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Habitat configuration affects colonisation of epifauna in a marine algal bed

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ARTICLE INFO

Article history:

Received 23 February 2005

Available online 16 September 2005

Keywords:

Patch size

Isolation

Algal beds

Matrix

Epifauna

Colonisation

ABSTRACT

Habitat fragmentation is a threat to the preservation of both terrestrial and marine biodiversity. While terrestrial systems have been well studied, relatively few studies have considered how changes to the spatial arrangement of habitats affect fauna in marine systems. In this study, sampling and manipulative experiments examined the effects of varying the size and isolation of habitat patches on the abundance of mobile invertebrates inhabiting an algal dominated rocky reef. Variation in the size of naturally occurring patches of the brown alga *Sargassum linearifolium* did not impact upon the abundance of any taxonomic groups, with the exception of polychaete worms, which were most abundant in small patches. When habitat patch size and isolation were manipulated, the abundance of colonising isopods increased with increasing isolation from contiguous habitat. Amphipods and ostracods colonised small patches to greater numbers than large patches. Sampling of the matrix was undertaken to examine the rarely tested assumption that the area between habitat patches is not a potential source of colonists to the habitat in question. The matrix was found to support a strikingly different community of invertebrates than did the algal habitats and thus was unlikely to be a source of colonists to isolated algal patches. The increased abundance on small and isolated patches for some taxa are inconsistent with traditional predictions of the effects of reduced habitat patch sizes and indicate that patchy landscapes should not necessarily be considered poor habitats. The variation in responses among taxonomic groups suggests that a range of patch sizes may be necessary to maintain species diversity.

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1. Introduction

Habitat fragmentation is a recognized threat to the conservation of biodiversity in both terrestrial and marine ecosystems (Bell et al., 2001; Tscharnkte et al., 2002). The process of fragmentation involves a reduction in the size of suitable habitat patches and increasing isolation among remnant habitat patches (Saunders et al., 1991; Fahrig, 2003). As well as the direct effects of reduced habitat area, further impacts include alterations to the dispersal and behaviour of organisms, isola-

tion of subpopulations and restricted gene flow (Zschokke et al., 2000). Indirect effects of habitat fragmentation may include enhanced invasibility of exotics, altered predator/prey interactions and fluctuating abiotic conditions due to the greater proportion of variable edge habitats (Tscharnkte et al., 2002). Alterations to the spatial configuration of habitat may also exacerbate the negative consequences of habitat loss (Shochat et al., 2001).

The effects of changes to the size and isolation of habitat patches have usually been examined by contrasting frag-

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0006-3207/\$ - see front matter © 2005 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2005.07.010

mented habitats to those that are considered to be contiguous (Fahrig, 2003). To do this, researchers have traditionally adopted one of three approaches. The first is to sample across habitat patches of varying size and isolation and record measures of abundance or species richness (Bell et al., 2001; Bowden et al., 2001; Shochat et al., 2001; Hill and Curran, 2003). Second, manipulative studies have created experimental landscapes to directly test the effects of specific processes associated with changes to habitat structure (Debinski and Holt, 1999). Finally, computer simulations have been used to examine dispersal and the persistence of populations in fragmented habitats (Wiens et al., 1997; Bevers and Flather, 1999).

In contrast to terrestrial ecosystems, it is only recently that the consequences of habitat fragmentation have been considered in marine habitats (Robbins and Bell, 1994; Bell et al., 2001). Human uses of marine environments including recreational activities and commercial developments often result in changes to the size and distribution of habitat patches (Duarte, 2002). Concern over anthropogenic impacts in marine systems, however, has predominantly centred on the removal of high trophic level organisms through overfishing (Pinnegar et al., 2000) and the impact of pollution (Shahidul Islam and Tanaka, 2004). Logistic problems associated with conducting landscape-scale ecology in subtidal marine environments have limited our understanding of the likely effects of habitat fragmentation and unlike terrestrial systems, detailed maps of habitat patch sizes and arrangement are rarely available (Robbins and Bell, 1994). Additionally, there have been few studies that have adopted an experimental approach to investigate how landscape configuration affects marine organisms and most of these have been conducted in a single habitat – that of seagrass beds (Irlandi, 1994; Robbins and Bell, 1994).

In this study, we use both sampling and experimental approaches to examine the effects of varying the size and isolation of habitat patches on the abundance and colonisation of mobile epifauna inhabiting subtidal algal beds. Marine macroalgae support very high densities of mobile invertebrates (especially amphipods, gastropods and polychaetes) which comprise a major component of coastal marine biodiversity (Brawley, 1992). Like seagrass beds, algal beds can be subject to fragmentation associated with anthropogenic developments and activities (Walker and Kendrick, 1998). The likely effects of this process on the mobile epifauna are poorly understood, with few studies examining the effects of fragmentation on invertebrates in algal habitats (Goodsell and Connell, 2002). We asked three specific questions: (1) Does the abundance of epifauna vary with the size of naturally occurring patches of the brown alga *Sargassum linearifolium*? (2) Do patch size and the degree of isolation affect the colonisation of epifauna in experimental landscapes? (3) Is the matrix between habitat patches a potential source of colonists?

2. Methods

2.1. Study site and organisms

Sampling and experiments were conducted on a sub-tidal rocky reef (2–5 m depth) supporting dense beds of the brown

macroalga *S. linearifolium* (Turner) C. Agardh at Shark Bay, Port Jackson, Sydney, Australia (33°51'9"S, 151°16'0"E). *S. linearifolium* is most abundant in the winter months (Poore and Steinberg, 1999), when it mostly occurs as large patches over tens of metres with occasional smaller patches and single algae in isolation among areas devoid of algae (bare rock or sand). The mean (\pm S.E.) distance among individuals at this time of year is 3.4 ± 0.6 cm ($n = 78$) (Poore, 2005).

