

Habitat complexity and community composition: relationships between different ecosystem engineers and the associated macroinvertebrate assemblages

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Abstract Several species of ecosystem engineers inhabiting coastal environments have been reported structuring different kinds of communities. The magnitude of this influence often depends on the habitat complexity introduced by the engineers. It is commonly accepted that an increase in habitat complexity will result in an increase in diversity and/or abundance in the associated fauna. The rocky salt marshes along the coast of Patagonia are dominated by cordgrasses, mussels, and barnacles forming a mosaic of engineered habitats with different complexity. This system allows us to address the following questions: how different is a macroinvertebrate assemblage when dominated by different ecosystem engineers? And, is there a positive relationship between increasing habitat complexity and the species richness, diversity and total density of the assemblages? To address these questions, we compared the three ecological scenarios with decreasing habitat complexity: cordgrass–mussel, mussel, and barnacle-engineered habitats. We found a total of 22 taxa mostly crustaceans and polychaetes common to all scenarios. The three engineered habitats showed different macroinvertebrate assemblages, mainly due to differences in individual abundances of some taxa. The cryptogenic amphipod

Orchestia gammarella was found strictly associated with the cordgrass–mussel habitat. Species richness and diversity were positively related with habitat complexity while total density showed the opposite trend. Our study suggests that species vary their relative distribution and abundances in response to different habitat complexity. Nevertheless, the direction (i.e., neutral, positive or negative) and intensity of the community's response seem to depend on the physiological requirements of the different species and their efficiency to readjust their local spatial distribution in the short term.

Keywords Ecosystem engineers · Habitat complexity · Macroinvertebrate assemblage

Introduction

The concept of ecosystem engineering is currently well recognized among ecologists worldwide and refers to the physical modification, maintenance, or creation of habitat by organisms (Jones et al. 1997). The engineer organisms can change the physical structure, complexity, and heterogeneity of the environment having a marked influence on the associated communities (Jones et al. 1994, 1997; Crooks 2002). Of these environmental features, habitat complexity encompasses the absolute abundance of individual structural components of the habitat and has long been considered one of the determinants of biological diversity (McCoy and Bell 1991). Thus, the magnitude of the influence of different engineer organisms often depends on the habitat complexity introduced by them, and the way this habitat complexity modulates the environmental forces and/or biological processes that shape the associated community, in terms of their species richness, diversity and

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density (Gutiérrez and Iribarne 2004; Hastings et al. 2007; Bouma et al. 2009).

Several species of ecosystem engineers inhabiting coastal environments have been reported structuring different sorts of communities by increasing habitat complexity as a consequence of providing living space with different structural components and/or by generating quantitative changes in the amount of living space. For instance, mussel beds, reef-building organisms and many species of plants form highly compact and imbricate structures above and below ground in soft bottom environments, increasing the availability of food, substratum for larvae settlement and supplying new refugia from predators and physical unfavorable conditions (Schwindt et al. 2001; Callaway 2006; Levin et al. 2006; Commito et al. 2008; Jackson et al. 2008; Buschbaum et al. 2009; Maggi et al. 2009).

It is widely accepted that an increase in habitat complexity will increase the diversity and/or abundance of the associated fauna (Crooks 2002; Bouma et al. 2009). The underlying hypothesis is that a greater amount of structure will provide more resources, habitats and niches (Connor and McCoy 2001). Many studies have been designed to evaluate the effect of a given ecosystem engineer on different faunal assemblages, and they usually compare presence versus absence of the ecosystem engineer (e.g., Castilla et al. 2004; Borthagaray and Carranza 2007). However, less effort has been directed to evaluate the effect of different engineers on a single faunal assemblage. Moreover, the papers compiled in Table 1 show that the direction of the effect exerted by ecosystem engineers with different habitat complexities may be hard to predict. In fact, the analysis and study of this ecological problem is strongly scale-dependent, because the notion and magnitude of structural complexity assigned to a given habitat will vary depending on the species under consideration. Indeed, meio- and microfaunal organisms such as nematodes, ostracodes, and ciliates are not likely to even respond to the same kind of differences in complexity than megafaunal organisms such as the sea lions, or even smaller organisms like cormorants and penguins, do. Nevertheless, since the study of large spectrum of habitat complexity (i.e., including macro and microscopic scales) is virtually impossible, scientists often advocated for partitioning their study systems.

The rocky salt marshes of Patagonia were recently described as an environmental intersection between rocky intertidal and salt marsh (Bortolus et al. 2009). In this environment, three well-known ecosystem engineers can be found coexisting and characterizing the intertidal: cordgrass, mussels, and non-native barnacle. Different species of cordgrass, mussels, and barnacles have been

reported to alter light, temperature, wave action, sedimentation, and food availability, which in turns have influenced with the abundance and distribution of invertebrate fauna (e.g. cordgrass: Capehart and Hackney 1989; Netto and Lana 1999; Hedge and Kriwokwen 2000; Bortolus et al. 2002; mussels: Thiel and Ullrich 2002; Adami et al. 2004; Prado and Castilla 2006; barnacles: Bros 1980; Barnes 2000; Harley 2006). However, the differences on the amount of structural components of these ecosystem engineers species supply three contrasting natural scenarios with increasing habitat complexity (from high to low: cordgrass–mussel-engineered, mussel-engineered, and barnacle-engineered habitats) that allow us to address the following questions: How different is a macroinvertebrate assemblage when dominated by different ecosystem engineers? And, is there a positive relationship between increasing habitat complexity and the species richness, density and total density of the assemblages?

