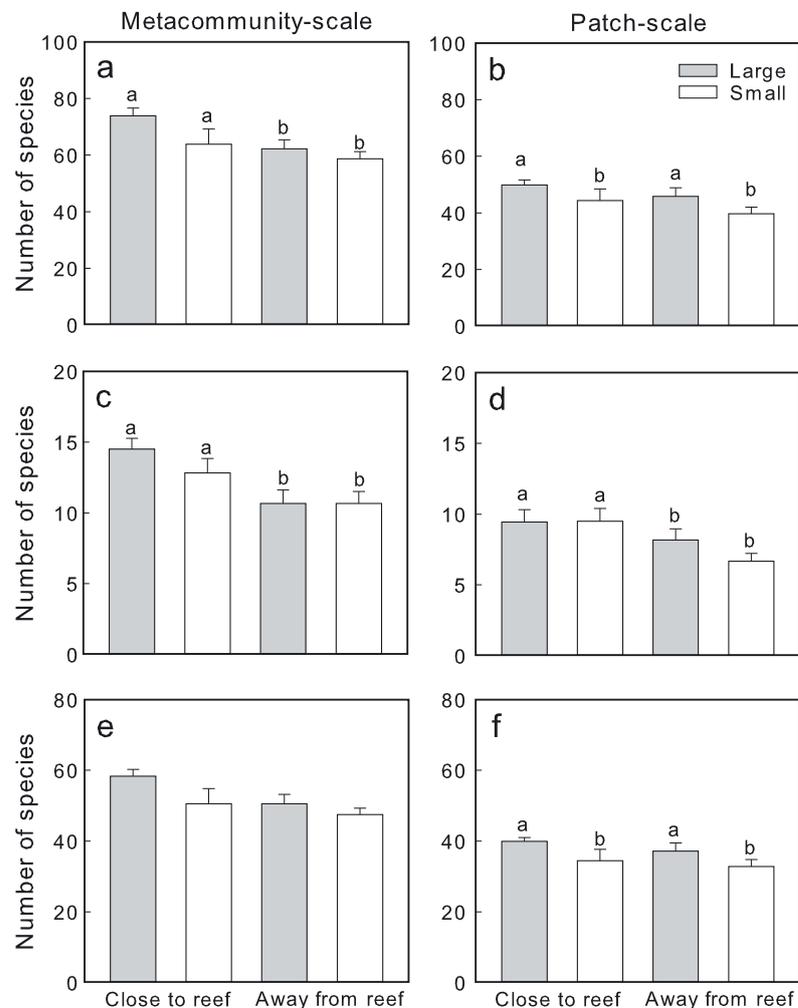


Fig. 1. Mean (+SE) numbers of species in metacommunities differing in size and proximity to reefs for (a,b) the assemblage as a whole, (c,d) the sessile component of the assemblage and (e,f) the motile component of the assemblage. Analyses were done at 2 scales: metacommunity (left panels) and patch (right panels). In each panel, different letters indicate significant differences between means (with significance set at $p < 0.05$; see Table S2 in the Supplement at www.int-res.com/articles/suppl/m569p015_supp.pdf)

33.6 ± 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).

For the whole assemblage, the output of multivariate analyses was generally similar at the 2 scales. A significant interaction was found between metacommunity size and location (as well as between proximity to the reef and location) for both the Bray-Curtis and Jaccard similarity indices (see Table S3 in the Supplement). Post hoc comparisons of these interaction terms showed consistent effects of both metacommunity size and proximity to the reef (i.e. effects were seen at both locations; Table 1).

When analysing data according to dispersal traits, we found that sessile assemblages did not respond to metacommunity size, but 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 (see Table S4 in the Supplement) revealed that most sessile taxa occurred more often in habitats close to the reefs. Motile assemblages responded significantly to size and proximity to the reef (Table 1). However, the latter was only significant when considering species abundances (Bray-Curtis), but not when relying only on changes in species identities (Jaccard). SIMPER analyses (Table S4) revealed that motile taxa were on average more abundant in large metacommunities. When considering the effect of proximity to the reef, most taxa were generally more abundant in metacommunities far from the reef.