S. linearifolium supports a diverse assemblage of mobile invertebrates including gammarid and caprellid amphipods, harpacticoid copepods, isopods, ostracods, polychaetes, decapods and gastropods. Further details on algal biomass at this site and factors affecting the distribution of amphipods can be found in Poore and Steinberg (1999), Poore et al. (2000) and Poore (2004).

2.2. Sampling of natural patches of varying size

The relationship between the size of naturally occurring patches of *S. linearifolium* and the abundance of epifauna within Shark Bay was examined by sampling 10 individuals of *S. linearifolium* from each of three different patch size classes in May, 2003. Patches were classified as small (a single alga), medium (greatest patch dimension 0.25–1.0 m) and large (greatest patch dimension larger than 1 m). Each patch was separated by at least 1 m from neighbouring habitat patches and within 3 m of large contiguous beds of *S. linearifolium*.

Individual *S. linearifolium* were quickly enclosed underwater in a 1 L plastic container. All samples were preserved in 5% formaldehyde, shaken repeatedly in freshwater to remove associated epifauna and rinsed through a 300 μ m sieve. Under a dissecting microscope, all invertebrates were counted and sorted to the following taxonomic groups: amphipods, isopods, polychaetes, copepods, bivalves, gastropods, anemones and ostracods. The wet mass of each alga was recorded and counts converted into densities (number of organisms/g wet mass of algae).

The abundance of amphipods, gastropods, isopods and polychaetes, the taxonomic groups exhibiting densities greater than 0.5 individuals/g algae, were contrasted among patch size classes by one-factor analysis of variance (ANOVA). The wet mass of the algae sampled did not differ significantly between any of the patch size classes ($F_{2,27} = 1.283$, $P = 0.294$).

2.3. Colonisation to patches of varying size and isolation

An artificial landscape was created to test how variation in patch size and isolation affects the colonisation of invertebrates to suitable habitat patches. Patch size and isolation were manipulated in a factorial design with individuals of defaunated *S. linearifolium* placed in patches of two size classes at three distances (0, 2 and 10 m) from existing algal beds (greater than 20 m \times 5 m). Cable ties were used to attach either one individual of *S. linearifolium* (small habitat patches) or an individual surrounded by four neighbours (large habitat patches) to squares of plastic mesh measuring 7 cm \times 7 cm with a mesh size of 1 cm². Epifauna were removed from algae using a fresh water rinse adapted from Holmlund et al. (1990).

Algae were placed in freshwater for 1 minute, followed by a short submersion in seawater and a subsequent minute of freshwater. The defaunation process does not affect the attractiveness of *S. linearifolium* to *Peramphithoe parmerong*, an abundant gammarid amphipod at Shark Bay (Poore, 2005).

Ten replicate patches were used for each of the six combinations of the patch size and isolation treatments. Mesh squares were bound by cable ties to a single eyehole dynabolt, drilled into the rock platform using a pneumatic drill attached to an SCUBA tank and labelled with fluorescent flagging tape to aid in recovery. All replicates were at least 5 m apart with no algae between the isolated treatments (2 and 10 m) and the contiguous algal beds.

After 5 days, 30 replicates were retrieved (five for each treatment), with the final 30 retrieved after 10 days. Five days is sufficient to allow abundant species of amphipods (the most abundant taxonomic group) to return to natural densities when colonising defaunated algae in close contact to existing unmanipulated algae (Poore, 2005). For large habitat patches, only the central individual of *S. linearifolium* was collected. Samples were preserved and sorted as described above. The densities of major taxonomic groups that exhibited mean densities greater than 0.5 individuals per g of algae were analysed with two-factor ANOVA with time and isolation treated as fixed factors and patch size treated as a random variable. Previous research has identified 5–10 days as an appropriate time period over which to examine returns to natural densities of epifauna. The wet mass of the alga sampled did not differ significantly among any of the treatments ($F_{1-2,48} > 0.310$, $P > 0.15$).

2.4. Matrix sampling

The effect of changes to the configuration of habitats is commonly examined by dividing the landscape into areas that support the organisms of interest (habitat patches) and the remaining areas (the matrix) (Wiens, 1995). This general approach, and the ability to manipulate the isolation of habitat patches used in this study, relies on the assumption that animals derived from the matrix do not influence the patterns of abundance in habitat patches (Ricketts, 2001). A relationship between variable abundances at different distances from contiguous patches may be confounded if the organisms studied are able to exploit various habitats, or if patterns of organism abundance in the matrix also vary with distances from contiguous patches. To exclude these possibilities we sampled invertebrates from the matrix habitat (bare rock and cover of associated sediments) among the patches of *S. linearifolium* at all distances from contiguous patches considered in the manipulative experiment.

Five plots of area 20 × 20 cm were sampled from each of the three levels of isolation used in the colonisation experiment (0, 2 and 10 m from contiguous algal beds). The plots were sampled with a venturi suction sampler (similar to designs described in Rostron and Survey, 2001). Particulate matter and associated invertebrates were sucked through the vacuum hose and collected in a 200 µm mesh bag. Each plot was subjected to 60 s of continuous suction fol-

lowed by 10 s of suction above the benthos to ensure all organisms still in the pipe and hose were collected in the mesh bag. The contents of the mesh bags were then transferred to 1 L plastic containers, preserved and sorted as described above.

The composition of major taxonomic groups within the matrix samples was contrasted to five randomly selected algal samples (only small patches were considered) from each of the levels of isolation with nonmetric multi-dimensional scaling and analysis of similarities. Given the contrasting types of samples, the numbers of each taxon were standardised to equal abundance per sample to provide a test of relative abundances only. The proportion of total number of individuals that belonged to each major taxonomic group was contrasted between matrix and algal habitats using 2 factor ANOVA with habitat (matrix or algal) and isolation (0, 2 and 10 m) as fixed factors. Amphipods were further classified to family to test the assumption that amphipod assemblages collected from the matrix were distinct from those associated with macroalgal habitats (10 samples contrasted from each habitat type).

