

Is habitat amount important for biodiversity in rocky shore systems? A study of South African mussel assemblages

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Abstract Habitat-forming species on rocky shores are often subject to high levels of exploitation, but the effects of subsequent habitat loss and fragmentation on associated species and the ecosystem as a whole are poorly understood. In this study, the effects of habitat amount on the fauna associated with mussel beds were investigated, testing for the existence of threshold effects at small landscape scales. Specifically, the relationships between mussel or algal habitat amount and: associated biodiversity, associated macrofaunal abundance and density of mussel recruits were studied at three sites (Kidd's Beach, Kayser's Beach and Kini Bay) on the southern and south-eastern coasts of South Africa. Samples, including mussel-associated macrofauna, of 10 × 10 cm were taken from areas with 100 % mussel cover (*Perna perna* or a combination of *P. perna* and *Mytilus galloprovincialis*) at each site. The amount of habitat provided by mussels and algae surrounding the

sampled areas was thereafter determined at the 4.0 m² scale. A number of significant positive relationships were found between the amount of surrounding mussel habitat and the abundances of several taxa (Anthozoa, Malacostraca and Nemertea). Likewise, there were positive relationships between the amount of surrounding algal habitat and total animal abundance as well as abundance of mussel recruits at one site, Kini Bay. In contrast, abundance of mussel recruits showed a significant negative relationship with the amount of mussel habitat at Kayser's Beach. Significant negative relationships were also detected between the amount of mussel habitat and species richness and total abundance at Kidd's Beach, and between amount of mussel habitat and the abundance of many taxa (Bivalvia, Gastropoda, Maxillopoda, Ophiuroidea, Polychaeta and Pycnogonida) at all three sites. No threshold effects were found, nor were significant relationships consistent across the investigated sites. The results indicate that the surrounding landscape is important in shaping the structure of communities

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associated with these mussel beds, with significant effects of the amount of surrounding habitat per se. The strength and the direction of habitat effects vary, however, between shores and probably with the scale of observation as well as with the studied dependent variables (e.g. diversity, abundance, mussel recruitment, species identity), indicating the complexity of the processes structuring macrofaunal communities on these shores.

Introduction

Ecosystems are subject to constant change and, occasionally, drastic shifts in community structure and function to an irreversible state may occur over a short period of time (e.g. Carpenter 2001; Muradian 2001; Scheffer et al. 2001). Such shifts can be characterized by threshold values of certain independent variables beyond which the dependent variables (e.g. abundance of a species or species diversity) change abruptly. An example would be changes in habitat amount. Species require specific environmental conditions in order to survive in an area, and such conditions will generally occur in relatively discrete parts of the environment, or patches. Habitat amount can then be defined as the proportion of the environment that is habitable within the mosaic of all patches that forms a landscape (Dunning et al. 1992; Fahrig 2001, 2003; Flather and Bevers 2002). Thus, habitat amount is estimated at a landscape scale, in contrast to the patch scale, e.g. at small, medium or large landscape scales. Biodiversity is expected to depend on the amount of suitable habitat in a landscape (Fahrig 2001, 2003), but the matrix or non-habitat surrounding habitable patches can also be important and can be estimated at the same scales. This is important because qualities of the matrix and the level of habitat fragmentation can affect the biodiversity and other properties of a given patch by influencing survival and fecundity as well as migration among habitat patches (Fahrig 2001; Goodsell and Connell 2008; Matias 2013). In theory, fecundity, migration and survival in the matrix influence the occurrence and nature of a possible threshold effect in the relationship between habitat amount and abundance, with the steepness of the curve affected by habitat fragmentation (Fahrig 2001). The effects of habitat fragmentation are commonly studied in terrestrial habitats (e.g. Andrén 1994; Fuhlendorf et al. 1996). Positive and negative relationships are known to occur between biodiversity and ecosystem functioning (Naeem et al. 1994; Tilman 1996; Kraufvelin et al. 2010), though most studies suggest a positive relationship between species richness and ecosystem stability (Prins et al. 1998; Gutiérrez et al. 2003; Hooper et al. 2005; Kiessling 2005; Ieno et al. 2006; Wahl et al. 2011), so that alterations to biodiversity may cause major changes to ecosystem functioning. Despite

being an important topic in terrestrial systems, few marine studies have focused on the consequences of habitat loss or fragmentation (e.g. Bell et al. 2001; Caley et al. 2001), and here the effects of habitat amount at small landscape scales are considered, including the possibility of threshold effects in the relationship between habitat amount and abundance/biodiversity.

In benthic marine systems, mussels are important through their enhancement of biodiversity by providing complex, heterogeneous habitats for a diverse range of fauna (Seed 1996; Kostylev 1996; Kostylev and Erlandsson 2001; Borthagaray and Carranza 2007). By modifying the habitat in both autogenic and allogenic ways, mussels affect nutrient levels, boundary layer characteristics, amount of organic matter and many other physical characteristics of the local environment (Seed 1996; McQuaid et al. 2000; Gutiérrez et al. 2003; Sousa et al. 2009; Zaiko et al. 2009). Within intertidal mussel beds, light intensity, temperature and water movement are reduced, while sediment accumulation and relative humidity are increased compared to neighbouring rock substrata (Menge and Branch 2000; Nicastró et al. 2012). Mussel habitats also increase the benthic surface area available for colonization (Seed 1996; Gutiérrez et al. 2003; Kostylev et al. 2005). Many microhabitats, resources and niches are thus offered by mussel beds and different species may coexist within them, contributing to the further diversification of these assemblages (Kostylev 1996; Gutiérrez et al. 2003; Kostylev et al. 2005). Earlier studies have shown that bigger patches of mussels support a higher biodiversity up to a maximum size, after which an asymptote is reached, i.e. equivalent to the species–area curve (Cain 1938; Seed 1996; Pettersson 2006; Norling and Kautsky 2008; Koivisto et al. 2011). Studies of the species–area relationship for mussel-associated invertebrates generally focus on the size of the clump examined (patch scale) (Peake and Quinn 1993), but do not consider the nature of the neighbouring habitat, i.e. the patch context. Consequently, it is not known whether a greater amount of mussel habitat surrounding a given mussel patch results in greater biodiversity, species richness, abundance or specific species compositions in the patch sampled. Additionally, it is not known whether variation in habitat amount affects the nature of possible threshold effects, as predicted by Fahrig (2001).

