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Original article

Mussels as ecosystem engineers: Their contribution to species richness in a rocky littoral community

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ABSTRACT

Mussels are important ecosystem engineers in marine benthic systems because they aggregate into beds, thus modifying the nature and complexity of the substrate. In this study, we evaluated the contribution of mussels (*Brachidontes rodriguezii*, *Mytilus edulis platensis*, and *Perna perna*) to the benthic species richness of intertidal and shallow subtidal communities at Cerro Verde (Uruguay). We compared the richness of macro-benthic species between mussel-engineered patches and patches without mussels but dominated by algae or barnacles at a landscape scale (all samples), between tidal levels, and between sites distributed along a wave exposition gradient. Overall, we found a net increase in species richness in samples with mussels (35 species), in contrast to samples where mussels were naturally absent or scarce (27 species). The positive trend of the effect did not depend upon tidal level or wave exposition, but its magnitude varied between sites. Within sites, a significant positive effect was detected only at the protected site. Within the mussel engineered patches, the richness of all macro-faunal groups (total, sessile and mobile) was positively correlated with mussel abundance. This evidence indicates that the mussel beds studied here were important in maintaining species richness at the landscape-level, and highlights that beds of shelled bivalves should not be neglected as conservation targets in marine benthic environments.

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1. Introduction

Ecosystem engineering (i.e. the creation, modification and maintenance of habitats by organisms (Jones et al., 1994) generates environmental heterogeneity and increases the diversity of habitats at the landscape level (Jones et al., 1997). Such increases in habitat diversity suggest that ecosystem engineers can positively affect ecosystem species richness. However, two conditions must be met to achieve higher species richness at this spatial scale. First, the engineer species must provide conditions not present elsewhere in the landscape and, second, some species must be able to live only in the engineered patches (Wright et al., 2002). Only if the engineer-created patches are sufficiently different from its surroundings (so that species otherwise excluded from the landscape can persist) will the addition of an engineer increase species richness via an increase in habitat diversity (Wright et al., 2002). This newly developed conceptual framework is a well-suited tool for management and monitoring issues, since it relates habitat-forming species with processes maintaining local and regional biodiversity.

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Ecosystem engineers can affect the availability of resources to other organisms either as a direct consequence of the structure created by them or by the modulation of biotic or abiotic forces by its structure (Jones et al., 1994, 1997) or their biological activity (e.g. Commito and Boncavage, 1989). Shell production and the subsequent creation of habitat by aquatic molluscs can affect other organisms via three general mechanisms, namely the provision of substrata for attachment, the provision of refuges to avoid predators or physical or physiological stress, and the control of the transport of particles and solutes in the benthic environment (Gutierrez et al., 2003). Mussels are known to control the above factors and processes in marine benthic environments (Fr chette et al., 1989; Crooks and Khim, 1999) suggesting that they can provide other organisms with unique resources. However, their effects on the macro-faunal community may depend upon habitat features varying along exposure and tidal gradients and with the spatial scales considered, since a high variability in the abundance of organisms at spatial scales within and among shores has been found in several intertidal studies (Benedetti-Cecchi, 2001a; Benedetti-Cecchi et al., 2001b; Adami et al., 2004). Mussel beds are a conspicuous feature of Uruguayan rocky shores. *Brachidontes rodriguezii* is the dominant mussel species in these beds but *Mytilus edulis platensis* and *Perna perna* are also present (Maytia and Scarabino, 1979; Neirotti, 1981). Although the biodiversity of Uruguayan rocky intertidal shores is comparatively well known (Caliari et al., 2003), mussel beds have only been studied at the population level, and specifically in relation to the commercial harvesting of some species (Riestra et al., 1992).

On the other hand, the contribution of mussels to the structure and species richness of intertidal and subtidal communities has received little attention in this region. Nevertheless, this is particularly important since intensive mussel harvesting might result in the loss of other species relying on critical resources only available at the mussel-created habitat.