2.5. Statistical analyses

Analyses of variance and Tukey's post hoc tests were conducted using SYSTAT Version 10 (SPSS Inc.). Assumptions of normality and heterogeneity of variance were tested for each variable by examining residual histograms and scatter plots of estimates vs. residuals, respectively (Quinn and Keough, 2002). Where necessary, data were log transformed to satisfy the assumptions of ANOVA. Nonmetric multi-dimensional scaling and analysis of similarities were conducted with Primer (Version 5.2.2, Primer-E Ltd.).

3. Results

3.1. Sampling of natural patches of varying size

The abundance of each of the major taxonomic groups with the exception of polychaetes did not vary significantly among the three size classes of naturally occurring *S. linearifolium* patches (Fig. 1, Table 1). Polychaetes were significantly more abundant on small habitat patches than the medium and large sized patches (Fig. 1(d), Table 1).

3.2. Colonisation to patches of varying size and isolation

Variation in the size and isolation of habitat patches in the artificially created landscape affected the colonisation of mobile invertebrates to these habitats. The effects, however, varied among the major taxonomic groups. Isopods were the only taxa to exhibit an isolation effect, colonising isolated habitat patches (i.e., 2 and 10 m) to greater abundance than those within contiguous habitat (Fig. 2(d), Table 2). The abundance of colonising amphipods, copepods, gastropods, ostracods and polychaetes did not differ significantly among levels of isolation of patches (Fig. 2(a)–(c) and (e)–(f), respectively, Table 2).

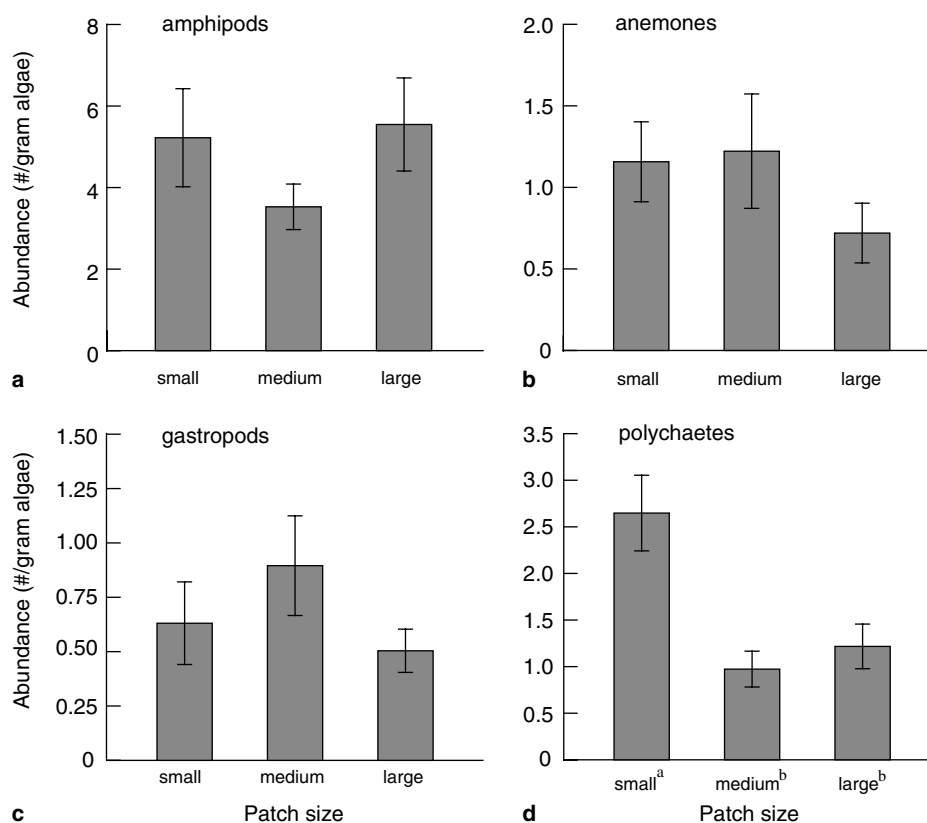


Fig. 1 – The abundance of: (a) amphipods; (b) anemones; (c) gastropods and (d) polychaetes sampled from naturally occurring patches of *Sargassum linearifolium* of varying size. Data are mean (\pm S.E) numbers per g wet mass alga, $n = 9\text{--}11$ per treatment). For polychaetes, treatments that share common letters are not significantly different according to Tukey’s pairwise comparisons.

Table 1 – Analyses of variance for abundances of abundant taxa sampled from naturally occurring patches of *Sargassum linearifolium* of varying size

Source	df	Amphipods ^a		Anemones		Gastropods ^a		Polychaetes	
		F	MS	F	MS	F	MS	F	MS
Size	2	0.45	0.225	1.21	0.736	1.02	0.668	9.82**	8.473
Error	27		0.449		0.609		0.656		0.863

Patch sizes were small (a single alga), medium (greatest patch dimension 0.25–1.0 m) and large (greatest patch dimension larger than 1 m).

Data were numbers per g wet mass alga.

^a Log transformed.

* Denotes a significant result ($0.01 < P = 0.05$).

** Denotes a significant result ($0.001 < P = 0.01$).

Patch size had an effect upon the abundance of amphipods and ostracods, both of which colonised small habitat plots to significantly greater numbers (Fig. 2(a) and (e), respectively, Table 2). The abundance of colonising copepods, gastropods, isopods and polychaetes did not differ significantly among patch sizes (Figs. 2(b)–(d) and (f), respectively, Table 2).