The South African coastline is characterized by filter feeders such as mussels, which are important for species diversity (McQuaid et al. 2000) and can be used to test the effects of habitat amount on biodiversity. The indigenous brown mussel *Perna perna* is an ecologically and socio-economically important species on the south and east coasts that is overexploited on parts of the east coast (Siegfried et al. 1985; Harris et al. 1998; Tunley 2009). Over-exploitation has led to extremely fragmented mussel beds and even local extinction in some areas (Dye et al. 1994; Calvo-Ugarteburu

and McQuaid unpubl. in Erlandsson et al. 2011a). In such cases, understanding the links between the size and fragmentation of populations of habitat-forming species and the effects of such ecological degradation on species diversity has important socio-ecological implications. Since many studies have shown correlations between biodiversity and ecosystem functioning (Hansen and Kristensen 1998; Prins et al. 1998; Gutiérrez et al. 2003; Ieno et al. 2006), it is possible that the whole ecosystem is affected if there is a relationship between habitat amount and biodiversity.

As mussel beds decrease in size, they tend to be replaced by coralline or filamentous algae (Siegfried et al. 1985; Lasiak and Field 1995, pers. obs.). New mussel larvae must therefore often settle onto algae and are then later forced to move to the primary hard substratum as they become bigger and unable to remain attached to the algae (Erlandsson and McQuaid 2004; Erlandsson et al. 2011a). Field studies and laboratory experiments indicate that the probability of recruits being able to move successfully from macroalgae to nearby mussel beds is remarkably low (Erlandsson et al. 2008, 2011a), so that the process of primary settlement onto macroalgae followed by secondary relocation into adult beds proposed by Bayne (1964) seems not to apply in this system. The negative effect of replacing adult mussels with algae from which larvae cannot successfully recolonize the primary substratum could therefore be a key driver for maintaining an ecological state in which there are few chances for natural recovery following over-exploitation. Along the South African coast, roughly half of *P. perna* larvae settle in mussel beds and the other half on macroalgae (McQuaid and Lindsay 2005; Erlandsson et al. 2008, 2011b). Consequently, where the density of mussels is low, it is likely that recruitment will also be low and that, as the ratio of algal to mussel cover on the shore increases, fewer individuals will reach the recruit stage (Lasiak and Barnard 1995; Erlandsson and McQuaid 2004; Erlandsson et al. 2011b). Thus, it becomes important to determine whether the amount of mussel habitat affects recruitment of new mussels into the same population and whether threshold values exist for mussel habitat amount, under which there is a drop in biodiversity.

The relationships between the amount of habitat provided by *P. perna* or macroalgae (mainly the red alga *Gelidium pristoides*) and a range of biological variables were examined on the south and south-east coasts of South Africa at small landscape scales. Five main hypotheses were posed: (1) positive or negative relationships exist between habitat amount of mussels/algae and biodiversity or abundance of associated macrofauna (total abundance or abundance of different taxonomic groups); (2) positive relationships exist between patch size and biodiversity or abundance of associated macrofauna; (3) positive relationships exist between amount of mussel/algae habitat and mussel recruitment; (4) positive relationships exist between

patch size and mussel recruitment; (5) threshold effects exist (nonlinear or partial regressions) in these relationships, with e.g. abundance or biodiversity decreasing dramatically at (and below) a certain habitat amount.

Since *P. perna* coexists with the invasive species *Mytilus galloprovincialis* in the western part of the south coast in South Africa (own observations), and some of the sampling was to take place there, the importance of the ratio between these two species was also investigated.

Materials and methods

Study sites

The study was carried out at three sites on the south and south-east coasts of South Africa: Kidd's Beach, (hereafter Kidd's 33°8,8573'S; 27°42,2104'E) and Kayser's Beach (Kayser's 33°12,6751'S; 27°36,7271'E), west of East London, and Kini Bay (Kini 34°1,30265'S; 25°22,7913'E), west of Port Elizabeth (Fig. 1). In contrast to shores farther east, where artisanal exploitation is intense, *P. perna* is abundant at these sites. All sites are exposed to strong wave action. Tides are semi-diurnal with an amplitude of ca 2 m for spring tides and ca 1 m for neap tides. Samples were collected from the mid mussel zone, where mussels form medium-sized patches interspersed with moderate to high abundance of the red alga *G. pristoides* and the barnacle *Tetraclita serrata*. Farther upshore, cover of algae and barnacles increase and mussel patches are more fragmented, while lower down, mussels create more uniform monolayered beds, generally with 100 % cover (Dye 1998; McQuaid et al. 2000; Menge and Branch 2000).

Sampling

Sampling was carried out during austral spring (September–October) in 2011. Two of the sites were sampled during one spring tide in September and the third (Kini) in one spring tide in October. To avoid possible natural fluctuations in biodiversity, it was necessary to complete sampling within one spring tide at each site. At each site, thirty samples were collected by scraping 10 × 10 cm quadrats placed haphazardly within patches of 100 % mussel cover. Patches were selected to provide a wide range of patch sizes in combination with a wide range of habitat amount surrounding these patches, allowing us to test our hypotheses. Mussels and all associated macrofauna were collected using a spoon and forceps and stored in 70 % ethanol until further analysis, which took place in random order. At Kidd's and Kayser's, adjacent samples were separated by a minimum distance of 2 m to avoid overlap in the surrounding habitat, which was estimated later. At Kini, the