In this paper we assessed the contribution of mussel-created habitat to the species richness of the benthic intertidal and shallow subtidal community at a Uruguayan rocky shore. In particular we quantified differences in macro-benthic specific richness between mussel-engineered patches (hereafter namely MEP) and non-mussel-engineered patches (hereafter namely NMEP) dominated by algae or barnacles and evaluated the consistency of the engineering effect across environmental gradients and different spatial scales. Further, we also focused on how species richness depends upon individual shell traits and spatial arrangement of shells.

2. Materials and methods

2.1. Study area

Cerro Verde (33°57'S, 53°30'W) is a rocky cape on the east coast of Uruguay (Fig. 1) affected by semidiurnal, low-amplitude tides (range <0.5 m) that are largely controlled by wind conditions (direction and speed). The rocky platforms have a smooth slope, with a width ranging from 15 to 23 m, and are exposed to different degrees of wave action according to its orientation. These platforms follow a classical zonation scheme (Stephenson and Stephenson, 1949), in which three zones can be identified: a high intertidal zone dominated by a cyanobacterial film; a middle intertidal zone dominated by barnacles; and a low intertidal and shallow subtidal zone characterized by a dense cover of mussels and/or macro-algae. This site harbours a rich hard-substrata benthic fauna, a yet undefined number of fish species (e.g. endangered sharks *Mustelus schmitti*, *M. fasciatus*, *Sphyrna bigelowi*), marine birds, mammals (*Otaria bryonia*, *Arctocephalus australis*) and sea turtles (*Chelonyx mydas*). It has been proposed as one possible marine protected area in Uruguay (IUCN Uruguayan Committee, 2002).

2.2. Sampling design

Sampling was carried out on intertidal and shallow subtidal (i.e. depth <1.5 m) rocky platforms of the Cerro Verde area during the summer months of 2005 and 2006 to minimize variations due to seasonal changes in climate and sea conditions. Three sampling sites 500 m apart were chosen along the coast: (1) wave-exposed; (2) wave-intermediately exposed; and (3) wave-protected (Fig. 1). Within each site, a variable number of quadrants of 20 × 20 cm were randomly sampled within each patch-type (mussel-engineered and non-mussel engineered, hereafter MEP and NMEP) and at each one of the three tidal levels above defined. Not all of the possible combinations of patch type and tidal level were found and the number of replicates taken within each patch type at a given tidal level varied, but ensured at least a minimum degree of replication within each condition in order to examine the main contrasts of interest. Organisms collected were fixed and identified and counted in the laboratory. In addition, all the mussels collected were counted, measured (shell length to the nearest 0.1 mm), oven-dried (40 °C over 48 h) and weighed to the nearest 0.01 g.

2.3. Data analysis

Each macro-faunal species was assigned to the following categories according to its occurrence: generalists (present in both MEP and NMEP); MEP specialists; and NMEP specialists. Sample-based rarefaction curves were constructed for MEP, NMEP and total (i.e. landscape) for meaningful standardization and comparison of datasets (Gotelli and Entsminger, 2001). Then, we calculated the following parameters in order to describe and quantify the engineer's effect: Landscape Area Engineered (LAE) (calculated as percentage of MEP/total patches); Relative Habitat Richness (RHR) as engineered richness/unengineered richness; Landscape Richness Enhancement (LRE) as $[\text{Engineered specialists} / (\text{Unengineered specialists} + \text{Generalists})] \times 100$; Landscape Insurance Potential (LIP) as percentage of generalists; and Habitat Rescue Potential