The abundance of no individual taxa differed significantly between the two collection times (Table 2). There were no significant interactions among the main effects (isolation, patch size and time) for any of the taxa analysed, with the exception

of a three-way interaction for the abundance of copepods (Table 2).

3.3. Matrix sampling

Sampling of invertebrates inhabiting the areas of bare rock and sediment between the algal habitats confirmed that these areas cannot be considered as suitable habitat for algal epifauna. The invertebrate assemblages inhabiting this matrix were not those found inhabiting *S. linearifolium* (Fig. 3). The composition of major taxa in the habitats differed

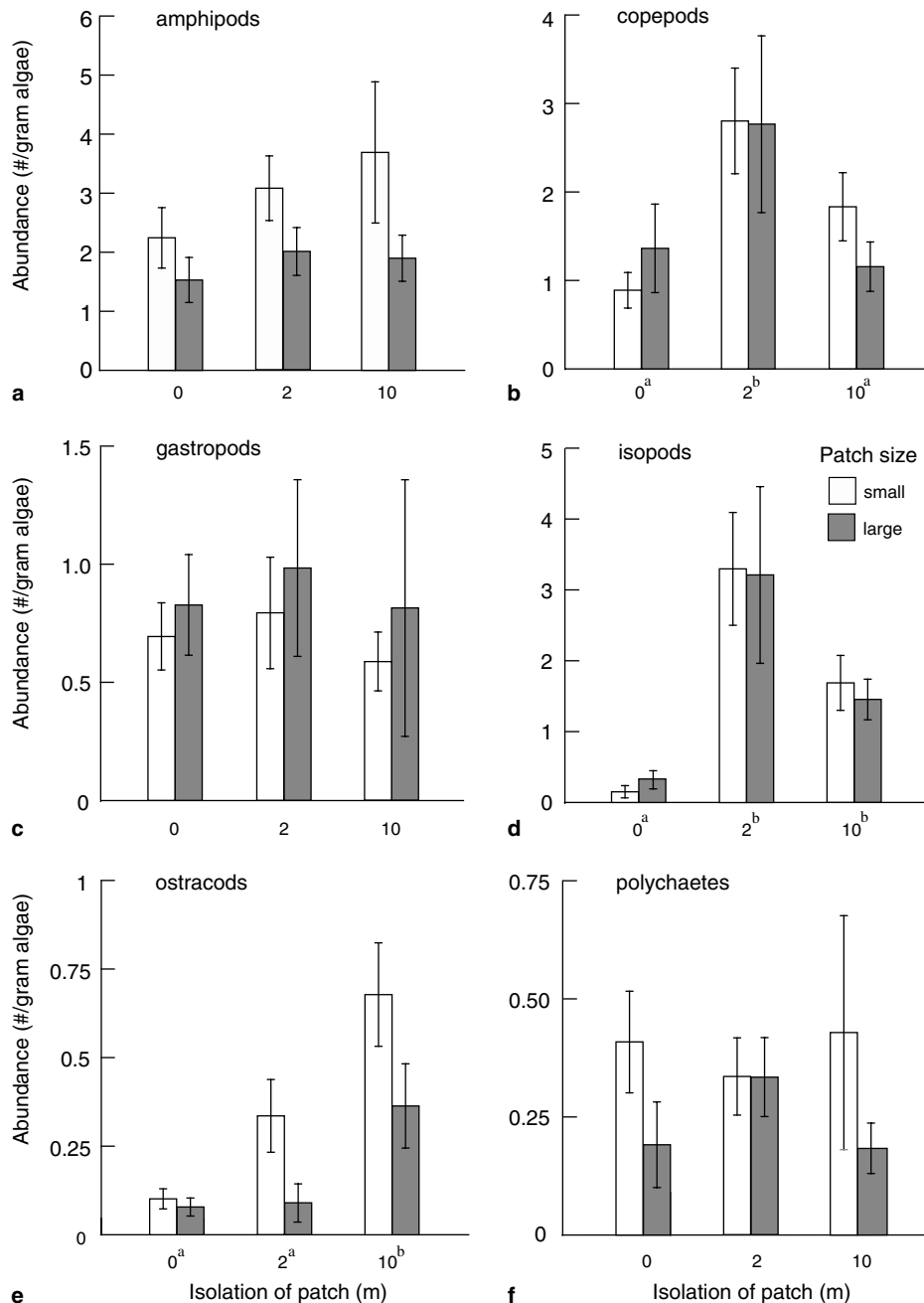


Fig. 2 – The abundance of: (a) amphipods; (b) copepods; (c) gastropods; (d) isopods; (e) ostracods and (f) polychaetes colonising habitat patches of varying size and isolation in an experimental landscape. Data are mean (\pm S.E) numbers per g wet mass alga ($n = 5$ per treatment). Distance treatments that share a letter are not significantly different according to Tukey's pairwise comparisons.

significantly (analysis of similarities, $R = 0.434$, $P = 0.001$). The matrix habitat supported high numbers of tanaids that were absent from algal communities (ANOVA contrasting the proportional abundance in the two habitats, $F = 236.2$, $P = 0.001$). Copepods ($F = 48.5$, $P < 0.001$), polychaetes ($F = 12.5$, $P = 0.001$), isopods ($F = 54.0$, $P < 0.001$) and ostracods ($F = 17.9$, $P = 0.001$) all comprised a significantly greater proportion of the total number of invertebrates found within algal assemblages than those within the matrix assemblages.

