A new non-indigenous *Crassostrea* species in Southwest Atlantic salt marshes affects mortality of the cordgrass *Spartina alterniflora*

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ABSTRACT

Biological invasions in marine and coastal systems may produce new trophic and nontrophic interactions influencing the structure of the invaded community. In the intertidal salt marshes of Samborombón Bay (36°19′20″S, 56°46′26″W; mouth of La Plata River; Argentina), there is a new non-indigenous oyster species, *Crassostrea* sp., which settles on the dominant smooth cordgrass *Spartina alterniflora*. Here, we analyzed if the oyster affects *S. alterniflora*. Sampling showed that density of live plant was similar across intertidal levels, but there were higher density of dead plant stems at low intertidal levels. This pattern coincides with higher density and larger shell size of *Crassostrea* sp. at the low intertidal where oysters are attached to the basal part of the plant stems. An experiment manipulating oysters attached to *S. alterniflora* stems and oyster mimics shows that *Crassostrea* sp. can indeed increase mortality of *S. alterniflora*. The negative effect of bivalves on plant could be because several oysters settle around the *Spartina* stem, and by growing during the year, strangle the plants increasing their mortality rate. Together, all these evidences strongly suggest that these non-indigenous oysters can control the lower intertidal level of plant distribution in this system.

1. Introduction

Biological invasions in marine and coastal systems may occur when a proper combination of conditions (e.g. resources, natural enemies, physical environment, and their spatial temporal variation) occur creating an open window for species to successfully invade new regions (e.g. Carlton, 1996; Shea and Chesson, 2002). When non-indigenous species establish in a new area, the recipient community develops new interactions (e.g. Cassey, 2005). Competition (e.g. Bando, 2006; Krassoi et al., 2008), predation (e.g. Bertness, 1984a) and facilitation (e.g. Bertness, 1984b; Sueiro et al., 2013) are the most common biological interactions influencing intertidal communities when a non-indigenous species is present. However, positive and negative non-trophic interactions (i.e. by non-indigenous introduced ecosystem engineering species; sensu Jones et al., 1994) can also be a major community structuring force (Dunstan and Johnson, 2003; Jones et al., 1994; Nugues et al., 2004). Thus, there is no doubt that non-indigenous species could be important structuring factors in invaded community.

In several Southwest Atlantic salt marshes, the cordgrass *Spartina densiflora* and *Spartina alterniflora* are the most common halophyte angiosperms inhabiting intertidal areas (Isacch et al., 2006). *S. alterniflora* is the dominating species in the lower marsh zone, which is daily flooded by tides (Daleo et al., 2008; González Trilla et al., 2009; Isacch et al., 2006). In Samborombón Bay (36°19′20″S, northern mouth of La Plata River, Argentina) *S. alterniflora* co-exists with an oyster species that settle on the lower part of their stems (B. Lomovasky, personal observation). Mitochondrial (16S and COI) and nuclear (ITS-2) sequence analyses show that this is a *Crassostrea* species that occurs in the West Atlantic closely related to an Indo-Pacific oyster species (Cavaleiro et al., in review). Although *Crassostrea gigas* was cited for the same area (Giberto et al., 2012), we never observed this species in the sampling location during the present study. Indeed, molecular markers showed that the only oyster species found in our study is a different species than *C. gigas* present in the Patagonian region of Argentina and Brazil and also different to the native oyster species of *Ostrea* genus (Cavaleiro et al., in review). Thus, *Crassostrea* sp. is a new non-indigenous species for the northern coast of Argentina (Cavaleiro et al., in review) that has been recently described in two different genetic analyses of specimens from the north of Brazil (first record: Canela Island, Bragansa; 00°47′02″S, 46°43′32.9″W; Varela et al., 2007; Melo et al., 2010) and southeast of Brazil (second record: estuarine region of Cananéia; 25°00′S, São Paulo State; Galvão et al., 2012) and all evidences suggest that it is a similar species to the one in the China Sea (Beihai, China; Varela et al., 2007; Liu et al., 2011). In our study site, *Crassostrea* sp. is only found attached around the basal part of *S. alterniflora* stems, likely due to the lack of hard substrata in this soft bottom environment.

