

Alteration of the configuration of bioengineers affects associated taxa

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ABSTRACT: Modification of the abiotic environment and creation of habitat by ecosystem engineers is an important ecological process. According to landscape ecology, the configuration (distance apart and spatial arrangement) of patches of engineered habitat within landscapes can also influence the physical environment and biodiversity. To examine the influence of a model engineer, the marine intertidal mussel *Trichomya hirsuta*, abiotic variables (sand deposition, temperature, and humidity) and biotic variables (species richness, numbers of unique species, densities of generalist species and entire assemblages) were compared between engineered and unmodified habitat and between different configurations of engineered patches. By keeping the number of habitat patches (i.e. mussels) constant, the effect of patch configuration (in terms of degree of patch aggregation) on the same abiotic and biotic variables was investigated. Mussels were found to trap large amounts of sand and engineer intertidal habitat that was cooler and, to a lesser extent, more humid during low tides. Mussels also had more species, more unique species and different assemblages compared to habitat without mussels. Different configurations of mussels had similar effects on the physical environment and had similar assemblages as a whole. Most importantly, regularly spaced solitary mussels had more edge and consequently more species, unique species and densities of generalists. These key findings suggest that the configuration of patches of habitat is a crucial factor affecting mussel bed biodiversity, and fragmentation of habitat into regularly spaced patches may have a positive influence on biodiversity due to the positive response of other species to habitat edges.

KEY WORDS: Configuration · Ecosystem engineer · Mussels · Biogenic habitat · Rocky shore · Landscape ecology · Positive interactions

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INTRODUCTION

The importance of positive interactions in determining the abundance and distribution of species requires better integration into current ecological theory (Bertness & Callaway 1994, Bertness & Leonard 1997, Bruno et al. 2003). Particularly striking examples of positive influences by plants or sessile animals have been termed 'physical ecosystem engineering' (Jones et al. 1997a). 'Ecosystem engineers' modulate the availability of resources (excluding the engineer as a direct source of food) by causing changes to the state of biotic or abiotic materials (Jones et al. 1994, 1997b). Modifi-

cation of the physical environment by ecosystem engineers can alter the abundance and diversity of assemblages (Badano & Marquet 2008). Ecosystem engineers have thus been the focus of many ecological studies (see Gutiérrez et al. 2003, Moore 2006, Hastings et al. 2007 for reviews). Although many different types of organisms are known to be ecosystem engineers, their ability to engineer habitat can vary from trivial to extensive (Wright & Jones 2006). Three important aspects determine the relative strength of engineers: (1) influences on the species richness, (2) the number of unique species added to a landscape, and (3) influences on the densities of different species common to

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habitats with or without engineers (Badano et al. 2006). Furthermore, it is necessary to show that the habitat-forming organism is modifying the environment before it should be considered an engineer (Badano et al. 2006).

In addition to potential differences in the relative strength of various engineers (Borthagaray & Carranza 2007, Wallentinus & Nyberg 2007), differences among habitats created by the same type of engineer may occur (Bruno & Kennedy 2000, Flecker & Taylor 2004, People 2006). Such variation may be attributed to the configuration (i.e. distance between individuals and the spatial arrangement of individuals within a group) of habitat patches within a landscape (Forman & Godron 1981, Fahrig 2003). The configuration of engineered habitats is particularly important because ecosystem engineers do not generally occur in isolation (Sousa 1984, Andren 1994). Landscapes with evenly distributed patches may differ from landscapes with the same number of patches that are aggregated, because greater aggregation leads to more interactions among patches and thus increased flow of resources (Forman & Godron 1981). When comparing landscapes with the same total number of patches of ecosystem engineers but with different configurations, one would predict physical and biological differences between the landscapes. Model systems are important for investigating both landscape ecology (Wiens et al. 1993) and ecosystem engineering (see Gutiérrez et al. 2003 for review). Many species of mussels have been considered ecosystem engineers because they provide refuge from thermal stress (Stephens & Bertness 1991), trap fine-grained sediments and organic particles (Tsuchiya & Nishihira 1985, Crooks & Khim 1999), provide surfaces for algae and epifauna (Seed & Suchanek 1992, Lohse 1993), form a matrix for infauna (Lawrie & McQuaid 2001, O'Connor & Crowe 2007), and provide greater protection from predators (Lintas & Seed 1994, Seed 1996, González & Downing 1999). Consequently, the presence of mussels as engineers and their degree of aggregation may influence their relative strength as engineers, in terms of how they modify the physical environment and how they affect species richness (the number of species), the number and type of unique species, and the density of generalists.