The proportion of the total number of individuals that were amphipods ($F = 2.0$, $P = 0.16$) and gastropods ($F = 0.51$, $P = 0.48$) did not differ significantly among the two habitats. The amphipod assemblages however, were dominated by species within different families. Within the matrix, most amphipods were from species within the families Aoridae and Ischyroceridae (50% and 45% of all amphipod individuals, respectively). In contrast, amphipods from algal samples were mostly species from the families Hyalidae and

Table 2 – Analyses of variance for abundance of epifauna colonising patches of *Sargassum linearifolium* in an experimentally fragmented landscapes

Source	df	Amphipods ^a		Copepods ^a		Gastropods ^a		Isopods ^a		Ostracods ^a		Polychaetes ^a	
		F	MS	F	MS	F	MS	F	MS	F	MS	F	MS
Isolation	2	12.98	0.755	4.88	4.670	2.69	0.482	30.86*	24.195	9.91	5.300	0.649	0.265
Time	1	8.88	1.775	0.04	0.087	0.95	0.131	1.57	0.111	20.78	2.265	0.968	0.511
Size	1	7.43**	3.019	0.60	0.430	0.02	0.014	0.08	0.072	7.36**	3.441	3.71	1.786
Isolation × time	2	1.58	0.843	0.40	1.005	0.31	0.551	1.08	0.566	0.28	0.189	0.51	0.219
Isolation × size	2	0.14	0.058	1.33	0.957	0.31	0.179	0.85	0.784	1.14	0.535	0.85	0.408
Time × Size	1	0.49	0.200	3.18	2.286	0.24	0.138	0.08	0.070	0.23	0.109	1.10	0.528
Isolation × time × size	2	1.31	0.533	3.48*	2.500	3.05	1.795	0.57	0.522	1.43	0.669	0.89	0.427
Error	48		0.406		0.719		0.588		0.924		0.468		0.482

The factors were isolation (0, 2 and 10 m from contiguous habitat), patch size (one and five algal individuals) and collection time (5 and 10 days from the start of the experiment).

Data were numbers per g wet mass alga.

a Log transformed.

* Denotes a significant result (0.01 < P = 0.05).

** Denotes a significant result (0.001 < P = 0.01)

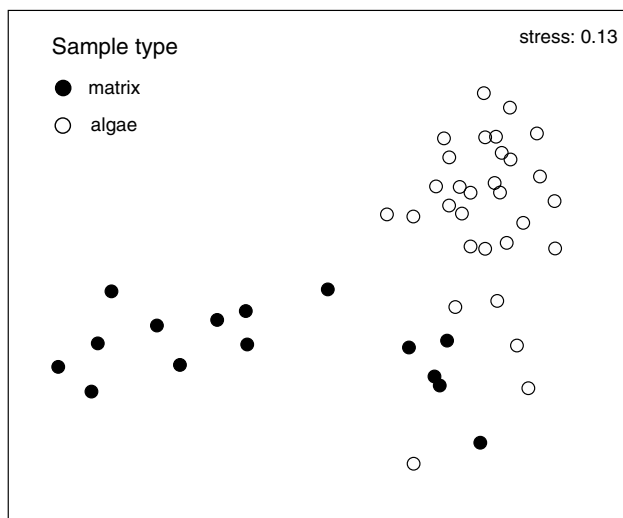


Fig. 3 – Nonmetric multi-dimensional scaling ordination of the samples from the matrix and algal habitats based on the composition of major taxonomic groups present in each (stress = 0.13).

Ampithoidae (40% and 15% of all amphipod individuals, respectively).

The abundance of isopods, ostracods, polychaetes and copepods within the matrix did not differ significantly among areas sampled from 0, 2 and 10 m from contiguous algal habitats (isopods: $F = 2.533$, $P = 0.121$, ostracods: $F = 2.600$, $P = 0.115$, polychaetes: $F = 1.649$, $P = 0.225$, copepods: $F = 0.864$, $P = 0.446$). This further supports the notion that the effects of habitat isolation observed in the above experiments for these taxa were not due to the matrix being a source of colonists to the algal habitats.

4. Discussion

4.1. Effects of varying patch size and isolation on algal epifauna

It is most often assumed that reductions in habitat patch size will result in reductions in the species richness and abundance of organisms associated with those habitats (Hill and Curran, 2003). In contrast to this prediction, reductions in the size of habitat patches of *S. linearifolium* were associated with either no effect on the invertebrates inhabiting this alga, or with increased abundances on smaller habitat patches. The effects of varying patch size differed among taxonomic groups and, for some taxa, between natural abundances and those recorded colonising patches in the manipulated landscape. While patch size did not affect taxonomic groups consistently, when an effect of patch size was found, invertebrates were always more abundant in small patches. Polychaetes were present at significantly higher abundance when sampled from naturally occurring small patches, while amphipods and ostracods colonised small experimental patches to significantly greater abundance in the patch size and isolation experiment. It must also be considered that attempts were not made to classify taxa to species, and that patch size effects at lower taxonomic levels may be masked.

These variable results are consistent with other marine studies which have found few predictable impacts of variation in patch size on the abundance of organisms in marine systems (Bell et al., 2001). The colonisation of the harpacticoid copepod *Scutellidium lamellipes* and the gammarid *Peramphithoe tea* has been shown to be reduced to small patches of the brown alga *Pelvetia fastigiata* (Gunnill, 1982). The prediction of reduced abundance with reduced patch size of seagrasses has been shown for species of infaunal bivalves (Irlandi, 1997) and for juveniles of the blue crab

Callinectes sapidus (Eggleston et al., 1998). Other manipulative experiments, however, have found greater colonisation of invertebrates to smaller habitat patches. Shrimps, amphipods and isopods have all been shown to be more abundant within smaller experimental patches of artificial seagrass and oyster reef habitats (Eggleston et al., 1998, 1999). These studies are comparable with the present study as they are short-term, small-scale experiments. Thus, our results add to the gathering evidence that simple patterns have not yet been identified as to the effects of patch size on organism abundance in marine systems.

