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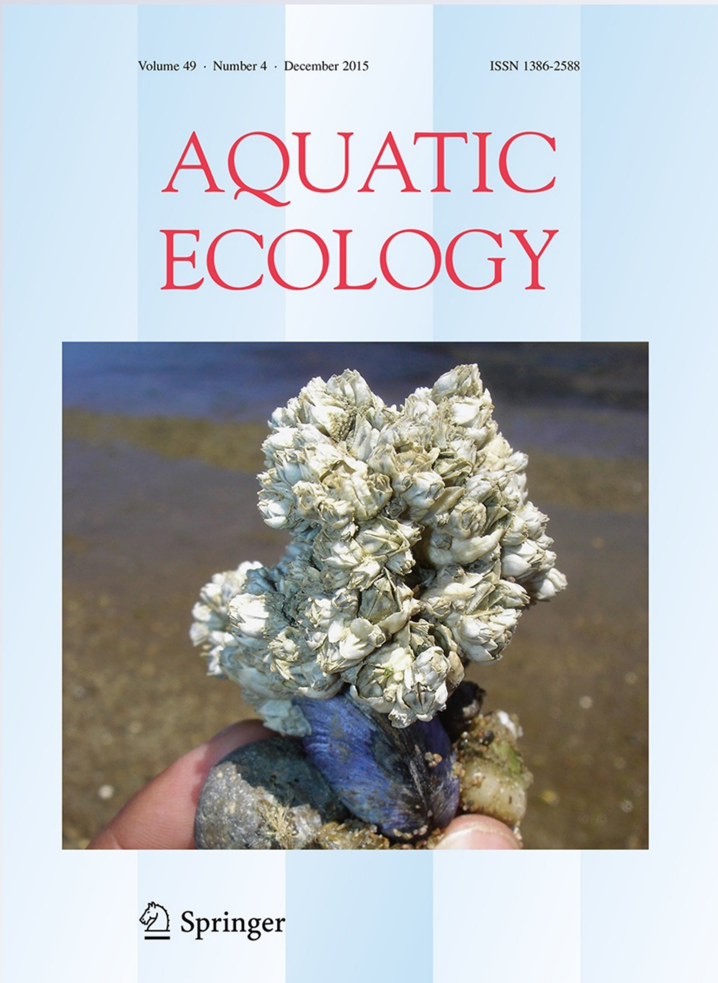

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Differential benthic community response to increased habitat complexity mediated by an invasive barnacle

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Abstract Invasive species threaten native ecosystems worldwide. However, these species can interact positively with local communities, increasing their richness, or the abundance of some species. Many invasive species are capable of influencing the habitat itself, by ameliorating physical stress and facilitating the colonization and survival of other organisms. Barnacles are common engineer species that can change the physical structure of the environment, its complexity, and heterogeneity through their own structure. *Balanus glandula* is a native barnacle of the rocky shores of the west coast of North America. In Argentina, this invasive species not only colonizes rocky shores but it also has successfully colonized soft-bottom salt marshes, where hard substrata are a limiting resource. In these environments, barnacles form three-dimensional structures that increase the structural complexity of the invaded salt marshes. In this work, we compared the composition, density, richness, and diversity of the macroinvertebrate assemblages associated with habitats of different structural complexity in two Patagonian salt marshes where *B. glandula* is well established. Our results showed differences in the relative distribution and abundances of the invertebrate species between habitats of different complexities. Furthermore, the response of the communities to the changes in the structural complexity generated by *B. glandula* was different in the two marshes studied. This highlights the fact that *B. glandula* facilitates other invertebrates and affect community structure, mainly where the settlement substrata (*Spartina* vs. mussels) are not functionally similar to the barnacle. Thus, our work shows that the rocky shore *B. glandula* is currently a critical structuring component of the native invertebrate community of soft-bottom environments where this species was introduced along the coast of southern South America.

Keywords Exotic species · Marine invasions · *Balanus glandula* · Habitat-forming species · Facilitation · Spartina · Patagonia

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Introduction

Coastal marine systems are often characterized by the presence of ecosystem engineer species (Jones et al. 1997). These organisms alter biotic and abiotic resources in the local environment, thus modifying and even creating habitats (Jones et al. 1997; Crooks 2002; Sousa et al. 2009). Several invasive species have a preponderant role as ecosystem engineers and could have profound architectural consequences on the ecosystem structure where they arrive (reviewed in Crooks 2002). The study of these cases is crucial due to the potential cascade effect over the entire invaded community (Crooks 2002; Wallentinus and Nyberg 2007; Sousa et al. 2009). Thus, although invasive species are considered among the top-five threats to native biodiversity (Vitousek et al. 1997; Sala et al. 2000), their arrival in a new environment could lead to an increase in local richness through positive interactions such as habitat modification (Jones et al. 1997; Crooks 2002). Furthermore, most of the studies on invasive ecosystem engineers show how these species positively interact with native fauna (Crooks 2002; Sousa et al. 2009; Sellheim et al. 2010). Nevertheless, in this complex ecological scenario, there are cases in which invasive species facilitate not only native species but they also have positive interactions with other invasive species, enhancing their establishment and spread (Simberloff and Von Holle 1999; Simberloff 2006).