Table 1. Summary of permutational ANOVAs comparing responses to size and proximity to reefs in whole assemblages, sessile species or motile species. Responses were calculated at the patch scale (i.e. average abundances) or at the metacommunity scale (i.e. sum of abundances across all patches). Analyses were performed using 2 different dissimilarity measures: Bray-Curtis and Jaccard. Levels of significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. See Table S3 in the Supplement at www.int-res.com/articles/suppl/m569p015_supp.pdf for full tables

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

Expt 2: short-term colonisation

In total, we identified 103 taxa (89 motile and 14 sessile) from 4289 individuals. Motile assemblages were dominated by amphipods (58%), gastropods (18%) and decapods (4%). Sessile assemblages were dominated by bryozoans (6%) and bivalves (5%). Most motile (71%) and a large number of the sessile (54%) species were found both close to and far from the reef.

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

Multivariate analysis showed that proximity to the reef generally did not determine the structure of whole assemblages (Bray-Curtis: $F_{1,53} = 191$, $p = 0.126$) although it appeared to have some effect on species identities (Jaccard: $F_{1,53} = 1.46$, $p = 0.083$). When analysing data according to the dispersal traits, again there were significant differences in the structure of assemblages of sessile species with proximity to reef (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 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 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 assemblages, proximity to reefs had no significant effect on the assemblage structure of motile species (Bray-Curtis: Location \times Time \times Proximity to reef $F_{2,51} = 1.34$, $p = 1.39$; Proximity to reef $F_{1,2} = 2.04$, $p = 0.167$; Jaccard: $F_{1,53} = 2.44$, $p = 0.110$).

DISCUSSION

Our study illustrates that, as expected, macrofaunal assemblages as a whole responded to differences in habitat configuration (metacommunity size and proximity to reef). More importantly, however, we found that the overall response of macrofauna varied according to species' post-settlement dispersal abilities. For instance, results showed that assemblages of sessile and sedentary invertebrates were ca. 30%

more diverse, and significantly so, in metacommunities deployed close to reefs, whereas motile invertebrates displayed no such pattern. Also, post-settlement dispersal ability determined responses to metacommunity size: motile assemblages were more diverse (at both the patch and metacommunity scales) in larger metacommunities, while sessile assemblages did not respond to metacommunity size.

Making the distinction between species that are able to actively disperse as adults and species that are not proved useful in contributing to a greater understanding of the responses observed to variation in habitat configuration and may provide insights about the underlying mechanisms. For instance, a greater number of species in larger habitats probably indicates that a greater number of individual patches sample more of the species pool and that upon arrival to a single patch, species can afterwards disperse to other patches within a metacommunity. Thus on average (and not only at the metacommunity scale), all patches within a metacommunity have more species. However, post-settlement species dispersal among patches within metacommunities is less likely in the case of sessile species; in accordance, there were no effects of size (at both the patch and metacommunity scales). The distinct response of sessile and motile taxa to changes in metacommunity size highlights the importance of recognizing post-settlement dispersal among habitat patches in mediating the response of species to habitat loss. Such considerations may prove particularly important, for instance, when considering the effects of variations in the spatial configuration of networks of marine protected areas on particularly important species (Shanks et al. 2003). In this regard, it would be important to investigate if 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 processes affecting the distribution of larval recruitment may be relatively more important at explaining such larger-scale distributions (among marine protected areas) than the post-settlement ability of species to disperse among habitat patches (addressed in this study), which likely is more important at smaller spatial scales, although this may still be important in distinguish some species (e.g. cryptic reef fish vs. benthic fish).