In this study, the hairy mussel *Trichomya hirsuta* (Lamarck) was used to examine the influence of an ecosystem engineer on intertidal rocky shores and how mussel configuration influences ecosystem engineering at different spatial scales (among degrees of aggregation and landscape). Specifically, I tested the prediction that in areas engineered by mussels there would be modification of the physical environment, enhanced species richness, more unique species, greater densities of generalists, and distinct assemblages. I also

hypothesised that aggregated engineers would have greater effects as ecosystem engineers (i.e. influences on the physical environment and on associated biodiversity) than engineers which were evenly distributed throughout a landscape.

MATERIALS AND METHODS

Study sites. This study was conducted at Chowder Bay (33° 30' 13" S, 151° 9' 10" E) located near the mouth of Sydney Harbour, Australia, a primarily marine habitat with little freshwater influence. Like most natural rocky shores in the region, Chowder Bay has gently sloping Hawkesbury sandstone platforms backed by native bushland. It has a tidal range of 1 to 1.5 m and has relatively little exposure to waves from oceanic swell because it is protected in the harbour.

Trichomya hirsuta occurs intertidally on the mid–low shore, often with many other habitat-forming species such as tubeworms, oysters and turfing algae (Underwood 1999). These mussels can occur either in dense beds (often metres in size), small clumps or as solitary individuals on many rocky shores in the Sydney region (pers. obs.), including in Sydney Harbour.

Experimental manipulation of the configuration of mussel beds. Experimental manipulation of mussels was necessary to remove any confounding effects of configuration from factors such as age of the substratum and position on the shore. *Trichomya hirsuta* were collected from intertidal rocky shores in Chowder Bay and kept overnight in an aquarium system within multiple tanks in a laboratory. Unfiltered seawater was collected from Sydney Harbour and maintained at 18°C (the temperature of the water in the harbour). The light/dark regime within the aquarium system used natural day and night cycles. Adult mussels (3 to 5 cm in length, MacIntyre 1959) were scrubbed clean of all associated taxa with a small brush, separated and randomly allocated to each treatment.

Five experimental treatments were used to test the hypotheses and to elucidate any artefacts associated with attaching mussels to the shore (Fig. 1). These treatments included (1) 9 regularly spaced solitary mussels, (2) 3 groups each of 3 mussels, (3) 1 group of 9 mussels, (4) a procedural control for any effect of the mesh (e.g. shading and alteration of water-flow), and (5) cleared substrata (rock). For the entire duration of the experiment, mussels were placed in large gauged (i.e. mesh hole size 2.5 cm), thin nylon mesh, secured with 1 cm strips of PVC woven through the mesh and attached with cable ties. Individual mussels or aggregations of mussels were separated by 5 cm, by using 1 cm strips of PVC woven through the mesh (Fig. 1). Each replicate was an 18 × 18 cm plot. During low tide,

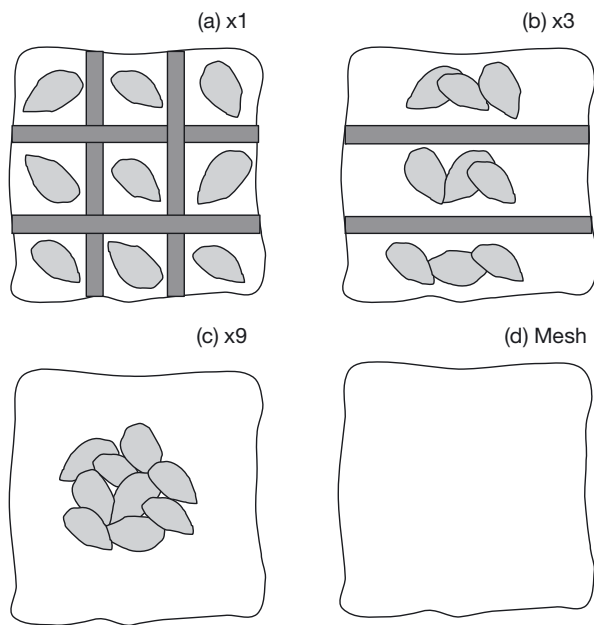


Fig. 1. Illustration of the experimental treatments: (a) 9 regularly spaced solitary mussels, (b) 3 aggregations of 3 mussels, (c) 1 aggregation of 9 mussels, and (d) mesh control

6 replicates of each treatment were attached to the mid-low shore in each of 2 randomly chosen locations within Chowder Bay (16 m stretches of rocky shore), separated by approximately 150 m. Two separate locations were chosen for spatial replication of the experiment. Areas in direct contact with the experimental treatments were scraped clear of epibiota to avoid direct influences of surrounding habitats (*sensu* Cole et al. 2007). Four holes were drilled into the rock and the mesh was secured by large washers and screws into each rawlplug in each hole. Mussels were left in the field for 2 mo during the austral summer of 2006–2007, and then collected by scraping all organisms and sediment from the substratum within the 18 × 18 cm plots.