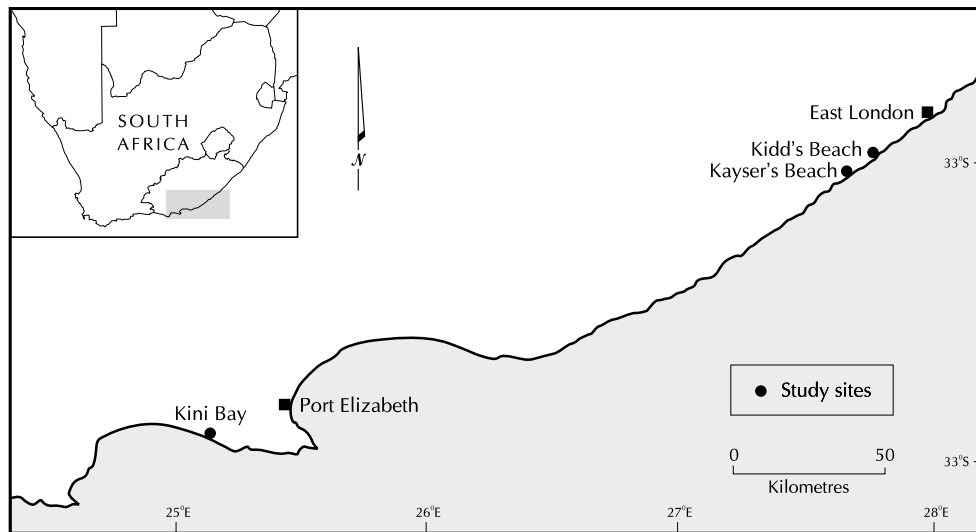


Fig. 1 Map showing the investigated field sites in South Africa: (from left to right) Kini, Kayser's and Kidd's

minimum distance between the samples was 1.5 m as fewer mussel patches were available.

The amounts of mussel and algal habitat surrounding each sample were estimated at the 4.0 m² scale, using a 50 × 50 cm quadrat marked with crossed strings making 25 intersections (Fig. 2). The 4.0 m² scale was chosen because it is the scale within which most mobile animals in mussel beds can move, thus enabling us to take migration between different habitat patches into consideration. A non-destructive point intercept method was used to estimate the percentage cover of the different habitats (Hawkins and Jones 1992), although at Kidd's, the algal data were not registered separately as filamentous/foliose or encrusting algae and thus only mussel habitat amount could be investigated at this site. The cover of mussels and algae within the 4.0 m² area was estimated with 16 non-overlapping quadrats (50 × 50 cm) with the sample in the centre of the total area (Fig. 2). Because estimates of both mussel and algal cover were necessarily made from the same surrounding area, these data can be viewed as non-independent (Underwood 1997). Nevertheless, the importance of the amount of algal habitat was considered as a possible explanation for patterns in the associated macrofauna and mussel recruitment, while recognizing that higher algal cover could possibly reflect lower mussel cover. The size of the mussel patch from which each 10 × 10 cm sample was taken was photographed except at Kini, where this was not possible, and therefore, patch sizes could not be estimated here. The photographs were then used to estimate patch sizes using the software ArcGIS (version 10.1). Sampled mussels were identified, counted and placed into size categories (0.5 mm–0.5 cm, 0.5–1 cm, 1–2 cm, 2–3 cm ... 11–12 cm), and associated macrofauna individuals bigger

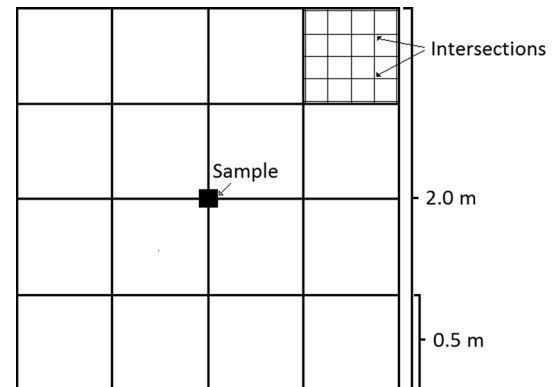


Fig. 2 Mussel and algal habitat amount around the 10 × 10 cm sample (black square in the centre) was estimated at the scale 4.0 m². This was done using a 50 × 50 cm quadrat with crossed strings making 25 intersections (upper right corner), which was placed out 16 times around the sample in the pattern indicated in the figure. By counting number of intersections covering mussels and algae, respectively, one can estimate the percentage in that square

than 0.5 mm were identified and counted. Mussel recruits were estimated directly from our samples, and individuals of 0.5–10 mm were defined as recruits (e.g. Erlandsson and McQuaid 2004). The proportions of *P. perna* and the non-indigenous mussel *M. galloprovincialis* were recorded for each sample at all sites. The associated macrofauna were identified to the lowest possible taxonomic level, which in most cases was the species level.

Statistics

Both univariate and multivariate statistical techniques were used to analyse the data. Regression analyses (linear and

nonlinear) were used to test the relationships between different variables, and the best-fit relationships were searched for using the models providing the highest R^2 values. To detect significant partial linear regressions, i.e. determining break points in the overall regressions suggesting possible threshold effects, a 3-step procedure was followed for each regression: (1) residual analysis, (2) regression analyses of the different slopes and (3) t tests comparing the different slopes. Step (1) Analysis of patterns among residuals (i.e. estimated differences between observed data points and the fitted regression line) was done to distinguish partial regression lines with different slopes and to determine the level of habitat amount where potential breaks between partial regressions occurred. Starting with the whole range of data points, the maximum positive or negative value (opposite sign to the first point value) of residual data was considered to correspond to a transition between partial regressions (see Kostylev and Erlandsson 2001; Erlandsson and McQuaid 2004). Step (2) Linear regression analysis was conducted for each partial regression and a statistically significant slope suggested that partial regressions should be considered. Step (3) As a last step in the detection of potential threshold effects, slopes of significant partial regressions were tested against each other using t tests in order to eliminate possible redundancy. If slopes of adjacent regressions were significantly different, then the partial regressions were considered valid. Since this procedure of partial regression analyses may include multiple tests, significance can be estimated using the Bonferroni correction.

All p values were corrected with Benjamini–Hochberg’s sequential correction (Benjamini and Hochberg 1995), with the false discovery rate at 5 %, to decrease the risk of making Type I errors. Simpson’s dominance index (1-D), total macrofaunal abundance and species richness were calculated, and multivariate statistical analyses were performed using PRIMER (version 6.1.13). Community data were analysed with nMDS analyses and one-way ANOSIM on Bray–Curtis similarities after square-root transforming the data to balance the relative influence of rare and dominant species. Differences between sites in biodiversity, abundance and species richness were tested using one-way ANOVAs. Prior to analysis, the data were tested for normality using Kolmogorov–Smirnov’s test and for homogeneity of variances using Levene’s test. Appropriate transformations were performed if the assumptions of the tests were violated.

