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Effect of *Spartina alterniflora* Loisel, 1807 on growth of the stout razor clam *Tagelus plebeius* (Lightfoot, 1786) in a SW Atlantic estuary

Mariana S. Addino *, Diana I. Montemayor, Mauricio Escapa, M. Fernanda Alvarez [1], Macarena S. Valiñas [2], Betina J. Lomovasky, Oscar Iribarne

Instituto de Investigaciones Marinas y Costeras (IIMyC), Laboratorio de Ecología, FCEyN, CONICET, Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

A B S T R A C T

Aquatic organisms that produce epibenthic structures such as saltmarsh plants play key roles in habitat functioning through their ecosystem engineering effects. Intertidal *Spartina* species are well known for modifying tidal hydrodynamic and sediment processes, affecting cohabiting infaunal organisms. The stout razor clam *Tagelus plebeius* is an infaunal filter-feeding species that inhabits a broad range of mudflats (MF) and *Spartina* saltmarshes (SM) along the American Atlantic coast. Through descriptive and experimental approaches conducted at the Bahía Blanca estuary (Argentina, 38°47′S, 62° 20′W), we evaluated ecosystem engineer effects of *Spartina alterniflora* (due to changes in sediment and water characteristics) on somatic and shell growth of *T. plebeius*. Comparison of bulk sediment parameters indicated that the sediment is more easily eroded in the SM than in the MF, but softer in the latest. In addition, food supply for clams (i.e., total particulate organic matter) was higher in the MF although food quality (i.e., percentage of organic matter in the water column) was in general higher in SM. Shell growth was higher but clam condition index (CI) was lower in the MF, and the opposite pattern was found in the SM. These results represent an uncoupling between shell and somatic growth with a positive effect of *S. alterniflora* on the CI of clams. Nevertheless, results of field experiments manipulating stems and roots of plants separately suggested that the effect of *Spartina* on clam's CI was not due to the structural changes generated by plant presence itself, although a better food quality in the SM may be related to the larger clams CI.

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1. Introduction

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species often modifying the community (Jones, 1994). Structures created by ecosystem engineers are diverse in dimension and composition and their physical properties are directly relevant to their effects, which are often considered as altered abiotic features (Jones et al., 1997). Thus, abiotic change and the consequent organisms response, is the result of structures interacting with kinetic energy and materials within an abiotic environment (Gutiérrez and Iribarne, 2004; Jones et al., 2010). Ecosystem engineers that modify key resources (e.g. space, nutrients, prey) often

have an important effect on the development of certain species into a particular habitat (Jones et al., 1997).

In the case of benthos, ecosystem engineering may at least equal trophic interactions in importance (Reise, 2002). This is the case of organisms that produce epibenthic structures, for example tubificid polychaetes (e.g. Friedrichs et al., 2000) or seagrass meadows and saltmarshes (e.g. Bouma et al., 2007). In the case of saltmarsh plants, *Spartina alterniflora* is a well known example of ecosystem engineering that modifies tidal hydrodynamic processes (Leonard and Luther, 1995), with consequences in suspended solids concentration (Leonard and Croft, 2006) and sedimentary characteristics (Leonard and Luther, 1995; Yang et al., 2008). These abiotic changes modify saltmarsh benthic biotic characteristics (Neira et al., 2005; Rader, 1984). Although there are attempts to generalize the effect of *Spartina* spp. on physical (Reise, 2002) and biotic features (Bertness et al., 2000), these effects largely depend on local plant morphology (Van Hulzen et al., 2007) and distribution (Leonard and Luther, 1995). Local water flow characteristics are also relevant and they will lead to different patterns of change in the sediments when the flow interacts with plants (Bouma et al., 2007). In fact, it may result in sediment erosion or deposition depending on plant density of the vegetated patches and water flow characteristics (Bouma et al., 2007). Moreover, benthic fauna shows

either positive or negative responses to plant presence (Neira et al., 2005; Whaley and Minello, 2002). Then, a combination of factors will determine the effect of plant presence on the abiotic environment and its consequences on organisms, leading to a context-dependent net ecosystem engineering effect.

Parallel to the studies evaluating abiotic variables modified by *Spartina alterniflora* (see above), there are several studies showing that abiotic features such as sediment characteristics (e.g., Azouzi et al., 2002; Vincent et al., 1994), hydrologic conditions (e.g. Grizzle and Morin, 1989; Saxby, 2002; Steffani and Branch, 2003) and consequently suspended food availability (e.g. Nakaoka, 1992; Rebelo et al., 2005) have significant effects on infaunal bivalve distribution and growth. Moreover, bivalve density may be different in vegetated and bare tidal flats. For example, in Paranaguá Bay (south Brazil 25°15′S, 48°40′W), a relatively high energy estuary, the density of different bivalves increases (e.g. *Anomalocardia brasiliana*) or decreases (e.g. *Lucina pectinata*) in relation to vegetation presence (da Cunha Lana and Guiss, 1991). Also, it was experimentally shown that *S. alterniflora* affects the growth of benthic estuarine bivalves both positively (e.g. *Mercenaria mercenaria*, Irlandi and Peterson, 1991) or negatively (e.g. *Macoma petalum*, Brusati and Grosholz, 2007). However, beyond the relationship with plant presence, few studies evaluate mechanistic approaches that link more than one abiotic feature modified by *S. alterniflora* with changes on bivalve traits inhabiting the marsh dominated area.