Due to loss of some samples from the first experiment (leaving 1 location, with $n = 3$ replicates of each treatment intact, except for the mesh control which was completely lost), a subset of the experiment was repeated. Treatments in the second experiment included undisturbed rock, cleared rock, mesh control, 9 solitary mussels and 1 group of 9 mussels. The experimental methods used were similar to those in the first manipulative experiment at the same 2 locations in Chowder Bay, with $n = 6$ replicates of each treatment at each location. In addition to the experimental controls in the previous experiment, areas without mussels were also sampled at the same time to determine if the experimentally cleared plots were fully colonised and repre-

sented established substrata. The second experiment remained in the field for 2 mo during the austral spring of 2007.

To determine the availability of edges of mussels as habitat, photographs were taken of 3 of the experimental plots of each configuration. The image analysis programme Image J was then used to determine the total length of the edges.

Measurement of modification to the physical environment. To determine the degree of modification of the physical environment by engineers, sediment accumulation, substratum temperature and relative humidity were measured in treatments with and without engineers and in treatments with engineers in different configurations.

Temperature and relative humidity of the substratum in each treatment for each manipulative experiment were recorded on 2 randomly chosen days within the 2 mo period, during daytime low tides of 1 December 2006 (Day 1) and 18 January 2007 (Day 2), and 26 September (Day 1) and 17 October 2007 (Day 2), for the first and second experiments, respectively. Temperature and relative humidity of the substratum amongst mussels and areas with mesh or bare rock were measured using thermocouples and humidity probes at the time of the lowest height of the tide, on days with low tides <0.5 m.

At the end of the experiments, samples were collected and fixed in 7% formalin buffered with seawater, then sieved through a 500 μm sieve. Organisms larger than 500 μm (macrofauna) were sorted, identified to the lowest taxonomic level possible and counted. The presence of colonial species and algae was recorded. From the same samples used to assess associated taxa, the mass (g) of sediment (sand, 63 to 500 μm) was measured by sieving samples (each 18 × 18 cm plot) through 500 μm and 63 μm sieves, drying the material collected on the 63 μm sieve at 30°C in an oven, and weighing the dried material repeatedly until the mass remained constant ensuring full removal of moisture.

Statistical analyses. Assemblages of organisms among different experimental treatments (i.e. between engineered and non-engineered and among different configurations) were compared in terms of the species and their densities at small (among degrees of aggregation) and large (landscape) spatial scales. In addition to traditional statistical analyses, calculations were also done using a framework developed by Badano et al. (2006) to determine the strength of ecosystem engineering by comparing treatments with or without mussels, and mussels in different configurations.

Effects of engineering on species richness: Species richness was determined for the number of species and number of only unique species among degrees of

aggregation and landscapes. Specifically, ANOVA was used to compare the numbers of species among the different treatments and between locations. In the first experiment, a single factor ANOVA compared the 4 treatments (rock, solitary, 3 groups of 3, and a group of 9, due to the loss of 1 location and the mesh treatment). In the second experiment, a 2 factor ANOVA incorporated the 2 randomly chosen locations, orthogonal to the 5 treatments (undisturbed substratum, cleared rock, mesh, solitary mussels, and a group of 9). There were $n = 3$ and $n = 6$ replicates of each treatment in the first and second experiment, respectively. Prior to analyses, data were tested for homogeneity of variances with Cochran's *C*-test. The data for many taxa did not require transformation, but for those that did few required the same transformation to create homogeneous variances. Therefore, in order to make simple comparisons among species, none of the data were transformed. The violation of homogeneity of variances was not considered to be a problem because ANOVA is relatively robust to heterogeneous variances for large designs such as this (Underwood 1997). When sources of variation were shown to be significant, Student-Newman-Keuls (SNK) tests were used to compare means relevant to the hypotheses of interest.

