

Independent effects of patch size and structural complexity on diversity of benthic macroinvertebrates

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Abstract. Despite a long history of work on relationships between area and number of species, the details of mechanisms causing patterns have eluded ecologists. The general principle that the number of species increases with the area sampled is often attributed to a sampling artifact due to larger areas containing greater numbers of individuals. We manipulated the patch size and surface area of experimental mimics of macro-algae to test several models that can explain the relationship between abundance and species richness of assemblages colonizing different habitats. Our results show that patch size and structural complexity have independent effects on assemblages of macroinvertebrates. Regardless of their structural complexity, larger habitats were colonized by more species. Patch size did not have a significant effect on numbers of individuals, so the increased number of species in larger habitats was not simply a result of random placement associated with sampling increased number of individuals. Similarly, random placement alone could not explain differences in numbers of species among habitats with different structural complexity, contrary to suggestions that the relationship between number of species and surface area might also be a sampling artifact due to more complex habitats having larger areas and therefore sampling more individuals. Future progress would benefit from manipulating properties of habitat in conjunction with experimental manipulations of area.

Key words: area; habitat; macroinvertebrates; passive sampling; random placement; structural complexity.

INTRODUCTION

The relationship between area and numbers of species—perhaps one of ecology’s few general “laws” (sensu Lawton 1999)—is a well-established ecological topic (Williams 1943, Coleman 1981). Larger numbers of species in increasing areas have been consistently demonstrated in a wide variety of habitats and organisms (see reviews by Connor and McCoy 1979, McGuinness 1984, Lomolino 2000), becoming a fundamental concept in studies of biogeography (e.g., MacArthur and Wilson 1967) and communities (e.g., Preston 1960). Studies exploring species–area relationships have also played an important role in conservation biology in general (e.g., Ney-Nifle and Mangel 2000), and particularly in the SLOSS debate (i.e., “single large or several small reserves”; Gilpin and Diamond 1980, Higgs and Usher 1980, Wilcox and Murphy 1985).

Greater numbers of species in larger areas have been explained by (1) purely mathematical processes, by which sampling more individuals increases the probability of finding more species (e.g., Coleman 1981); (2) the increased probability of larger patches “sampling”

more individuals from the population (“passive sampling” or “target area” hypotheses; Simberloff 1976, Connor and McCoy 1979); (3) larger areas having a greater diversity of ecological niches and associated species (“habitat diversity” hypothesis; Williams 1943, Ricklefs and Lovette 1999); and (4) greater rates of colonization (or immigration), thus reducing the probability of extinction (“area per se” hypothesis; MacArthur and Wilson 1967). Most of these explanations involve extensive discussions of associated mathematical, conceptual and ecological issues (see reviews by Connor and McCoy 1979, Hill et al. 1994). These commonly tested hypotheses are, however, not necessarily mutually exclusive explanations of species–area relationships. It is also unlikely that any of these hypotheses would be supported in all types of habitats or groups of organisms. For example, the species–area relationships for bryophytes and for lichens in the same areas do not support the same hypothesis (e.g., Lobel et al. 2006). Similarly, it has been shown that benthic assemblages at different stages of colonization (i.e., early and late colonization) show patterns that support different hypotheses (Anderson 1999).

An alternative explanation for patterns of distribution and abundance of species is spatial variation in the physical structure of the environment, which is often referred to as structure (or complexity) of habitats

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TABLE 1. Models, hypothesis and tests of effects of patch size and surface area on number of species (S) and number of individuals (N).