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In this sense, filter feeding non-indigenous bivalves commonly associated with seagrasses (Peterson and Heck, 1999; Reusch and Williams, 1998) and salt marshes (Bertness, 1984b) may increase the benthopelagic coupling bringing planktonic production to the benthos (Ruesink et al., 2005), thereby having the possibility of increasing submerged or intertidal aquatic vegetation growth by increasing the nutrients available to the rhizosphere (Bertness, 1984b; Peterson and Heck, 1999). Indeed, biodeposits of suspension feeding bivalves are high in nitrogen and phosphorus (Bertness, 1984b). However, some negative effects have been observed with the presence of non-indigenous bivalves' species such as the case of the introduced mussel *Musculista senhousia*, which negatively affects the growth of eelgrass *Zostera marina* rhizome and its consequent asexual propagation in San Diego Bay (California State, USA, 32°43′25″N, 117°11′19″W, Reusch and Williams, 1998). This may be the product of the spatial interference between the two species given that the mussel carpet is a much stable substrata than the ambient sediment (Reusch and Williams, 1998). Thus, the potential outcome of these new interactions is unpredictable but could be important in the structure of the invaded community.

Intertidal salt marsh habitats occur across strong gradients of physical stress (flooding and/or salinity) and plant competition, which are in general responsible for the pronounced zonation pattern of marsh plants (Alberti et al., 2010; Daleo et al., 2008; Pennings et al., 2005). This trade-off between physical stress and plant competition typically leads to competitively superior plants dominating the least stressful zones (i.e., less frequently-flooded, high marsh habitats) and displaces competitively subordinate marsh plants to more stressful zones such as regularly-flooded low marsh habitats (Pennings and Callaway, 1992). However, in some areas the inferior salt marshes are also influenced by biotic interaction such as herbivory that can become an important control process of plant distribution (Alberti et al., 2007, 2010; Bertness, 1984a,b; Costa et al., 2003; Silliman and Bortolus, 2003). Our observations suggest that in the Southwest Atlantic estuaries the presence of a new non-indigenous oyster species attached on the inferior part of the cordgrass *S. alterniflora* stems also affects plant mortality rate, thus having the potential to be an important controlling factor of *S. alterniflora* lower distribution.

Given this background, and based on descriptive and experimental approaches, the objectives of this work were to analyze (i) the distribution, recruitment and growth of *Crassostrea* sp. and (ii) the effect of oysters on mortality, density and growth rate of *S. alterniflora* across the intertidal.

## 2. Material and methods

2.1. Study area

The study was performed between February 2009 and June 2010 at the Samborombón Bay, a site located at the southern mouth of La Plata River (Tapera de Lopez, 36°19′20″S, 56°46′26″W; Argentina; Fig. 1). This is a brackish water area with muddy sediments, with mean tidal amplitude of 0.75 m and annual rainfall of 950 mm (Isacch et al., 2006). Both the oyster *Crassostrea* sp. and high-density patches of *S. alterniflora* are in this area. Samples and experiments were carried out at three intertidal levels parallel to the shore with different aerial exposition time: Low = 0.40 m above mean low tide (hereafter abbreviated amlt), Medium = 0.54 m amlt and High = 0.75 m amlt.

2.2. Recruitment and growth of Crassostrea sp. on S. alterniflora

Bimonthly samplings for the analysis of recruitment and growth of *Crassostrea* sp. were carried out since February 2009 up to May 2010 at the intertidal levels described before. Ten live plants and 10 dead plants of *S. alterniflora* were randomly obtained by excavating the sediment at each sampling date and intertidal level in order to evaluate if oysters showed a settlement preference for one or the other. All plants were observed under a binocular microscope and oysters were counted, and shell height (H) from the umbo to the ventral margin was measured (precision: ±0.01 mm). The number of oysters settled by stems was counted and the null hypothesis of no difference in the mean values between tidal levels, dates and settlement places (live and dead plants) was tested by a three-way ANOVA with subsequent Tukey's HSD test (Zar, 1999).

To identify recruitment patterns the oysters size frequency distribution (n = 1903) was analyzed by date, intertidal level and settlement place (live or dead plants). Given that assumptions of normality and homogeneity of variances were rejected, a non-parametric Kruskal–Wallis test was used to test the null hypothesis of no difference in the median shell height between dates, tidal levels and, settlement places. Then, a multiple comparison test of mean ranks was used when differences were found (Zar, 1999).