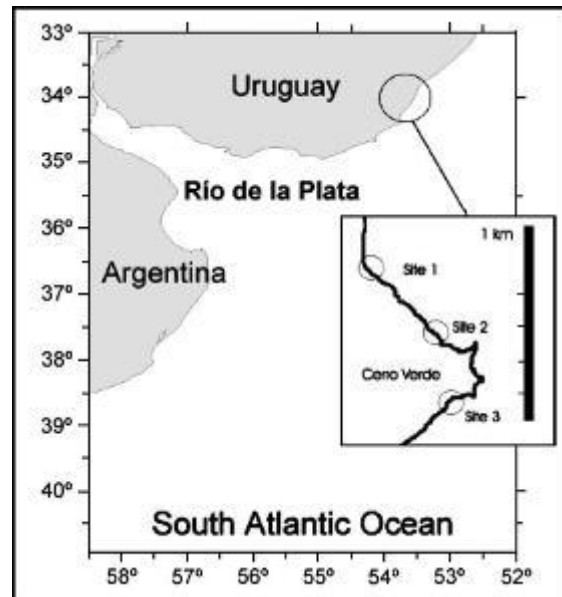


Fig. 1 – Map of the South American Atlantic coast, showing the study region along the coast of Uruguay.

(HRP) as percentage of generalist species whose mean abundance (density in patch) and incidence (number of occurrences) was at least two times greater in engineered patches than in unengineered patches. Statistical significance of differences in abundance were assessed by means of Kolmogorov–Smirnov two sample test for independent samples ($p < 0.05$).

The overall effect of patch type on macro-faunal species richness was assessed by means of a Student's t-test for independent samples ($p < 0.05$). The consistency of the engineer effect along the exposure and tidal gradient was evaluated by means of the significance of the interaction term in two separated two-way analysis of variance (ANOVA). Factors for the first analysis were Site (fixed, three levels) and Patch type (fixed, two levels), while Tidal Level (fixed, three levels) and Patch were used for a second analysis. Further, the effects of Tidal Level, Patch, and Tidal Level × Patch interaction were evaluated within each Site. Cochran's C-test was used to check the assumption of homogeneity of variances and, when necessary, data were log-transformed to remove heterogeneous variances. In cases where homogeneity was not achieved, we set the critical level to a value equal to the p-value for variance homogeneity (Underwood, 1997). All analyses were done separately for each one of the three faunal groups (total, sessile and mobile species).

Regression analyses were used to evaluate if species richness was correlated with mussel density and the mean and standard deviation of mussel shell length and dry weight at each sampling quadrant. In addition, we examined the correlations between the abundance of mussels and shell traits in order to remove density-dependent effects on these variables. In all cases, possible non-linear responses of the independent variables were investigated by means of the examination of the significance of the second-order coefficient of a fitted polynomial function. Otherwise, a linear function was adjusted. Regression analysis was also done separately for total, sessile and mobile macro-fauna. Log transformed data (both dependent and independent variables) were used for the regression analysis due to heterocedasticity.

3. Results

A total of 37 species (or operative taxonomic units) of benthic invertebrates, distributed in 7 major taxa were found in the 59 quadrants sampled. These were: 16 crustaceans, 9 molluscs, 3 cnidarians, 4 polychaetes, 2 pycnogonids, a nemertean, a ophiuroidean and a platyhelminth (Table 1). In addition, three mussel species were present in the assemblage: *Brachidontes rodriguezii*, *Perna perna* and *Mytilus edulis platensis*. Another mytilid, *Modiolus carvalhoi*, was present as a single specimen in one quadrant, and considered as a macro-faunal species. From the analysed samples, 37 were classified as MEP and 22 as NMEP.

Within the samples more than half of the total sampled area was engineered (61%), while the maximum Relative Habitat Richness was 1.29. We also found that 10 species were added to the landscape by the engineer (Landscape Richness Enhancement, 37%). Generalist species (species present in the combined engineered and unengineered patches) represented 67.57% of total species (i.e. Landscape Insurance Potential). Of these species, 84% showed at least double the incidence of engineered patches (Habitat Rescue Potential). Also, 46% of the generalist species showed a mean increase in abundance from NMEP to MEP, but only 7 species showed statistically significant differences (Table 1).

Rarefaction curves showed that total species richness reached the asymptotic maximum after approximately 40 sampling units while species richness at MEP did the same after 27 samples. However, NMEP did not reach an asymptotic value. The total (landscape) curve lay above MEP and NMEP curves on all the scales, with the latter displaying the lowest values across the scales. However, there were no significant differences among the species richness curves, as shown by the overlapping of the curves' 95% confidence intervals.