The stout razor clam *Tagelus plebeius* is an euryhaline filter feeder species distributed along the American Atlantic coast from Massachusetts (42 °N, Leal, 2002) to the Northern Argentinean Patagonia (41°S, Scarabino, 1977). This is a deep-burrowing species that inhabits permanent burrows of up to 70 cm depth in unvegetated mudflats (Holland and Dean, 1977) and in *Spartina* saltmarshes (Teal, 1962) with cohesive sandy silt sediments. The burrow walls have the same characteristics as the surrounding sediments. It is not mucous lined but easily distinguished due to its compacted nature (Holland and Dean, 1977). Superficial sediments constantly collapse into the burrow, which is also affected by tides and related bed load transport (Gutiérrez and Iribarne, 2004). Thus, it was suggested (see Gutiérrez and Iribarne, 2004) that this clam maintains its burrow as a permanent structure by exerting pressure against the burrow walls through vertical movements and gaping. Silts

and clays increase the stability of burrows and siphon tubes by filling interstitial spaces between sand particles in such a way that they bind together (Holland and Dean, 1977). Then, a higher content of silt and clay in the sediment may lead to smaller cost on burrow maintenance. In fact, there is higher clam density in areas characterized by a greater content of silt, clay and organic matter (Gutiérrez and Iribarne, 1998). Moreover, areas with high sand and low silt and clay content are not inhabited by *T. plebeius* (Holland and Dean, 1977). Given this pattern, changes in sediment characteristics due to the presence of *Spartina alterniflora* could affect the settlement and/or burrow maintenance of *T. plebeius* and then may affect the energy availability or allocation for their development.

In addition, stable isotope analysis in the Southwest Atlantic intertidals revealed that phytoplankton and benthic microalgae comprise the food supply for *Tagelus plebeius* (Botto et al., 2005). Like in other filter feeders (see Dame, 1996), higher food supply in the water column (i.e. organic matter content) was associated with higher clams growth (Abrahão et al., 2010). Benthic microalgae biomass may be higher in saltmarshes (e.g. Janousek, 2009) and their resuspension is often an important input to the water column (De Jonge and Van Beuselom, 2003) and thus to food availability for suspension feeders. However, the strength and direction of saltmarsh plants effects are context dependent and thus the final outcome may be positive or negative. Thus, changes in amount and/or composition of suspended material generated by saltmarsh plants may also be relevant for clam energy availability or allocation.

In some areas of the Bahia Blanca estuary (Villa del Mar, Argentina, 38°47′S, 62°20′W, Fig. 1), the presence of *Spartina alterniflora* in the intertidal generates sediment erosion (Pratolongo et al., 2010) associated with a less cohesive sediment in the saltmarsh. In this context, the objectives of this study were 1) to compare density, length-height relationships and condition index of *Tagelus plebeius* between the saltmarsh and the bare mudflat and, 2) to evaluate the effect of *S. alterniflora* on shell and somatic growth of clams. We hypothesize that clam density, shell and somatic growth are lower in the vegetated areas because less cohesive sediment leads to a higher energy cost in burrow construction and maintenance and/or because of lower food availability.
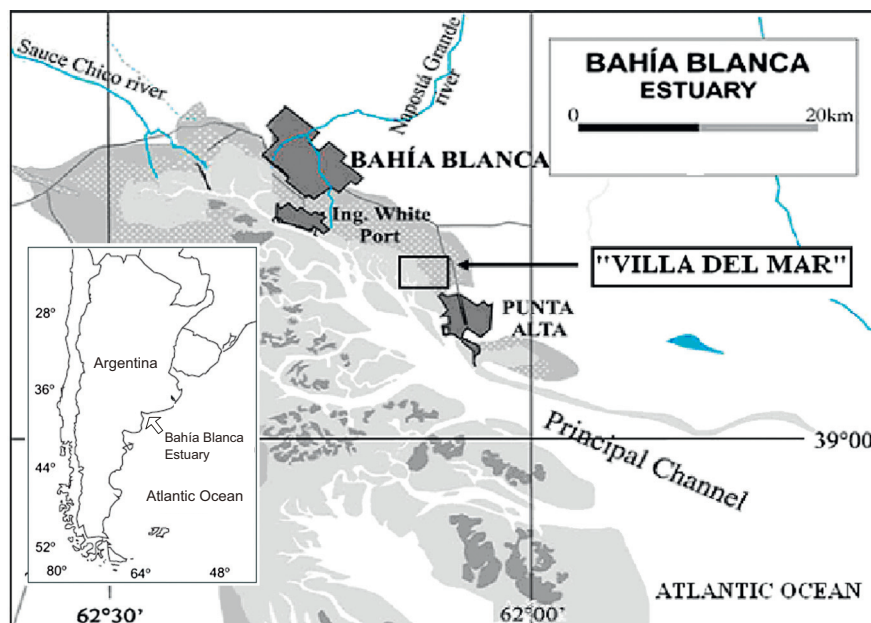

Fig. 1. Map of the study site.

2. Materials and methods

2.1. Study area

Samplings and experiments were performed from October 2007 to July 2010 in the middle-outer reach of the principal channel of the Bahia Blanca estuary (Villa del Mar; Fig. 1). In this site, the intertidal mudflat covers approximately 6 km², where *Spartina alterniflora* marshes form a fringe of about 150 m wide (Pratolongo et al., 2009). The semidiurnal tides reach up to 3.5 m (Perillo and Piccolo, 1999). The bed morphology at the saltmarsh/mudflat boundary often shows a patchy and higher elevation on the bare mudflat in the seaward side of the saltmarsh (Pratolongo et al., 2010).

