Complexity in the relationship between matrix composition and inter-patch distance in fragmented habitats

P. J. Goodsell · S. D. Connell

Abstract The connectivity of fragmented landscapes is a function of the physical distance between suitable habitats and the characteristics of the habitat through which the animal is moving, i.e. the matrix. Experimental manipulations done to explain how spatial arrangement and composition of habitats affects biota remain scarce, particularly in marine systems. Holdfasts of the common kelp, *Ecklonia radiata*, are discrete units of habitat for small invertebrates (e.g. amphipods, isopods, molluscs, annelids) that can be isolated from other holdfasts by habitat, which may be less suitable (e.g. other species of algae or relatively bare space). We compared assemblages, which colonised defaunated holdfasts in experimentally created small-scale landscapes where patches of habitat (holdfasts) were distant versus close together and which had *Sargassum* spp. versus relatively bare space in the matrix. We also compared colonisation across matrices of crushed fucoid algae to assess whether the structural or chemical nature of algae in the matrix had the most influence on the colonisation. Assemblages in defaunted holdfasts differed between those that were close to and those that were distant from undisturbed holdfasts, where the matrix was devoid of vegetation.

Where *Sargassum* spp. was present in the matrix, however, this difference disappeared and was possibly due to the chemical, rather than structural, characteristics of the fucoid matrix. The extent to which matrix habitat is a barrier to movement of invertebrates among holdfasts thus depends on not only how extensive it is but what type of habitat it contains. As within terrestrial systems, the nature of the matrix is also likely to be a fundamental component of the connectivity within marine systems.

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Introduction

The fragmentation, or break up, of continuous habitat inevitably results in unsuitable or less suitable habitat separating remnant patches of suitable habitat by varying distances (Fahrig 2003). Isolated patches of habitat can, however, remain connected within fragmented landscapes because they are neither too distant nor the intervening environment impermeable. Our challenge, if we are to understand the consequences of habitat fragmentation, is to detect the components of landscape pattern that facilitate (or hinder) the persistence of populations via dispersal among and colonisation of remnant habitats (Henle et al. 2004; Tischendorf et al. 2005).

The persistence of populations in discrete patches of habitat requires that rates of immigration are sufficient to overcome local extinction in patches of habitat (in addition to successful reproduction; MacArthur and Wilson 1967; Brown and Kodric-Brown 1977). Biodiversity is threatened in fragmented landscapes because greater mortality is associated with travelling larger distances through relatively inhospitable habitat to utilise or supplement resources in remnant patches (Andrén 1994; Hanski et al. 2000). Historically, the extent to which remnant habitats are available to

organisms and thus the structural connectivity of the landscape, was assessed using measures of distance between remnant habitats (e.g. from a metapopulation approach; Hanski 1994). It is now realised that the structural connectivity of fragmented landscapes is likely to be affected by the characteristics of the surrounding landscape; i.e. the matrix (Taylor et al. 1993; Ricketts 2001; Murphy and Lovett-Doust 2004). The type of habitat and its suitability, or lack thereof, in the matrix can determine the ease at which animals are able to move among the landscape. The matrix can be a barrier to colonisation because movement among fragmented habitats is physically impeded (e.g. Johnson et al. 1992). Alternatively, colonisation of distant habitats may be facilitated because the matrix provides structure similar to the primary habitat (e.g. Gascon et al. 1999). It is likely, therefore, that connectivity of fragmented landscapes is not only a function of the distance among primary habitats but is also a function of the nature of the matrix through which animals disperse.