Materials and methods

Study system

The Patagonian rocky salt marshes develop on top of wave-cut platforms of sedimentary rock and are dominated by a dwarf ecotype of the austral cordgrass *Spartina densiflora* Brong. (the Patagonian ecotype; see Bortolus 2006; Fortuné et al. 2008; Bortolus et al. 2009) covering about 40% of the substratum. The unvegetated areas are dominated either by a dense bed of the native mussels *Perumytilus purpuratus* (Lamarck 1819) and *Brachidontes rodriguezii* (d'Orbigny 1846) or by the only intertidal species of barnacle in this region, the non-native *Balanus glandula* Darwin 1854 while the occurrence of bare rock is virtually nil in this area. In this system, the cordgrasses have a very compact and thick mat of roots and rhizomes (mean biomass of 22 ± 10 g 100 cm⁻²; Sueiro, unpublished data), which in turn is covered by a dense mat of mussels (mean density of 133 ± 51 ind 100 cm⁻²; Sueiro, unpublished data) underneath a homogeneous 30 cm height canopy (mean biomass of 4 ± 2 g 100 cm⁻²; Sueiro, unpublished data) (Bortolus et al. 2009; Fig. 1). As a result, these patches provide the highest amount of available space and microhabitats with their different structural components, thus generating the more complex habitat. The next lower level of habitat complexity is presented by the mussels, which are also found in the rocky shores devoid of cordgrass. In this case even though the mussels are the only structural component, they form highly dense and multilayer beds, providing an intermediate amount of available space and microhabitats (mean density 160 ± 42 ind 100 cm⁻²; Sueiro, unpublished data, Fig 1) (Adami

Table 1 Studies showing examples of increasing habitat complexity generated by different ecosystem engineers and the response of the associated communities

Engineered habitats compared	System examined	SP	De	Di	Source
More complex	Less complex				
Seagrasses (<i>Halophila ovalis</i> and <i>Zostera capricorni</i>)	Alga (<i>Caulerpa taxifolia</i>)	+	0	Na	McKinnon et al. 2009
<i>Fucus vesiculosus</i>	Barnacle	+	–	Na	Thompson et al. 1996
Rough and bushy artificial kelp	Smooth artificial kelp	+	+	Na	Christie et al. 2007
Filamentous artificial alga	Foliose artificial alga	+	+	Na	Edgar and Klumpp 2003
Macrophyte (<i>Najas microcarpa</i> , <i>Utricularia foliosa</i> , <i>Egeria najas</i> , <i>Cabomba frucata</i> and <i>Eichhornia azurea</i>)	Macrophyte (<i>Nymphaea amazonum</i>)	+	+	Na	Thomaz et al. 2008
Algae (<i>Cystoseira barbatula</i> , <i>Cystoseira spinosa</i> , <i>Sargassum vulgare</i> , <i>Halopteris scoparia</i>)	Algae (<i>Dictyota fasciola</i> and <i>Dictyota dichotoma</i>)	+	+	+	Chemello and Milazzo 2002
Algae (<i>Ceramium nodulosum</i> and <i>Cladophora rupestris</i>)	Algae (<i>Corallina officinalis</i> and <i>Chondrus crispus</i>)	+	+	+	Hull 1997
Bryozoan (<i>Watersipora subtorquata</i>)	Sea squirt (<i>Ascidia ceratodes</i>) and mussel (<i>Mytilus galloprovincialis</i>)	+	0	+	Sellheim et al. 2010
Halophyte (<i>Phragmites australis</i>)	Halophyte (<i>Spartina alterniflora</i>)	+	+	Na	Angradi et al. 2001
Alga (<i>Codium fragile</i> spp. <i>tomentosoides</i>)	Algae (<i>Laminaria longiciruris</i> and <i>Laminaria digitata</i>)	+	0	+	Schmidt and Scheibling 2006
Monolayer of mussel (<i>Perumytilus purpuratus</i>)	Multilayer of mussel (<i>P. purpuratus</i>)	0	0	Na	Prado and Castilla 2006
Bryozoan (<i>W. subtorquata</i>)	Sea squirt (<i>A. ceratodes</i>) and mussel (<i>M. galloprovincialis</i>)	0	0	0	Sellheim et al. 2010
Oyster (<i>Crassostrea gigas</i>)	Mussel (<i>Mytilus edulis</i>)	0	–	Na	Kochmann et al. 2008
Macrophyte (<i>Thalassia testudinum</i>)	Macrophyte (<i>Halodule wrightii</i>)	0	0	Na	Lewis 1984
Alga (<i>Macrocystis pyrifera</i>)	Alga (<i>Undaria pinnatifida</i>)	+	+	+	Raffo et al. 2009
Hybrid halophyte (<i>S. alterniflora</i> x <i>Spartina foliosa</i>)	Halophyte (<i>S. foliosa</i>)	0	–	0	Brusati and Grosholz 2006
Mussel (<i>M. galloprovincialis</i>)	Alga (<i>Corallina</i>)	0	–	Na	Chapman et al. 2005
Mussel (<i>P. purpuratus</i>)	Algae (<i>C. officinalis</i> var. <i>chilensis</i> , <i>Gelidium chilense</i> and <i>Gastroclonium cylindricum</i>)	0	0	Na	Kelaheer et al. 2007
Halophyte (<i>Spartina anglica</i>)	Seagrass (<i>Zostera noltii</i>)	0	+	–	Bouma et al. 2009
Halophyte (<i>S. anglica</i>)	Seagrass (<i>Z. noltii</i>)	0	0	Na	Cottet et al. 2007