Unique species at the treatment level were compared using a ratio outlined by Badano et al. (2006). This ratio was calculated as number unique to Habitat A (A) plus the number of species common to both habitats (G), divided by the number of species in Habitat B (B) and (G), i.e. 'Relative importance of unique species' = $(A + G)/(B + G)$. Unique species were also determined at the landscape scale. Numbers of species which were unique to Habitat A were compared with the total number of taxa (i.e. generalists and species unique to each of the habitats A and B), 'Contribution of unique species in Habitat A' = $A/(A + B + G)$, reflecting the contribution of unique species that are due to the presence of a specific configuration in a landscape (Badano et al. 2006), giving estimates of beta diversity (e.g. Caley & Schluter 1997, Koloff et al. 2003, Ricklefs 2004).

Effects of engineering on generalists: The combined effects of engineering on generalists were determined by analysing the ranked treatments using non-parametric tests. Densities of generalists were ranked and Kruskal-Wallis tests compared rank sums for each treatment to determine the overall differences among treatments for all generalist species (Sokal & Rohlf 1995). Effects of engineering were also determined at the landscape (site) scale by calculating the number of generalists as a percentage of the total number of taxa in a landscape, i.e. 'Percentage of generalists' = $G/(A + B + G) \times 100$ (Badano et al. 2006).

Effects of engineering on assemblages of species: Untransformed data of assemblages were compared

graphically using non-metric multi-dimensional scaling (nMDS) ordinations using Bray-Curtis dissimilarity matrices (Bray & Curtis 1957) calculated in PRIMER 5 (PRIMER-E 2002). Permutational multivariate analysis of variance (PERMANOVA, Anderson 2005) based on Bray-Curtis dissimilarities was used to analyse differences in assemblages. Factors were the same as those for the univariate analyses comparing numbers of species. Significance of *F*-ratios was determined from 999 randomisations of the data (Anderson 2005).

RESULTS

Modification of the physical environment

Nine solitary mussels had a total edge of 136.0 ± 11.7 cm, 3 aggregations of 3 mussels had a total edge of 80.6 ± 9.6 cm, and a single aggregation of 9 mussels had a total edge of 53.1 ± 3.7 cm. The amount of edge significantly differed among treatments ($F_{2,6} = 22$, $p < 0.01$) such that solitary mussels had significantly more edges than aggregations of 3 or 9 mussels (SNK, $p < 0.01$).

Treatments with mussels (solitary or mussels aggregated in groups of 3 or 9) had greater sediment mass than treatments without mussels (undisturbed substratum, substrata that were cleared and mesh control), although this was not significant for Expt 2 at Location 2 (Expt 1: $F_{3,8} = 7.44$, $p < 0.05$; Expt 2: $F_{4,50} = 5.55$, $p < 0.001$, SNK, $p < 0.05$).

In the first experiment, treatments with mussels of all configurations were cooler than treatments where mussels were not present (Day 1: $F_{4,4} = 13.23$, $p < 0.05$; Day 2: $F_{4,4} = 36.67$, $p < 0.05$). In the second experiment, mussels in either configuration were also cooler than treatments without mussels, although this was not significant for the Day 1 (Day 1: $F_{3,3} = 2.23$, $p > 0.05$; Day 2: $F_{3,3} = 176.08$, $p < 0.001$). With respect to humidity, in the first experiment there was a significant location by treatment interaction (Day 1: $F_{4,50} = 3.58$, $p < 0.01$; Day 2: $F_{4,50} = 3.93$, $p < 0.01$). Although it was more humid in treatments with mussels (regardless of the configuration), differences were only significant at one time for one location (SNK, $p < 0.01$). In the second experiment, treatments with mussels had greater humidity but this was significant for Day 2 only (Day 1: $F_{3,3} = 2.79$, $p > 0.05$; Day 2: $F_{3,40} = 7.07$, $p < 0.001$, SNK, $p < 0.05$).

Effects of ecosystem engineering on species richness

Comparison of the number of species indicated that there were significantly more species associated with treatments with mussels than treatments without mus-

sels (Expt 1: $F_{3,8} = 49.5$, $p < 0.001$; Expt 2: $F_{3,3} = 2898$, $p < 0.001$, SNK, $p < 0.01$). Although there were no significant differences among different configurations of mussels in the first experiment (SNK, $p > 0.05$), the second experiment showed significantly more species associated with solitary mussels compared to those in a group (SNK, $p < 0.01$).