Ecosystem engineers that increase habitat complexity or heterogeneity usually also increase abundances and/or species richness (Sueiro et al. 2011, 2012), whereas those that decrease complexity tend to have the opposite effect (Crooks 2002). This tendency is consistent with the hypothesis that more complex habitats provide more resources that will in turn be utilized by a larger number of species (Connor and McCoy 2001; Kelaher et al. 2007b). However, a growing number of studies showed that an increase in habitat complexity may have a neutral effect on the associated community (Almany 2004; Duarte et al. 2006) or even a negative one (Callaway 2003; Neira et al. 2006). Many studies have also shown that once a certain level of complexity has been reached, the subsequent increases will not have any significant further effect on community parameters (Prado and Castilla 2006; Kelaher et al. 2007a; Sellheim et al. 2010; Sueiro et al. 2011). Besides, the effects that a given ecosystem engineer exerts on the community can vary depending on where the study is conducted (Mussels: Thiel and Ullrich 2002; Duarte et al. 2006; Buschbaum et al. 2009. *Spartina*: Netto and Lana 1999; Neira et al. 2005; Sueiro et al. 2013). These differences occur because the effect of the species depends on the ecological interactions between engineers and the local fauna and a variety of specific characteristics, such as its tolerance to extreme temperature or moisture (Jones et al. 1997; Crooks 2002; Buschbaum et al. 2009). Consequently, the direction and the magnitude of the effect driven by the ecosystem engineers are usually hard to predict.

Barnacles are considered autogenic ecosystem engineer species or habitat-forming because they change the physical structure, complexity, and heterogeneity of the environment through their own structure (reviewed in Barnes 2000). On rocky shores, a large variety of organisms use the microhabitats generated by barnacles to settle and to avoid predation and desiccation (reviewed in Barnes 2000). The acorn barnacle *Balanus glandula* was accidentally introduced to Argentina in the early 1970s. The species, native to the Pacific coast of North America, now covers 17 latitudinal degrees of the Argentinean coast, from San Clemente del Tuyú (36°S) to Río Grande (53°S) (Spivak and L'Hoste 1976; Schwindt 2007). This barnacle dominates the high intertidal zone and forms a dense layer of up to 40,000 individuals per square meter (Schwindt 2007). Recently, the species has successfully colonized salt marshes; a surprising finding given the fact that *B. glandula* is an emblematic rocky shore species (Schwindt et al. 2009; Sueiro et al. 2013; Mendez et al. 2014). In the southern Argentina salt marshes, *B. glandula* settle on different substrata forming large three-dimensional structures (hereafter aggregates, Schwindt et al. 2009; Mendez et al. 2013). Aggregates generally have semi-elliptical shape and can reach the size of a lemon. Moreover, in salt marshes, the living substrata utilized by *B. glandula* to settle are ecosystem engineers as well (Mendez et al. 2013; Sueiro et al. 2013). This is the case of the halophyte *Spartina alterniflora* currently considered native and the cryptogenic *Mytilus* sp. mussels. Therefore, the structural complexity determined by the ecosystem engineers originally present is increased by the presence of the invasive *B. glandula*. As a result, this scenario provides the opportunity to evaluate the effect of an increased habitat complexity on the abundance and/or species richness of the community. In addition, since settlement substrata utilized are different between marshes, it is possible to assess whether these primary engineers influence the effect exerted by the barnacles. In this work, we compare the composition, density, richness, and diversity of the macroinvertebrate assemblages associated with zones of different structural complexity in two Patagonian salt marshes where *B. glandula* is currently well established. Besides, organic matter content and sediment grain size were compared among the zones of different complexities.

Materials and methods

Study sites

The study was performed in Loros marsh (hereafter Loros, 41°01′S, 64°06′W; Fig. 1) and Riacho marsh (hereafter Riacho, 42°24′S, 64°37′W; Fig. 1). The low and high marsh levels were +3.5 and +7.6 m, respectively, for Loros and +4.4 and +5.8 m, respectively, for Riacho (relative to the Argentinean hydrographic zero supplied by the Servicio de Hidrografía Naval 2012; for further description, see Bortolus et al. 2009). The Loros study site is characterized by monospecific grassland of *Spartina alterniflora* with only some small patches of *Sarcocornia perennis* scattered along the highest level of the shore (Isacch et al. 2006; Bortolus et al. 2009). In Riacho, *S. alterniflora* and *Spartina densiflora* dominate the low marsh and *S. perennis* dominates the high marsh (Isacch et al. 2006; Bortolus et al. 2009). Both marshes are colonized by the invasive barnacle *Balanus glandula* (Schwindt et al. 2009). The distribution of the barnacles in the marshes is patchy, and they are found exclusively on substrata located on tidal channels, where the seawater flows constantly with the tides. *B. glandula* uses all the hard substrata present in the marshes to settle, and this versatility is likely to favor its success and persistence within the Patagonian salt marshes (Mendez et al. 2013). *Mytilus* sp. mussel valves are the most frequent type of substrata utilized in Riacho marsh, whereas the base of the stems of dominant halophyte *Spartina alterniflora* is the substratum most utilized in Loros marsh, where mussels are less abundant (Schwindt et al. 2009; Mendez et al. 2013). The species forms three-dimensional aggregates in salt marshes, which reach larger sizes on mussels at Riacho, and on *S. alterniflora* at Loros.