Table 1 continued

Engineered habitats compared	System examined	SP	De	Di	Source
More complex	Less complex				
More dense <i>C. officinalis</i> turf	Less dense <i>C. officinalis</i> turf	–	–	Na	Kelaher 2003
Algae (<i>Cladophora rupestris</i> and <i>Laminaria digitata</i>)	Alga (<i>Fucus serratus</i>)	Na	+	+	Hooper and Davenport 2006
Alga (<i>Sargassum globulariataefolium</i>)	Alga (<i>Hormosira banksii</i>)	Na	0	Na	Schreider et al. 2003
Tubeworm (<i>Ficopomatus enigmaticus</i>)	Oyster (<i>Ostrea conchaphila</i>)	Na	+	Na	Heiman et al. 2008

We classified the cases where habitat complexity was not measured, as more or less complex considering the density and/or diversity of structural elements. Responses are indicated in terms of positive (+), negative (–) or neutral (0) relationship between species richness (SP), density (De) or diversity (Di) in the more complex versus the less complex engineered habitat. *Na* not assessed in the study

et al. 2004; Bertness et al. 2006; Prado and Castilla 2006). Finally, the simplest habitat complexity level in the rocky marshes is generated by carpets (mono-layers less than 1 cm height) formed by barnacles on the rocky bottom (mean density 146 ± 59 ind 100 cm^{-2} ; Sueiro, unpublished data) without mussels or cordgrasses (Schwindt 2007; Savoya and Schwindt 2010; Fig. 1). The non-native *Balanus glandula*, the only structural component in these patches, is strongly cemented to the substratum and prevents the formation of the sub-superficial community of invertebrates often found underneath the mussel beds that are attached to the substratum with abundant byssal threads. The existence of different combinations of these same habitats is possible, but not pertinent within the context of this study. Field surveys were conducted in rocky salt marshes distributed along the shore of the Nuevo Gulf in the Argentinean Patagonia ($42^{\circ}36'S$, $64^{\circ}49'W$; Fig. 1). The climate is mostly arid with low precipitations ($< 200 \text{ mm year}^{-1}$), annual temperatures ranging from 39°C to -7.5°C , and strong, cold winds predominantly from the southwest with a mean annual speed of up to 22 km h^{-1} and gusts that may exceed 100 km h^{-1} . All samples were collected at $\sim 3.50 \text{ m}$ above the Argentinean hydrographic zero.

Sample design

To investigate the macrofaunal assemblages associated with the three engineered habitats, $20 \times 20 \text{ cm}$ samples were obtained seasonally from 2007 to 2009 and placed into the following three categories: (1) samples engineered by cordgrasses and mats of mussels covering their roots and rhizomes ($n = 30$, hereafter *S-M*); (2) samples engineered by mussels ($n = 30$, hereafter *M*) and (3) samples engineered by barnacles ($n = 30$, hereafter *B*). In the field, samples were carefully placed in plastic bags with ice. At the laboratory, the macrofauna of *S-M* samples was macroscopically sorted from above-ground and below-ground plant material, followed by a second sorting through a 0.5-mm mesh. The rest of the samples (*M* and *B*) were sorted through a sieve of 0.5-mm mesh. The retained material was always fixed in 10% formalin for 48 h and then preserved in 70% ethanol. Organisms retained on the sieve (excluding mussels and barnacles when they formed the engineered habitats) were counted and identified to the lowest possible taxonomic level. A voucher of each specimen collected was deposited in the invertebrate collection of the CENPAT (www.cenpat.edu.ar).