Results

Species diversity and species composition at site level

The overall species richness exceeded 79 at Kidd’s, 81 at Kayser’s and 74 at Kini. These values are conservative,

since a number of closely related species were lumped together into higher taxonomic groups (for full species/taxa list see Table 1). The taxonomic groups that were particularly well represented were Bivalvia, Gastropoda, Malacostraca, Maxillopoda and Polychaeta, which are also prominent in other mussel communities (Seed 1996). Despite the high total species richness, the abundances of associated fauna were dominated by only a few species and there were no significant differences in diversity among the three sites. NMDS analyses indicated that species composition at Kini differed from Kidd’s and Kayser’s (Fig. 3). Although, strictly, the stress value of 0.22 exceeded what is considered to be reliable by Kruskal (1964), it is not unusually high for such a large number of samples. ANOSIM further revealed significant overall differences between the sites (Global $R = 0.546$, $p < 0.001$) and pair-wise ANOSIM demonstrated that all three sites differed significantly from one another at $p < 0.001$. Kini differed most from Kidd’s ($R = 0.726$) and Kayser’s ($R = 0.671$), whereas Kidd’s and Kayser’s were most similar in species composition ($R = 0.262$).

A one-way ANOVA showed that the total abundance of fauna differed significantly between sites ($F_{2,87} = 11.34$, $p < 0.001$). Pair-wise a posteriori Bonferroni analyses revealed that the average total abundance was significantly higher at Kidd’s (on average 463 individuals per sample) than at Kayser’s (329 individuals, $p = 0.029$) and at Kini (265 individuals, $p < 0.001$). The total abundance per sample at Kayser’s and Kini did not differ significantly from each other. The abundance data were fifth root transformed.

Mussel versus algal habitat amount

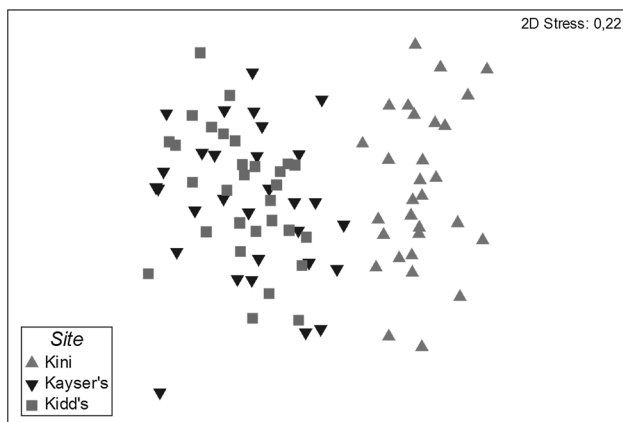
The total amount of mussel and filamentous/foliose macroalgal cover together at 4.0 m² ranged from 18 to 82 % at Kini and from 26 to 92 % at Kayser’s, indicating that estimation of both mussels and algae from the same quadrats could lead to some issues of negatively correlated data at these two sites. However, this was specifically checked for by running individual regression analyses between mussel habitat amount on the x -axis and algal habitat amount on the y -axis, and no significant negative relationships were found.

Relationships between mussel (and algal) habitat amount and biodiversity/species richness/abundance

Regression analyses revealed significant negative linear relationships between mussel habitat amount (independent variable) and species richness and total abundance of macrofauna (dependent variables) at Kidd’s (Table 2; Fig. 4). No significant relationship was found between mussel habitat amount and biodiversity.

Table 1 List of species/taxa that were found at the three investigated sites

Species (unknown)	Echinoidea	<i>Thais capensis</i>	<i>Sphaeramene polytylotos</i>	<i>Phyllodoce</i> sp. 1–2
Species 1–4	<i>Parechinus angulosus</i>	<i>Tricolia capensis</i>	<i>Stenothoidae</i> spp.	Polychaete sp. 1–7
Actinopterygii	Gastropoda	<i>Tricolia neritina</i>	Maxillopoda	<i>Pomatoleios kraussii</i>
<i>Muraenoclinus dorsalis</i>	<i>Afrolittorina africana</i>	<i>Turritella carinifera</i>	<i>Balanus amphitrite</i>	<i>Pseudonereis</i> sp. (juv.)
Anthozoa	<i>Burnupena lagenaria</i>	Holothuroidea	<i>Balanus venustus</i>	<i>Pseudonereis variegata</i>
Actiniaria sp. 1	Clionella sp. 1	<i>Pentacta doliolum</i>	Balanidae sp. (juv.)	<i>Serpulidae</i> sp. 1–2
<i>Anthothoe chilensis</i>	Columbellidae sp.	<i>Pentacucumis spyridophora</i>	Balanidae sp. 1	<i>Spirorbis</i> spp.
<i>Aulactinia reynaudi</i>	<i>Crepidula porcellana</i>	Insecta	<i>Chthamalus dentatus</i>	<i>Syllis exogoninae</i>
<i>Bunodosoma capensis</i>	<i>Cymbula oculus</i>	Coleoptera sp.	<i>Notomegabalanus algicola</i>	<i>Syllis prolifera</i>
Arachnida	<i>Eatoniella nigra</i>	Insecta sp.	<i>Octomeris angulosa</i>	<i>Syllis variegata</i>
<i>Desis formidabilis</i>	<i>Eatoniella</i> sp. 1–2	Malacostraca	<i>Tetraclita serrata</i>	<i>Thelepus</i> spp.
Mite species 1–3	<i>Epitonium kraussi</i>	Amphipoda sp.	Nematoda spp.	Polyplacophora
Asteroidea	<i>Fissurella mutabilis</i>	<i>Anthuridae</i> sp. 1–3	Nemertea spp.	<i>Acanthochiton garnoti</i>
<i>Patiriella exigua</i>	Gastropoda sp.	<i>Caprellidae</i> sp.	Ophiuroidea	<i>Ischnochiton textilis</i>
Bivalvia	Gastropoda sp. (juv.) 1–4	<i>Cirolana cranchii</i>	<i>Amphipholis squamata</i>	Pycnogonida
Bivalvia sp. 1–5	<i>Gibbula</i> sp. 1–2	<i>Cirolana incisicauda</i>	Polychaeta	<i>Nymphopsis cuspidata</i>
<i>Brachidontes semistriatus</i>	<i>Helcion pruinosus</i>	<i>Cirolana venusticauda</i>	<i>Ceratonereis mirabilis</i>	<i>Pycnogonida</i> sp.
<i>Cardita variegata</i>	<i>Melanella algoensis</i>	<i>Cyamidae</i> sp.	<i>Cirriformia capensis</i>	<i>Tanystylum brevipes</i>
<i>Choromytilus meridionalis</i>	<i>Natica tecta</i>	<i>Dexaminidae</i>	<i>Euphrosinidae</i> sp.	Rhabditophora
<i>Hiatella arctica</i>	<i>Nucella dubia</i>	<i>Dynamenella australis</i>	<i>Fabricinae</i> sp.	<i>Notoplana patellarum</i>
<i>Lasaea</i> spp.	<i>Nucella squamosa</i>	<i>Dynamenella huttoni</i>	<i>Gunnarea capensis</i>	Platyhelminthes sp. 1–5
<i>Musculus cuneatus</i>	<i>Onchidiidae</i> sp.	<i>Ingollfiellida</i> sp.	<i>Lepidonotus durbanensis</i>	Sipuncula
<i>Mytilus galloprovincialis</i>	<i>Patellogastropoda</i> sp.	<i>Jaeropsis</i> spp.	<i>Lumbrineris coccinea</i>	Sipuncula sp.
<i>Perna perna</i>	<i>Polinices dictyrna</i>	<i>Mesanthura catenula</i>	<i>Naineris</i> spp.	Sipunculidea
<i>Petricola</i> sp.	<i>Pusia patula</i>	<i>Ochlesis lenticulosus</i>	<i>Orbiniidae</i> sp.	<i>Golfinga capensis</i>
	<i>Scutellastra granularis</i>	<i>Plagusia chabrui</i>	<i>Phylloce madeirensis</i>	