Model and hypothesis	Null	Tests of hypothesis
Random placement—sampling more individuals increases the probability of finding more species:		
H_1 : Positive relationship between S and N .	H_0 : No relationship between S and N .	Regressions of S and N in (1) all samples, irrespectively of patch size or surface area; (2) habitats of the same size, irrespectively of type of surface area; (3) habitat of the same surface area, irrespectively of patch size.
Passive sampling or target area—larger islands “sample” more colonists (i.e., have greater immigration) than do smaller islands:		
H_2 : Differences in N (per unit area) between habitats of different sizes.	H_0 : No difference in N (per unit area) between habitats of different sizes.	ANOVA of N in habitats of different sizes (i.e., 100, 200, and 300 cm ²).
H_5 : Differences in N (per unit area) in between habitats of with larger surface area.	H_0 : No difference in N (per unit area) between habitats with different surface area.	ANOVA of N in habitats with different surface area (i.e., A, B, and C).
Area per se—greater rates of colonization (or immigration), thus reducing the probability of extinction:		
H_3 : Greater S in larger habitats.	H_0 : No differences in S in habitats of different sizes.	ANOVA of S (per unit area) found in habitats of different sizes.
H_4 : Greater S in habitats with greater surface area.	H_0 : No difference S in habitats with different surface area.	ANOVA of S (per unit area) found in habitats with different surface area (i.e., A, B, and C).

(reviewed by McCoy and Bell [1991]). Structurally complex habitats generally have more species because they can provide a greater diversity of niches or different ways of exploiting resources (MacArthur and MacArthur 1961). Thus, complexity is an important influence on the diversity of assemblages. Independently of the way structure is defined or measured, such influences of complexity on diversity of organisms have been observed in terrestrial (e.g., Pianka 1966) and aquatic habitats (e.g., Hovel and Lipcius 2001).

The effects of these two attributes of habitat—patch size and structural complexity—have rarely been distinguished in manipulative studies, possibly because effects of increasing area and habitat heterogeneity can be extremely difficult to separate (e.g., Ricklefs and Lovette 1999, McGuinness 2000). There are additional difficulties associated with manipulative experiments at large and ecologically relevant spatial scales to test explanations for species–area curves (McGuinness 2000). At finer scales, the effects of structural complexity and surface area are also often confounded because surface area generally increases with greater surface complexity (Johnson et al. 2003). Several studies have reported independent effects of structural complexity and patch size on individual species. For example, survival of crabs has been shown to be correlated with increased structural complexity (i.e., shoot density), regardless of patch size of seagrass (Hovel and Lipcius 2001). Species sometimes respond to local structural complexity rather than to the overall patch size of habitat, although there have been relatively few examples of responses of entire assemblages (but see Taniguchi et al. 2003).

The aim of this study is therefore to test three general models that can potentially explain effects of patch size of and structural complexity on diversity of benthic

assemblages (Table 1). Predictions from these models were tested by manipulating patch size and surface area of artificial mimics of macroalgae. Larger habitats provided greater overall surface area without changing the structural complexity of components of habitat per unit area. Effects of surface area were investigated by manipulating the density and length of fronds, to modify the surface area provided by the habitat (e.g., Sirota and Hovel 2006). Here, surface area was used as an estimate of structural complexity because it is well-correlated with fractal complexity (e.g., Johnson et al. 2003, Kostylev et al. 2005) and is a good descriptor of structure of artificial habitats. Habitats with greater surface areas are often colonized by more individuals (Attrill et al. 2000).

These artificial habitats are colonized by diverse assemblages of mollusks from a range of families, different life-history traits, feeding modes, reproduction, development, mobility, and dispersal (Beesley et al. 1998). These organisms are quite small, ranging from 0.5 to 3 mm in size, and have been found to respond consistently in accordance with predictions based on models usually tested at larger scales (e.g., habitat heterogeneity; Matias et al. 2007). Note, however, that the width of artificial habitats is more than 200 times their average body lengths (i.e., <1 mm; M. G. Matias, unpublished data). This is relevant because, although, many gastropods colonize an area by passive advection through the water column (Beesley et al. 1998), it has been shown that they actively crawl and show preferences for particular types of habitats (Olabarria et al. 2002). Previous work manipulating the structure of habitat at finer scales has shown that assemblages of mollusks respond to differences in structure of habitat at the scale of <0.15 m (e.g., Matias et al. 2007), which

TABLE 2. Dimensions of artificial habitats with different sizes and types of structural components.