Invertebrates associated with the presence of *Balanus glandula*

In order to compare the composition, density, richness, and diversity of macroinvertebrates associated with zones of different complexities, samples were collected in the two marshes mentioned above. Samples were obtained in three zones following a gradient of habitat complexity. The high-complexity zones (hereafter high) corresponded to sectors of the marshes with *B. glandula* settle on *S. alterniflora* or mussels (Fig. 1). The middle-complexity zones (hereafter middle) corresponded to sectors of the marshes with the settlement substrata, but without *B. glandula*

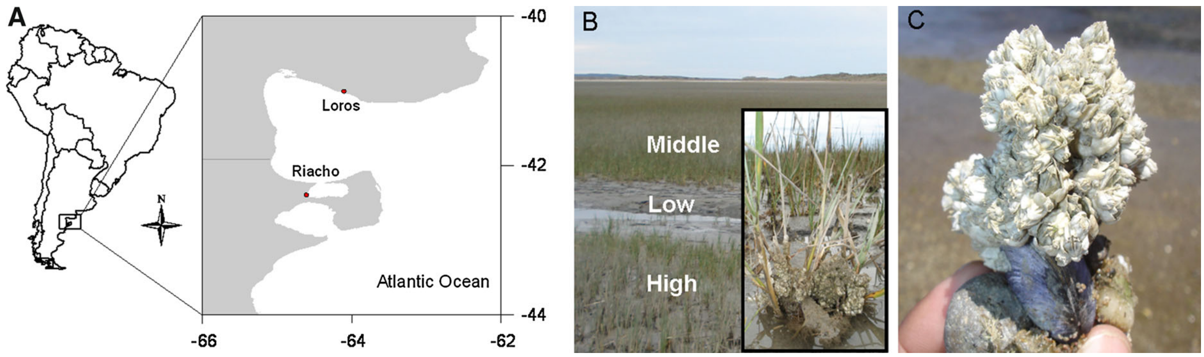

Fig. 1 Map of South America showing the location of the marshes studied (**a**). Photograph showing the distribution of the zones of different complexities (High: high-complexity zone, Middle: middle-complexity zone, and Low: low-complexity zone) in Loros marsh, and a detail of an aggregate (**b**). Photograph of typical aggregate of barnacles in Riacho (**c**). Photograph credits: A. Bortolus

(Fig. 1). The low-complexity zones (hereafter low) corresponded to sectors of the marsh characterized by bared loamy sandbanks devoid of any settlement substrata (Fig. 1). For the selection and the delimitation of these zones, we carefully surveyed Loros and Riacho marshes and identify areas that differed exclusively by the presence/absence of *B. glandula* and the settlement substrata. Thus, the zones of different complexities were similar in terms of major characteristics such as height (relative to the line of low tide), flooding time, positioning along the tidal gradient, *Spartina* or mussels density, and proximity to channels. The marshes were selected as these represent the largest marshes in Patagonia invaded by the species, and they have similar appearance at the landscape scale.

From each of the three zones in the two marshes, 10 samples were collected using a plastic core (Loros, diameter: 15 cm, depth: 20 cm, volume: 3532 cm^3; Riacho, diameter: 15 cm, depth: 10 cm, volume: 1766 cm^3) on eight occasions during 1 year (November and December 2009, January, February, May, June, July, and September 2010. n total = 240 for each marsh). The samples collected contained a belowground (infauna) and an aboveground portion (*Balanus* aggregates and settlement substrata; Figure 1). To collect the samples, the core was placed on top of a *Balanus* aggregate (formed over *Spartina* or mussels) and then buried into the sediment (20 cm in Loros and 10 cm in Riacho). All the samples collected were interspersed within each zone and through the study sites. Samples were then sieved through a 0.5-mm mesh. The organisms retained on the mesh were fixed in 4 % formalin and preserved in 70 % ethanol. In the laboratory, all organisms were identified to the lowest taxonomic level possible under a dissecting stereo microscope (80×). Considering the unwanted potential consequences of taxonomic misidentifications (Bortolus 2008, 2012), we performed an extensive literature review in which we obtained updated taxonomic keys and we requested the assistance of taxonomic specialists for each taxon. A voucher of the taxa collected was deposited in the CENPAT invertebrate collection (CNP, http://www.cenpat-conicet.gob.ar/). Afterward, total density (individuals/100 cm^3), richness, and Shannon diversity (Shannon and Weaver 1949) were calculated for each sample.