To investigate if there were individuals of different ages, a subsample of oysters (n = 20) was analyzed identifying internal shell growth
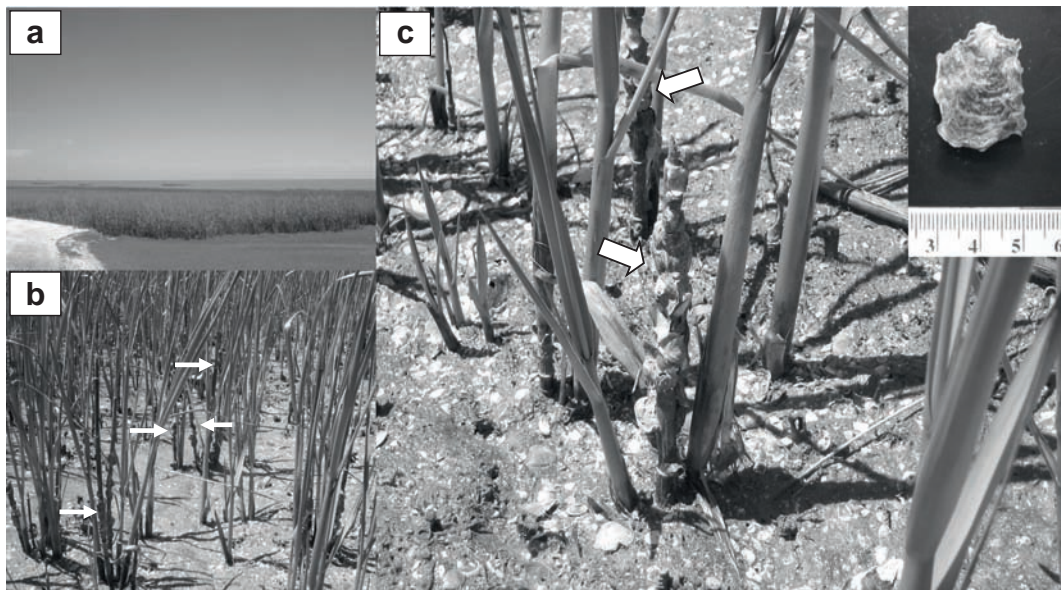
Fig. 1. (a) Salt marshes of *Spartina alterniflora* at Tapera de Lopez, Samborombón Bay, Argentina; (b) oysters on *S. alterniflora* stems; and (c) detailed of several oysters attached on dead *S. alterniflora* stems. Arrows: clusters of oysters.

bands (see for procedure Jones et al., 1990; Lomovasky et al., 2002a, 2007). These bands can be identified as translucent (i.e. narrow and dark) and opaque bands (i.e. wide and white; Jones et al., 1990). In bivalves, the presence of translucent growth bands indicates a period of very slow or even halted shell growth (Rhoads and Lutz, 1980; Richardson, 2001), which may be caused by low metabolic rates related to low environmental temperatures in autumn and winter seasons, as already seen in other bivalves species for this region (Lomovasky et al., 2002a,b, 2005). Thus, the number of translucent growth bands of each individual could be considered as a proxy of age. Each right valve was embedded in epoxy resin and sectioned along the axis of maximum growth in height. The cross-sections were polished on lapidary wheels using grids of 400, 600, 1200 and 2400 grade and etched with DE-CAL agent at 0.5%. Polished shell cuts were examined under a stereo microscope using a reflecting light (Rhoads and Lutz, 1980). Additionally, to evaluate if there were reproductively mature individuals a macroscopically analysis of gonads (color, turgidity) and gonadal smears under a microscope to identify the presence of gametes was analyzed.

2.3. Effect of oysters on mortality and growth rate of S. alterniflora

Given the oyster settlement on S. alterniflora (see results 3.1), samplings were done to evaluate the prevalence of plants with oysters and the possible effects of their presence on plant density. The density of live and dead plants in relation with the presence of oysters was measured at each intertidal level and sampling date using a 30×30 cm core. All plants were measured in height (precision ± 1 mm) to characterize the height plant distribution across the intertidal. The null hypothesis of no difference in the mean density and height between intertidal levels and dates was tested with a two-way ANOVA with subsequent Tukey's HSD test (Zar, 1999). When assumptions of normality and homogeneity of variances were rejected, we used a nonparametric test (Kruskal–Wallis test: K–W, Zar, 1999).

To evaluate if there is an effect of oysters on plant height growth and mortality (see results 3.2), two sets of field experiments were carried out. In the first one (March 2009 to April 2010) and at the 3 intertidal levels, sixty plants from 15 to 68 cm height (n = 180) were marked with a numbered soft plastic label and randomly assigned to each of 3 treatments: "control" with un-manipulated plants, "removed" where all oysters settled on plants were removed during the experimental time and "plant strangled" where it was added an adhesive tape of 20 mm width (similar to mean oyster shell height) fixed with a small wire surrounding the stem of each plant at the same height that oysters attached (from 5 to 10 cm height). This treatment was done to simulate the presence and strangle produced by oysters and only on plants that originally did not have oyster. The initial height of each plant was measured at the beginning of the experiment (March 2009) and then bimonthly, recording the plant survival. The methodology used to the plant strangled setups was only effective in the first two sampling dates while the wire tension on the adhesive tape of each stem was maintained. For the second sampling date, most of the strangled plants were dead, thus statistical analyses were only carried out for that period of time (see results). ANCOVA analyses were used to evaluate the plant growth in height between intertidal level and treatment in each sampling date using the growth increment as the response variable and the initial height as the covariable. The percentages of dead plants were calculated at each intertidal level, treatment and sampling date. A chi-square test (Zar, 1999) was used to evaluate if the cumulative percentage of dead plants in the considered period differed between "control" vs. "removed" and "plant strangled" setups and between "plant strangled" vs. "removed" treatments.