2.2. Habitat characteristics in the mudflat and the saltmarsh

Fifteen squares (40 cm side) separated by at least 10 m from each other, were randomly selected in the saltmarsh (hereafter SM) and the number of plant stems were counted (stem density, # m⁻²). Additionally, we randomly selected and measured (precision ± 0.1 cm) the total height of one stem into each square (n = 15) to estimate mean stem height.

For grain size distribution, five sediment cores (5 cm diameter and 20 cm depth) were randomly taken in the intertidal mudflat (hereafter MF) and in the SM. Hereafter, to analyze sediment characteristics in the SM samples, roots were separated from the sediment. Sediment samples were wet-sieved through 6 steel sieves of 2, 1, 0.5, 0.25, 0.125, 0.063 mm; the fraction <0.063 mm was also preserved. The material retained in each sieve was dried at 80 °C to constant weight (precision ± 0.01 g). Weight percentages of sand (<1 and > 0.063 mm) and silt-clay (<0.063 mm) were calculated for each sample.

To evaluate water content (% of water in the sediment), sediment organic mater content (OM) and bulk density (g cm⁻³), ten sediment samples of 20 cm³ were randomly taken from MF and SM. Samples were wet weighted and then dried at 80 °C to constant weight (precision ± 0.01 g) to estimate water content. Then, the dried sediment was burned at 450 °C during 8 hours and weighted again to estimate the OM content. Additionally, dry weight of sediment was divided into sample volume (20 cm³) to estimate bulk density.

For sediment penetrability and shear strength we performed fifteen measurements of the force necessary to penetrate the sediment with a hand penetrometer (precision ± 0.01 kg cm⁻²) and ten measurements of the torsional force needed to shear the sediment with a Torvane shear-strength meter (precision ± 0.01 kg cm⁻²), in the MF and the SM. Measures were randomly taken and separated by at least 10 m from each other. All measurements described above were carried out between October and December 2007.

To evaluate bed load transport, ten tubular plastic sediment traps were deployed in the MF and the SM (following Emerson and Grant, 1991). Each trap consisted in a PVC tube (3 cm diameter, 40 cm length) inserted in the substrate with the opening levelled at the sediment surface, with another smaller PVC tube (2.5 cm diameter, 40 cm length) introduced into the first one to collect sediment. All traps were deployed during low tide and filled with clean water to avoid sedimentation by incoming water (see Botto et al., 2006; Emerson and Grant, 1991). Sediment retained in the traps was collected after 1 tidal cycle (12 h) and the sampling was repeated monthly between March and June 2010. Sediment retained on the traps was then dried at 80 °C until constant weight (precision ± 0.01 g).

For particulate organic matter content in the water column (hereafter POM) ten tidal water samples were taken with plastic bottles of 500 ml, in the MF and the SM immediately after the sites were flooded. The procedure was repeated every ~30 d between July 2009 and May 2010. Samples were filtrated onto pre-weighted, 4.7 cm diameter and 1.2 μm mesh size, glass-fiber filters GF/C Whatman. Each filter with the retained material was dried at 80 °C to constant weight (precision ±

0.01 g) and then burned in a muffle furnace at 450 °C during 8 hours to calculate total POM (g L⁻¹). Additionally, organic matter percentage was calculated for each sample (%OM).

All variables were compared between MF and SM by unequal variance t_c-test (corrected t-test, Welch approximation, Zar, 1999). In the case of bed load transport and POM, this analysis was carried out separately for each sampling date. In all cases and hereafter, the correspondent assumption's fulfilling was evaluated before each statistical analysis (Zar, 1999).

2.3. Comparison of population features of Tagelus plebeius between the MF and the SM

Clam density was calculated by excavating and counting all living clams into nine blocks of 40 cm in side and 70 cm in depth (maximal depth registered for *Tagelus plebeius*, Abrahão et al., 2010), separated by a distance of at least 10 m in the MF and the SM (clams m⁻²). The null hypothesis of no difference in mean density of clams between sites was tested with t_c (Zar, 1999).

For shell morphometrics and condition index (hereafter CI), 119 clams were randomly extracted from MF and 126 from SM between September and October 2007 using a shovel (hereafter referred as 1st sampling). All individuals were measured in shell length (L: anterior-posterior axis; precision ± 0.01 mm) and shell height (H: umbo-ventral axis). Size (L) frequency distribution was compared between sites with Kolmogorov-Smirnov test (Zar, 1999). The relationship between H and L of clams was evaluated using simple regression models and then compared between sites with ANCOVA analysis, with H as covariate. The equality of slopes (relationship H-L) from each site was tested before the analysis (Zar, 1999).

The CI of each clam was calculated using the dry weight of soft tissue (dried at 80 °C to constant weight) and L of clams with the following equation (Clausen and Riisgård, 1996):

$$CI = soft\ tissue \cdot L^{-b}$$

where b (2.9) is the slope of the regression curve between L and soft tissue. The null hypothesis of no difference in mean CI between sites was compared with t_c (Zar, 1999). Given that CI showed differences between sites in the 1st sampling (see 3.2.), three additional samplings (hereafter referred as 2nd, 3rd and 4th sampling) were made between July 2009 and March 2010 to evaluate if the differences maintained through time. In each additional sampling, approximately 30 clams were extracted from each site, measured and CI was calculated as described above. The null hypotheses of no difference in mean CI between sites were evaluated with t_c for each sampling date (Zar, 1999).