Marine systems are thought to have greater connectivity than terrestrial systems because the fluid medium promotes dispersal and recruitment. That said, terrestrial plants with propagules and flying animals which disperse through the air (another fluid medium) have been shown to be affected negatively by experimental fragmentation of their habitat (Freemark and Merriam 1986; Collinge and Forman 1998; Murphy and Lovett-Doust 2004). Indeed, there is a growing body of literature, which shows that marine organisms are affected by the fragmentation of their habitat (Eggleston et al. 1999; Bell et al. 2001; Goodsell and Connell 2002; Roberts and Poore 2006; Tanner 2006). The current experiment was done within forests of kelp, which support a diverse suite of marine fauna (Witman and Dayton 2001) and are increasingly threatened by human development in Australia (Connell 2007). The common kelp *Ecklonia radiata* is particularly conspicuous and widespread across temperate Australia (Goodsell et al. 2004). Understanding how the spatial configuration and composition of habitat influences ecological patterns and processes should be done not at scales relevant to human perception, but at the scale appropriate to the movement of organisms across its landscape (e.g. Wiens and Milne 1989; Collinge and Forman 1998). Individual holdfasts of *E. radiata* form discrete "patch" habitats for a diverse assemblage of invertebrates (including crustaceans, polychaetes, molluscs and echinoderms) (Smith et al. 1996). Many of these invertebrates are highly mobile exhibiting rapid exchange of individuals across small spatial scales (Gunnill 1982a; Howard 1985; Virnstein and Curran 1986) and most species of holdfast fauna move among kelps rather than remain associated with one individual plant (Edgar 1991; Norderhaug et al. 2002).

We tested the hypothesis that colonisation of patches of habitat (close versus distant) is affected by the nature of the intervening matrix (alternate vegetation versus relatively bare space). Two main types of matrix between individuals of *E. radiata* can occur in fragmented forests: (1) canopy-forming species of fucoid algae (e.g. *Sargassum* spp.) and (2) relatively bare substrata lacking canopy-forming macro-algae (>20 cm in height). Holdfasts of *Sargassum* spp. are solid, discoid and relatively small and as such, should be less suitable as habitat for invertebrates, which use the complex and branched holdfasts of *E. radiata* as habitat. In addition, differences in plant chemistry between laminarian *E. radiata* and fucoid *Sargassum* spp. could affect the suitability of this habitat (e.g. Poore and Steinberg 1999), hence we assessed whether the structural or chemical nature of algae in the matrix had the most influence on the colonisation of fragmented habitats. Relatively bare space is predicted to be even less suitable as habitat because it is mostly devoid of suitable habitat. We predicted that the presence of vegetation in the matrix between habitats would better facilitate colonisation compared to matrices of bare space. Hence, assemblages that colonise close habitats would be similar to those that colonise distant habitats when alternate vegetation exists in the matrix, but not when the matrix is bare.

Methods

Study site

The current experiment was done in forests of *E. radiata* at Edithburgh, South Australia (35°5′S, 137°45′E) at depths of 3–6 m in Austral summer 2002 (Fig. 1). The forest was at an average depth of 3–6 m and the experiment was done in dense (>5 individuals per m²), monospecific stands (>80% of the canopy was *E. radiata*). Experimental plots were chosen to be 1 m² because of known experimental effects of the structure of *E. radiata* canopies measured at this scale on invertebrates within holdfasts (Goodsell and Connell 2002). The substratum was limestone covered with encrusting-coralline red algae, hereafter referred to as relatively bare substratum cf substratum covered with holdfasts of *E. radiata* or *Sargassum* spp.