Effects of ecosystem engineering on unique species were estimated at the level of experimental treatments and location. Mussels had many unique species, particularly macroalgae, molluscs and crustaceans (Table 1). Furthermore, regularly spaced solitary mussels had in total a greater number of unique species than mussels which were more aggregated and substrata without mussels (Fig. 2). In Expt 1, unique species contributed relatively little to the total number of species in each comparison of degree of aggregation

Table 1. Summary of species unique to mussels (regularly spaced solitary mussels, 3 groups of 3 mussels and 1 group of 9 mussels) but not associated with substrata without mussels (undisturbed substratum without mussels, cleared substratum without mussels and the mesh control), combining data from both experiments. All taxa were unique to regularly spaced solitary mussels except for those indicated with a superscript (1 = solitary, 3 = groups of 3, 9 = groups of 9)

Taxon	Species
Algae	<i>Antithamnion</i> sp.
	<i>Ceramium</i> sp. ^{1,3}
	<i>Cladophora</i> sp.
	<i>Gelidium</i> sp.
	<i>Herposiphonia</i> sp.
	<i>Laurencia</i> sp.
	<i>Polysiphonia</i> sp.
	<i>Ralfsia verrucosa</i> ^{1,3}
	<i>Sargassum</i> sp.
	<i>Ulva lactuca</i>
<i>Wrangelia</i> sp.	
Polychaeta	<i>Chrysopetalum debile</i>
	<i>Exogone gambiae</i>
	<i>Scoloplos</i> sp.
Mollusca	<i>Cantharidella picturata</i>
	<i>Chiton pelliserpentis</i>
	<i>Crassostrea gigas</i> ³
	<i>Crepidula</i> sp.
	Olividae
	Phaselidae
	<i>Risoella</i> sp.
<i>Saccostrea glomerata</i>	
Arthropoda	<i>Balanus amphitrite</i>
	<i>Balanus trigonus</i>
	<i>Hexaminius covertus</i> ³
	Ostracoda ³
	Pycnogonida
	<i>Tetraclitella purpurascens</i> ⁹
Other	Nemertea
	<i>Watersipora</i> spp.

(Table 2a), indicated by values close to 1 (sensu Badano et al. 2006). In Expt 2, there were relatively more unique species associated with regularly spaced mussels than those in a group of 9, indicated by a value

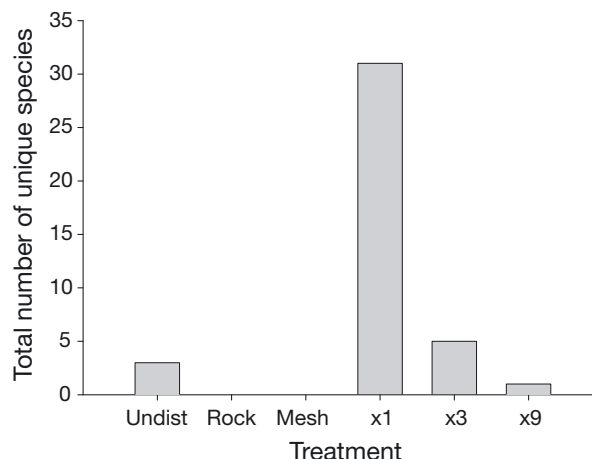


Fig. 2. Total number of unique species (from both experiments) from the undisturbed substratum without mussels (undist), substratum without mussels (rock), mesh control (mesh), 3 aggregations of 3 mussels (x3), 1 aggregation of 9 mussels (x1), and 9 regularly spaced solitary mussels (x9)

Table 2. Summary of comparisons of total species calculations using the framework developed by Badano et al. (2006) to determine the (a) relative importance of unique species, (b) contribution of unique species associated with an experimental treatment, and (c) percentage of generalists. The treatments were: undisturbed substratum without mussels (undisturbed); substratum without mussels (rock); mesh control (mesh); 9 regularly spaced solitary mussels (x1); 3 aggregations of 3 mussels (x3); 1 aggregation of 9 mussels (x9). Expt 1 had treatments rock, x1, x3 and x9. Expt 2 had treatments undisturbed, rock, mesh, x1 and x9. Data for the 2 locations in Expt 2 were combined

Comparison	(a)	(b)	(c)
Expt 1			
Rock vs. x1	4.1	3.3	18
Rock vs. x3	3.8	3.1	18
Rock vs. x9	3.9	3.1	21
x1 vs. x3	0.9	0.2	59
x1 vs. x9	1.0	0.2	62
x3 vs. x9	1.0	0.3	59
Expt 2			
Undisturbed vs. rock	0.7	0.1	55
Undisturbed vs. mesh	0.7	0.1	51
Undisturbed vs. x1	2.1	1.3	33
Undisturbed vs. x9	0.9	0.3	49
Rock vs. mesh	1.2	0.5	50
Rock vs. x1	4.4	3.5	19
Rock vs. x9	1.9	1.1	38
Mesh vs. x1	4.1	3.2	22
Mesh vs. x9	1.5	0.8	43
x1 vs. x9	1.6	0.7	59

of 1.6 (Table 2a). In both experiments, similar patterns were also found at the landscape level (Table 2b).