2.4. Field experiments evaluating the effect of Spartina alterniflora on shell growth and CI of Tagelus plebeius

To determine the effects of *Spartina alterniflora* on growth of clams, a transplant experiment was performed between April 2008 and May 2009. In order to protect clams from predation by oystercatchers (see Bachmann and Martínez, 1999) and attacks from burrowing crabs (see Lomovasky et al., 2006), plastic square cages (1 cm mesh and 50 cm side) were randomly placed in the saltmarsh comprising "transplant" treatment (n = 10) and in the bare mudflat comprising "transplant control" treatment (n = 10). Eighty clams were extracted from the mudflat, measured in L and marked with a plastic number glued to the periostracum surface with cyanoacrylate (superglue) to be identified later. Four of that clams, between 45 and 51 mm in L, were transplanted into each cage at each site. Given the impossibility to perform artefact (cage) controls because we could not avoid the predation inside them, before the end of the experiment we measured the physical characteristics inside and outside cages, which may be modified by the presence of *S. alterniflora* and thus affect clams. Sediment

and water samples were taken and processed as described in 2.2. Then, the null hypotheses of no difference in mean percentage of sand and silt-clay, mean OM and mean POM between inside and outside cages were evaluated separately for each treatment (transplant and transplant control) by a t_c (Zar, 1999). At the end of the experiment, six cages from "transplant" and four cages from "transplant control" could be recovered (the rest were swept by tide) accounting for a total of 19 live, marked clams for which CI, calculated as describe above (see Section 2.3.), and the increment in L (final L – initial L, mm) were calculated. The relationship between shell L increment and initial L was evaluated by simple regression models. There was no relationship between these variables (see 3.3.), thus the mean increment could then be used in further statistical analysis. In order to perform a more powerful test, we looked for differences between replicates (cages) into each treatment (transplant and transplant control) with ANOVA. Then, as there were no differences (see 3.3.), data were pooled into each treatment. The null hypotheses of no difference in mean CI as well as mean shell L increment between clams from both treatments were tested using t_c (Zar, 1999).

To discriminate the effect of stems and roots on clams, two more field experiments were conducted. The first experiment (hereafter *Experiment 1*) consisted of 18 experimental units of 100 m² that were delimited in the saltmarsh in September 2009 and was comprised by three treatments. In 6 experimental units all the stems of *Spartina alterniflora* were removed constituting the "pruned" treatment, other 6 were walked above and used as the "pruning control" treatment (walking on during pruning may have an effect *per se* on clams and thus it was necessary to differentiate both sources of disturbance) and the 6 remaining experimental units were not modified and used as "natural controls". Nine months later, according to the low clam density in the saltmarsh, 5 clams between 48 and 67 mm in L were extracted from a smaller area in the centre of each experimental unit in order to avoid border effects. CI was calculated for each clam as described above (see 2.3).

The second experiment (hereafter *Experiment 2*) consisted of 20 experimental units of 1 m², comprising four treatments randomly located in the saltmarsh within the first 5 m landward to the mudflat-saltmarsh boundary, in January 2010. In 5 experimental units all plants (with the associated sediment) were completely removed with a shovel and 1 month later the resultant moat were naturally filled again with mud. Mimics of *Spartina alterniflora* stems were then deployed on each square to constitute the "mimic treatment". The mimics consisted in plastic flexible grass, around 20 cm length and 0.5 cm diameter which was glued with Epoxy putty (its use and safety was full proved, e.g. Bazterrica et al., 2007) to a plastic mesh matching the natural stem form and density. Then the mesh with mimics was attached to the floor with stakes. In another 5 experimental units we disturbed the sediment by burying a shovel 30 cm into the sediment and moving it from side to side approximately each 5 cm, but the plants were left there in order to function as "removal control". In other 5 experimental units we attached only plastic mesh as "mimic control" and finally the remaining 5 experimental units were not modified and used as "natural controls". Eighty clams between 44 and 68 mm in L were extracted from the saltmarsh, marked as explained for the transplant experiment, and 4 of them were placed into each experimental unit. Five months later all live, marked clams were recovered and CI was calculated as explained above. For *Experiment 1* and *Experiment 2*, the null hypothesis of no difference in mean CI of clams between treatments (fixed factor) and experimental units (EU, random factor, nested in treatments) was tested using a nested ANOVA model following Underwood (1997).

3. Results

3.1. Habitat characteristics in the mudflat and the saltmarsh

Stem density in the saltmarsh was 267 stems m⁻² (SD = 114), with a mean height of 17.52 cm (SD = 5.99). We found higher percentage of sand in the SM and higher percentage of silt-clay in the MF. Additionally, OM and water content were higher in the MF, while bulk density was higher in the SM, which can be related to grain size distribution. The force necessary to penetrate the sediment as well as the shear strength was higher in the SM than in the MF, which indicated that sediment is more easily penetrated in the latter. Bed load transport showed differences between sites in three of the four sampling dates being always higher in the SM (Fig. 2), which is consistent with the other sediment parameters. Mean POM showed differences in four of the six sampling dates, in three of them it was higher in the MF (Fig. 3); however, %OM in the water column in those dates was in general higher in the SM. Statistical data referred to these analyses together with mean (SD) values are summarized in Table 1.