Data analysis

Multivariate approaches were used to examine macroinvertebrates assemblages in each engineered habitat. These

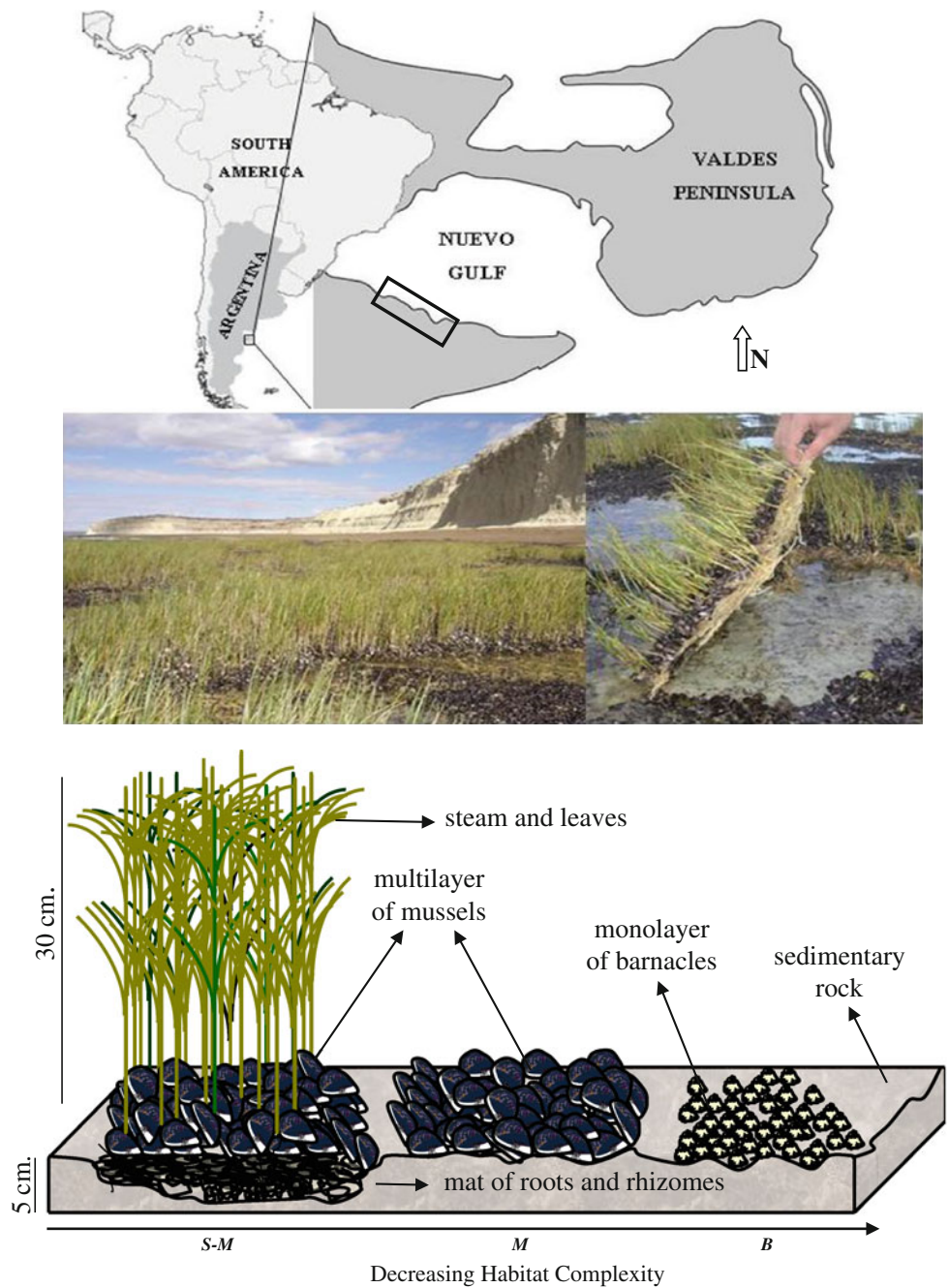


Fig. 1 *Top*: map showing the location of the study site. *Center*: landscape physiognomy of a typical Patagonian rocky salt marsh and close-up of the cordgrass–mussel-engineered habitat. *Bottom*: schematic representation of the studied ecosystem engineers inhabiting

rocky salt marshes. Cordgrass–mussel-engineered habitat (*S-M*), mussel-engineered habitat (*M*), and barnacle-engineered habitat (*B*) (Photograph credits: A. Bortolus)

analyses were carried out using Primer Statistical software (Clarke and Warwick 1994). The data matrix of all invertebrate species was 4th-root transformed in order to down-weight the abundant species. Non-metric multidimensional scaling (MDS) was used to explore community similarities and differences for macroinvertebrates assemblages in the engineered habitats. Stress values <0.1 and <0.2 indicate good and useful resolutions, respectively, of the

two-dimensional MDS plot (Clarke and Warwick 1994). Pairwise comparisons for significant differences in macroinvertebrates assemblages between engineered habitats were made using a one-way analysis of similarity (ANOSIM), and a similarity percentage (SIMPER) analyses were used to determine the taxa responsible for the differences between groups. These analyses were based on Bray-Curtis similarity indexes.