Effects of engineering on generalists

Generalist taxa included taxa from a range of taxonomic groups (Table 3). In the first experiment it was clear that mean densities of generalists were greater where mussels were present, regardless of the configuration, compared to cleared substratum (Table 3a). In the second experiment the distinction between mussels and substrata without mussels (undisturbed, cleared rock or the mesh control) was less clear, particularly due to the undisturbed substratum ranking highly (Table 3b). It was, however, clear that less aggregated mussels had greater densities of generalists than did more aggregated mussels (Table 3b). At a landscape level, the different configurations of mussels had a large proportion of generalist taxa, indicated by relatively high percentages (Table 2c). Mussels in all

Table 3. Number of times each treatment ranked according to the density of generalists in (a) Expt 1, 10 times for 10 taxa, for each of 4 treatments; (b) Expt 2, 22 times for 22 taxa, for each of 5 treatments, in 2 locations. The treatments were: undisturbed substratum without mussels (undisturbed); substratum without mussels (rock); mesh control (mesh); 9 regularly spaced solitary mussels ($\times 1$); 3 aggregations of 3 mussels ($\times 3$); 1 aggregation of 9 mussels ($\times 9$). Expt 1 had treatments rock, $\times 1$, $\times 3$ and $\times 9$. Expt 2 had treatments undisturbed, rock, mesh, $\times 1$ and $\times 9$

	Number of times ranked				
	1	2	3	4	5
(a) Expt 1^a		$(\chi^2 = 23.09, 3 \text{ df}, p < 0.001)$			
Rock	0	0	0	10	
$\times 1$	3	4	3	0	
$\times 3$	4	3	3	0	
$\times 9$	3	3	4	0	
(b) Expt 2^b		$(\chi^2 = 38.30, 4 \text{ df}, p < 0.0001)$			
Undisturbed	5	9	1	5	2
Rock	0	2	6	8	6
Mesh	1	4	4	6	7
$\times 1$	17	4	0	1	0
$\times 9$	0	4	8	7	3

^aAmphipoda, *Acanthochitona retrojecta*, *Cellana tramoserica*, *Montfortula rugosa*, *Mytilus galloprovincialis*, *Patelloida* spp., *Neanthes biseriata*, Spirorbinae, and juvenile *Trichomya hirsuta*

^b*Acanthochitona retrojecta*, Amphipoda, *Amphithalamus incidata*, *Austrobalanus imperator*, *Capitella capitata*, *Cellana tramoserica*, *Cirriiformia* sp., *Galeolaria caespitosa*, *Limonia marina*, Isopoda, *Lasaea australis*, *Montfortula rugosa*, *Mytilus galloprovincialis*, *Neanthes biseriata*, Nematoda, *Patelloida alticostata*, *Patelloida mufria*, *Saccostrea glomerata*, *Siphonaria denticulata*, *Halicarcinus ovatus*, *Syllis prolifera*, *Tesseropora rosea*

configurations had fewer species in common with the rock than with each other, indicated by low percentages (Table 2c).

Effects of engineering on assemblages of species

nMDS ordinations of multivariate data indicated clear patterns of difference between assemblages of taxa associated with mussels and treatments without mussels (Fig. 3). In the first manipulative experiment there was a significant effect of treatment ($F_{3,8} = 3.29$, $p < 0.05$) such that assemblages associated with mussels (solitary mussels, 3 groups of mussels aggregated in threes, and mussels aggregated in groups of 9, Pairwise tests, $p < 0.05$) significantly differed from assemblages on the substratum without mussels (Pairwise tests, $p < 0.05$). In the second manipulative experiment, although assemblages significantly differed between the locations ($F_{1,30} = 6.65$, $p < 0.001$), there was a significant effect of treatment ($F_{8,30} = 2.97$, $p < 0.001$) such that treatments without mussels (undisturbed rock, previously cleared rock and the mesh control) signifi-