3.2. Comparison of population features of Tagelus plebeius between the MF and the SM

Mean clam density was higher in the MF (10 clams m⁻², SD = 5.3) than in the SM (4 clams m⁻², SD = 4.4; t_c = 2.59, df = 16, p = 0.02). Size frequency distribution showed no differences between sites (D_{max} = 0.127, p > 0.1; Fig. 4). Shell L and H of clams showed linear relationships in both sites (F = 903 and 1101, df = 116 and 121, p < 0.0001, r^2 = 0.87 and 0.90; MF and SM, respectively). Comparison of slopes showed no difference between sites (F = 1.49, df = 237, p = 0.22), being the intercept value higher for the MF than for the SM, indicating that shells are more elongated in the first one (intercept: MF = 1.33, SM = 0.21; F = 14.37, df = 238, p < 0.001; Fig. 5). CI also showed differences between sites in all samplings being always higher in SM than MF (Table 2, Fig. 6).

3.3. Field experiments evaluating the effect of Spartina alterniflora on shell growth and CI of Tagelus plebeius

In the transplant experiment, the comparison of physical characteristics (mean sand, silt-clay, OM percentages and mean POM) between inside and outside cages of "transplant" treatment showed no cage effect in any of the analyzed variables (Table 3). In the "transplant control" treatment, we only found an artifact effect on mean percentage of sand and silt-clay that were lower and higher respectively inside cages (Table 3). Additionally, the comparison of shell increment and CI between replicates of each treatment showed no differences (Transplant: "Increment": F = 1.99, df = 4, p = 0.23, "CI": F = 0.01, df = 4, p = 0.95;
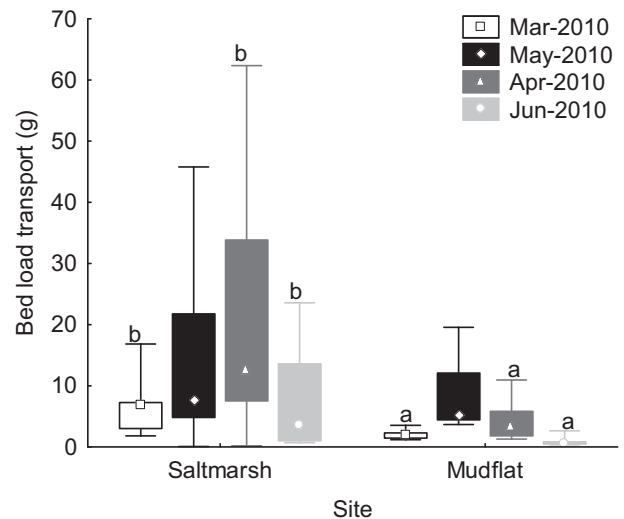

Fig. 2. Bed load transport in the SM and the MF in each date of sampling. Middle point shows the median, box limits show 25 and 75% percentiles and the bars indicate maximum and minimum values. The dates that showed differences between sites are indicated with letters that denote values in ascendant order.

Fig. 3. POM in the SM and the MF in the different dates of sampling. Middle point shows the median, the box limits show 25 and 75% percentiles and the bars indicate maximum and minimum values. The dates that showed differences between sites are indicated with letters that denote values in ascendant order.
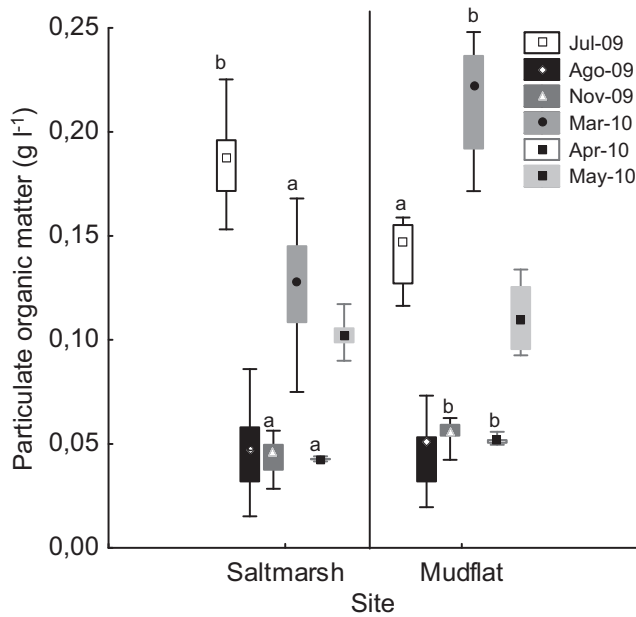
Transplant control: "Increment": $F = 0.64$, $df = 5$, $p = 0.56$, "CI": $F = 0.39$, $df = 5$, $p = 0.70$). Thus, the data into each treatment could be pooled (see 2.4.).

There was no relationship between initial L and shell increment of clams in any treatment ($F = 2.11$ and 0.13, $df = 8$ and 7, $p = 0.18$ and 0.73; for "transplant" and "transplant control", respectively). Mean shell L increment was smaller in "transplant" than in the "transplant control" (transplant $= 2.80$ (1.75), transplant control $=
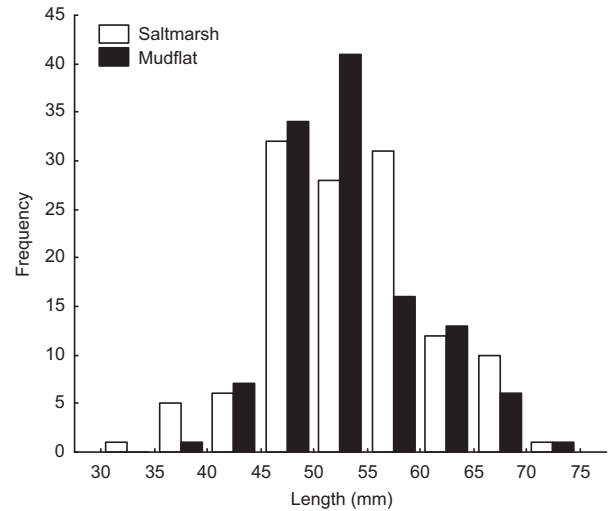

Fig. 4. Size (L, mm) frequency distribution of clams from SM and MF.