Habitat	Area (cm ²)	Fronds per cm ²	Length of fronds (cm)	Surface area of fronds (cm ²)
A1	100	66.2	1	26.5
A2	200	66.2	1	53.0
A3	300	66.2	1	79.5
B1	100	22.6	2	18.5
B2	200	22.6	2	36.1
B3	300	22.6	2	54.1
C1	100	16.2	4	25.9
C2	200	16.2	4	51.8
C3	300	16.2	4	77.8

reinforces the idea that, for the small snails studied here, a patch of heterogeneous habitat of 200 cm² can properly be considered to be a landscape (sensu Fahrig and Merriam 1985, Wiens 1990, Steffan-Dewenter et al. 2002).

METHODS

Study site

This study was done on intertidal rock platforms at the Cape Banks Marine Research Area, on the northern headland of Botany Bay (NSW, Australia), in July–September, 2007. Experiments were done in two locations with similar orientation and exposure to waves on gently sloping low-shore rock platforms or large boulders, 0.3 to 0.6 m above mean low water. Artificial habitats were interspersed amongst meadows of algal turf dominated by *Corallina officinalis* L. and were attached to the rock with stainless steel screws and rubber washers. Assemblages associated with coralline habitats vary with slope (Akioka et al. 1999), height on shore (Kelaheer et al. 2003) and show small-scale patchiness (Olabarria and Chapman 2001). Artificial habitats of each treatment were scattered at random over areas that were previously chosen because they had similar characteristics.

Design of the experiment

Assemblages colonizing artificial turfs respond to changes in density and length of fronds (Kelaheer 2003a, b). Three types of artificial turf (Grassman Pty Ltd., NSW, Sydney, Australia) with different densities and length of fronds were selected (A, B, C in Table 2). These artificial turfs were chosen because they differ in length (A < B < C) and also in density of fronds (A > B > C), which maximized the structural differences needed to test our hypotheses about different types of habitats. Previous studies have shown that assemblages of mollusks colonizing artificial habitats respond negatively to greater densities of fronds (Kelaheer 2003a) and positively to longer fronds (Kelaheer 2002). Therefore, the assemblages that colonize our artificial habitats were affected by the combined effect of density and length of fronds.

Experimental sub-habitats were squares of turf (5 × 5 cm²), cut as described in previous experimental work (Matias et al. 2007). Experimental habitats were of three sizes: small (made up of four units); intermediate (eight units), and large (12 units) with areas of 100, 200, and 300 cm², respectively. Previous experiments showed that artificial habitats of these sizes are appropriate to test our hypotheses (Matias et al. 2007). Each unit of turf was glued to squared pieces of rubber and attached to wire mesh with minimal distances between units (see detailed design in Appendix A; Matias et al. 2007).

Artificial habitats were retrieved 60–65 days after being deployed. Previous studies have demonstrated that artificial turfs are rapidly colonized by numerous invertebrates after 14 days of deployment (Olabarria 2002, Kelaheer 2005). After 50 days of deployment there are significant differences between assemblages colonizing habitats with different structural diversity (Matias et al. 2007). The diversity and abundance of invertebrates in artificial turfs at 2, 4, and 12 months after deployment are not different from those in natural turfs (i.e., *Corallina* spp.; Kelaheer 2003a), which suggests that they are consistent with the natural assemblages. Thus, the time of deployment used here is to test hypotheses about differences in patch size and structure of habitats.

Fauna and epiphytes may easily be dislodged from the units of turf when habitats are removed from the shore. To prevent this, artificial habitats were retrieved using a grid of 50 × 50 mm squared plastic corers (similar to an ice cube tray), which isolated units so that they could be sampled separately, but simultaneously. The grid of corers was carefully placed over the artificial habitat and then pressed firmly down to enclose the whole patch. The screws were then undone, so that each sub-habitat in the artificial habitat was in a separate corer and each corer was emptied into a separate plastic bag, guaranteeing that the epiphytes and fauna associated with each sample were completely recovered. All units were labeled and preserved in 7% formalin. Three units were randomly selected from each habitat. Each unit was then washed in a 500-μm sieve and all invertebrates sorted and counted under a binocular microscope at 16× magnification. All mollusks were identified to the finest possible taxonomic resolution, either species or morphospecies. Each replicate was derived from pooling data from three units.