Also, at the landscape scale the total species richness was significantly higher at MEP compared with NMEP ($t_{(1,57)} \frac{1}{4} 5.25$, $p < 0.01$). Mussel-engineered patches also showed a significantly higher richness of sessile ($t_{(1,57)} \frac{1}{4} 3.88$, $p < 0.01$) and mobile ($t_{(1,57)} \frac{1}{4} 4.88$, $p < 0.01$) macro-fauna. A significant Patch \times Site interaction was found for total (ANOVA; $F_{(2,53)} \frac{1}{4} 11.255$, $p < 0.05$), sessile ($F_{(2,53)} \frac{1}{4} 6.20$, $p < 0.05$) and mobile ($F_{(2,53)} \frac{1}{4} 5.04$, $p < 0.05$) species richness, while Level \times Patch interactions were not significant.

At the site scale in the protected site, a significant patch effect was detected for all three faunal groups [total (S), sessile (SS) and mobile (MS) specific richness], but Tidal Level affected only sessile ($F_{(2,17)} \frac{1}{4} 6.7557$, $p < 0.05$) and total ($F_{(2,17)} \frac{1}{4} 4.6116$, $p < 0.05$) macro-fauna. At the Exposed site, the effect of tidal level was significant for Total ($F_{(2,12)} \frac{1}{4} 8.1336$, $p < 0.05$) and mobile species ($F_{(2,12)} \frac{1}{4} 4.2866$, $p < 0.05$); no patch effects were detected. Patch effects within the intermediately exposed site could not be estimated due to insufficient samples.

The richness of total (regression analysis, $r_2 \frac{1}{4} 0.44$, $p < 0.05$), mobile ($r_2 \frac{1}{4} 0.34$, $p < 0.05$) and sessile macro-faunal species ($r_2 \frac{1}{4} 0.33$, $p < 0.05$) were positively correlated with mussel abundance. Sessile macro-faunal specific richness was positively correlated with the standard deviation of mussel dry weight ($r_2 \frac{1}{4} 0.17$; $p \frac{1}{4} 0.01$). Mean and standard deviation of mussel length and weight were not correlated with mussel density.

Table 1 – Classification of macro-invertebrate species or operative taxonomic units (OTUs) according to their occurrences and motility

Occurrence	Species OTUs	Major taxa	
G	<i>Cymadusa</i> sp.	Amphipoda	Motile
G	<i>Hyale</i> sp.	Amphipoda	Motile
G	<i>Jassa</i> sp.	Amphipoda	Motile
G	<i>Caprella pennantis</i>	Amphipoda	Motile
MEP	<i>Ampithoe</i> sp.	Amphipoda	Motile
G	<i>Ostreola equestris</i>	Bivalvia	Sessile
G	<i>Modiolus carvalhoi</i>	Bivalvia	Sessile
MEP	<i>Sphenia fragilis</i>	Bivalvia	Sessile
MEP	<i>Entodesma patagonicum</i>	Bivalvia	Sessile
G	<i>Actinia bermudensis</i>	Cnidaria	Sessile
G	<i>Actinaria</i> spp.*	Cnidaria	Sessile
MEP	<i>Bunodosoma cangicum</i>	Cnidaria	Sessile
G	<i>Balanus improvisus</i> *	Cyrripedia	Sessile
G	<i>Chtamalus bisinuatus</i>	Cyrripedia	Sessile
G	<i>Pachycheles haigae</i>	Decapoda	Motile
G	<i>Cyrtograpsus altimanus</i>	Decapoda	Motile
G	<i>Sesarma</i> ? sp.	Decapoda	Motile
G	Pannopeidae indet.	Decapoda	Motile
MEP	<i>Pilumnus reticulatus</i>	Decapoda	Motile
NMEP	<i>Cyrtograpsus angulatus</i>	Decapoda	Motile
MEP	<i>Amphipholis squamata</i>	Echinozoa	Motile
G	<i>Siphonaria lessonii</i>	Gastropoda	Sessile
G	<i>Lottia subrugosa</i> *	Gastropoda	Sessile
MEP	<i>Costoanachis sertulariarum</i>	Gastropoda	Motile
MEP	<i>Stramonita haemastoma</i>	Gastropoda	Motile
NMEP	<i>Echinolittorina lineolata</i>	Gastropoda	Motile
G	<i>Idothea baltica</i>	Isopoda	Motile
MEP	<i>Synidothea marplatensis</i>	Isopoda	Motile