In this study, isolation of habitat patches of *S. linearifolium* within the experimental landscape had a strong effect upon the abundance of isopods, which demonstrated greater colonisation to isolated patches (2 and 10 m) than patches in contact with contiguous algal stands. This result is consistent with that of Virnstein and Curran (1986) who demonstrated that epifaunal crustaceans rapidly colonised isolated artificial seagrass habitats to higher densities than contiguous habitats, and Tanaka and Leite (2004) who showed similar patterns for gammarid amphipods colonising *S. stenophyllum*. However, Gunnill (1982) found reduced colonisation of *S. lamellipes* and *P. tea* with distance from contiguous patches of *P. fastigiata*. For intertidal microgastropods, distance between patches of coralline algae was not found to affect colonisation (Olabarria, 2002).

Evidence from observational and experimental studies increasingly suggests that varying patch size and isolation has inconsistent impacts upon fauna (Fahrig, 2003; Grez et al., 2004). Despite expectations of negative impacts of reducing patch size and increasing isolation of patches, experimental studies in a wide range of habitats have shown positive, negative or no effects upon the abundance of organisms (Debinski and Holt, 1999). This variability in results to date may be attributable in part to the range of spatial and temporal scales over which such research has been conducted (Debinski and Holt, 1999). For example, research into the effects of habitat fragmentation has occurred across a wide variety of spatial scales, from regions (Fjeldsa, 1992) to cm (Wiens et al., 1997; Parker and Mac Nally, 2002; Williamson, 2003), and across temporal scales from days (Wiens et al., 1997) to millennia (Fjeldsa, 1992).

In contrast, existing marine research has taken place across much more uniform temporal and spatial scales. It is logistically difficult to replicate sampling across sub-tidal habitats on very large scales, and marine researchers have been largely limited to short-term, small-scale studies (Robbins and Bell, 1994). Even on these scales, however, patterns may vary with spatial scale. In this study, the discrepancy between the results of the sampling and manipulative approaches for some taxa (e.g., polychaetes) may be explained by variation in the sizes of habitat patches used in each approach. Natural patches sampled were much larger than those created experimentally in our artificial landscape. Further manipulative experiments in marine environments are required to establish how variation in the scales of habitat structure may impact benthic assemblages. Also needed are studies that test the effects of fragmenting existing habitats on marine assemblages, rather than creating artificial landscapes of known habitat configuration as was done

here and in similar previous research (Hovel and Lipcius, 2002).

4.2. Processes affecting abundance in habitat fragments

Variation in the effects of patch size and isolation on algal epifauna in this study, and more generally among existing studies, may arise from a wide range of processes affecting the abundance of organisms in patchy landscapes. These include those that affect the ability of organisms to disperse among habitat patches and their subsequent persistence once within patches. The rapid colonisation of experimental landscapes by epifauna provides a potentially powerful tool for assessing the relative importance of these mechanisms.

The structure of many subtidal habitats has been shown to affect water flows by attenuating strong currents (Bologna and Heck, 2000). These attenuated flows often facilitate an increase in the passive settlement of individuals within those habitats (Bologna and Heck, 2000). Landscape characteristics that alter local hydrodynamics may therefore affect supply of both larvae and passively dispersing animals (Bell et al., 2001; Tanner, 2003). For example, small patches with greater edge to centre ratios may attenuate currents more efficiently, enhancing the deposition of organisms to these patches (Bologna and Heck, 2000). Thus, structural aspects of patchy landscapes may alter the supply of organisms to an area, an important source of variation in the abundance and species composition of marine benthic assemblages (Underwood and Keough, 2001). Furthermore, the physical structure of habitats may covary with the degree of patchiness (Healey and Hovel, 2004). The use of artificial seagrass (Healey and Hovel, 2004), or in this study, the relocation of algal habitats from a consistent source allows for tests of patch size and isolation per se, that are not confounded by possible variation in within-patch habitat structure.

Virnstein and Curran (1986) proposed a “nearest refuge hypothesis” to explain increased abundances of fish and crustaceans observed on isolated habitat patches in seagrass beds. This hypothesis assumes that organisms disperse widely among habitat patches (predominantly at night) then return to the nearest possible suitable habitat for refuge. For organisms that have travelled some distance from suitable habitat, isolated clumps of habitat would provide the nearest refuge for more animals than less isolated patches (Virnstein and Curran, 1986). This hypothesis was derived from studying colonisation of artificial seagrass units by mobile invertebrate epifauna at distances of up to 15 m from seagrass beds. This is on a scale comparable to our own and therefore the abundance of isopods on isolated habitat patches is consistent with this process.

It is likely that the relationship between colonisation and isolation of habitat patches is dependent upon the scale of the habitat structure (Banks, 1998). While Virnstein and Curran's (1986) nearest refuge hypothesis may operate over scales comparable to the foraging range of the organism, increased isolation over much larger scales would be expected to limit colonisation. If ecologists are to formulate general theories from small scale experimentation, incorpo-

rating the spatial scale of habitat structure as a factor in their analyses may be a necessary approach (Banks, 1998).

In addition to processes affecting colonisation, variation in patch size and isolation may also alter post-colonisation processes such as rates of predation. Differences in predation pressure between fragmented and contiguous habitats may shape the responses of entire communities to habitat configuration (Irlandi, 1994; Hovel and Lipcius, 2002; Laurel et al., 2003). If predation pressure is enhanced at patch edges, small patches with a greater proportion of patch edge to interior habitat offer lower protection from predation than do large patches (Hovel and Lipcius, 2002). Alternatively, predators of benthic organisms in marine systems may aggregate within and concentrate foraging efforts upon larger patches (Connell and Anderson, 1999; Laurel et al., 2003). In this study system, the effects of fish predation on epifauna are unknown and the importance of predators in responses to fragmentation remains unresolved.