The relationship between numbers of individuals and numbers of species (hypothesis 1, Table 1) was tested by examining the correlations between numbers of species and numbers of individuals in every habitat ($n = 54$ habitats). In addition, the slopes of the relationships between numbers of species and numbers of individuals in habitats of same structural complexity (i.e., $n = 18$ habitats in each of 3 complexities) were tested for heterogeneity of slopes (Underwood 1997). Hypotheses 2, 3, and 5 were tested by comparing habitats with different areas and types of components, using a three-way analysis of variance (Table 1). *Type* was a fixed

comparison among habitats with different type of sub-habitats (A, B, or C); *patch size* was a fixed comparison between artificial habitats of different area (100, 200, and 300 cm²); *location* was random with two levels; there were three replicate habitats of every combination of type and size and location. All analyses were preceded by Cochran's test, which detects the type of heterogeneity of variances that can compromise analysis of variance. Numbers of individuals had heterogeneous variances and were transformed using square root($x + 1$), which is appropriate for this type of data and removes the relationships between means and variances for Poisson-type variables (Sokal and Rohlf 1995, Underwood 1997, Quinn and Keough 2002). Other transformations of data were used (e.g., $\log[x + 1]$), in response to comments by reviewers, but these did not change the outcome of any analyses.

There were no a priori hypotheses about which model would best describe the species–area relationship, therefore any model (e.g., linear, power function, exponential) provides a valid test of our hypothesis. We tested the hypothesis that more species should be found in habitats with larger surface area (hypothesis 4, Table 1) using a linear model on untransformed numbers of species and surface area (cm²) for (1) all 54 habitats (three replicates of nine combinations of type and size in each of two locations); (2) the 18 habitats of the same structural complexity for each of the three types (i.e., three replicate habitats for each of three sizes in the two locations); and (3) the 18 habitats of the same size for each of the three types (i.e., three replicate habitats for each of three types in the two locations). These analyses were also done with log-log transformation and yielded the same similar results.

RESULTS

Habitats with greater numbers of individuals had more species ($r = 0.86$, $P < 0.001$, 52 df). This pattern was significant ($P < 0.001$, 16 df) for each type of structure: type A, $r = 0.71$; type B, $r = 0.96$; type C, $r = 0.89$. Differences among slopes were significant (test for homogeneity of slopes, $F_{2,48} = 3.5$, $P < 0.05$, Fig. 1). Although there was a clear positive relationship between numbers of species and numbers of individuals (i.e., rejecting hypothesis 1), the slopes of this relationship were not the same for habitats of different structural complexity.

Patch size did not affect the numbers of individuals ($F_{2,40} = 5.9$; $P > 0.05$; see ANOVA table in Appendix B and means in Appendix C). Although there were significant differences in numbers of individuals between locations, there was no interactive effect with any of the main factors. This result does not reject the null hypothesis of no differences in numbers of individuals per unit area among habitats of different sizes (hypothesis 2).

There was a consistent increase in number of species with increasing area of habitats (Fig. 2: patch size).

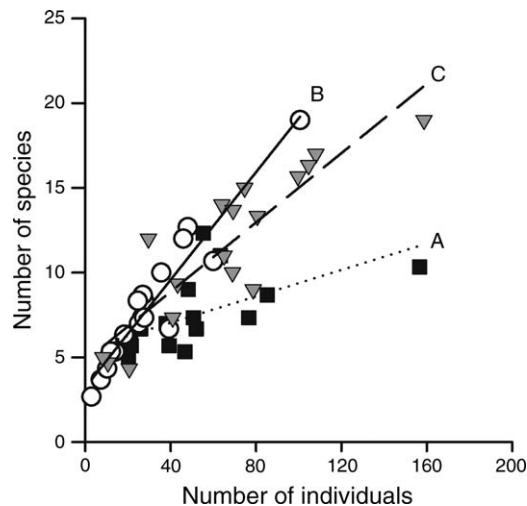


FIG. 1. Regressions of relationships between number of species and number of individuals per habitat: black squares are habitats made of components of type A; white circles are habitats made of components of type B; gray triangles are habitats made of components of type C. See Table 1 for characteristics of habitat types.