Table 2 Mean density \pm standard deviation of invertebrate species (ind 100 cm⁻²) on data pooled over four sampling seasons

	<i>S-M</i>	<i>M</i>	<i>B</i>
Crustacea			
<i>Orchestia gammarella</i> (Pallas) 1766	7 \pm 11	0.2 \pm 0.7	0.04 \pm 0.11
<i>Amphitoe valida</i> Smith, 1873	0.01 \pm 0.06	0	0.1 \pm 0.4
<i>Melita palmata</i> (Montagu, 1804)	0.1 \pm 0.5	2 \pm 5	0.1 \pm 0.8
<i>Monocorophium insidiosum</i> (Crawford, 1937)	0.2 \pm 0.3	1 \pm 3	2 \pm 5
<i>Tanais dulongii</i> (Audouin, 1826)	29 \pm 27	44 \pm 27	20 \pm 24
<i>Exosphaeroma</i> sp.	2 \pm 6	2 \pm 4	1 \pm 4
<i>Pseudosphaeroma</i> sp.	14 \pm 12	6 \pm 10	28 \pm 32
<i>Idotea</i> sp.	0.01 \pm 0.03	0	0
<i>Cyrtograpsus altimanus</i> Rathbun, 1914	2 \pm 2	2 \pm 2	0.3 \pm 0.9
Polychaeta			
<i>Eulalia</i> sp.	1 \pm 1	1 \pm 1	0.4 \pm 0.5
<i>Boccardia polybranchia</i> (Haswell, 1885)	1 \pm 2	9 \pm 16	55 \pm 34
<i>Scoletoma tetraura</i> (Schmarda, 1861)	0.04 \pm 0.10	0	0
Syllidae	0.3 \pm 0.6	0.1 \pm 0.3	1 \pm 1
Capitellidae	0.1 \pm 0.4	1.6 \pm 2.5	0
Orbiniidae	0.8 \pm 1.4	1.3 \pm 3.2	0.2 \pm 0.5
Bivalvia			
<i>Lasaea</i> sp.	0.2 \pm 0.4	0.1 \pm 0.3	1 \pm 2
<i>Mytilus</i> sp.	2 \pm 2	1 \pm 1	0.2 \pm 0.5
Gastropoda			
<i>Siphonaria lessoni</i> Blainville, 1824	6 \pm 4	11 \pm 5	14 \pm 6
<i>Trochon geversianus</i> (Pallas 1769)	0.01 \pm 0.02	0	0
Nemertea			
Actinaria	4 \pm 5	2 \pm 4	0.01 \pm 0.04
Ofiuroida	0.01 \pm 0.03	0.01 \pm 0.03	0
Total richness	22	18	17

Cordgrass–mussel-engineered habitat (*S-M*), mussel-engineered habitat (*M*), and barnacle-engineered habitat (*B*)

In addition, species richness, diversity (Shannon's index H), and total density (ind 100 cm⁻²) were compared among engineered habitats within each season using ANOVA tests or the nonparametric Kruskal–Wallis test when variances were heterogeneous and could not be stabilized after different transformations. Significant results were analyzed a posteriori with the Scheffé test after the ANOVAs, or with multiple comparisons of mean ranks after Kruskal–Wallis test (Zar 1999).

Results

A total of 103,287 individuals of 22 species of benthic macroinvertebrates were found in the three engineered habitats in which the most common taxa were crustaceans and polychaetes (Table 2). The replication was originally planned to be balanced ($n = 30$ per category), however, due to non-planned logistic constraints the final replicate number involved in this description was 30 for *S-M*, 20 for *M*, and 10 for *B*. In order to prevent biased analysis and flawed interpretations, but also trying to avoid the

unnecessary sacrifice of valid replicates, we randomly chose a balanced set of ten plots per category and compared them statistically. After repeating this procedure three times, with three different sets of 10 randomly chosen replicates we always found the results consistent and never different from the unbalanced analysis (i.e. including $n = 30, 20$ and 10). The dominant species found showed a differential distribution among engineered habitats: the cryptogenic *Tanais dulongii* was more abundant at *M* habitat (Kruskal–Wallis test: $H = 30.84, P < 0.01$, post hoc test, $M > S-M = B, P < 0.01$), the isopod *Pseudosphaeroma* sp. at *B* habitat (Kruskal–Wallis test: $H = 51.18, P < 0.01$, post hoc test: $B > S-M = M, P < 0.01$), and the limpet *Siphonaria lessoni* at *M* and *B* habitats (Kruskal–Wallis test: $H = 75.96, P < 0.01$, post hoc test, $M = B > S-M, P < 0.01$). Of the total taxa identified, 70% were common to the three engineered habitats and just the isopod *Idotea* sp., the gastropod *Trochon geversianus*, and the polychaete *Scoletoma tetraura*, were exclusively found in habitat from *S-M* but at very low density (≤ 0.01 ind 100 cm⁻², Table 2). However, the amphipod *Orchestia gammarella* was found almost exclusively at high density