Size of the aggregates and associated fauna

To evaluate a possible relationship between the size of the aggregates and the abundance, richness, and diversity of macroinvertebrates, we randomly collected 30 individual aggregates for the 8 months mentioned in "Invertebrates associated with the presence of *Balanus glandula*" (except for January and July in Riacho where 28 and 26 aggregates were obtained, respectively. n total Loros = 240 aggregates, n total Riacho = 234 aggregates). The aggregates were collected by hand and contained barnacles and the settlement substrata (Fig. 1). The volume of the aggregates was calculated by water displacement (expressed in cm^3). Aggregates were then carefully washed on a 0.5-mm sieve, and organisms retained treated as in the previous section. Total density (individuals/100 cm^3), richness, and Shannon diversity were calculated per aggregate. This survey also allowed us to compare the macroinvertebrate assemblages between marshes in order to evaluate whether the effects of *Balanus* were site-specific.

Repeated measures permutational analysis of variance (PERMANOVA) was used to determine whether there were significant differences in the invertebrate community composition among zones in each marsh using Primer 6 PERMANOVA+ extension software version 6.1.7 (Anderson et al. 2008). PERMANOVA compares the F statistics to a distribution generated by multiple random permutations of the analyzed data, thus liberating it from the formal assumptions of traditional ANOVA (Anderson 2001; Anderson et al. 2008). Repeated measures PERMANOVA model was employed with structural complexity (zones) as fixed factor and the sampling months as repeated measures (9999 permutations). Pairwise comparisons were performed among all pair of levels for the factor zone to identify where the differences occurred. The abundance of all invertebrate species was fourth-root transformed in order to down-weight the abundant species. To explore similarities and differences among assemblages, non-metric multidimensional scaling (MDS) was used, and a similarity percentage analysis (SIMPER) was performed to determine the taxa responsible for the differences between groups. PERMANOVA and MDS were made with a Bray–Curtis similarity matrix using a dummy variable. The PERMANOVA routine creates a nonparametric, permutational analogue of ANOVA when applied to univariate data (Anderson 2001; Anderson et al. 2008). Therefore, repeated measures PERMANOVA models were also employed to determine whether there were significant differences in density, richness, and diversity of invertebrates among zones for the two marshes (9999 permutations). For these three variables, pairwise comparisons were performed to identify where the differences among each pair of zones occurred.

Repeated measures PERMANOVA was used to determine whether there were significant differences in the invertebrate community composition, density, richness, and diversity between marshes (data from subsection b). For this PERMANOVA model, marsh was considered as fixed factor and the sampling months as repeated measures (9999 permutations). For each variable, pairwise comparisons were performed to identify where the differences among marshes occurred. MDS and SIMPER were also made to compare the marsh assemblages. Lastly, independent parametric correlations were used to evaluate a possible relationship between the size of the aggregates and the abundance of macroinvertebrates, richness, and diversity in each marsh (Zar 1999).

Organic matter content and grain size distribution

The organic matter content (OMC) and the grain size distribution were studied in four of the months mentioned before (November 2009, January, May and July 2010). For OMC, six sediment samples were collected in each zone with the same sampling design above described (diameter: 3.5 cm, depth: 25 cm, volume: 240 cm^3). In addition, one sample for standard mechanical-sieving grain analysis (diameter: 6 cm, depth: 25 cm, volume: 706 cm^3) was obtained from each zone. OMC was determined from the samples combusted individually at 450 °C for 4 h, obtaining ash-free, dry weight. Grain size distribution was determined by sieving the samples through a series of five screens with mesh size ranging from 1000 to 62 µm. Sediment samples were previously processed following Carver (1971). The OMC was compared using a repeated measures PERMANOVA model with structural complexity (zones) as fixed factor and the sampling months as repeated measures (9999 permutations). Pairwise comparisons were performed to identify where the differences among zones occurred.

Results

Invertebrates associated with the presence of *Balanus glandula*

A total of 23 taxa of macroinvertebrates were found in Loros marsh and 28 in Riacho (Table 1). In Loros, community composition, density, richness, and diversity differed significantly between zones of different habitat complexity (repeated measures PERMANOVA: zone, month, and their interaction were significant. Online Resource 1A). Furthermore, communities from the most-structured habitat (high-complexity zone) were clearly dissimilar to assemblages from the middle and non-structured habitat (middle- and low-complexity zones) (Fig. 2a. SIMPER ∼55 % dissimilarity. Online Resources 2A and 3A), while middle and low zone did not differ so much from each other (SIMPER ∼32 % dissimilarity. Online Resources 2A and 3A). The amphipod *Monocorophium insidiosum* and crabs were the most abundant species in high zone. In the low zone, Spionidae, Capitellidae, and *Darina solenoides* were typical (Table 1. Online Resource 3A). Density was generally lower in the high-complexity zone than in the middle- and low-complexity zone (Fig. 3a. Online Resource 2A). The gastropod *Heleobia australis* was the most common species in middle and low zones, contributing more than 75 % of the total macroinvertebrate abundance (Table 1), and therefore, it is likely to cover up any potential effect on the density of the other taxa. In fact, when this species was excluded in the density comparisons, density was generally higher in the high-complexity zone (repeated measures PERMANOVA: pseudo-$f_{zone} = 10.07$, pseudo-$f_{month} = 33.82$, pseudo-$f_{zonexmonth} = 8.83$; $p < 0.05$). Richness and diversity were generally higher in the high-complexity zone and lower in the zone of middle complexity (Fig. 3b, c. Online Resource 2A). However, these differences among zones changed during the course of the study (Online Resource 2A). For example, high- and low-complexity zones did not differ significantly in May and June. Also, middle- and low-complexity zones did not differ significantly from each other in November and December (Online Resource 2A).