Larger habitats had more and more species per unit (Fig. 2: patch size; SNK tests, $P < 0.05$). These results were consistent in the two locations and among habitats of different structural complexity (Appendix A), rejecting the null hypothesis of no differences in number of species among habitats of different area (supporting hypothesis 3). There was an overall positive relationship between surface area and number of species when all habitats were pooled ($r = 0.51$, $P < 0.001$, 52 df). This relationship was significant ($P < 0.001$, 16 df) for each type of habitat when pooled across the 3 sizes: type A, $r = 0.85$; type B, $r = 0.71$; type C, $r = 0.78$). When habitats of the same size were examined, pooled across the 3 types, the relationship between number of species and surface area was only significant for the largest habitats: 100 cm², $r = 0.53$, $P > 0.05$; 200 cm², $r = 0.30$, $P > 0.05$; 300 cm², $r = 0.34$, $P < 0.001$.

In each location, habitats made of type C had more species than did habitats of types A or B (SNK tests, $P < 0.05$; Fig. 2: type of structure; Appendix B). Number of species per unit (i.e., the mean number in the 3 sub-habitats sampled per habitat) showed a similar pattern, but means could not be separated using multiple comparisons (SNK tests, $P > 0.05$; Fig. 2; Appendix B). Similarly, there were no differences among numbers of individuals in habitats with different structural complexity ($F_{2,4} = 3.7$; $P > 0.05$; Appendix B). These results do not support the prediction that habitats with greater surface area should have more individuals (hypothesis 4) and reject the prediction of no differences in number of species between habitats with different surface area (hypothesis 5, Table 1).

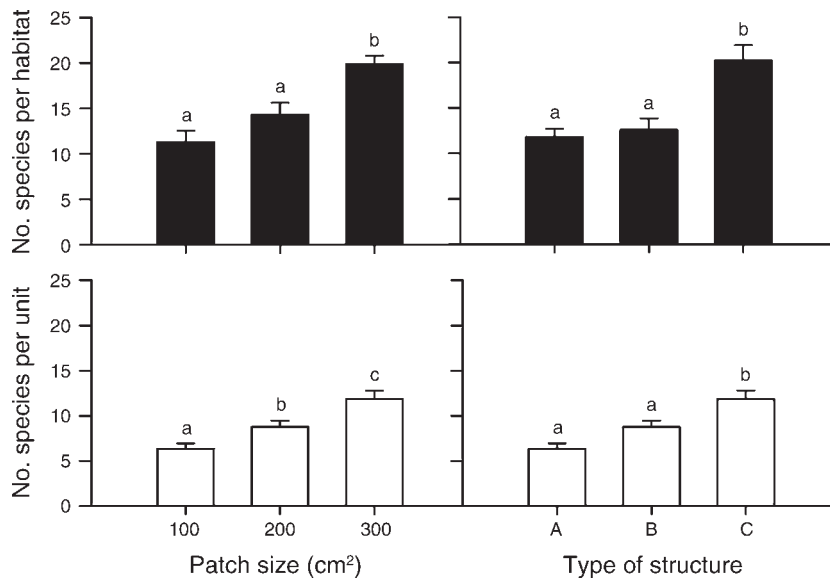


FIG. 2. Diversity of assemblages in habitats with different (a) patch size and (b) type of structure; open bars are the mean (+SE) number of species per unit; black bars are the mean (+SE) number of species per habitat. Different letters denote significant differences at $P < 0.05$.

DISCUSSION

Species and area

The numbers of species colonizing habitats were closely associated with the numbers of individuals when all habitats were analyzed together, regardless of their size or structural complexity. It was predicted that, if individuals were randomly allocated to patches of habitat (sensu Coleman 1981; hypothesis 1 in Table 1), samples of equal area (i.e., 75 cm²) taken from habitats of different overall areas (100, 200, or 300 cm²) should yield the same numbers of species (e.g., Simberloff 1976). Our results showed that assemblages colonizing larger habitat had more species, regardless of the structural complexity of habitat. This clearly demonstrates that the random placement hypothesis alone cannot explain differences in numbers of species among habitats of different sizes. Moreover, neither patch size nor surface area affected numbers of individuals per unit area, which rejects the hypothesis that numbers of individuals would differ among habitats of different sizes (hypotheses 2 and 4). In general, for a particular patch size, habitats with more individuals had more species, but this cannot be generalized to explain the greater number of species in larger habitats. These results indicate that random placement of individuals can occur at the scale of habitat (i.e., patches with more individuals have more species), but this does not explain the increased number of species in larger habitats.