Manipulation of matrix cover and distance between habitats

Using SCUBA, experimental plots (1 m × 1 m) were randomly assigned to monospecific areas of *E. radiata* and permanently marked. A central individual (target sample) was chosen in the centre of each plot and temporarily marked with flagging tape. Surrounding individuals of *E. radiata* were then removed to standardise density within each plot at 5 plants per m² based on previous results that invertebrates respond to fragmentation of *E. radiata* to this
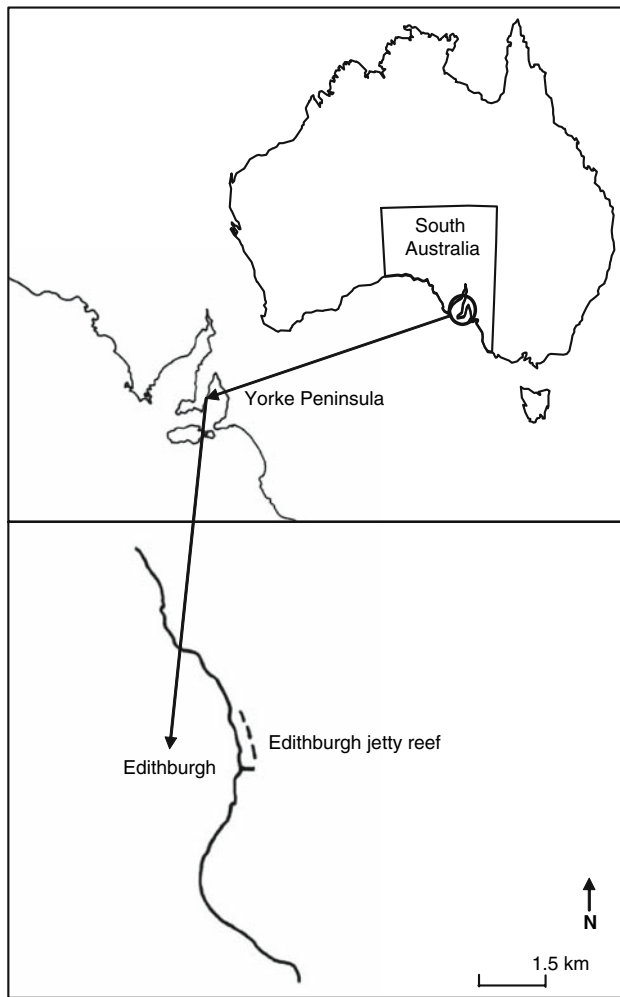
Fig. 1 Map of study site at *E. radiata* at Edithburgh, South Australia, Australia

amount (Goodsell and Connell 2002). To assess the effect of the matrix distance on colonisation, thinning was done so that the central individual was separated from all neighbouring habitats of *E. radiata* by either "distant" (>20 cm) or "close" (<10 cm) distances. Whilst such distances may appear to be small, separation of habitat at this scale has been shown to be sufficient to change the structure of assemblages of invertebrates in holdfasts of *E. radiata*; i.e. this is the spatial scale at which these organisms respond to features of the landscape (Goodsell and Connell 2002). A total of 48 plots were set up; *n* = 24 plots for each distance.

The volume of kelp holdfasts is known to affect the diversity of the associated assemblages (Smith et al. 1996) so central individuals were chosen to be of similar size and the volume of holdfasts (done during final sampling) were not different from one another (ANOVA; $F_{3,40} = 1.2$, $P > 0.05$). Only central individuals were removed for defaunation by carefully levering the holdfast from the substratum with a spatula. These individuals were then taken to

the surface and the holdfast was immersed in a 1% solution of formalin and freshwater. This procedure adapted from Gunnill (1982a) and Poore (2004) effectively removes invertebrates and does not damage the alga nor affect the behaviour of colonising invertebrates (see also Edgar 1992). Holdfasts were then kept in aerated seawater for 24 h to remove any traces of formalin or freshwater. Individuals were attached to a plastic mesh grid (15 cm × 15 cm with a mesh size of 25 mm) using several small cable ties wrapped around the haptera of the holdfast and re-attached to the substratum in the experimental plots by hammering small metal stakes through the grid into the substratum.

We compared assemblages that colonised defaunated holdfasts separated from undisturbed holdfasts by a matrix of bare space (mostly no habitat) or an alternate, but less suitable habitat of fucoid algae (*Sargassum* spp.). To do this, we collected individuals of *Sargassum* spp. from nearby areas of the forest and attached these to mesh grids using small cable ties attached around the stipe. These were rinsed in freshwater to remove any invertebrates so that reinvasion was not confounded by taxa more commonly associated with the matrix than the primary habitat, *E. radiata*. *Sargassum* spp. were then "planted" between the defaunated individual of *E. radiata* and the surrounding *E. radiata* in the six plots where *E. radiata* were "close" together and six plots where *E. radiata* were "distant". In another six of each of the "close" and "distant" arrays, the matrix was left relatively bare (Fig. 2).