In Riacho, community composition, density, richness, and diversity differed significantly between zones of different habitat complexity (repeated measures PERMANOVA: zone, month, and their interaction were significant. Online Resource 1B). In this

Table 1 Mean density of invertebrate taxa (ind/m^3) for the three zones of different complexities (*H* high, *M* middle, and *L* low) of Loros and Riacho marsh

	Taxa	Loros			Riacho		
		High	Middle	Low	High	Middle	Low
Polychaeta							
Syllidae		732	4	7	1430	1430	410
Spionidae		32	209	2682	4685	1408	623
Capitellidae		110	142	4650	28	50	2144
Phyllodocidae			18	212			
Maldanidae		4		28	106	142	1798
Lumbrineridae					92	729	7
Orbiniidae					962	106	7
Cirratulidae					14	7	
Polynoidae						7	
Eunicidae				4	7	14	
Nereididae				71	50	7	2902
Nephtyidae			4				
Onuphidae						7	
Decapoda							
Crabs		4420	276		2130	226	28
Halicarcinus planatus	(Fabricius, 1775)	4					
Tanaidacea							
Tanais dulongii	(Audouin, 1826)	156	4		16093	29356	92
Isopoda							
Pseudosphaeroma sp.			4		6561	14	
Exosphaeroma sp.					715		
Excirolana armata	(Dana, 1853)				7	35	7
Amphipoda							
Monocorophium insidiosum	(Crawford, 1937)	6571	14	4	354	9172	7
Ampithoe valida	Smith, 1873	92	21		28	587	
Orchestia gammarella	(Pallas, 1766)				35		
Melita palmata	(Montagu, 1804)				290	14	
Insecta							
Chironomidae		11	4		3843	262	7
Arachnida							
sp. indet.			4				
Gastropoda							
Siphonaria lessoni	Blainville, 1824	18	4		163	28	
Trophon geversianus	(Pallas, 1774)				7		
Heleobia australis	(d'Orbigny, 1835)	45085	188666	178567			
Bivalvia							
Lasaea sp.					170		205
Tellina petitiana	d'Orbigny, 1846						15
Darina solenoides	(King & Broderip, 1832)	4	410				
Mytilus sp.		492	32				
Actiniaria							
sp. indet.		180	11		163	28	

Table 1 continued

Taxa		Loros			Riacho		
		High	Middle	Low	High	Middle	Low
Nemertea							
Ramphogordius sanguineus	(Rathke, 1799)	x	x	x	x	x	x

Neohelice granulata, *Cyrtograpsus altimanus*, and *Cyrtograpsus angulatus* were grouped together since most of the individuals were juveniles in which the correct species identification was not possible (named as crabs). For the nemertean *Ramphogordius sanguineus*, the presence is indicated since species fragment easily when handled

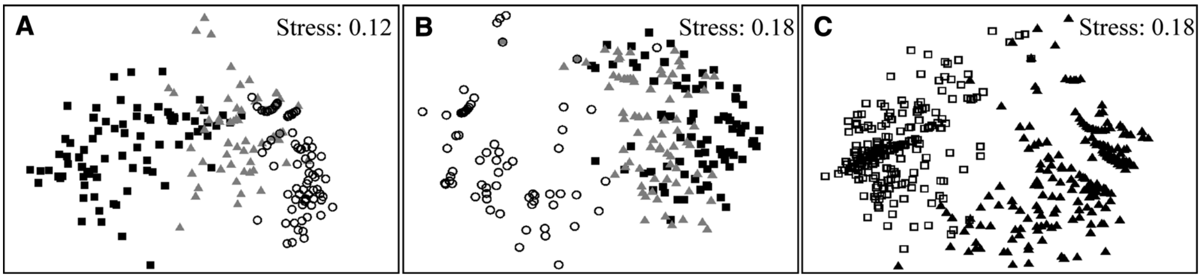

Fig. 2 Two-dimensional MDS ordination comparing macroinvertebrate assemblages associated with the three zones in Loros (**a**) and Riacho (**b**): High-complexity zone: *black squares*, middle: *gray triangles*, and low: *white circles*. Two-dimensional MDS ordination comparing marshes in the aggregates survey (**c**): Riacho: *black triangles* and Loros: *white squares*

marsh, communities from the non-structured habitat (low-complexity zone) were clearly dissimilar to assemblages from structured habitats (high- and middle-complexity zones) (Fig. 2b. SIMPER ~90 % dissimilarity. Online Resources 2B and 3B), while high and middle zones did not differ so much from each other (SIMPER ~50 % dissimilarity. Online Resources 2B and 3B). Capitellidae, Maldanidae, and Nereididae were the most abundant taxa in the low-complexity zone, while *Monocorophium insidiosum*, *Tanais dulongii*, *Pseudosphaeroma* sp., Spionidae, and Chironomidae were typical of middle and high zones (Table 1. Online Resource 3B). Density in structured habitats was generally higher than in non-structured habitat (Fig. 3a. Online Resource 2B). Richness and diversity were also usually higher in structured habitats, but these differences were not consistent over the course of the study (Fig. 3b, c. Online Resource 2B). For instance, richness in high- and low-complexity zones did not differ significantly from each other in February, May, and June. Also, richness and diversity did not differ significantly in middle- and low-complexity zones in November, December, and September (Online Resource 2B).