**Fig. 3** NMDS ordination for the sampling sites Kini (upward triangles to the right), Kidd's (squares) and Kayser's (downward triangles to the left)

One significant positive relationship was found between algal habitat amount and total macrofaunal abundance at Kini. No other significant relationships were found between algal habitat amount and total

Table 2 Results from regression analyses on relationships between mussel habitat amount at the scale 4.0 m² and Simpson's dominance index, number of species and total abundance of fauna at the three study sites

Variable	Site	R ²	p value	Relationship
Simpson	Kidd's	0.136	0.138	Quadratic
	Kayser's	0.067	0.167	Neg. linear
	Kini	0.015	0.513	Pos. linear
Species richness	Kidd's	0.154	0.032*	Neg. linear
	Kayser's	0.105	0.081	Neg. logarithmic
	Kini	0.022	0.434	Pos. power
Total abundance	Kidd's	0.165	0.025*	Neg. linear
	Kayser's	0.107	0.217	Quadratic
	Kini	0.055	0.213	Neg. linear

The significant *p* values remained significant after a sequential Benjamini–Hochberg correction and are shown in bold face

macrofaunal abundance, neither were there any significant relationships between algal habitat amount and biodiversity or species richness at any of the sites (Table 3).

Relationship between mussel (and algal) habitat amount and *P. perna* recruitment and size

The number of *P. perna* recruits in the samples ranged from 0 to 13 per 10 × 10 cm quadrat at Kidd's, from 5 to 39 at Kayser's and from 4 to 23 at Kini. No significant positive relationship was found between mussel recruit density and habitat amount at any site, though there was a significant negative relationship at Kayser's (Table 4; Fig. 5). For relationships between habitat amount and mean mussel size, there was also one significant relationship, a positive power function at Kini (Table 4). When testing recruit density against algal habitat amount, there was one significant relationship, a quadratic one at Kini (Table 3; Fig. 6). This relationship was based on a distinct outlier for which algal habitat was particularly high and recruit density particularly low. If the outlier is ignored, the relationship becomes a positive power function (Fig. 6). In all cases, the R^2 values were very low.

Relationship between mussel habitat amount and different taxonomic groups

The analysis of the relationships between abundances of separate phyla/classes/species and mussel habitat amount resulted in several significant results (Table 5). Most taxa were investigated for such relationships, leaving out only groups where the total number of individuals per site was less than 50. At Kini 11.6 %, at Kayser's 9.4 % and at Kidd's, only 3.7 % of all individuals fell into the category that was not investigated. Positive relationships, either linear or nonlinear, were found for the classes Anthozoa and Malacostraca and the phylum Nemertea and individual species belonging to these taxonomic groups. Negative relationships, also either linear or nonlinear, were found between mussel habitat amount and the classes Bivalvia, Maxillopoda, Ophiuroidea, Polychaeta and Pycnogonida and species within these classes. Taken over all, the class Gastropoda showed a negative relationship with mussel habitat amount, but *Fissurella mutabilis* showed a positive relationship. A quadratic relationship was found for the cushion star *Patiriella exigua* and Maxillopoda against mussel habitat amount at Kayser's.

Relationship between mussel patch size and biodiversity/abundance/recruitment

Actual patch size (the size of the patch from which the sampled quadrat was taken) varied between 0.014 and 1.8 m² at Kidd's and between 0.014 and 2.0 m² at Kayser's (patch size could not be measured at Kini). No significant relationships were found between patch size and the dependent variables biodiversity, species richness, total abundance or recruit density ($p > 0.05$ in all cases).

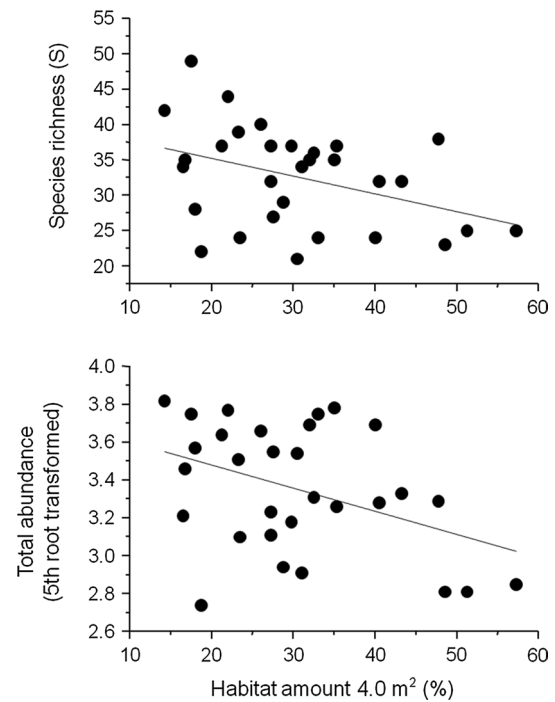


Fig. 4 Relationship between amount of mussel habitat at 4.0 m² at Kidd's and species richness in the *upper graph* ($R^2 = 0.154$, $y = -0.250x + 40.203$, $F = 5.087$, $p = 0.032$), and total macrofauna abundance in the *lower graph* ($R^2 = 0.165$, $y = -0.012x + 3.72$, $F = 5.578$, $p = 0.025$)