To distinguish between the effects of the physical structure of the fucoid matrix and its chemistry, we crushed whole individuals of defaunated *Sargassum* spp. using a pestle and mortar at the sea surface and placed the crushed tissue in fine meshed cloth bags (one individual per bag). These bags were attached to the plastic grids and put between the defaunated individual of *E. radiata* and the surrounding *E. radiata* in the experimental plots, again in six of the "close" and "distant" arrays. Empty cloth bags were attached to plastic grids and put between the defaunated *E. radiata* and its neighbours in six of each of "close" and "distant" arrays as a procedural control for the cloth bags. Every treatment contained plastic grids (all defaunted holdfasts were attached to a grid) such that a procedural control for the plastic grid was unnecessary.

We predicted that the assemblages, which colonised the vacant holdfast would differ depending on how far (close vs. far) and through what matrix (fucoid vs. crushed fucoid vs. bare) they migrated from holdfasts of the surrounding *E. radiata* (Fig. 2). All plots were interspersed within the same forest, such that each experimental plot was surrounded by similar amounts of *E. radiata*. Recolonisation of invertebrates to vacant habitats can be very rapid (within days) and little changes occur in the structure of assemblages

Fig. 2 Diagram representing the experimental 1 m × 1 m plots. The primary habitat, a central individual of *E. radiata* (*filled circle*) was "distant" and "close" to all other *E. radiata* (*open circle* holdfasts). The matrix was "planted" with fucoid algae (*open diamond*), crushed fucoid algae (*multi symbol*), control (*open square*) or left relatively bare. Colonisation into the defaunated central holdfast was measured
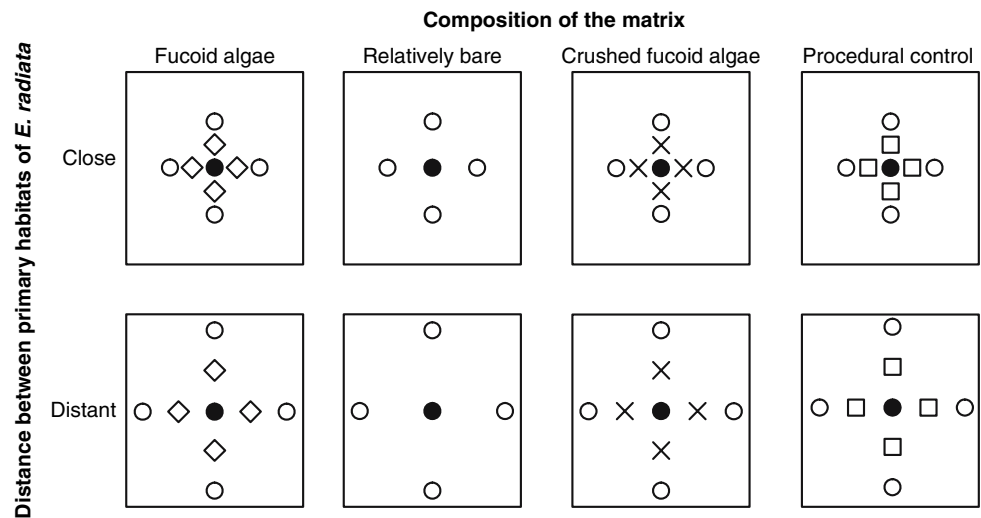
thereafter (Howard 1985; Virnstein and Curran 1986; Edgar 1992). So, the experiment was left for three days to allow for sufficient colonisation but reduce the effect of other post-colonisation processes occurring once individuals arrived in the new habitat such as competition. The central individual of *E. radiata* was sampled by cutting the fronds from the holdfast at the stipe and quickly sealing a plastic bag to the substratum over the holdfast that was then levered off the substratum and the bag enclosed around it. Each sample was fixed in 10% formalin/seawater solution. Holdfasts were dissected and the fauna separated through a 0.5 mm sieve. Identification of the mobile fauna was formally done to the level of family because further taxonomic resolution was time-consuming or the taxonomy unknown. Many studies on similar organisms have shown that coarser levels of resolution show similar patterns to that fine (Chapman 1998; Gray et al. 1998).