Random placement may be a good model to explain number of species at coarser scales but not for finer areas (Plotkin et al. 2000). At finer scales, processes that might influence the probabilities of finding different species are spatial aggregation (Hill et al. 1994) and

intraspecific competition among individuals at finer scales (Plotkin et al. 2000). Moreover, intertidal gastropods show great variability in abundances at fine scales as a result of variability of patches of habitat (e.g., Olabarria and Chapman 2001) and dispersal after settlement (e.g., Underwood 2004). Assemblages colonizing artificial habitats (i.e., plastic scourers) have been shown to vary significantly among patches 20 cm apart (Chapman and Underwood 2008), which suggests that small-scale variability in abundance is likely to influence the probabilities of finding individuals in each habitat independently of the patch sizes used in this experiment.

An alternative to investigate random placement is to use rarefaction, which assumes that individuals are randomly distributed (Magurran 2004) and are randomly sampled (Gotelli and Colwell 2001). These assumptions of independence are unrealistic for many benthic assemblages. Random patterns are rarely observed; most species exhibit some sort of spatial aggregation (e.g., Chapman and Underwood 1996). Rarefaction could have led to biased estimation of numbers of species in smaller habitats (Clarke and Warwick 2001). The same would be true when using species-per-individual ratios to correct for unequal numbers of individuals, because this assumes that species richness increases linearly with abundance, which has been shown not to be true for benthic assemblages (Gray 1997). Patterns of abundance in these assemblages are rarely this extreme and therefore the species-per-abundance ratio would have distorted patterns of number of species.

More species in larger habitats could potentially be explained by differences in numbers of microhabitats between habitats of different sizes. For example, smaller habitats generally have a greater perimeter-to-area ratio

and therefore more edges. Any resource being concentrated near edges would support increased abundances of any species reliant on it (Ries and Sisk 2004). If the numbers of individuals differ between middles and edges of patches, sampling the patches as in the present study would represent smaller and larger patches differently. Randomly sampling three units from each patch would, on average, sample more of the edge units in smaller patches than in larger ones. This would matter if sampling of larger patches included microhabitats that do not exist in smaller patches (Anderson 1999) or where the probability of larval settlement differs between edges and middle areas of patches (Mullineaux and Butman 1990). Alternatively, individuals in assemblages in larger patches might colonize edges preferentially, but have a reduced overall number of species when compared to assemblages in smaller patches (Anderson 1999). These processes could cause the number of species per unit area to be underestimated in larger habitats. Previous studies on assemblages of microgastropods have shown no differences between the numbers of individuals colonizing edges when compared to interiors of natural patches of turfs (Olabarria 2002), but these possibilities are being investigated (M. G. Matias, *unpublished data*).

Species and complexity

The relationship between number of individuals and numbers of species in habitats of Type B had a steeper slope than in habitats Type A and C (Fig. 1), which suggests that turnover of species does not match the overall differences in diversity between types of habitat. This result is somewhat unexpected because, structurally, Type B has characteristics intermediate between those of Types A and C. This is analogous with some patterns observed in ecological boundaries (or ecotones sensu Smith et al. 1997), where areas of transition are colonized by species from two or more different types of adjoining habitats, resulting in a greater turnover of species. From this, one possible explanation of this result is that habitats of Type B are colonized by species that are found in habitats of Type A and C, as a result of its intermediate structure or its being a “transition” habitat. There were, however, 11 species that were exclusive to B and C, as opposed to only three species shared between Types B and A, which suggests that, although, Type B has an intermediate structure between Types A and C, it shares more species with habitats of Type C. This result suggests that the relationship between structural complexity and number of species may not be linear (Kelaher 2003a), and has implications for future studies using artificial habitats, because which types of habitat are chosen for experiments may affect the outcomes.