4.69 (1.16) mm; $t = 2.74$, $df = 17$, $p = 0.014$). CI of clams did not show differences between treatments (mean CI (SD): 0.0063 (0.001), $df = 17$, $t_c = -0.49$, $p = 0.63$). However, the power of this analysis was 7 % ($t = 2.11$, Power analysis $= 0.076$). Thus, this indicates that the tendency to higher CI values in the transplant treatment [mean CI (SD): 0.0064 (0.001) and 0.0061 (0.0009)] for transplant and transplant control, respectively) may be interpreted as a result in agreement with the pattern found in samplings.

Mean CI showed no differences between treatments and experimental units (EU) for both *Experiment 1* [Treatment: $F = 1.38$, $df = 2$, $p = 0.3$; EU (treatment): $F = 0.88$, $df = 15$, $p = 0.6$; mean CI (SD): 0.00395 (0.0021)] and *Experiment 2* [Treatment: $F = 0.61$, $df = 3$, $p = 0.6$; EU (treatment): $F = 1.05$, $df = 16$, $p = 0.4$; mean CI (SD): 0.00407 (0.0028)].

Table 1

Mean (SD) values for percentages of sand, silt and clay and organic matter, water content, bulk density, penetrability, bed load transport, POM and percentage of OM in the water column in the MF and the SM; and the correspondent statistics for the comparisons between sites in different dates of sampling. Bold letters denote significant differences.

Variable	Sampling date	Mudflat	Saltmarsh	df	t_c-value	p-value
Sand (%)		66.3 (3.9)	80.7 (7.3)	8	−3.9	**0.005**
Silt and clay (%)		30.8 (4.4)	18.0 (7.1)	8	3.4	**0.009**
OM (%)		2.94 (1.71)	1.38 (0.33)	9.69	−2.81	**0.012**
Water content (%)		38.2 (6.21)	24.7 (1.46)	9.99	6.71	**<0.001**
Bulk density (gr cm^{-3})		0.98 (0.16)	1.38 (0.08)	13.06	−7.15	**<0.001**
Penetrability (kg cm^{-2})		0.16 (0.06)	1.15 (0.32)	14.9	−11.58	**<0.001**
Share strength (kg cm^{-2})		0.17 (0.06)	0.41 (0.13)	12.69	−5.21	**<0.001**
Bed load transport (g)	March 10	2.0 (0.7)	6.9 (4.3)	9.5	3.53	**0.006**
	April 10	4.5 (3.3)	19.5 (19.3)	9.5	2.43	**0.037**
	May 10	8.4 (5.9)	14.8 (16.5)	11.3	1.15	0.27
	June 10	0.9 (0.7)	7.3 (8.5)	9.1	2.41	**0.039**
POM (g l^{-1})	July 09	0.143 (0.015)	0.187 (0.022)	18	5.25	**<0.001**
	August 09	0.047 (0.018)	0.048 (0.021)	18	0.05	0.963
	November 09	0.056 (0.006)	0.045 (0.009)	18	−3.27	**0.004**
	March 10	0.215 (0.026)	0.127 (0.027)	18	−7.37	**<0.001**
	April 10	0.052 (0.002)	0.043 (0.001)	18	−16.42	**<0.001**
	May 10	0.111 (0.016)	0.102 (0.007)	18	−1.57	0.133
%OM in water column	July 09	4.55 (1.84)	5.46 (0.63)	18	1.47	0.159
	August 09	1.55 (0.39)	1.65 (0.29)	18	0.68	0.506
	November 09	1.36 (0.10)	1.22 (0.16)	18	−2.33	**0.032**
	March 10	6.13 (0.55)	7.37 (1.43)	18	2.55	**0.020**
	April 10	12.7 (0.70)	18.59 (2.10)	18	8.40	**0.003**
	May 10	9.35 (1.21)	8.94 (0.66)	18	−0.95	0.355
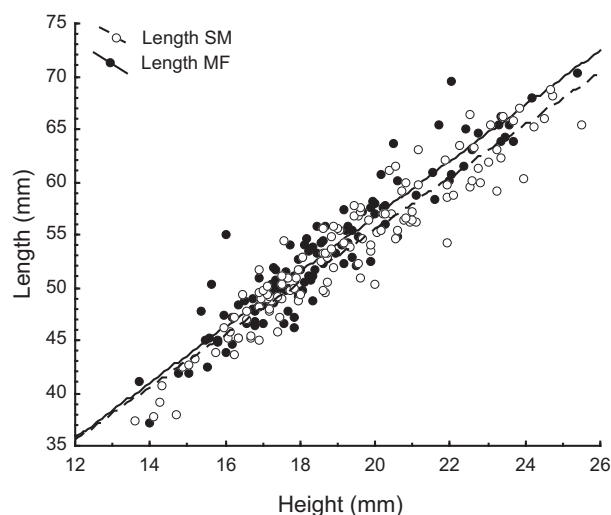
Fig. 5. Relationships between length and height of clams in the SM and the MF.

Fig. 6. Condition index of clams in the SM and the MF in the different dates of sampling. Middle point shows the median, the box limits show 25 and 75 % percentiles and the bars indicate maximum and minimum values. The dates that showed differences between sites are indicated with letters that denote values in ascendant order.