Table 3 Results from regression analyses on relationships between algal habitat amount (on the scale 4.0 m²) and number of mussel recruits at Kini, as well as biodiversity and species richness at Kayser's and Kini

Variable	Site	R^2	p value	Relationship
Mussel recruits	Kini	0.380	0.002**	Quadratic
Mussel recruits without outlier	Kini	0.249	0.006**	Pos. power
Total abundance	Kayser's	0.02	0.461	Quadratic
	Kini	0.181	0.019*	Pos. logarithmic
Simpson	Kayser's	0.032	0.343	Neg. power
	Kini	0.057	0.204	Pos. linear
Species richness	Kayser's	0.026	0.393	Neg. logarithmic
	Kini	0.106	0.079	Pos. logarithmic

All significant p values remained significant after a sequential Benjamini–Hochberg correction and are shown in bold face

Role of the ratio between *P. perna* and *M. galloprovincialis*

At Kini, where *M. galloprovincialis* was abundant, the influence of the proportion of *P. perna* on species richness and total abundance of fauna was also examined and significantly positive linear relationships were found. The more *P. perna* there were in a sample, the higher the species richness

Table 4 Results from regression analyses on relationships between mussel habitat amount (on the scale 4.0 m²) and number of mussel recruits and mean mussel size at the three study sites

Variable	Site	R ²	p value	Relationship
Mussel recruits	Kidd's	0.043	0.290	Neg. linear
	Kayser's	0.181	0.019*	Neg. linear
	Kini	0.006	0.691	Pos. exponential
Mussel size	Kidd's	0.118	0.063	Pos. linear
	Kayser's	0.131	0.049*	Pos. linear
	Kini	0.225	0.008**	Pos. power

The significant *p* values that remained significant after a sequential Benjamini–Hochberg correction are shown in bold face

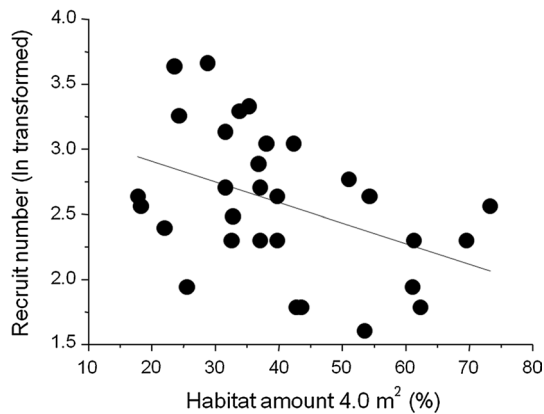


Fig. 5 Relationship between amount of mussel habitat at 4.0 m² and number of *P. perna* recruits at Kayser's ($R^2 = 0.181$, $y = -0.02x + 3.22$, $F = 6.193$, $p = 0.019$)

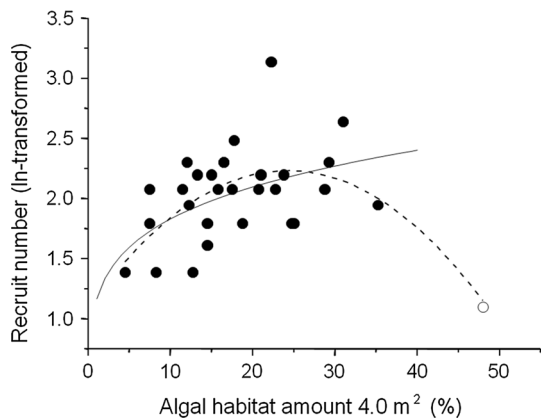


Fig. 6 Relationship between algal habitat amount at the 4.0 m² scale and the density of mussel recruits at Kini ($R^2 = 0.38$, $y = 1.091 + 0.0938x - 0.00193x^2$, $F = 8.29$, $p = 0.002$) showed by the *dashed line*. If the outlier to the right (*open circle*) is ignored, there is a significantly positive power relationship between the variables ($R^2 = 0.249$, $y = 1.170x^{0.195}$, $F = 8.932$, $p = 0.006$) which is shown by the *fully drawn line*

Table 5 Results from regression analyses on relationships between mussel habitat amount (4.0 m²) and different taxonomic groups and species