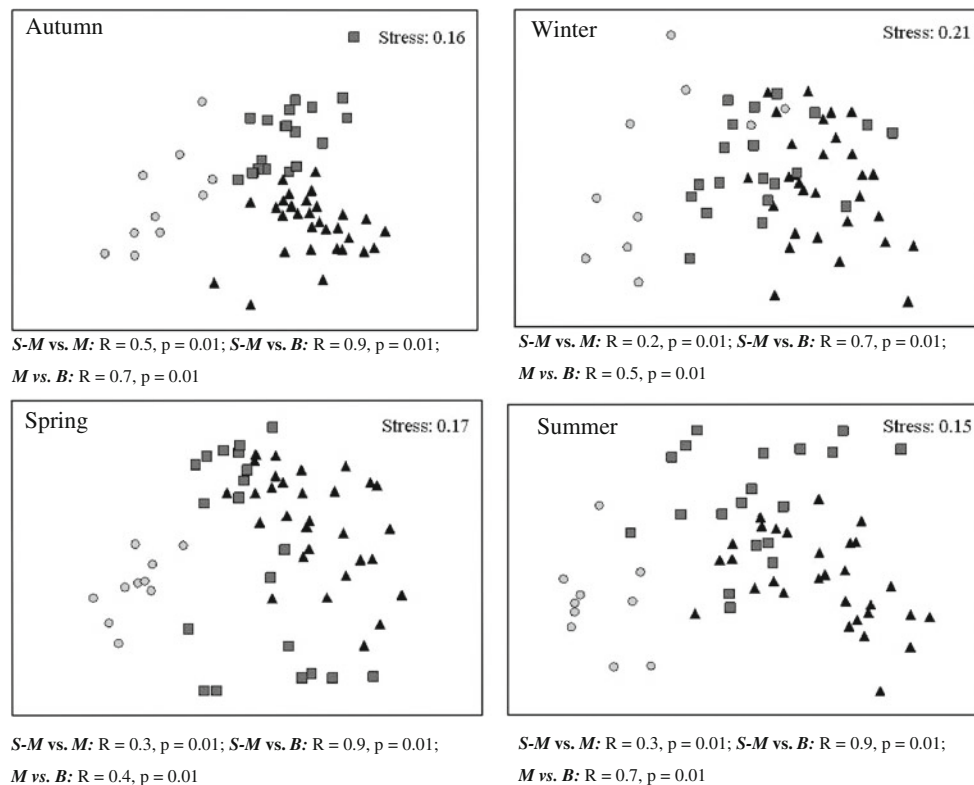


Fig. 2 Two-dimensional MDS ordination comparing macroinvertebrates densities associated with cordgrass–mussel-engineered habitat and results of pairwise comparisons using ANOSIM test at each season. Cordgrass–mussel-engineered habitat: *black triangles*;

mussel-engineered habitat: *dark gray squares*; barnacle-engineered habitat: *gray circles*. Data were 4th-root transformed in order to down-weight abundant species

in *S-M* habitats (Kruskal–Wallis test; $H = 71.88$, $P < 0.01$, post hoc test, $S-M > M = B$, $P < 0.01$, Table 2).

The MDS plots jointly with the ANOSIM procedure showed that macroinvertebrates assemblages in *B* clearly separated from *S-M* and *M* in all seasons while *S-M* and *M* showed a certain degree of overlapping (Fig. 2). Since most of the taxa were shared by the three engineered habitats, these results were mainly due to differences in individual densities. The most discriminating taxa among engineered habitats along all the seasons were the polychaete *Boccardia polybranchia* and the crustaceans *Orchestia gammarella*, *Pseudosphaeroma* sp. and *Tanais dulongii* (Table 3). Large abundances of *B. polybranchia* and *Pseudosphaeroma* sp. were characteristic of *B* habitats while higher densities of *O. gammarella* and *T. dulongii* were characteristic of *S-M* and *M*, respectively (Table 3). The mussel *Mytilus* sp., the sea anemones, and the nemerteans also accounted for differences among engineered habitats, but to a lesser extent (Table 3).

Species richness, diversity, and total density differed significantly among the engineered habitats (Table 4). *S-M* and *M* habitats were more species rich and diverse than *B* (Table 4). This greater richness showed by *S-M* and

M resulted from the presence of some rare species in these habitats. On the other hand, *B* showed significantly higher total densities over all seasons (Table 4), which was mainly drive by the high density of the worm *Boccardia polybranchia*.

Discussion

As we expected, the macroinvertebrate assemblages we studied showed a variable species relative distribution and abundance in presence of different ecosystem engineers. Although we found similar suites of species, the relative density of many individual species was markedly different among contrasting engineered habitats. Moreover, while species richness and diversity increased jointly with the habitat complexity provided by the ecosystem engineers, the total density showed the opposite trend.