Size of the aggregates and associated fauna

The sampling of the individual aggregates yielded one new species, the ophiuroid *Amphipholis squamata*, observed at very low densities in Riacho (1 ind/dmP^3). Fourteen and 18 taxa of macroinvertebrates were found in Loros and Riacho, respectively. Community composition, density, richness, and diversity differed significantly among marshes (repeated measures PERMANOVA: marsh, month, and their interaction were significant. Online Resource 1C). Furthermore, communities from Loros were clearly dissimilar to assemblages from Riacho (Fig. 2c. SIMPER ~90 % dissimilarity. Online Resources 2C and 3C). *Monocorophium insidiosum*, Syllidae, and crabs were the most abundant taxa in Loros, while *T. dulongii* and *Pseudosphaeroma* sp. and Chironomidae were typical of Riacho (Online Resource 3C). Density, richness, and diversity were generally significantly higher in Loros than in Riacho (Fig. 3a–c), and only in four cases, no differences among marshes were detected (Online Resource 3C). The mean size of the aggregates was 19.37 cm^3 (SD = 11.41) in Loros and 15.58 cm^3 (SD = 9.5) in Riacho. The range size was from 2 to 91 cm^3 in Loros and from 1 to 70 cm^3 in

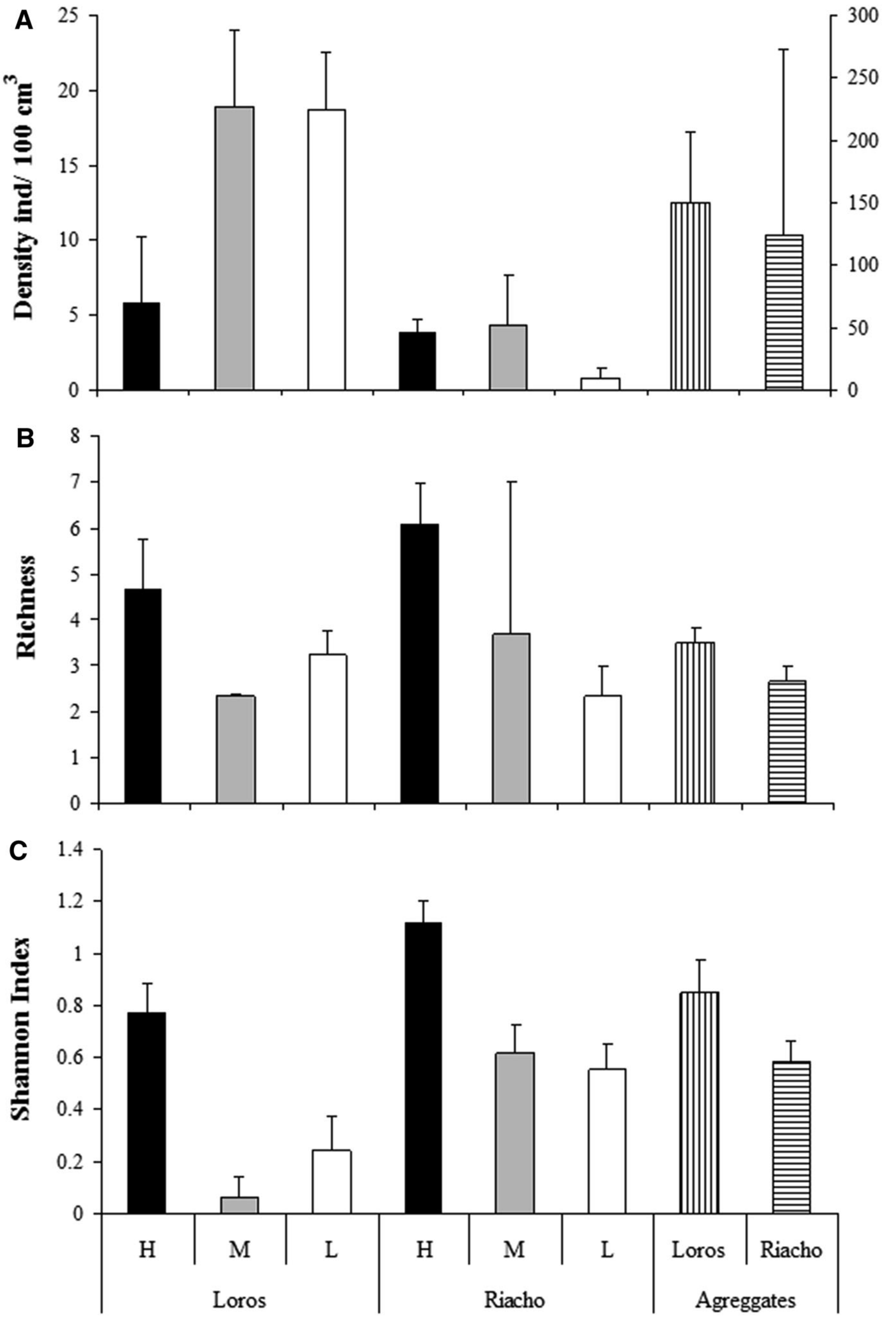

Fig. 3 Density (**a**), richness (**b**), and diversity (**c**) (mean + SD) of macroinvertebrates associated with the different zones of the marshes and the aggregates survey. Values were averaged across all months. For aggregate survey density, scale is displayed on the secondary axis. *H* high-, *M* middle-, and *L* low-complexity zones

Riacho. The size of the aggregates was positively and significantly correlated with abundance of macroinvertebrates in both marshes ($r_{\mathrm{Loros}} = 0.54$, $t = 9.93$, $p < 0.05$. $r_{\mathrm{Riacho}} = 0.58$, $t = 10.67$, $p < 0.05$). Even though the size showed a positive significant relationship with the richness in both marshes and with diversity in Loros, correlation coefficients were low (size and richness: $r_{\mathrm{Loros}} = 0.4$, $t = 6.74$, $p < 0.05$. $r_{\mathrm{Riacho}} = 0.29$, $t = 4.6$, $p < 0.05$. Size and diversity: $r_{\mathrm{Loros}} = 0.32$, $t = 5.15$, $p < 0.05$).

Organic matter content and grain size distribution