Finally, relationships between patch structure and the abundance of mobile epifauna could arise if the matrix was a source of potential colonists. Whilst patchy habitats are usually considered to consist of two habitats, patches and matrix, most studies have focused only upon abundances within habitat patches (Ricketts, 2001). Some evidence exists, however, to suggest that the structure of the matrix is also important in mediating responses to habitat patchiness (Ricketts, 2001). If functional isolation is to occur, the matrix must not be a significant source of colonists for habitat patches. The possibility of algal-associated invertebrates residing in the matrix was tested and disputed by directly sampling the matrix habitat, and therefore cannot explain the results of the colonisation experiment.

4.3. Conclusions

Many marine habitats may be fragmented through human activities such as coastal developments and recreational activities (Uhrin and Holmquist, 2003). Understanding the role of changes to habitat configuration in algal-dominated habitats is essential as these support diverse assemblages of associated fauna that provide trophic links between primary producers and predatory fish (Taylor, 1998). Using experimental techniques in a novel habitat, this study adds to existing evidence from seagrass beds that demonstrate variable responses of fauna to habitat structure. Effects of decreased patch size and increased isolation have varied in magnitude and among taxonomic groups, but when present have usually had positive effects upon densities of invertebrates.

This growing evidence from small-scale manipulative marine studies indicates that patchy habitats are not necessarily poor quality and that combinations of patchy and contiguous habitats may be required in a given area to maximise diversity, particularly if certain taxa demonstrate an affinity for isolated habitat patches (Healey and Hovel, 2004). The results of such research in marine habitats can help in identifying and prioritising areas in need of conservation, and in the design of potential restoration strategies (Eggleston et al., 1998). Experimental manipulation of habitat configuration is

a powerful tool that can guide the design of such strategies (Robbins and Bell, 1994; Bell et al., 2001).

Acknowledgements

Field work would not have been possible without the assistance of Graeme Clark and Nicole Hill. We thank Peter Banks, Emma Johnston and two anonymous reviewers for detailed comments that have improved this manuscript. All research was conducted with the permission of New South Wales Fisheries (Scientific Research Permit # P01/0047). This research was supported by the Australian Research Council Discovery Project DP0208481.

REFERENCES

- Banks, J.E., 1998. The scale of landscape fragmentation affects herbivore response to vegetation heterogeneity. *Oecologia* 117, 239–246.
- Bell, S.S., Brooks, R.A., Robbins, B.D., Fonseca, M.S., Hall, M.O., 2001. Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. *Biological Conservation* 100, 115–123.
- Bevers, M., Flather, C.H., 1999. Numerically exploring habitat fragmentation effects on populations using cell-based coupled map lattices. *Theoretical Population Biology* 55, 61–76.
- Bologna, P.A.X., Heck, K.L., 2000. Impacts of seagrass habitat architecture on bivalve settlement. *Estuaries* 23, 449–457.
- Bowden, D.A., Rowden, A.A., Attrill, M.J., 2001. Effect of patch size and in-patch location on the infaunal macroinvertebrate assemblages of *Zostera marina* seagrass beds. *Journal of Experimental Marine Biology and Ecology* 259, 133–154.
- Brawley, S.H., 1992. Mesoherbivores. In: John, D.M., Hawkins, S.J., Price, J.H. (Eds.), *Plant-animal interactions in the marine benthos*. Clarendon Press, Oxford, pp. 235–263.
- Connell, S.D., Anderson, M.J., 1999. Predation by fish on assemblages of intertidal epibiota: effects of predator size and patch size. *Journal of Experimental Marine Biology and Ecology* 241, 15–29.
- Debinski, D.M., Holt, R.D., 1999. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14, 342–355.
- Duarte, C.M., 2002. The future of seagrass meadows. *Environmental Conservation* 29, 192–206.
- Eggleston, D.B., Etherington, L.L., Elis, W.E., 1998. Organism response to habitat patchiness: species and habitat-dependent recruitment of decapod crustaceans. *Journal of Experimental Marine Biology and Ecology* 223, 111–132.
- Eggleston, D.B., Elis, W.E., Etherington, L.L., Dahlgren, C.P., Posey, M.H., 1999. Organism responses to habitat fragmentation and diversity: habitat colonization by estuarine macrofauna. *Journal of Experimental Marine Biology and Ecology* 236, 107–132.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecological and Evolutionary Systematics* 34, 487–515.
- Fjeldsa, J., 1992. Biogeographic patterns and evolution of the avifauna of relict high-altitude woodlands of the Andes. *Stenstrupia* 18, 9–62.
- Goodsell, P.J., Connell, S.D., 2002. Can habitat loss be treated independently of habitat configuration? Implications for rare and common taxa in fragmented landscapes. *Marine Ecology Progress Series* 239, 37–44.