Analytical methods

Differences in the average composition and relative abundance of taxa number of taxa colonising holdfasts among the different treatments were analysed using a 2-factor fixed model PERMANOVA (formerly NP-MANOVA; Anderson 2001, 2005). This analysis partitions the variance in multivariate dissimilarity measures, producing a pseudo *F*-ratio with a permuted null distribution. Our hypotheses predicted differences among certain, but not all treatments, so planned post hoc comparisons were done where differences were significant in the initial analysis. A non-metric multidimensional scaling plot was done to provide a visual assessment of the effects of matrix composition and inter-patch distance on the structure of assemblages in each treatment. This was done on the centroids of each group because our hypothesis was about the average difference among treatments. Distances between points on the plot

correspond to dissimilarities between the centroids of each treatment (Clarke 1993).

In addition to the abundances and frequencies of taxa, we also tested for differences in the number of taxa among treatments using ANOVA. Where significant differences were detected, Student–Newman–Keuls tests were used post hoc to define among, which group differences existed.

Results

Overall we found 41 families from 6 different phyla. An average of 10 families and 69 individuals colonised a single holdfast (sample). This is consistent with the fauna found in holdfasts of similar volume, which have not been modified (Goodsell and Connell 2002; Goodsell et al. 2004) suggesting that the assemblages in our samples were representative of those, which occur naturally. The most frequent and numerous fauna were amphipods (e.g. lysianassids, colomastigids, aroids and hyalids) and isopods (e.g. limnorids and gnathids). Polychaetes, nematodes, ostracods, gastropods and chitons were also present in the colonising fauna. For a list of fauna often found in the holdfasts of *E. radiata* in South Australia see Goodsell and Connell (2005).

A significant interaction between the type of matrix and the distance between habitats was detected for the composition and relative abundance of taxa, which colonised vacant holdfasts (Table 1, Fig. 3). Planned comparisons were done post hoc to compare the structure of assemblages colonising close habitats to those colonising distant habitats when the matrix was: (1) fucoid versus bare to test for the effect of fucoid algae in the matrix, (2) fucoid versus crushed fucoid to test whether an effect of fucoid algae is due to chemistry or structure and (3) crushed fucoid algae versus the control (empty bags) to test for experimental artefacts. Fauna that colonised holdfasts with the empty bag matrix

Table 1 Results of PERMANOVA testing the relative and interactive effects of the distance between habitats (close and distant) and the matrix separating habitats (bare, fucoid algae, crushed fucoid algae, control) on the composition and relative abundance of invertebrates

PERMANOVA	df	MS	F	P
Proximity	1	128.0	5.2	**
Matrix	3	35.9	1.5	0.09 (NS)
Proximity × Matrix	3	40.6	1.7	*
Residual	40	24.5		
Pairwise comparisons			t	P
Close versus distant	Bare matrix		1.8	***
	Fucoid matrix (FM)		1.4	0.05 (NS)
	Crushed fucoid matrix (CFM)		2.2	**
Bare versus FM	Close habitats		1.7	*
	Distant habitats		1.1	NS
FM versus CFM	Close habitats		1.3	NS
	Distant habitats		1.4	0.06 (NS)
Empty bag versus CFM	Close habitats		1.4	NS
	Distant habitats		1.3	NS

Gower's distance measures were used (Gower 1971). Data was fourth root transformed to provide more a more equal weighting of numerically less and more dominant taxa (Clarke 1993). Those pairwise comparisons, which are relevant to the hypotheses (planned a priori) are given for the significant interaction term

NS: $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

were similar to those that colonised holdfasts within the crushed fucoid matrix in close (PERMANOVA; $t = 1.4$, $P > 0.05$) and distant ($t = 1.3$, $P > 0.05$) arrays suggesting that the presence of the cloth bag did not affect colonisation.