In Loros and Riacho, organic matter content (OMC) differed significantly between zones of different habitat complexity (Fig. 4a. Loros: repeated measures PERMANOVA: zone, month, and their interaction were significant. Online Resource 1A. Riacho: Repeated measures PERMANOVA: zone, month, and their interaction were significant. Online Resource 1B). The OMC was generally higher in the structured habitats than in the non-structured habitats, in both marshes. However, this effect was not consistent over the course of the study (Loros: Online Resource 2A. Riacho: Online Resource 2B). In Loros, for example, OMC differed significantly in middle- and low-complexity zones in November and July. In Riacho, instead, OMC did not differ significantly in high- and middle-complexity zones in November and January. Moreover, the marshes showed different grain size distributions. Riacho showed a coarser composition than Loros. Fine sand, very fine sand, and silt and clay were the dominant fractions in Loros (Fig. 4b). Gravel, coarse sand, and middle sand were the dominant fractions in Riacho (Fig. 4b). Only in Riacho a differentiation of the sediment composition among zones was observed. In this marsh, the low-complexity zone showed a finer composition than high and middle zones (Fig. 4b).

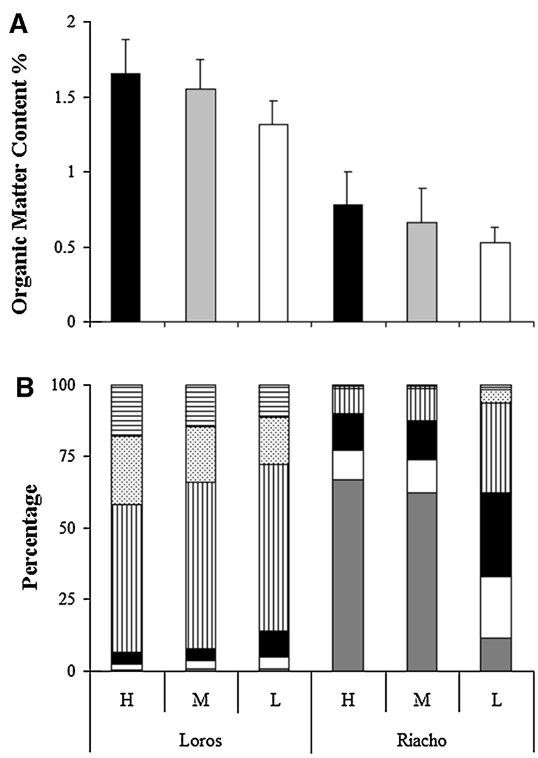

Fig. 4 Organic matter content % (+SD) (**a**) and percentages of the different grain size fractions (**b**) associated with the different zones of the marshes. *H* high-, *M* middle-, and *L* low-complexity zones. Gravel: *gray*, coarse sand: *white*, medium sand: *black*, fine sand: *vertical lines*, very fine sand: *black dots*, and silt + clay: *horizontal lines*

Discussion

Overall, our results suggest that the increase in structural complexity mediated by the presence of the invasive barnacle *B. glandula* enhances the habitat quality by increasing the availability of settling spaces, food, and/or refuge. Our results also suggest that this invasive secondary engineer facilitates invertebrates and affects community structure where the primary facilitator species (as settlement substratum) is not functionally redundant with the barnacles. Nonetheless, considering that *B. glandula* has been found in a small number of marshes along the Argentinean coast, as the invasion process continues, to carry out research in order to assess whether our results and inferences are consistent at broader geographical scales, will be very useful. Given the expansion observed for *B. glandula* along the Argentinean coast and, more recently, in other countries such as Japan and South Africa (Schwindt 2007; Kado 2003; Simon-Blecher et al. 2008, respectively), we predict that potential habitat alteration of the invaded coasts will occur in the short term in the invaded regions. However, the effect on the native communities might vary strongly among regions and sites.