G		<i>Lineus rubens</i> *		Nemertea		Motile
G		<i>Alita succinea</i>		Polychaeta		Motile
G		<i>Halodysynella</i> sp.*		Polychaeta		Motile
G		Syllidae indet.*		Polychaeta		Motile
G		<i>Phragmatopoma</i> sp.		Polychaeta		Sessile
G		<i>Pycnogonum pamphorum</i> *		Pycnogonida		Motile
MEP		<i>Anoplodactylus petiolatus</i>		Pycnogonida		Motile
G		Polycladida indet.		Plathelminthes		Motile
G		Tanaidacea indet.		Tanaidacea		Motile

Occurrence: (MEP) inhabits only engineered patches; (NMEP) inhabits only rocky substrata not engineered by mussels; (G) inhabits both (generalist). Motility: (1) mobile able to change spatial location; and (2) sessile are attached to primary or secondary substrata (included vagile species, i.e. with very low mobility). Species with statistically significant differences in abundance (Kolmogorov–Smirnov two sample test for independent samples; $p < 0.05$) between habitat types are denoted with (*).

4. Discussion

Our study demonstrated that at a landscape scale, species richness is increased by the engineering activity of mussel species, producing shells that introduce complexity into benthic communities. The positive effect of mussel beds in macro-faunal species richness did not depend upon site and tidal level. This increase in species richness at the landscape scale reflects a significant addition of new species to the intertidal rocky community that otherwise would remain excluded. However, this effect seems to be scale-dependent, since differences in mean richness between MEP and NMEP within sites were not significant in all cases. The same fact can be observed in the rarefaction curves, where confidence intervals overlapped at small spatial scales.

We also found a positive effect on the abundances of 60% of generalist taxa, which showed higher abundances in mussel beds than in other patches. The same result has been found in several studies dealing with the positive effect of mussel mats, but most are restricted to comparisons between bare soft sediment and mussel beds (Ragnarsson and Raffaelli, 1999; Commito et al., 2005, 2006). Our results are likely to be extrapolated to other neighbouring rocky shores with similar characteristics. In this vein, Cerda and Castilla (2001) reported that macro-invertebrate diversity did not show differences between sites at a local scale in Antofagasta Bay (Chile), which suggests that the effect of the exotic engineer *Pyura praeputialis* on the increase of species richness was similar along the coast of the bay (Castilla et al., 2004).

The positive effect of mussels supports the suggestion of Crooks (2002), who stated that engineers that increase “habitat complexity” tend to favour either the diversity or abundance of organisms. Conversely, engineers that decrease habitat complexity should have a negative effect on diversity or abundance. Chapman et al. (2005) showed that most invertebrate taxa, especially the more widespread and numerous ones, were generally more abundant in turf (coralline algae) than in mussel beds. However, Commito et al. (2005) reported a reduction of species diversity in mussel bed patches compared with the unengineered bare sediment, in a situation in which the engineers increased spatial heterogeneity and complexity.

Tokeshi and Romero (1995) have shown that specific groups of organisms are favoured in mussel beds. For example, our results showed that mobile polychaetes are several times more abundant in mussel beds (ranging from 29 to >1000) than on an engineered rock surfaces. These species may be favoured by the structurally complex substrata with interstitial spaces generated by mussels, thus providing shelter on the otherwise exposed rocky substrate. In addition, direct and/or indirect trophic interactions account for the presence of several species in mussel beds. Polyclad flatworms, for instance, belong to a group of species known to predate on oysters (Watanabe and Young, 2006) and are exclusively found on mussel beds, whereas the whelk *Stramonita haemastoma* preys on bivalves and on Sabelariid polychaetes (Suchanek, 1978, 1985; Lintas and Seed, 1994). Decapod crustaceans and some amphipods probably require the secondary space afforded by mussels as a refuge from water movement and desiccation (Bain, 1991; Piel, 1991; Genzano,