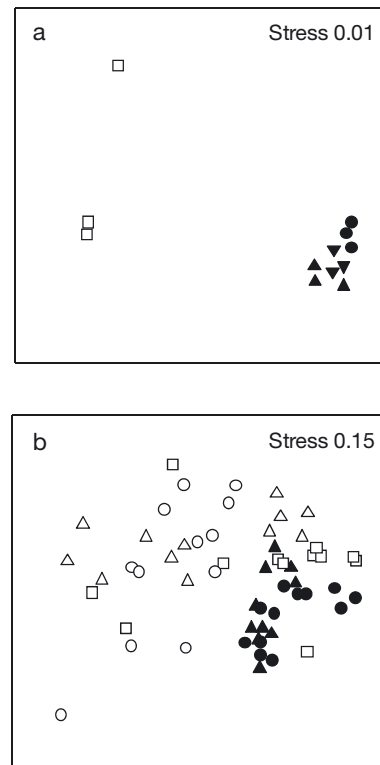


Fig. 3. nMDS plots of (a) Expt 1 and (b) Expt 2 showing assemblages from the undisturbed substratum without mussels (\square), substratum without mussels (Δ), mesh control (\circ), 9 regularly spaced solitary mussels (\bullet), 3 aggregations of 3 mussels (\blacktriangledown), and 1 aggregation of 9 mussels (\blacktriangle)

cantly differed from treatments with mussels (solitary mussels and mussels in aggregated groups of 9, Pairwise tests, $p < 0.05$). Regardless of the configuration of the mussels, their assemblages were similar (Pairwise tests, $p > 0.05$).

DISCUSSION

There are 2 striking findings from this study. First, *Trichomya hirsuta* was experimentally demonstrated as an ecosystem engineer by all methods of comparison (of biotic and abiotic variables) with substrata without these mussels. Mussels engineered the abiotic environment by trapping sand and creating habitat that was cooler, and to a lesser extent, more humid during low tide. Mussels also had biotic influences, by having more species, many unique species (particularly species of macroalgae, molluscs and barnacles), greater densities of generalists, relatively few species in common with the substrata without mussels, and overall different assemblages. Second, configuration had no measurable abiotic effects and there was a positive influence of decreased aggregation on associated taxa. Regularly spaced solitary mussels had more species, many unique species (mostly macroalgal species), and greater densities of generalists.

Consistent with other studies on mussels as ecosystem engineers (see Gutiérrez et al. 2003 for review), *Trichomya hirsuta* altered the abiotic environment. To determine the abiotic effects of ecosystem engineering, previous studies have measured the alteration of the abiotic environment and availability of resources by measuring the temperature of the substratum, the amount of moisture in the soil and the availability of mineral nutrients (e.g. Badano et al. 2006, Jouquet et al. 2006). There are many abiotic factors that influence assemblages on intertidal rocky shores but those influencing desiccation during low tide are important (Southward 1958). Compared to bare rocky substrata, *T. hirsuta* altered the abiotic environment by trapping more sediment and creating habitat that was much cooler and more humid during low tides. Such alteration to the abiotic environment is important for many intertidal organisms (e.g. Altieri et al. 2007). For example, many studies have shown that mortality during low tide due to high temperatures and desiccation limits the distribution of intertidal organisms (Cornelius 1972, Menge 1976, Underwood & Denley 1984). Intertidal ecosystem engineers such as mussels may ameliorate desiccation effects through retention of water and increasing humidity during low tide (Bailey-Brock et al. 1980, Dias & Paula 2001). Although the direction of differences in temperature and humidity was consistently similar, these were snapshot measurements.

Helmuth & Hoffman (2001) suggest that the temporal history of body temperatures represent the true thermal stress of intertidal organisms. These snapshot differences in temperature suggest that further investigation of the thermal history of assemblages associated with *T. hirsuta* would reveal reduced thermal stress compared to assemblages living on substrata without mussels.

Positive effects of engineering by *Trichomya hirsuta* were detected at the small scale of experimental treatment and at the larger landscape scale. Assemblages associated with mussels were different from those associated with substrata without mussels. Moreover, many organisms positively responded to the presence of mussels, including numbers of unique taxa and densities of generalists. The species which were unique to mussels encompassed the broad taxonomic groups: Algae, Mollusca, Polychaeta, Arthropoda, Nemertea and Bryozoa. Similarly, generalist taxa were also represented by a range of taxonomic groups. It can therefore be proposed that not only the entire assemblage of organisms was influenced by the presence of mussels, but also unique and generalist taxa separately. Such strong influences by *T. hirsuta* on the biota suggest that loss of mussels from intertidal rocky shores, particularly this study system, will lead to a loss in diversity (due to loss of unique taxa) and a reduction in overall abundances (due to loss of abundances of generalist taxa). Effects on generalist taxa are, however, probably limited due to the relatively small percentage of generalists in landscapes consisting of mussels and substrata without mussels.