The *S-M*-engineered habitat was characterized by the exclusive presence of the gammaridean amphipod *Orchestia gammarella*, a likely introduced species (Orensanz et al. 2002) that was virtually absent from *M* and *B*. Other related species of amphipod have been reported as a characteristic component of salt marsh communities

Table 3 Results of the SIMPER routine showing the species, which made the greatest contributions to dissimilarity in significant contrast between engineered habitats at each season ranked by decreasing power (%)

	Taxa	Av. density	Av. density	Contrib. %	Cum. %
		S-M	M		
Autumn	<i>Pseudosphaeroma</i> sp.	37.30	6.80	14.87	14.87
Groups S-M & M	<i>Orchestia gammarella</i>	8.00	0.00	13.44	28.31
Av. dissimilarity = 31.99	<i>Boccardia polybranchia</i>	1.00	23.35	12.63	40.94
	<i>Mytilus</i> sp.	3.78	2.28	9.31	50.25
		S-M	B		
Groups S-M & B	<i>Boccardia polybranchia</i>	0.25	53.38	24.71	24.71
Av. dissimilarity = 43.81	<i>Cyrtograpsus altimanus</i>	3.61	0.10	10.88	35.59
	<i>Orchestia gammarella</i>	7.24	0.00	10.83	46.43
	<i>Mytilus</i> sp.	2.33	0.18	8.66	55.09
		M	B		
Groups M & B	<i>Boccardia polybranchia</i>	5.84	53.38	17.13	17.13
Av. dissimilarity = 40.86	<i>Pseudosphaeroma</i> sp.	1.70	15.60	13.95	31.08
	<i>Cyrtograpsus altimanus</i>	4.19	0.10	12.34	43.42
	Nemertea	2.81	0.18	10.12	53.55
		S-M	M		
Winter	Actinaria	5.08	2.46	12.71	12.71
Groups S-M & M	<i>Boccardia polybranchia</i>	1.11	7.10	11.92	24.63
Av. dissimilarity = 25.76	<i>Orchestia gammarella</i>	2.45	0.33	10.38	35.01
	<i>Pseudosphaeroma</i> sp.	11.36	7.86	9.62	44.63
	<i>Mytilus</i> sp.	2.39	0.95	8.96	53.59
		S-M	B		
Groups S-M & B	<i>Boccardia polybranchia</i>	1.11	39.00	17.02	17.02
Av. dissimilarity = 36.44	Actinaria	5.08	0.03	11.36	28.38
	<i>Pseudosphaeroma</i> sp.	11.36	48.18	9.97	38.35
	<i>Tanais dulongii</i>	45.36	38.73	9.19	47.54
	<i>Monocorophium insidiosum</i>	0.32	4.85	8.82	56.36
		M	B		
Groups M & B	<i>Pseudosphaeroma</i> sp.	7.86	48.18	14.36	14.36
Av. dissimilarity = 31.21	<i>Boccardia polybranchia</i>	7.10	39.00	13.78	28.13
	<i>Tanais dulongii</i>	58.93	38.73	10.62	38.76
	<i>Monocorophium insidiosum</i>	0.69	4.85	10.39	49.15
	Actinaria	2.46	0.03	9.37	58.52
		S-M	M		
Spring	<i>Pseudosphaeroma</i> sp.	19.01	10.61	14.13	14.13
Groups S-M & M	<i>Orchestia gammarella</i>	6.88	0.13	12.26	26.69
Av. dissimilarity = 33.84	Actinaria	4.30	2.61	11.48	38.17
	<i>Boccardia polybranchia</i>	1.17	7.46	10.58	48.76
	<i>Tanais dulongii</i>	27.27	40.55	9.91	58.67
		S-M	B		
Groups S-M & B	<i>Boccardia polybranchia</i>	1.17	76.03	24.20	24.20
Av. dissimilarity = 43.79	Actinaria	4.30	0.00	11.34	35.54
	<i>Orchestia gammarella</i>	6.88	0.05	10.70	46.23
	<i>Mytilus</i> sp.	1.40	0.00	10.59	56.83
		M	B		
Groups M & B	<i>Boccardia polybranchia</i>	7.46	76.03	24.12	24.12
Av. dissimilarity = 40.05	<i>Pseudosphaeroma</i> sp.	10.61	13.25	12.27	36.38
	<i>Tanais dulongii</i>	40.55	12.53	9.65	46.03
	Nemertea	2.11	0.10	9.38	55.38

Table 3 continued

	Taxa	Av. density	Av. density	Contrib. %	Cum. %
		S-M	M		
Summer	<i>Orchestia gammarella</i>	9.56	0.42	13.93	13.93
Groups S-M & M	<i>Boccardia polybranchia</i>	1.51	14.92	13.58	27.52
Av. dissimilarity = 31.96	<i>Pseudosphaeroma</i> sp.	17.82	4.99	13.26	40.77
	<i>Tanais dulongii</i>	25.75	37.86	10.37	51.14
		S-M	B		
Groups S-M & B	<i>Boccardia polybranchia</i>	1.51	50.95	20.30	20.30
Av. dissimilarity = 45.59	Actinaria	3.51	0.00	12.30	32.60
	<i>Orchestia gammarella</i>	9.56	0.05	11.57	44.16
	<i>Mytilus</i> sp.	2.10	0.00	10.91	55.07
		M	B		
Groups M & B	<i>Pseudosphaeroma</i> sp.	4.99	35.60	15.61	15.61
Av. dissimilarity = 40.71	<i>Boccardia polybranchia</i>	14.92	50.95	14.95	30.56
	Nemertea	3.00	0.08	11.12	41.68
	Actinaria	1.80	0.00	9.16	51.49