4. Discussion

Clam density and shell growth were lower in the saltmash, in association with less cohesive sediment, which agrees with our main hypothesis. However, clam condition index showed the opposite; that is a positive effect of S*partina alterniflor*a on clam somatic growth which, contrary to our hypothesis, would be explained by a better food quality in the saltmarsh. Overall, these results support our suggestions (see Introduction) about the effect of *S. alterniflora* on energy availability or allocation for clams, through sediment and water changes. Moreover, they emphasize the importance of studies assessing inter-specific relationships and mechanistic approaches for ecosystem engineering effects.

The higher proportion of silt, clay, OM and sediment water content in the MF, as well as higher proportion of sand, higher bulk density and bed load transport in the SM may indicate that at least the superficial sediment is more easily eroded (Grabowsky et al., 2011) in the SM. Indeed, silt, clay and OM increase the erosion threshold (i.e. energy necessary to initiate erosion). Meanwhile sand (which is typically associated with higher bulk density) has lower erosion threshold (Grabowsky et al., 2011) often resulting in a positive correlation between bulk density and erosion (e.g. Gerbersdorf et al., 2005). Moreover, sediments with less than 2 % of OM, such as we found in the SM, are generally considered erodible (Morgan, 2005). In general, saltmarsh plants are recognized to favor sedimentation especially of smaller particles like silt and clay (Reise, 2002). However, the combination of sediment characteristics described above contradicts such generalization, although they agree with a previous study carried out in the same site (i.e., Pratolongo et al., 2010). That study showed that these marsh plants neither attenuate the currents nor damp the waves and thus sedimentation do not occur within the marsh canopy but mild erosion does (Pratolongo et al., 2010). The
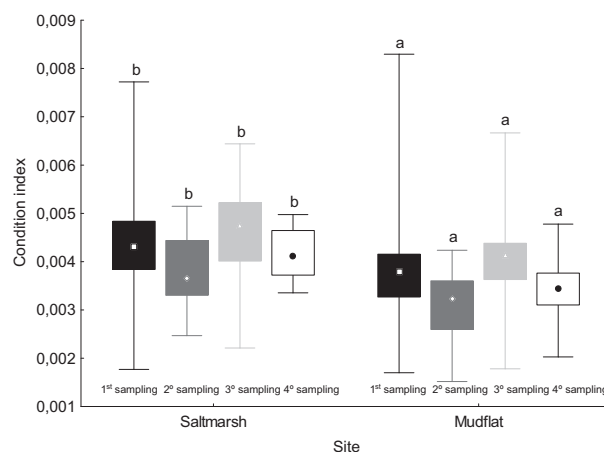
cylindrical shape of the stems may contribute to the productions of small scale eddies and consequently enhanced turbulence (Nowell and Jumars, 1984) that may lead to sediment erosion especially if stem density is low (Bouma et al., 2009; Leonard and Luther, 1995; Nowell and Jumars, 1984). In this sense, in laboratory flow experiments with water speed similar to those observed in our study site (35 cm.s^{-1}, see Cuadrado et al., 2003), *Spartina* densities between 200 and 800 stems m^{-2} generated sediment erosion, while densities higher than 1500 stems m^{-2} generated sedimentation (Bouma et al., 2009). Then, grain size distribution (and associated water content, bulk density and OM content) together with bed load transport found in the SM may be explained by the low stem density (267 stems.m^{-2}, see Section **3.1**) of *Spartina alterniflora* observed in our study site and the probably enhanced turbulence.

Easily eroded sediments are related to low sessile bivalves density (Dame, 1996). In fact, there are lower densities of *Tagelus plebeius* in sediments with higher sand content both in North American (Holland and Dean, 1977) and South American estuaries (Gutiérrez and Iribarne, 1998). In accordance, in our study clam density in the SM was more than twice lower than in the MF. The superficial erosion threshold of the sediment and thus the amount of sediment transported over the bottom surface can be related to the density of benthic bivalves given that a higher erosion and transport may generate 1) unfavorable conditions to larval settlement or 2) resuspension (Williams and Heck, 2001) and burying of newly settled larvae (Dame, 1996). For example, newly settled spats of the soft clam *Mya arenaria* are transported across sediment surface together with the transported sediments, which is related to a lower clam density (Emerson and Grant, 1991). Thus, the higher sediment transport in the SM (this study) may cause the lower clam density found in this site, at least if new settled clams allocate near the sediment surface such as it is suggested by the presence of recruits in adult siphon holes (B. Lomovasky, pers. obs.) and the correlation between length and burrowing depth of clams (Iribarne et al., 1998).

Table 2
Statistics for comparison of mean CI between SM and MF in the random samplings. Bold letters denote significant differences.

Sampling	Site	t-value	df	p-value
1st	SM	4.4	231	<**0.001**
	MF			
2nd	SM	4.07	61	<**0.001**
	MF			
3rd	SM	2.22	63	**0.029**
	MF			
4th	SM	4.79	57	<**0.001**
	MF			

Table 3
Comparison of physical characteristics between inside and outside cages (artifact effect) in the transplant experiment. Bold letters denote significant differences.