Distinction between sessile and motile species also proved useful in understanding the responses of macrofauna to experimental changes in proximity to reef (or source of colonists). Our prediction was that distance to a nearby reef plays an important role in structuring communities (e.g. Chase & Ryberg 2004)

with habitats farther away from the reef supporting lower numbers of species. In accordance, assemblages of invertebrates with sessile adult stages were significantly influenced by the proximity to the reef, with habitat patches deployed away from the reef supporting less diverse assemblages. Assemblages of invertebrates with motile adult stages, however, did not respond as predicted (and in 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 community composition. Given the perceived and documented importance of habitat isolation for many organisms, including species with high levels of motility (reviewed by Cadotte 2006), it may be tentatively suggested that larval dispersal ability of the motile invertebrates during the 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 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 abundance of individuals recorded in patches farther away from reefs was also shown by Virnstein & Curran (1986) for some amphipods.

While results were generally similar regardless of scale (patch or metacommunity), there were a few exceptions, most notably the fact that when considering the assemblage as a whole, significant effects of proximity to reefs were found only at the metacommunity scale. A possible explanation for this result might be attributed to the fact that probabilities of sampling rare species depend on the scale at which one measures species diversity (i.e. patch vs. metacommunity). Differences between different habitat types might be driven 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, rare species often colonised a single patch within the metacommunity, and thus their contribution to species diversity is reduced when diversity is measured at the patch scale (i.e. numbers of species were averaged from 3 patches within each metacommunity). In contrast, metacommunities were colonised by multiple rare species (i.e. the sum of rare species in each of the 3 patches) that all contribute to species diversity at the metacommunity scale. For this reason, the contribution of rare species is greater at the metacommunity scale when compared to the patch scale, providing a better 'sample' of benthic organisms, since there were clearly fewer rare species away from the reef. These results 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 the effects of isolation.

Although post-colonisation processes for community assembly may clearly be important (e.g. Chase et al. 2010), our complementary experiment investigating the short-term effects of habitat proximity to the reef on early patterns of species colonisation showed that patterns were consistent with those observed during the main experiment (no effect of proximity to reef on species with motile adult stages, greater richness of species with sessile adult stages close to the reef). Such consistent responses found between the 2 experiments imply a rather influential role of larval dispersal or colonisation over post-colonisation processes for community assembly in terms of patch isolation (proximity to reef). Note that the overall numbers of species colonising the individual patches in this short-term experiment (3 d) was relatively small for species with sessile adult stages (see Fig. S4b in the Supplement). The small number of sessile species colonising habitat patches may affect our ability to extrapolate these results to a wider assemblage of sessile species (as found in the main experiment), which also suggests that dispersal ability clearly affects the way species colonise new patches. While species with sessile adult stages are dependent on larval recruitment from plankton (which is influenced by species reproductive seasonality), species with motile adult stages appear to be able to arrive at and colonise new habitat patches both via larval recruitment from plankton and via dispersal of adult individuals. Although we have not tested the short-term colonisation effect on species response to changes in metacommunity size, this result may suggest that proximity to reef and metacommunity size differently affect the distribution of species according to life-cycle stage; proximity to reef may be relatively more important in determining the ability of larvae colonising experimental patches, whereas metacommunity size may be relatively more important in determining post-settlement dispersal of adults (for motile species).

Interpretation of the output from analyses was in some cases based on trends ($p < 0.1$) rather than strictly statistically significant ($p < 0.05$) responses (i.e. see response of species richness in the whole assemblage to metacommunity size). We believe that lack of statistical significance in some cases was likely driven by the overall low number of replicates used ($n = 3$). Such a low number of replicates results from the fact that (1) sorting, identifying and enumerating macrofauna is a laborious task and (2) we adopted a hierarchical framework in which individ-

ual habitat patches were grouped as metacommunities. In our case, we sampled 3 individual habitat patches per replicate metacommunity, which tripled the number of samples. We believe that even though this approach reduced statistical power to detect significant effects, it was also important as it allows us to distinguish scale-dependent effects.

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