At the low intertidal a second field experiment was carried out from February 2010 to June 2010 where oysters were more abundant (see results) to simulate "constant" strangling effects on the plants. This experiment differ from the previous one in which the wire tension

on adhesive tape for each stem was maintained for only 3 months because of the dead of external leaf and with reduction of the leaf width. Forty plants were marked with numbered soft plastic labels in the middle part of the plant and randomly assigned to each of two treatments: "control" with un-manipulated plants without oysters, and "plant strangled" which differed from the first experiment, a piece of elastic band of 10 mm width was tied around the stem between 5 to 10 cm of plant height and used to simulate the constant oysters strangling. After four months a chi-square test (Zar, 1999) was used to evaluate if the percentage of survival plants differs between "control" and "plant strangled" setups.

3. Results

3.1. Recruitment and growth of Crassostrea sp. on S. alterniflora

Oysters settled on the inferior part of S. alterniflora stems were observed in live and dead plants (Fig. 1b). They cover the entire surface around the stem forming a cluster of oysters around most plants (Fig. 1c). Mean density of oysters settled by stems showed a higher number in dead plants than in live plants and at the low intertidal than medium and high intertidal for most of the sampling dates (Interaction F = 9.44, p < 0.05; Fig. 2). At the low intertidal the maximum density reached up to 54 oysters per stem in dead plants and 17 oysters
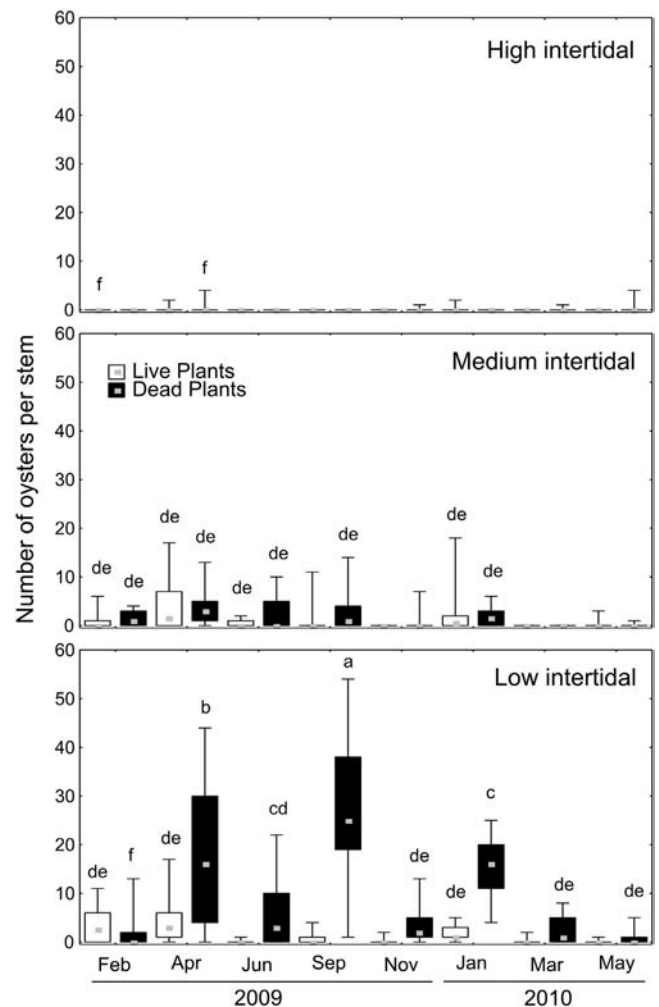

Fig. 2. Number of oysters attached on live and dead *Spartina alterniflora* stems at the low, medium and high intertidal and sampling date. Box plots are constructed with limits of boxes being the 75th and 25th percentile and vertical bars represent maximum and minimum values, points inside boxes indicate medians. Different letters denote significant difference in descendent order (p < 0.05).

in live plants, while at the medium intertidal the density reached 14 and 18 oysters in dead and live plants respectively and at the high intertidal 4 and 2 oysters per stem in dead and live plants respectively.

The shell height frequency distribution of oysters (Fig. 3) showed an important recruitment (size < 2 mm H) in February 2009 in both dead and live plants. However, higher individuals in dead plants (>12 mm H) indicated the presence of older individuals (i.e. related to previous recruitments). In April and June 2009 recruits were present at lower densities and no recruitment was observed in the summer of 2010.