Variable	Site	R ²	p value	Relationship
Anthozoa	Kidd's	0.053	0.220	Pos. linear
	Kayser's	0.064	0.409	Quadratic
	Kini	0.331	0.001***	Pos. linear
<i>Aulactinia reynaudi</i>	Kidd's	0.047	0.252	Pos. linear
	Kayser's	0.088	0.192	Pos. logarithmic
	Kini	0.337	0.023*	Pos. logarithmic
(Asteroidea)	Kidd's	0.031	0.354	Neg. logarithmic
<i>Pateriella exigua</i>	Kayser's	0.33	0.004**	Quadratic
	Kini	0.099	0.245	Quadratic
	Kidd's	0.250	0.005**	Neg. linear
Bivalvia	Kayser's	0.256	0.004**	Neg. linear
	Kini	0.122	0.058	Neg. logarithmic
	Kidd's	0.255	0.004*	Neg. linear
<i>Lasaea</i> spp.	Kayser's	0.208	0.011	Neg. linear
	Kini	0.130	0.05	Neg. logarithmic
	Kidd's	0.07	0.159	Neg. exponential
Gastropoda	Kayser's	0.302	0.002**	Neg. logarithmic
	Kini	0.082	0.316	Quadratic
	Kidd's	0.050	0.500	Quadratic
<i>Fissurella mutabilis</i>	Kini	0.163	0.027*	Pos. logarithmic
	Kidd's	0.010	0.877	Quadratic
	Kayser's	0.043	0.274	Neg. linear
<i>Helcion pruinosus</i>	Kini	0.32	0.001**	Neg. logarithmic
	Kidd's	0.027	0.383	Neg. linear
	Kayser's	0.121	0.059	Neg. exponential
<i>Scutellastra granulularis</i>	Kini	0.157	0.03*	Neg. logarithmic
	Kidd's	0.000	0.937	Pos. linear
	Kayser's	0.200	0.049*	Quadratic
Malacostraca	Kini	0.151	0.034*	Pos. power
	Kidd's	0.061	0.187	Neg. logarithmic
	Kayser's	0.058	0.447	Quadratic
<i>Jaeropsis</i> spp.	Kini	0.187	0.017*	Pos. power
	Kidd's	0.316	0.019*	Pos. linear
	Kayser's	0.044	0.421	Neg. linear
<i>Stenothoidae</i> spp.	Kini	0.146	0.072	Neg. logarithmic
	Kidd's	0.036	0.314	Neg. linear
	Kayser's	0.210	0.041*	Quadratic
Maxillopoda	Kini	0.152	0.033*	Neg. logarithmic
	Kidd's	0.729	0.141	Quadratic
	Kayser's	0.025	0.407	Neg. logarithmic
Nemertea	Kini	0.143	0.040*	Pos. logarithmic
	Kidd's	0.253	0.005**	Neg. logarithmic
	Kayser's	0.031	0.587	Neg. logarithmic
Ophiuroidea	Kini	0.086	0.332	Neg. linear

Table 5 continued

Variable	Site	R^2	p value	Relationship
Polychaeta	Kidd's	0.121	0.06	Neg. linear
	Kayser's	0.154	0.032*	Neg. logarithmic
	Kini	0.239	0.006**	Neg. exponential
<i>Naineris</i> spp.	Kidd's	0.246	0.005**	Neg. logarithmic
	Kayser's	0.164	0.027*	Neg. logarithmic
	Kini	0.203	0.012*	Neg. logarithmic
<i>Spirorbis</i> spp.	Kidd's	0.290	0.003**	Neg. exponential
	Kayser's	0.002	0.807	Neg. logarithmic
	Kini	0.142	0.048*	Neg. linear
<i>Syllis prolifera</i>	Kidd's	0.011	0.577	Neg. linear
	Kayser's	0.166	0.025*	Neg. linear
	Kini	0.043	0.553	Quadratic
Pycnogonida	Kidd's	0.109	0.075	Neg. logarithmic
	Kayser's	0.366	0.006**	Neg. logarithmic
	Kini	0.153	0.206	Quadratic

Taxonomic groups/species with no significant relationships to mussel habitat amount at any of the sites are omitted from the table. The significant p values that remained significant after a sequential Benjamini–Hochberg correction are shown in bold face

($R^2 = 0.201$, $F = 7.027$, $p = 0.013$) and the higher the total abundance of associated animals ($R^2 = 0.161$, $F = 5.383$, $p = 0.028$), though in both cases R^2 values were low, indicating that there were other important sources of variation.

Discussion

Earlier studies on the relationships between mussels and biodiversity were done mainly at the patch scale, without taking the patch context, e.g. the matrix and surrounding habitat, into account (e.g. Tsuchiya and Nishihira 1985; Dittmann 1990; Peake and Quinn 1993; Hammond and Griffiths 2006; Koivisto et al. 2011; see however Koivisto and Westerbom 2012) and often indicated positive relationships between the two (e.g. Norling and Kautsky 2008; Zaiko et al. 2009). The present study showed several significant relationships, either negative or positive, between habitat amount and various other variables. Critically, however, no thresholds could be detected using residual analysis to suggest break points between partial regressions (Kostylev and Erlandsson 2001) in any of the relationships that were tested, even though some of the significant quadratic relationships suggested nonlinear trends. Thus, at the small scale at which the effects of habitat amount were studied, there was no evidence for abundance or biodiversity dramatically decreasing below a certain level of habitat amount. However, this does not exclude the possibility that this kind of pattern exists at larger or smaller landscape scales.

Habitat loss has been shown to have negative effects on processes that are important for population dynamics and persistence such as population growth, foraging, reproduction, dispersal and predation (Fahrig 2003 and references therein, Kraufvelin et al. 2006a, b; Bulleri et al. 2012). Small and more isolated patches, which are likely to result from habitat loss and fragmentation, may not be as effective as larger patches at sustaining local populations of species, partly because small and often slow moving animals may not be able to migrate through the matrix, which increases in size as habitat is lost (Fahrig 2001). Furthermore, small patches result in increased amounts of edge habitat, and this can cause higher migration rates to the matrix (Fahrig 2003) and simulations indicate that more habitat is required for regional population survival, if the emigration rate becomes higher (Fahrig 2001). Therefore, less matrix and more surrounding habitat should allow more animals to migrate to other mussel patches (or parts of the patches) and thus contribute to a generally higher biodiversity. On the other hand, if habitat fragmentation does not include habitat loss, it may have more positive than negative effects due to habitat complementarity and reduced isolation of patches (Dunning et al. 1992; Fahrig 2003). Thus, some studies indicate that habitat fragmentation affects abundances in a community only if the overall habitat amount is low (Fahrig 1998; Trzcinski et al. 1999). Although not explicitly investigated here, it is thus possible that patterns of fragmentation could explain the absence of any significant relationship between mussel habitat amount and biodiversity and total abundance at Kayser's and Kini (Table 2).

The observed large differences (in nMDS and in ANOSIM) in community structure between Kini and the two other sites could be due to the relatively large geographical distance separating Kini (e.g. Branch et al. 1999) or by the higher proportion of *M. galloprovincialis* at Kini than at Kidd's and Kayser's, where *P. perna* was clearly dominant. Iwasaki (1995) showed that different species can dominate the associated faunal community depending on which mussel species dominates the mussel population. On the other hand, no strong differences in the biodiversity of communities associated with *P. perna* as opposed to *M. galloprovincialis* have previously been detected (Hammond 2001; Jordaan 2010). Consequently, there was no direct evidence of a strong mussel species effect on associated communities in our system, and in fact earlier work indicates that, instead, the infaunal community is strongly affected by the size structure of mussel populations (O'Connor and Crowe 2007; Cole and McQuaid 2010). This suggests a mechanism for species-specific effects as the two mussel species often differed in size (*P. perna* being bigger in our samples than *M. galloprovincialis*), though manipulative experiments using *P. perna* provided no support for the effects of mussel bed structure (Cole and McQuaid 2011).