Although positive responses to engineering by mussels have been previously observed (e.g. Borthagaray & Carranza 2007), this should not detract from the role of *Trichomya hirsuta* as an ecosystem engineer. After a range of rigorous tests, *T. hirsuta* was found to be an ecosystem engineer, influencing a range of abiotic and biotic variables. Although the abiotic properties (more sand, cooler temperatures and in some cases greater humidity) which were measured may not be unique to mussels, the relative differences between mussels and substrata without mussels are genuine. The undisturbed substratum was often quite complex (e.g. Chapman 1994) and had other types of engineers present, e.g. turfing coralline algae or tubeworms (Cole et al. 2007). Nevertheless, when compared to the undisturbed substratum, the entire range of taxa showed a positive response to the presence of *T. hirsuta*. This suggests that organisms are not responding solely to the provision of additional space provided by mussel shells (which is not engineering, sensu Jones et al. 1994) but also the shelter that mussels provide. These taxa were algae, sessile animals and mobile animals and thus were not only responding to the provision of

matrix or sediment but rather to a range of factors/resources that mussels provide. Most intertidal organisms are faced with the risk of desiccation, therefore the role of heat stress on organisms associated with habitat engineered by mussels is likely to be an important driving factor and should be further investigated.

In both experiments there were strong differences between treatments with and without mussels. However, the first experiment did not show a strong effect of configuration, whereas the second experiment did. It should be noted that the 2 experiments were done in different seasons, summer and spring. Although the first experiment had less replication than the second experiment, observed differences may be contingent on the seasonal delivery of recruits (*sensu* Keough 1983).

In summary, landscape ecology theory proposes that the configuration of habitat units is an important factor determining resource flow and production such that more aggregated units will have a more altered environment (Forman & Godron 1981). Furthermore, the large amount of edge associated with less aggregated units may facilitate greater flow and delivery of food (Irlandi et al. 1995). I found no evidence of configuration influencing the abiotic environment, and mussels that were aggregated did not alter the abiotic environment any differently from regularly spaced solitary mussels. Configuration of mussels also did not affect the total species richness or overall assemblages of associated taxa. Strikingly, any biotic responses to configuration were contrary to the hypothesis; there were more species, more unique species and greater densities of generalists associated with regularly spaced solitary mussels. Specifically, there were more unique taxa, particularly macroalgae, associated with regularly spaced solitary mussels. Generalist taxa, mostly small mobile crustaceans (e.g. crabs, isopods and amphipods) and limpets also responded positively to solitary mussels. These differences may be attributed to the significantly greater edges of solitary mussels than mussels which are aggregated. Landscape ecologists predict that there are increases of abundances of organisms near edges when resources differ between patches because being near the edge increases access to both sets of resources (Ries & Sisk 2004). With respect to the current study system, the role of positive edge effects seems a likely explanation for the observed findings. Positive responses to edges have been commonly observed in many different systems, for example forests (Cappuccino & Martin 1997, Didham et al. 1998), seagrass meadows (Irlandi et al. 1995, Warry et al. 2009) and freshwater lakes (Treibitz & Nibbelink 1996).

Effects of fragmentation and the consequent changes of spatial arrangement of patches of habitat within

landscapes affect dispersal of marine organisms among patches of habitat of the same type or different types (e.g. Tokeshi & Romero 1995, Eggleston et al. 1999). Disturbances such as smothering by sand (Zardi et al. 2006, Airolidi & Hawkins 2007) and large storms (Underwood 1999) may fragment mussel beds. Effects of fragmenting mussel beds, or more generally fragmenting any habitats which are created by physical ecosystem engineers, are complex. At a landscape scale, fragmentation may lead to a greater range of habitats, including small and large patches. Such fragmentation of large patches of habitat into smaller patches may, however, not decrease the quality of the habitat (Fahrig & Merriam 1994), but may positively influence biodiversity due to the positive responses of organisms to increased habitat edges. Positive responses to habitat subdivision may also be due to smaller pieces of habitat providing refugia from predators which can only occur in large patches, higher rates of immigration among a larger number of smaller patches, increased landscape complementation, and positive edge effects (Fahrig 2003).

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