Source of variation	Transplant control			Transplant		
	df	t$_c$-value	p-value	df	t$_c$-value	p-value
% sand	4.3	4.14	**0.012**	8	−0.25	0.810
% silt and clay	4.4	−4.23	**0.011**	8	0.18	0.863
% OM	16	−1.26	0.226	17	−0.44	0.664
POM	7.0	2.07	0.077	17	1.86	0.080

Morphometric relationships of clams showed that shells are more elongated in the MF, while a higher CI of clams was found in the SM indicating a better somatic growth in this site. This pattern, which is also temporally constant, indicates that plant presence affects clam growth. Moreover, the consequent uncoupling of shell and somatic growth between sampling sites was partially confirmed in the transplant experiment, where shell increment was higher in clams kept in the MF but CI showed a tendency to higher values in clams transplanted to the SM. For this experiment, measurement of physical characteristics inside and outside cages showed that there was not an artifact effect on sediment characteristics in the SM (transplant), which allowed us to attribute the differences found in clam growth to the presence of *Spartina alterniflora*. The higher shell growth in the MF (transplant control) in addition to the L-H relationship pattern found in population samplings may be also related to the differences in sediment characteristics. More elongated shells are typical of bivalves inhabiting more cohesive sediments (Abrahão et al., 2010; Eagar, 1978) like those in the MF given that they make burrowing easier (Stanley, 1970). Furthermore, this is in agreement with previous results on the clam *Mya arenaria* which experimentally showed that shell length growth is faster in finer than in coarser sediments (Newell and Hidu, 1982). Thus, ecosystem engineering by *S. alterniflora* on the sediment would be influencing shell growth of *Tagelus plebeius*.

Clam CI was consistent in all population samplings being always higher in the SM. Also in the transplant experiment clams in the SM showed a tendency to higher values. Differences in CI are often associated with food availability; in the sense of better somatic tissue condition with higher food availability (e.g. Rebelo et al., 2005). However, food availability (i.e. POM) was in general higher in the MF than in the SM with some monthly variability such as in other regional estuaries (e.g. Martinetto et al., 2007). Thus, it would indicate that the amount of food itself does not explain the difference between clams of both habitats. Nevertheless, food quality in terms of its composition; that is detritus or phytoplankton/microphytobenthos, is probably implicated. In fact, in some sampling dates, parallel to the higher POM over the MF the percentage of OM in the water column was higher in the SM which would indicate a better food quality in this site. Differences in food quality (instead of quantity) are known to alter reproductive potential, mortality, growth and condition of bivalves (e.g. Grizzle and Morin, 1989; Marsden, 2004); especially in suspension feeders given that they use both fresh phytoplankton and particulate organic matter (dead substrates) for nutrition (Dame, 1996). In general, there is a positive correlation between chlorophyll *a* concentration and CI of bivalves, but a little nutritional value was reported for dead organic matter (e.g. Marsden, 2004; Petersen et al., 1997; Rheault and Rice, 1996). Concerning *Tagelus plebeius*, phytoplankton and suspended benthic microalgae constitute its major food source (Botto et al., 2005). In this sense, benthic microalgae biomass may reach higher values inside vegetated patches independently of sediment physical characteristics (e.g. Janousek, 2009), often with an important contribution to suspended material in the water column (e.g. around 30% in the EMS estuary (Holland), 53°20′N 7°6′E, De Jonge and Van Beuselom, 2003). Thus, we can hypothesize that higher biomass of benthic microalgae in the SM (i.e. better food quality for these clams) is the cause of the higher individuals CI in this site compared with the adjacent MF.

The fact that neither the roots nor the aerial part of *Spartina alterniflora* separately showed any effect on the CI of clams, dismiss the effect of other structural changes likely generated by plants that may lead to the higher CI found in the SM. Nevertheless, there is higher superficial sediment erosion in the vegetated area (Pratolongo et al., 2010) that, in agreement with our hypothesis, would result in smaller clam density in the SM (this study). However, and contrary to that hypothesis, CI was not negatively affected in the SM. This indicates that, despite coarser sediment, burrow maintenance cost is not higher in this site or that it is supported by the hypothetical better food quality proposed above. In general, studies concerning vegetation effects on

bivalve growth take into account somatic growth (e.g. Bologna and Heck, 1999) or, and more often, shell growth (e.g. Brusati and Grosholz, 2007; Irlandi and Peterson, 1991; Peterson et al., 1984). Both variables are indifferently interpreted as fitness indicators of the studied species considering that a better growth, either shell or somatic, indicates a better reproductive capacity (Bologna and Heck, 1999; Irlandi and Peterson, 1991). However, taking into account that in filter feeders somatic tissue carries out all the physiological activity including reproduction (Dame, 1996), the higher CI of clams in the SM may be interpreted as a result of better abiotic conditions for somatic tissue maintenance and thus better fitness in this site. Contrary, individuals inhabiting the MF would need to spend a higher portion of their energy reserves in shell elongation. In this sense, through samplings and experiments, changes in resources allocation due to vegetation presence were found in the estuarine filter feeder clam *Anadara trapezia*, which inhabit intertidal and shallow subtidal habitats in Australia (Wright and Gribben, 2008). Thus, a differential energy budget allocation in *Tagelus plebeius* would be determined by physical habitat conditions, which in our study area are modified by the presence of *S. alterniflora*.

In conclusion, the effect of *Spartina alterniflora* as ecosystem engineer leads changes in life history traits of clams and thus, the secondary production of the habitat since clams comprise a high proportion of infaunal biomass. In fact, this is the unique native infaunal bivalve species in the area. Besides, the rapid response of this bivalve to the habitat changes evaluated here represents a good indicator of its phenotypic plasticity. Given that phenotypic variations are subject to natural selection, our results add evidence to the current intend to demonstrate how ecosystem engineers increase the interaction between ecology and evolution.

Acknowledgements

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