Several studies have found that invasive species could increase local richness through positive interactions such as habitat modification (Jones et al. 1997; Crooks 2002). Nevertheless, our results suggest that the response of benthic community to the additional complexity provided by *Balanus glandula* might not be as predictable as expected. In Loros marsh, the most complex habitats showed the highest macroinvertebrate diversity and abundance. However, the zone of middle and lowest complexity usually did not differ from each other. This intrigued us because the middle-complexity zone was dominated by the ecosystem engineer *Spartina alterniflora* and where we expected to find a significantly higher diversity and abundance compared to the bared mudflat (see supporting literature Netto and Lana 1999; Hedge and Kriwokwen 2000; Neira et al. 2006; Sueiro et al. 2011). In a similar vein, the zones of high and middle complexity presented a similar macroinvertebrate assemblage in Riacho, suggesting that in this marsh, the presence of *B. glandula* adds no significant effect to that generated by mussels. In both situations, we observed that when a certain level of structural complexity is reached, any subsequent increment will not alter significantly the effects on the communities (Prado and Castilla 2006; Kelaher et al. 2007a; Sellheim et al. 2010; Sueiro et al. 2011).

In our study, a secondary engineer (*Balanus glandula*) utilizes and interacts with two different settlement substrata (*Spartina alterniflora* in Loros and mussels in Riacho). Facilitation processes and modification of habitat generated in these cascades can produce different effects on benthic organisms (Altieri et al. 2010; Thomsen et al. 2010). In fact, the effects that many ecosystem engineers have on the associated community tend to be site-specific (Thiel and Ullrich 2002; Neira et al. 2005; Buschbaum et al. 2009) and are also conditioned by the ecological interactions with the local fauna and its characteristics (Crooks 2002; Buschbaum et al. 2009; Thomsen et al. 2010). Our results show that the same ecosystem engineer may affect overall species richness, diversity, and composition differently in each site. Furthermore, when the marshes were compared through the sampling of individual aggregates, the assemblages associated with each marsh were different, and Loros showed higher density, richness, and macroinvertebrate diversity than Riacho. These results suggest that aggregates in Loros improve habitat quality for the species in this marsh compared to the aggregates in Riacho. Therefore, *B. glandula* is likely to facilitate invertebrates and to affect community more intensely where the primary facilitator species (i.e., *Spartina* vs. mussels) do not have the same ecological function than barnacles. Investigations focussed on potential site effects are currently limited by the low number of marshes found colonized by *B. glandula* within the region.

By providing new microhabitats, invasive species were found able to facilitate not only the establishment and spread of native species but also other invasive species as well (Simberloff and Von Holle 1999; Simberloff 2006). In Loros marsh, the amphipod *Monocorophium insidiosum* and the crabs *Neohelice granulata*, *Cyrtograpsus altimanus,* and *Cyrtograpsus angulatus* showed higher density in the habitat where *Balanus glandula* was present. The amphipod *M. insidiosum*, a known invasive species for this region (Orensanz et al. 2002), was the only non-native species found in our surveys, and we also recorded four cryptogenic species: the tanaid *Tanais dulongii* and the amphipods *Ampithoe valida*, *Orchestia gammarella,* and *Melita palmata* (Orensanz et al. 2002). While the amphipods were recorded at low densities during the study, the tanaid *T. dulongii* showed high densities within the barnacle zone at Riacho marsh, suggesting a potential positive interaction between these species that will need further attention.

Factors such as predation, density-dependent processes, and physicochemical characteristics are capable of influencing the density and distribution of benthic species (Adam 1990; Mitsch and Gosselink 2000). During the field work of this and other studies conducted in the same marshes, we observed that the main predators were occasional seabirds. Besides, it is well known that the physicochemical characteristics of the environments can determine the distribution of marsh fauna as they define the abundance of food, the mobility of species, and the availability of O_2, among others (Adam 1990; Mitsch and Gosselink 2000). Grain size, for instance, is one of the most important characteristic that controls the spatial distribution of infaunal organisms (Hall 1994). We found differences in grain size distribution only in high and middle zones compared to low-complexity zone in Riacho, and generally did not fluctuate throughout the year. These differences in the grain size between zones could explain the pattern found in Riacho, where the zone with finer grain size (low-complexity zone) was characterized by the dominance of Capitellidae, Maldanidae, and Nereididae polychaetes which are typically infaunal families. The OMC, instead, differed significantly among zones in both marshes. However, we did not find a consistent pattern of these fluctuations over the months, and the differences in OMC were not correlated with the variations found for density, richness, and/or diversity. Together, these results suggest that the physicochemical characteristic studied were not influencing significantly the distribution and abundance of the fauna.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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