The comparison of median shell height between intertidal levels showed larger sizes at the lower intertidal in February, April and September 2009 on dead plant and, June and November 2009 on live plants than other intertidal levels (p < 0.05). At each intertidal level,

the shell height showed differences across the year showing the smaller median values between February and April 2009 when recruits are present and larger individuals in the other sampling dates (p < 0.05; Fig. 4).

Observation of the internal shell growth bands of this species showed individuals with a maximum of 5 translucent bands. We also found presence of gonadal development in all analyzed individuals. These results suggest the presence of adult individuals of several years old.

3.2. Effect of oysters on mortality and growth rate of S. alterniflora

The *S. alterniflora* height showed higher values in January, March and May 2010 at the low intertidal than the rest of the year and intertidal levels (Interaction F = 2.41, p < 0.05, Fig. 5). The mean density of live *S. alterniflora* was similar between intertidal levels (ANOVA F = 0.22, p > 0.05) with 118.89 (SD = 64.72) plants m^{-2} at the high, 122.59 m^{-2} (61.34) at the medium and, 127.46 plants m^{-2} (69.82) at the low intertidal. The percentage of live plants with oyster presence was higher at the low intertidal in all the sampling dates (Table 1) reaching 60% in February, 90% in April 2009 and 80% in January 2010 showing higher prevalence of oysters at the low intertidal than at the
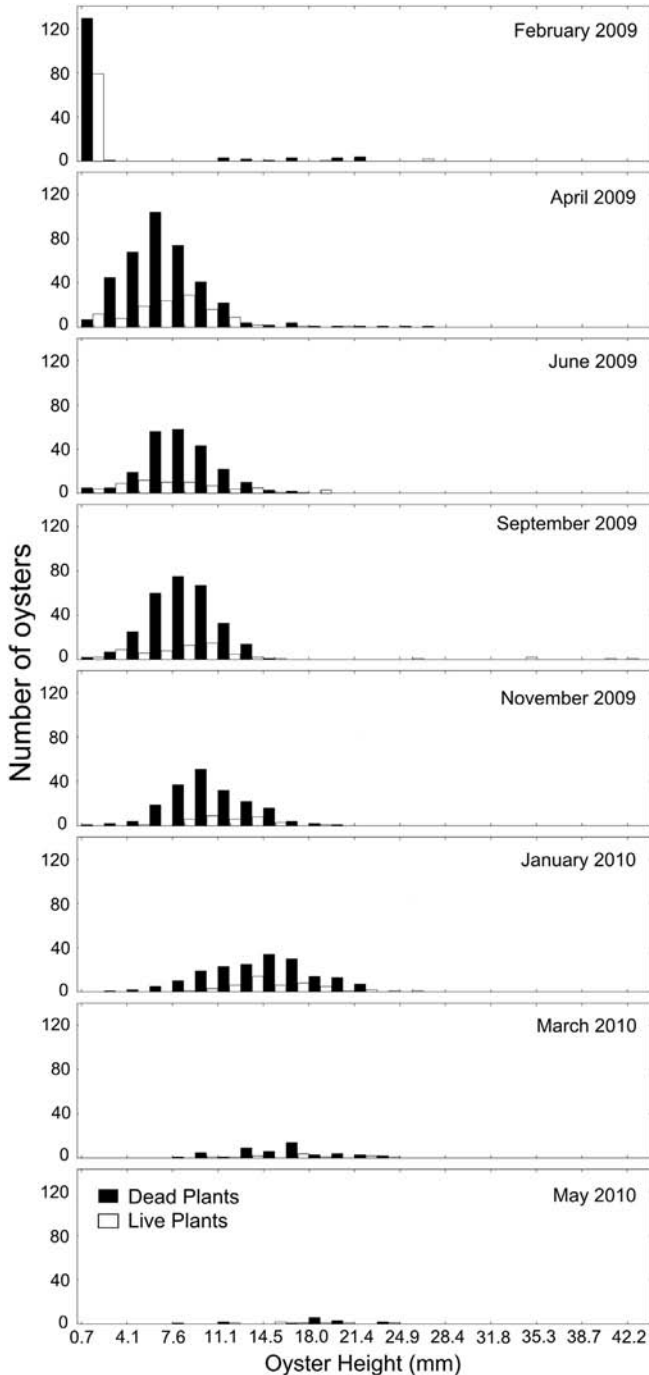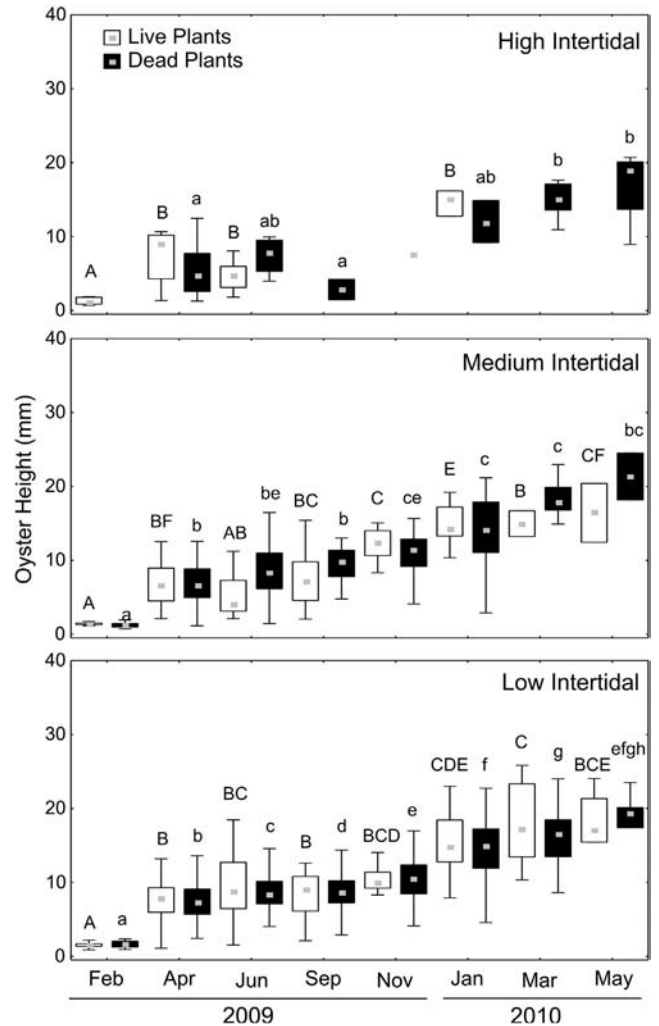