Assemblages in distant habitats were different to those in close habitats when the matrix was bare. The presence of fucoid algae in the matrix, however, caused assemblages in close habitats to be more similar to those in distant habitats (Fig. 3, Table 1). Post hoc comparisons also showed that assemblages differed between bare matrices and fucoid matrices when habitats were close together but not when they were distant. No differences were detected between assemblages colonising distant or close habitats surrounded by fucoid matrices (Fig. 3, Table 1). Interestingly, assemblages which colonised close habitats were different to those that colonised distant habitats when the matrix was crushed fucoid algae (Table 1). The average dissimilarity within groups (i.e. the within-group variability) was negligible for all treatments (ranging from 4 to 9%).

The type of matrix had no significant effect on the number of taxa colonising vacant holdfasts (Table 2). ANOVA did, however, detect greater number of families in habitats that were distant than in those that were close together (Table 2, Fig. 4). Few differences (ANOVA: $P > 0.05$)
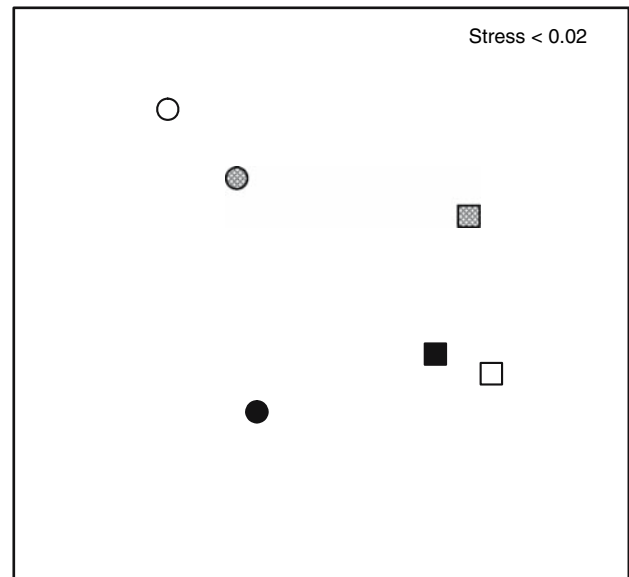

Fig. 3 nMDS plot of the average composition and relative abundance of taxa from close (*circles*) and distant (*squares*) habitats with different types of matrix. *Open symbols* represent samples with bare matrix between suitable habitats, *filled symbols* represent samples from habitats with a matrix of fucoid algae, and *shaded symbols* represent samples with a matrix of crushed fucoid algae

were detected between treatments by analysis of variance on the family richness and abundance of main groups of taxa (e.g. amphipods, echinoderms and molluscs). Some families (e.g. isopods and annelids) did, however, show similar results to analysis of the total the number of taxa, i.e. that there were a greater number of these taxa in distant than in close habitats regardless of the type of matrix (ANOVA: $P < 0.05$). Families, which contributed the most (>5%) to differences between close and far habitats with bare matrices (and to differences between habitats with fucoid and bare matrices where habitats were close) were ostracods, sipunculids, isopods, annelids and gammarid amphipods (Table 3). No differences were, however, detected in the individual abundance of these taxa among treatments (ANOVA: $P > 0.05$), with the exception of nematodes, which colonised close habitats in significantly greater abundance than far habitats regardless of the type of matrix (ANOVA: $P < 0.05$).

Discussion

Few habitats are truly isolated (Wiens 1992) and the nature of the matrix between remnant patches of habitat plays an important role in the connectivity of fragmented landscapes (Taylor et al. 1993; Ricketts 2001; Bender and Fahrig 2005). The isolation of habitats-by-distance remains an influential determinant of dispersal among animal populations in fragmented habitats. Yet, distance does not act

Table 2 Results of ANOVA testing for differences in the number of taxa in habitats separated by different distances (close vs. distant) and matrices of (1) fucoid algae, (2) crushed fucoid algae, (3) bare and (4) control

Source of variation	df	MS	F	P
Proximity	1	111.0	7.9	***
Matrix	3	2.9	0.2	ns
Proximity × Matrix	3	13.2	0.9	ns
Residual	40	14.1		

"Proximity" and "Matrix" were treated as fixed factors and orthogonal. Variance values were homogenous at $P > 0.05$ (Cochran's C test)