Taxonomic groups differed in their relationships with habitat amount, but this was not unexpected (Fahrig 2013), and there may be several explanations for such different patterns. One explanation relates to differences in the life cycles of the various species. For example, larvae settling among mussels may be buried in the large amounts of faeces and pseudofaeces that mussels produce. Species with larval stages that are more tolerant to anoxic conditions thus seem to have higher chances for survival among mussel beds (Commito and Boncavage 1989). Species with a pelagic larval stage are also prone to mussel predation when they settle in the intertidal, since they may be filtered by the mussels themselves (Mileikovsky 1974 and references therein, Porri et al. 2008). This could result in different relationships with mussel cover for species with planktonic larvae as opposed to those that brood their offspring or encapsulate the embryo (Dean 1978; Commito and Boncavage 1989). Species with direct development or species where the larvae are well developed or have already become small juveniles before they enter the adult population also have a higher probability of survival in mussel habitats than other species (Thiel and Ullrich 2002). The link between foraging by mussels and the reproductive strategies of associated fauna could thus help explain the negative nature of some relationships between mussel habitat amount and abundances of different species and taxonomic groups. For example, bivalves and many polychaetes (with pelagic larval stages) showed negative relationships to mussel habitat amount. Amphipods and isopods, on the other hand, are direct developers (Väinölä et al. 2008; Wilson 2008) and most showed positive correlations with mussel habitat amount. In addition to being very abundant at all three sites, the class Malacostraca and a few species within it (e.g. the isopods *Jaeropsis* spp.) had significant positive relationships with mussel habitat amount. Not having a long larval stage in their life cycle could thus have influenced their abundance among the mussels. Amphipods, and other mobile groups of species, are also more likely to benefit from a larger habitat amount due to their mobility.

The relationship between adult and recruit densities in mussel beds varies with the scale at which it is examined (Reaugh-Flower et al. 2011). This often indicates a strong positive relationship between recruit density and abundance or percent cover of adult mussels at the patch scale (Erlandsson and McQuaid 2004; McQuaid and Lindsay 2007), but in the present study no positive relationships were found between recruitment and the size of surrounding mussel habitat considered. Furthermore, a significantly positive relationship between mussel habitat amount and mean size of the mussels was found at Kini (Table 4). This may be because older, larger mussels create larger mussel beds (Norling and Kautsky 2007, own observations) that have had longer to recruit infauna and undergo succession,

but again, it is uncertain that mussel size itself has a direct effect. To our knowledge, no other studies have focused on the relationship between recruit density and the amount of habitat surrounding a patch. The negative relationship between mussel habitat amount and recruit density at Kayser's (Table 4; Fig. 5) had extremely low predictive power, but was counter to our hypothesis 3 and we have no explanation for it.

Algal habitat amount seemed to have a positive effect on total abundance of associated macrofauna, but only at Kini. Koivisto and Westerborn (2010) found a positive relationship between the presence of algal structures and biodiversity in *Mytilus edulis* communities and ascribed this pattern to the larger surface area and additional complexity offered by the algae. Some species can also find a hiding place among the algae, while grazers might find more food (e.g. periphytic microalgae) on and among the macroalgae. Algal habitat amount also had a positive effect on mussel recruit density, which could reflect small-scale movement of recruits to nearby mussel habitats. Earlier studies, however, have shown that this is unlikely (Erlandsson et al. 2008, 2011b). Such results should therefore be interpreted with caution, but cannot be ruled out as possible local factors. Additional caution should be applied with regard to the possible non-independence between amounts of mussel and algal habitat (Underwood 1997). These were estimated from the same quadrats, making it impossible to disentangle the relative importance of higher amounts of algae from those of possibly lower amounts of mussels. Nevertheless, this issue was considered as a minor one since there was no significant negative correlation between the two habitat amounts.

The introduction of non-indigenous species has caused changes to many ecosystems (Hooper et al. 2005; Harley et al. 2013; Kraufvelin 2013, 2014; Garbary et al. 2014). In South Africa, *M. galloprovincialis* was introduced to the west coast more than 30 years ago and has spread along the coast since then (Grant and Cherry 1985; McQuaid and Phillips 2000) and outcompeted the ribbed mussel *Aulacomya ater* on the west coast (Van Erkom and Griffiths 1990). *P. perna* and *M. galloprovincialis* can, however, co-exist on the south coast, partly because of a delicate balance between different competitive and facilitative interactions (Rius and McQuaid 2006, 2009) that results in each dominating a different zone, with overlap and co-existence in the mid mussel zone (Bownes and McQuaid 2006; Erlandsson et al. 2011b). According to earlier studies, relatively few species seem to have been directly negatively affected by this introduction (Hanekom 2008), though these negative effects can be very powerful (e.g. Steffani and Branch 2003, 2005) and it is not clear how the rocky shore ecosystem may be affected by the further spread eastwards of *M. galloprovincialis*. In the present study, positive

relationships were found between the relative amount of *P. perna* and total abundance of associated animals, although this may have been caused by the response of just a few species. Nevertheless, it could indicate that the possible negative influence of *M. galloprovincialis* on the biodiversity of mussel-associated macrofauna may be greater than previously reported.

In conclusion, this study showed that there are significant relationships between the amount of mussel habitat surrounding a patch at small landscape scales and numerous response variables in mussel-associated species assemblages. Even though only a few significant relationships were found between mussel habitat amount and species richness and total macrofauna abundance, the mussel habitat amount still seemed to have an effect on the abundance of many specific taxonomic groups and the results suggest that this may be linked to mode of reproduction. No threshold effects in the relationship between habitat amount and abundance/biodiversity were observed at the scale investigated. Our study highlights the important, but complex landscape effects that reflect relationships between habitat amount, species composition and species abundances in the marine environment. The results also show that habitat amount per se is a factor structuring the fauna associated with South African mussel beds, but that the strength of its effects varies between shores and probably with scale, as well as with the studied dependent variable, including species identity.

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