Fig. 3. The shell height frequency distribution of oysters on live and dead *Spartina alterniflora* stems across the year at the low, medium and high intertidal.

Fig. 4. Box plots of oyster shell height on live and dead *Spartina alterniflora* stems at the low, medium and high intertidal and sampling date. Box plots are constructed with limits of boxes being the 75th and 25th percentile and vertical bars represent maximum and minimum values, points inside boxes indicate medians. Different letters denote significant difference in ascendant order (p < 0.05). Capital letter: between sampling date at live plants and small letter: between sampling date at dead plants.
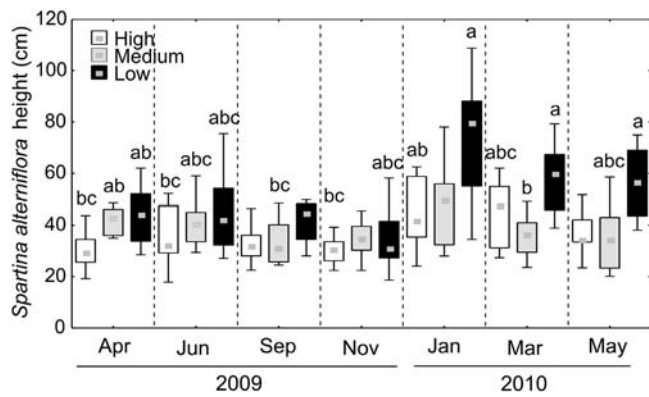
Fig. 5. *Spartina alterniflora* height at the low, medium and high intertidal and sampling date. Box plots are constructed with limits of boxes being the 75th and 25th percentile and vertical bars represent maximum and minimum values, points inside boxes indicate medians. Different letters denote significant difference in descendent order (p < 0.05).

other levels. Mean density of dead plants was higher at the low intertidal with 61.43 plants m^{-2} (42.51) than medium 30.56 (26.33) and high intertidal 24.89 (21.48) (ANOVA F = 20.77; p < 0.05). The percentage of dead plants with oysters attached on their stems was of 88.79% (18.24) at the low intertidal, 25.53% (29.78) at medium and 0% (0) at the high intertidal across the year.

The annual experiment showed that after three months all the *S. alterniflora* plants with oysters attached were dead (control treatment, low and medium, no oysters were present at the high intertidal level). In April 2009 the strangled setups showed also plant mortality at all intertidal levels. However, the plants from the "removed" treatment (those where oysters were removed) showed the opposite pattern than the control with higher mortality at the high intertidal than at the medium and low level (Table 2). In the next sampling date (June 2009), in the control setup no plants with oysters attached were found, thus the objective of the present field experiment for the following sampling dates was not possible to carry out. Additionally, the strangled setup treatment was not running after two sampling dates (see Section 2.3). The cumulative percentage of dead plants in the two sampling dates (Table 2) showed higher percentage of dead plants in control than oysters removed treatment at the low intertidal (χ^2 = 19.78, p < 0.001). There were no differences at the medium and high intertidal level (χ^2 = 2.08, p = 0.149 and χ^2 = 0.51, p = 0.474 respectively) and also between control and strangled set up at the 3 intertidal levels (χ^2 = 2.08, p = 0.149 at high, χ^2 = 2.91, p = 0.088 at medium and χ^2 = 0.50, p = 0.479 at low respectively). The strangled treatment showed a higher percentage of dead plants when compared to the removed treatment at the low intertidal (χ^2 = 14.25, p < 0.001) with no difference at the other two intertidal levels. In the first experiment, the plant growth showed higher increments at low intertidal than medium and high with no difference between treatments in April 2009 (ANCOVA; F = 2.66; p < 0.05). No differences were observed in June 2009 between intertidal levels and treatments (p > 0.05).