- Greze, A., Zaviero, T., Tischendorf, L., Fahrig, L., 2004. A transient, positive effect of habitat fragmentation on insect population densities. *Oecologia* 141, 444–451.
- Gunnill, F.C., 1982. Macroalgae as habitat patch islands for *Scutellidium lamellipes* (Copepoda: Harpacticoida) and *Ampithoea* (Amphipoda: Gammaridae). *Marine Biology* 69, 103–116.
- Healey, D., Hovel, K.A., 2004. Seagrass bed patchiness: effects on epifaunal communities in San Diego Bay, USA. *Journal of Experimental Marine Biology and Ecology* 313, 155–174.
- Hill, J.L., Curran, P.J., 2003. Area, shape and isolation of tropical forest fragments: effects on tree species diversity and implications for conservation. *Journal of Biogeography* 30, 1391–1403.
- Holmlund, M.B., Peterson, C.H., Hay, M.E., 1990. Does algal morphology affect amphipod susceptibility to fish predation. *Journal of Experimental Marine Biology and Ecology* 139, 65–83.
- Hovel, K.A., Lipcius, R.N., 2002. Effects of seagrass habitat fragmentation on juvenile blue crab survival and abundance. *Journal of Experimental Marine Biology and Ecology* 271, 75–98.
- Irlandi, E.A., 1994. Large and small-scale effects of habitat structure on rates of predation: how percent coverage of seagrass affects rates of predation and siphon nipping on an infaunal bivalve. *Oecologia* 98, 176–183.
- Irlandi, E.A., 1997. Seagrass patch size and survivorship of an infaunal bivalve. *Oikos* 78, 511–518.
- Laurel, B.J., Gregory, R.S., Brown, J.A., 2003. Predator distribution and habitat patch area determine predation rates on Age-0 juvenile cod *Gadus* spp. *Marine Ecology Progress Series* 251, 245–254.
- Olabarria, C., 2002. Role of colonization in spatio-temporal patchiness of microgastropods in coralline turf habitat. *Journal of Experimental Marine Biology and Ecology* 274, 121–140.
- Parker, M., MacNally, R., 2002. Habitat loss and the habitat fragmentation threshold: an experimental evaluation of impacts on richness and total abundances using grassland invertebrates. *Biological Conservation* 105, 217–229.
- Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.L., Hereu, B., Milazzo, M., Zabala, M., D'Anna, G., Pipitone, C., 2000. Trophic cascades in benthic marine ecosystems: lessons from fisheries and protected-area management. *Environmental Conservation* 27, 179–200.
- Poore, A.G.B., 2004. Spatial associations among algae affect host use in a herbivorous marine amphipod. *Oecologia* 140, 104–112.
- Poore, A.G.B., 2005. Scales of dispersal among hosts in a herbivorous marine amphipod. *Austral Ecology* 30, 219–228.
- Poore, A.G.B., Steinberg, P.D., 1999. Preference-performance relationships and effects of host plant choice in a herbivorous marine amphipod. *Ecological Monographs* 69, 443–464.
- Poore, A.G.B., Watson, M.J., de Nys, R., Lowry, J.K., Steinberg, P.D., 2000. Patterns of host use among alga- and sponge-associated amphipods. *Marine Ecology Progress Series* 208, 183–196.
- Quinn, G.P., Keough, M.J., 2002. *Experimental design and data analysis for biologists*. Cambridge University Press, Cambridge.
- Ricketts, T.H., 2001. The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist* 158, 87–99.
- Robbins, B.D., Bell, S.S., 1994. Seagrass landscapes: a terrestrial approach to the marine subtidal environment. *Trends in ecology and evolution* 9, 301–304.
- Rostron, D.M., Survey, S., 2001. Procedural guideline No. 3–10: Sampling marine benthos using suction samplers. In: Davies, J., Baxter, J., Bradley, M., Connor, D., Khan, J., Murray, E., Sanderson, W., Turnbull, C., Vincent, M. (Eds.), *Marine Monitoring Handbook*, March 2001. Joint Nature Conservation Committee, UK, pp. 293–305.
- Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation, a review. *Conservation Biology* 5, 18–32.
- Shahidul Islam, M., Tanaka, M., 2004. Impacts of pollution on coastal and marine ecosystems including coastal and marine fisheries and approach for management: a review and synthesis. *Marine Pollution Bulletin* 48, 624–649.
- Shochat, E., Abramsky, Z., Pinshow, B., 2001. Breeding bird species diversity in the Negev: effects of scrub fragmentation by planted forests. *Journal of Applied Ecology* 38, 1135–1147.
- Tanaka, M.O., Leite, F.P.P., 2004. Distance effects on short-term recolonization of *Sargassum stenophyllum* by mobile epifauna, with an analysis of gammarid life habits. *Journal of the Marine Biological Association of the United Kingdom* 84, 901–910.
- Tanner, J.E., 2003. Patch shape and orientation influences on seagrass epifauna are mediated by dispersal abilities. *Oikos* 100, 517–524.
- Taylor, R.B., 1998. Short-term dynamics of a seaweed epifaunal assemblage. *Journal of Experimental Marine Biology and Ecology* 227, 67–82.
- Tscharntke, I.S., Kruess, A., Thies, C., 2002. Characteristics of insect populations on habitat fragments: A mini review. *Ecological Research* 17, 229–239.
- Uhrin, A.V., Holmquist, J.G., 2003. Effects of propeller scarring on macrofaunal use of the seagrass *thalassia testudinum*. *Marine Ecology Progress Series* 250, 61–70.
- Underwood, A.J., Keough, M.J., 2001. Supply-side ecology: The nature and consequences of variations in recruitment of intertidal organisms. In: Bertness, M.D., Gaines, S.D., Hay, M.E. (Eds.), *Marine Community Ecology*. Sinauer Associates Inc., Massachusetts, pp. 183–200.
- Virnstein, R.W., Curran, M.C., 1986. Colonization of artificial seagrass versus time and distance from source. *Marine Ecology Progress Series* 29, 279–288.
- Walker, D.I., Kendrick, G.A., 1998. Threats to macroalgal diversity: marine habitat destruction and fragmentation, pollution and introduced species. *Botanica Marina* 41, 105–112.
- Wiens, J.A., 1995. Landscape mosaics and ecological theory. In: Hansson, L., Fahrig, L., Merriam, G. (Eds.), *Mosaic Landscapes and Ecological Processes*. Chapman & Hall, London, pp. 1–26.
- Wiens, J.A., Schooley, R.L., Weeks Jr., R.D., 1997. Patchy landscapes and animal movements: do beetles percolate. *Oikos* 78, 257–264.
- Williamson, M., 2003. Species-area relationships at small scales in continuum vegetation. *Journal of Ecology* 91, 904–907.
- Zschokke, S., Dolt, C., Rusterholz, H., Oggier, C., Braschler, B., Thommen, G.H., Lüdin, E., Erhardt, A., Baur, B., 2000. Short-term responses of plants and invertebrates to experimental small-scale grassland fragmentation. *Oecologia* 125, 559–572.