2002). Pycnogonids, in turn, are commonly found along with sessile or sluggish invertebrates that are associated with mussels, including sea anemones and hydroids on which they prey (Genzano, 2002). Strong interactions with mussel associated species may occur during early phases of the life cycle. For example, the endoparasitic larvae of the sea spider *A. Petiolatus* were reported to be associated with colonies of Bouganvillid Hydrozoans. In this context, the presence of *P. pamphorum* (one occurrence within unengineered patches dominated by algae *Ulva* sp.) may be ascribed to dislodgement from neighbouring mussel beds. Mussels also provide secondary substrata for attachment (*L. subrugosa*, *S. lessonii*) and may enhance the likelihood of settlement of some species (e.g. the bivalves *S. fragilis*, *M. carvalhoi*, *E. patagonicum*, *Balanus* sp.). In addition, Ophiuroideans and polychaetes are able to colonize the sediment trapped between mussel beds and the bare rock surface (Prado and Castilla, 2006).

On the other hand, other species or functional groups may be negatively affected by mussel engineering. The presence of specialists on patches not engineered by mussels may be indicative of a negative interaction between mussels and these species. Nevertheless, only one of the species collected (the crab *C. angulatus*) was exclusively associated with macroalgae. Other putative engineering organisms, like the barnacle *Chthamalus bisinuatus*, which occur at high densities on the rocky platform, were associated only with the gastropod *Echinolittorina lineolata* and restricted mainly to supra and mesolittoral levels (reflecting the species vertical zonation pattern in response to physical gradients).

Total, sessile and mobile species richness within MEP were positively correlated with mussel abundance. The positive correlation between the richness of sessile macro-fauna and mussel density could be explained because of the expected relationship between mussel density and substrate area available. Mobile macro-fauna, in turn, might depend upon crevices generated between mussels. This suggests that the patterns in abundance and occurrence of different functional groups did not respond in the same way to the engineering effect and that dispersal capabilities and body size might affect the way in which the organisms interact with their environments (Collins and Glenn, 1991).

Although other studies have shown that species richness and diversity of the associated fauna increased with age and size of mussel patches (Tsuchiya and Nishihira, 1985, 1986), the variables that measured individual shell traits (i.e. mean shell length and mean dry weight) were not correlated with specific richness. Similarly, variables measuring heterogeneity in individual shell traits (i.e. length SD and dry weight SD) were not correlated with patch species richness, except for the positive correlation between sessile macro-faunal and dry weight SD. This positive correlation may reflect a positive response to increasing heterogeneity in mussel beds. In general, mean and standard deviation of mussel length as well as mean mussel dry weight were not useful in explaining variation in species richness. In this vein, mussel densities and length–frequency distributions may interact in a complicated fashion. According to Commito and Rusignuolo (2000), an intermediate percentage cover of mussels of different sizes would have a highly irregular surface and large values of fractal dimension (i.e. a measure of habitat complexity), while similar-sized, densely packed mussels at 100% cover might have a relatively smooth surface and small values.

Thus, if micro-scale habitat complexity is indeed an important control then maximum values of specific richness are expected at large values of fractal dimension. However, recent studies concluded that habitat heterogeneity may not be an accurate indicator of faunal diversity (Le Hir and Hily, 2005). For conservation and management purposes, the identification of key processes that maintain mussel-bed structure are of outmost importance, since these structures control the local richness of benthic species. The mussel beds studied here are key structures that add species to the landscape and it is therefore vital that shelled bivalves are not neglected as conservation targets. Quantitative research on the relationship between different community traits (species richness and composition, abundance distribution) and environmental factors (exposure, habitat complexity, energy input, seascape configuration, pollution) is needed to understand community structure and to ensure a proper management of protected areas.

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