The percentage of survival plants recovered after the four-month field experiment (second experiment) from un-manipulated "control" and "strangled" treatment showed higher percentage in control than strangled plants (93% and 11% respectively; χ^2 = 134.70, p < 0.01).

Table 2
Percentage of dead plant in the first field experiment to evaluate the effect of oysters settled on *S. alterniflora* in the 3 intertidal levels (high, medium and low) with 3 treatments: "control" with un-manipulate plants, "removed" and "plant strangled".

Treatment	Intertidal level	April 2009	June 2009	Cumulative %
Control	High	0	45	45
	Medium	15	20	35
	Low	25	25	50
Plant strangled	High	5	30	35
	Medium	10	14	24
	Low	15	30	45
Oyster removed	High	20	40	40
	Medium	5	40	45
	Low	0	20	20

4. Discussion

Our study shows that a new non-indigenous species of *Crassostrea* oyster increases the mortality rate of the cordgrass *S. alterniflora* mainly at the lower intertidal salt marshes of Samborombón Bay. *Crassostrea* sp. produces mortality of *S. alterniflora* by possible direct mechanical effects when several oysters settle around their stems and, while growing, strangle the plants. The negative effect of oysters is higher at the lower intertidal level where oysters showed higher density and reached larger sizes.

Several non-indigenous bivalves introduced to a diversity of environments (Green and Crowe, 2013; Hebert et al., 1991; Kimmerer et al., 1994; McMahon, 1983; Reusch and Williams, 1998; Ruesink et al., 2005) strongly affect native species often altering the habitat through modification of the access to resources for other species (Jones et al., 1994; Padilla, 2010). The presence of biological invasions like oysters occurs worldwide and in most cases due to aquaculture purposes (Ruesink et al., 2005). In the Southwest Atlantic the only known introduced oyster is *C. gigas* introduced in 1982 for aquaculture purposes (northern part of the Argentinean Patagonia, San Blas Bay at 40°32′S; Orensanz et al., 2002). In these salt marshes they form dense reefs attached to hard surface such as limestone, empty shells, shell of a native small mussel *Brachidontes rodriguezii* and, the basal portion of *S. alterniflora* (Escapa et al., 2004; Orensanz et al., 2002). However, there are no evidences of negative effects of this oyster on the native cordgrass. The *Crassostrea* species described here is a new non-indigenous species (but see discussion on Cavaleiro et al., in review) for the north coast of Argentina and it is different than the introduced *C. gigas* and others native oysters from Brazil and Argentina (Cavaleiro et al., in review). The presence of sexual maturity and a maximum of five translucent bands (highly likely related to age) in the oysters analyzed suggest that these are aged adult individuals, which compared with *C. gigas*, they reached smaller maximum size (maximum shell length found 45 mm) and thus, pose lower growth rate (see Borges, 2005).

In contrast with *C. gigas* of the southern region (Escapa et al., 2004; Orensanz et al., 2002), *Crassostrea* sp. is found only attached on the basal part of *S. alterniflora* stems, possibly related to the lack of other hard substrata in the studied area. They cover the entire surface around the stem of *S. alterniflora* forming a cluster of oysters in most of the plants. Higher densities and larger oysters occur at the low intertidal. These differences in density and shell size are also observed in other

Table 1
Percentage of live *Spartina alterniflora* with oysters attached on their stems by sample date and intertidal level.

	Feb/2009	Apr/2009	Jun/2009	Sep/2009	Nov/2009	Jan/2010	Mar/2010	May/2010
High	0	20	0	0	0	10	0	0
Medium	40	60	30	20	0	50	0	10
Low	60	90	20	40	20	80	10	10

filter feeder bivalves inhabiting intertidal areas (e.g. oyster species, Crosby et al., 1991; Kingsley-Smith et al., 2009) where their distribution and size are related with filtering activity and temperature exposition having better conditions (shorter emersion time) at the low intertidal and more stressful condition at the high intertidal (Gosling, 2003; Reise, 1998). Intertidal oysters exposed to physical stresses, such as high temperatures, allocate more energy to metabolic maintenance, and thus being in detriment of somatic growth (Dame, 1972). However, biological interactions such as competition (Cognie et al., 2006) and/or predation (Bartol et al., 1999; Bologna and Heck, 1999) could be responsible for oyster distribution and size. For example, there is higher mortality due to predation at lower intertidal or shallow subtidal habitats (Bartol et al., 1999; Gosling, 2003). Thus, we can hypothesize that the distribution pattern and oyster characteristics observed in our study may respond to metabolic necessities of this species at the high intertidal and biological interactions at the low intertidal.