More species were found in Type C habitats, which had the largest surface area, but the numbers of individuals colonizing artificial habitats were not affected by differences in surface area. This suggests that increased numbers of species cannot be a result of random placement associated with sampling increased numbers

of individuals, contrary to suggestions that the relationship between surface area and number of species might be a sampling artifact as result of increased sample size (Attrill et al. 2000). Furthermore, if surface area alone explained the numbers of individuals and numbers of species, there should be no differences between samples of equal amount of habitat (i.e., equal number of fronds per unit area) taken from habitats of different sizes. As indicated above, there were more species in larger habitats than in samples of equal size taken from smaller habitats, rejecting the null hypothesis of no differences in numbers of species in samples of the same surface area.

The relationship between surface area and number of species was only significant in larger habitats; surface area alone did not explain differences in number of species in small and intermediate sized habitats (100 and 200 cm²). This result is not consistent with the lack of statistical interactions between differences among types of habitat and differences among sizes of habitats in the numbers of species and of individuals. Surface area may be a better predictor of structure of these assemblages in larger habitats (i.e., 300 cm²). This is not surprising given the hierarchical nature of structure of habitats whereby assemblages respond to changes in structure of habitats at different scales (e.g., patch size; Kotliar and Wiens 1990). It is also further evidence that measurements of structure of habitat may quantify attributes in ways that are different from the ways organisms respond to them. Understanding the effects of structure of habitats at different scales must include discussions of the appropriateness of the measures used at different scales.

Comparisons between habitats with different surface areas are confounded by other attributes of habitat, such as density and length of fronds (e.g., Attrill et al. 2000, Kelaher 2003a, b, Sirota and Hovel 2006). The physical structure of habitat depends not just on the shape of structural components, but also on the available space associated with these structures. Therefore, several indices should be used jointly to capture different aspects of structure of habitat (e.g., fractal geometry; Warfe et al. 2008). Structural complexity (as measured by fractal geometry) can influence the number of species, even after correcting for the increased surface availability on more complex surfaces (Johnson et al. 2003). These assemblages are responding to differences in structure of the habitats (as measured by surface area), although what causes these differences cannot be attributed to a sampling artifact. No previous work has critically examined which indices of structural complexity might better describe the structure of these complex, turf-like habitats.

Conclusions

The use of experimental micro- and mesocosms to test conceptual models is quite common across the ecological literature (e.g., Kneitel and Chase 2004, Srivastava 2006). These experimental systems are all, by definition, small habitats, which enable appropriate

replication, but also provide the versatility to test relevant hypotheses that are often difficult to test at larger scales (see review by Srivastava et al. 2004). The artificial habitats used here share most of these advantages, such as rapid colonization, tractability and size of experimental units, and, unlike laboratory experiments, are deployed across the natural habitats, which they mimic. This study clearly showed that patch size and structural complexity are independent attributes of habitats and accentuate the need for proper experimental manipulations to determine the relative contributions of such attributes.

If habitats are manipulated at the appropriate scales at which organisms respond to the environment, the information obtained from these studies can be extremely valuable to the interpretation of observational studies at larger scales, which are difficult to manipulate. Understanding how these different attributes of habitats influence assemblages is essential for predicting their responses to reductions of patch size (Bender et al. 1998, Bell et al. 2001) at a time when the loss and modification natural habitats are considered to be major threats to global biodiversity (Gray 1997, Pimm and Raven 2000). Reduced natural variation in structural complexity of habitats may also affect the numbers of species (e.g., “habitat” homogenization; McKinney and Lockwood 1999). In order to predict and explain species’ responses to such dramatic changes in natural habitats, it is essential to develop an understanding of why species inhabit such habitats in the first place.

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APPENDIX A

Photographs of experimental habitats (*Ecological Archives* E091-129-A1).

APPENDIX B

Analyses of abundance and diversity of mollusks in patches of different size and structural complexity (*Ecological Archives* E091-129-A2).

APPENDIX C

Figures showing mean abundances in habitats with different patch size and type of structure (*Ecological Archives* E091-129-A3).