NS: $P > 0.05$, *** $P < 0.05$

independently of the nature of the matrix within fragmented landscapes. Our results suggest that when the matrix is very different to the primary habitat (i.e. relatively bare space), the distance between habitats exert strong effect on the colonisation of fragmented habitats.
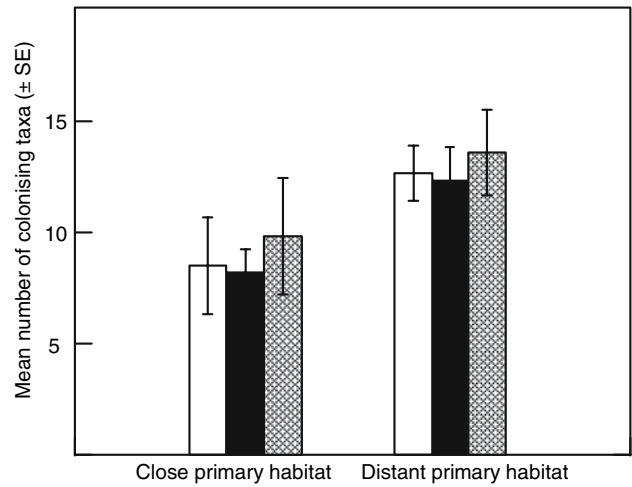

Fig. 4 The number of taxa (taxonomic richness ± SE) in close and distant habitats separated by different types of matrix. *Open bars* represent samples with bare space in the matrix, *filled bars* represent samples from habitats with a matrix of fucoid algae and *shaded bars* represent samples with a matrix of crushed fucoid algae

Table 3 The percentage contribution of taxa (>5%) to differences between close and distant holdfasts with fucoid, crushed fucoid and bare matrices

		Close Crushed Fucoid	Close Bare	Distant Fucoid	Distant Crushed Fucoid	Distant Bare
Close Fucoid		**NS** Ostracoda 10 Lysianssidae 8 Paratanaidacea 8 Colomastigidae 5 Limnoridae 5 Maldanidae 6	**46 %** Ostracoda 13 Paratanaidacea 7 Nematoda 6 Hyalidae 5 Limnoridae 5 Lysianssidae 5 Melitidae 5 Nereididae 5 Sipuncula 5	**NS** Melitidae 10 Colomastigidae 8 Hyalidae 8 Lysianssidae 8 Aoridae 6 Corophiidae 5 Jaeropsidae 5 Paratanaidacea 5 Eunicidae 5 Maldanidae 5	N/A	N/A
	Close Crushed Fucoid	N/A	N/A	**71 %** Lysianssidae 16 Ostracoda 9 Colomastigidae 5 Hyalidae 7 Melitidae 7 Paratanaidacea 7	N/A
	Close Bare	N/A	N/A	**64 %** Ostracoda 12 Lysianssidae 10 Melitidae 8 Limnoridae 5 Maldanidae 5 Sipuncula 5
	Distant Fucoid			**NS** Melitidae 11 Corophiidae 8 Aoridae 7 Anthuridae 7 Jaeropsidae 7 Paratanaidacea 6 Colomastigidae 5 Lysianssidae 5 Eunicidae 5	**NS** Melitidae 9 Colomastigidae 8 Hyalidae 7 Jaeropsidae 7 Aoridae 6 Anthuridae 5 Paratanaidacea 5
	Distant Crushed Fucoid				N/A

NS no significant difference between groups ($P > 0.05$), *NA* comparisons not relevant to the hypotheses

Assemblages colonising close and distant habitats were different only when the matrix contained crushed, but not intact, fucoids. This suggests that the chemical nature of the fucoid matrix may be more important than the structural characteristics. Many authors are aware that the morphology of plants is often correlated with variation in the diversity and abundance of fauna (e.g. Taylor and Cole 1994), yet our results support concerns that the qualitative aspects of plant identity may play a major role in the dynamics of animal populations (i.e. the idiosyncratic hypothesis; Lawton 1994; Parker et al. 2001). Indeed, Poore (2004) showed that rates of colonisation to macroalgal habitat was affected by the identity of the surrounding algae. We add to the understanding that the matrix does matter (Ricketts 2001; Vandermeer and Carvajal 2001; Murphy and Lovett-Doust 2004; Tanner 2006) and suggest that detailed physicochemical properties of the matrix may need to be known to better understand the ways animals use fragmented landscapes.