Lists were truncated whenever cumulative percentage reached 50%. Cordgrass–mussel-engineered habitat (**S-M**), mussel-engineered habitat (**M**), and barnacle-engineered habitat (**B**)

Table 4 Results of the ANOVA and the Scheffé tests comparing community parameters among the three ecosystems engineered habitats (EE) at each season

Seasons	Factor	Diversity			Species richness			Total density		
		F _{2,57}	P	Scheffé test	F _{2,57}	P	Scheffé test	F _{2,57}	P	Scheffé test
Autumn	EE	9.70	<0.01	B < M = S-M	1.83	0.17		14.90	<0.01	B > M = S-M
Winter	EE	0.68	0.51		8.98	<0.01	B < M = S-M	60.80	<0.01	B > M = S-M
Spring	EE	14.01	<0.01	B < M = S-M	11.22	<0.01	B = M < S-M	11.50	<0.01	B > M = S-M
Summer	EE	12.54	<0.01	B < M = S-M	20.09	<0.01	B < M = S-M	9.00	<0.01	B > M = S-M

Cordgrass–mussel-engineered habitat (**S-M**), mussel-engineered habitat (**M**), and barnacle-engineered habitat (**B**)

(Laffaille et al. 2001; Agnew et al. 2003; Idaszkin 2006; Cattrijsse and Hampel 2006; Bortolus et al. 2009). The absence of this amphipod at **M** and **B** habitats and its strong association with **S-M** seem linked to the shelter and food provided by plants, which supports the hypothesis that the austral cordgrass *Spartina densiflora* supplies a particular habitat that resulted in the net addition of new species to the invertebrate community commonly characterizing the local rocky shores (Adami et al. 2004). This addition implies an important ecological event since *O. gammarella* amphipods are able to modulate ecosystem variables such as primary production by feeding on plant detritus (Agnew et al. 2003; Dias and Hassall 2005). These crustaceans are even capable of acting as important links between semi-terrestrial and marine ecosystems since they have been reported to be an important food source for coastal fishes (Laffaille et al. 2001; Ludlam et al. 2002; Cattrijsse and Hampel 2006) and nemerteans (McDermott and Roe 1985).

The habitat created by the non-native barnacle *Balanus glandula* showed the highest density of the tubicolous

spionid worm *Boccardia polybranchia*, a common cryptogenetic species in the intertidal zone of the area. The Spionidae is one of the most abundant families of Polychaeta, and it is able to inhabit any kind of substratum in shallow waters (Fauchald and Jumars 1979). We found this polychaete within burrows or in tubes made of mud and detritus in the crevices in-between barnacles where it probably finds protection from predation and/or from harsh environmental conditions such as heat stress, dehydration, and the impact of waves.

Among the three engineered habitats we studied, the species richness and diversity were significantly higher in those more complex. Our results support the hypothesis that greater amounts of structure and physical dimensions increase the availability of surface and therefore greater resources, which in turn increase the number of possible niches to exploit. It seems unlikely, however, that the relationship between complexity and diversity is linear. The highest values of total density were found associated with the least complex habitat—the barnacles—contrary

to that general pattern. Some of the authors in Table 1 hypothesized that extremely complex habitats could actually exclude organisms, which implies that the maximal density would be in some intermediate level of habitat complexity. The fact that we did not find a difference in species richness, diversity, and total density between the most complex (*S-M*) and the intermediate (*M*) habitats suggest the need to consider either a greater spectrum of possibilities or a stronger contrast in complexity among the habitats considered in order to have a more complete picture of the problem. Several studies have reported the occurrence of similar species composition in similar habitats (Table 1), and a parsimonious hypotheses explaining this pattern refers to the potential redundancy in habitat provision by the engineers, since many of the engineers can accomplish the same essential ecological role (Kelaher et al. 2007). This can also be seen in our results where the pool of species found associated with *S-M* and *M* overlapped greatly. The neutral relationship we found between these two habitats indicates that, once a certain level of complexity is reached, additional complexity would not significantly alter the richness, diversity, and/or total density of the associated species.

In summary, our study strongly suggests that the species vary their relative distribution and abundances in presence of the different habitats complexities generated by *S-M*, *M*, and *B*. However, the direction (i.e., neutral, positive or negative) and intensity of the community response to the ecosystem engineer organisms may be conditioned by the physiological requirements of the different species and their efficiency to readjust their local spatial distribution in the short term.

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