S. alterniflora has a gradient in height across the intertidal with tall forms at tidal creek banks (maximum > 1.3 m, at the low intertidal) to short forms into marsh interior (<0.35 m, high intertidal; our study). This pattern was confirmed by the observations related to our first experiment, with higher plant growth at the low intertidal, such as was also observed in other salt marshes of *S. alterniflora* in the Northern hemisphere (Mendelssohn and Morris, 2000). The maximum plant height found in our study, higher than previous reported for the area (Daleo et al., 2008; Isacch et al., 2014), was also observed in eutrophized *S. alterniflora* salt marshes in northern Patagonia (39°01′S–56°25′W, Bahía Blanca; Cardoni et al., 2011; Isacch et al., 2014). The season of maximum plant height (summer) coincided with the oyster's recruitment, but not the effect was observed on plant height growth due to the presence of oysters. The density of live plants was similar between intertidal levels but the percentage of dead plants was higher at the low intertidal showing also higher mortality rate as was observed in salt marshes which support a high crab herbivore pressure (Alberti et al., 2007). In our study area, crabs are at very low density and do not form beds (area with a high crab burrow density; B. Lomovasky, pers. obs.), and assuming that the grazing intensity has a positive relation with crab density in this systems (Alberti et al., 2007), the pattern of higher stem mortality found in the present study at the low intertidal could not be related to crab herbivory. The pattern of live plant density found in this study differs from other *S. alterniflora* marshes where a higher density of live plants was observed at the low intertidal (González Trilla et al., 2009). The higher density of oysters attached to dead plants could be related with the cumulative recruitments that occur in dead stems (of few cm of height above the sediments) across several years. The latter is confirmed by the presence of cohorts of different oyster size and the limited time that live plants survive to oyster's presence (our results). Thus, it shows more incidences of oyster's effects at the low intertidal (see above) altering the plant mortality rate.

The effects of non-indigenous bivalves on native plant species are negative (Reusch and Williams, 1998), positive (Bertness, 1984b; Green and Crowe, 2013; Torchin et al., 2005) or there are no effects (Reusch and Williams, 1998) depending on the environment, the analyzed response variable and the bivalve characteristics (i.e. presence–absence of byssus, substrate preference, reef formation). The effects that the mussel *M. senhousia* have on native eelgrass in San Diego Bay (USA) are negative on the asexual propagation, positive on the leaf growth and have no effect on the shoot density of eelgrass (Reusch and Williams, 1998). Other invasive bivalve species such as *Geukensia demissa* shows positive effects on the leaf growth of *S. alterniflora* (Bertness, 1984b) and *Spartina foliosa* (Torchin et al., 2005). Something similar shows the non-indigenous blue mussels *Mytilus edulis* on the native eelgrass *Z. marina* (Reusch et al., 1994) where biodeposition of feces and pseudofeces by bivalves can increase ammonium availability for rooted angiosperms. In either case, the mechanisms involved could be species-specific and related to initial environmental conditions (Green and Crowe, 2013; Padilla, 2010; Reusch and Williams, 1998).

In our study the oysters negatively affects survival of *S. alterniflora*. This effect may be due to tissue lesions or mechanical abrasion on the stem surface where oysters attached themselves, or the alteration of the exchanges performed at the air/stem interface and/or effects of the oyster dissolved or particulate excretion on the plant. However, our results and observations suggest that it is due to the mechanical strangling when several oysters settle around their stems and while growing they strangle the plants. In either case, oysters enhance plant mortality.

The pronounced zonation pattern of marsh plants is determined across strong gradients in physical stress (flooding and/or salinity) at the low intertidal and plant competition at the high intertidal (Pennings and Callaway, 1992; Pennings et al., 2005). However, in other natural communities the lower intertidal distribution is being controlled by herbivory (Alberti et al., 2007; Bertness, 1984a,1984b; Costa et al., 2003; Silliman and Bortolus, 2003). In our system, considering that oyster density is higher at the low intertidal and that plants with oyster survive only a short time (our study), we can conclude that if *Crassostrea* sp. finally became a successful invader it could develop into a control factor of the lower distribution limit of *S. alterniflora*.

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