We were surprised that the nature of the matrix was only important when habitats were close together, yet this result supports the notions that the matrix may be particularly important when sources of immigrants are close by (Ås 1999). Many species are capable of using the matrix as habitat (Gascon et al. 1999) even when the surrounding matrix is much less suitable than the source habitat (e.g. urban matrices; Brown et al. 2006; Goodsell et al. 2008). Moreover, the nature of the matrix may not be an important factor for invertebrates capable of dispersal over large distances. Surprisingly, assemblages that colonised close habitats separated by a matrix of fucoid algae resembled those that colonised habitats situated further apart (regardless of the type of matrix). It seems plausible that particular assemblages of invertebrates are more strongly associated with isolated habitats or those, which have alternate vegetation in matrices between habitats. Little is known about the life-history characteristics of taxa that inhabit holdfasts such that it is difficult to discuss the mechanisms behind individual responses to modification and fragmentation of their landscapes. Nonetheless, most of the fauna that colonised vacant holdfasts were crustacean taxa (brooders with adult dispersal) and those that appeared in most replicates of most treatments (common) were small-bodied and compact individuals with large shield like coxae (e.g. Lysianassidae, Colomastigidae). This body shape is notable for its resistance to buffeting from wave action (Yassini et al. 1995) and capacity for dispersal (Franz and Mohamed 1989), which could explain their ability to colonise isolated habitats. Because surrounding holdfasts (source habitats) were unmodified, it is unlikely only a subset of the total available pool (i.e. only highly mobile taxa) colonised holdfasts in the current study.

That we found a greater number of invertebrate taxa in isolated holdfasts suggests that diversity of these assemblages is not suppressed by increasing distance between habitats. Gunnill (1982b) and Virnstein and Curran (1986) reported greater abundance of invertebrate taxa in habitats that were distant from each other compared to aggregated habitats. Whilst many of these fauna are very mobile (amphipods, isopods, etc.), Virnstein and Curran (1986) propose "the nearest refuge hypothesis" that motile invertebrates disperse over areas of non-habitat (bare) and then concentrate in isolated habitats because habitats in isolation are the nearest available refuge (see also Edgar 1992; Holmquist 1998). Processes affecting dispersal and migration of invertebrates in fragmented landscapes are no doubt complex and await further testing in the field. For example, the primary mode of transport between habitats for organisms that can swim and crawl should be investigated (e.g. Taylor 1998). Nonetheless, as is the case in terrestrial systems (Fahrig 2002; Lee et al. 2002), the effects of fragmentation for marine systems are as likely to be positive, as they are negative.

Experiments necessary to uncover the effects of fragmented landscapes on biodiversity are often difficult because of ethical concerns associated with the manipulation of landscape pattern at scales appropriate to organisms with large ranges of dispersal (McGarigal and Cushman 2002). Given that small animals perceive their landscape at small scales, experiments done within so-called "microlandscapes" are particularly useful to gain an understanding about how the elements of a landscape (e.g. matrix composition and isolation of remnant habitat) influence ecological patterns and processes in the associated fauna (Wiens and Milne 1989). Indeed, the chief concepts of landscape ecology should apply to any landscape regardless of its spatial scale because landscapes should be defined at the scale relevant to the organism, rather than some human perspective (Wiens 2002).

In the current study, the distance between remnant kelp habitats on invertebrate diversity was dependent on the nature of the matrix. The matrix was particularly important when animals disperse small distances between fragmented habitats. Sustainability of biodiversity in fragmented landscapes relies on connectivity among remnant patches and their relative isolation was in the current study, and may indeed be for other systems, a product of distance and the nature of the intervening matrix.

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