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Abiotic stress mediates top-down and bottom-up control in a Southwestern Atlantic salt marsh

**Juan Alberti · Agustina Méndez Casariego ·
Pedro Daleo · Eugenia Fanjul · Brian Silliman ·
Mark Bertness · Oscar Iribarne**

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Abstract Increasing evidence has shown that nutrients and consumers interact to control primary productivity in natural systems, but how abiotic stress affects this interaction is unclear. Moreover, while herbivores can strongly impact zonation patterns in a variety of systems, there are few examples of this in salt marshes. We evaluated the effect of nutrients and herbivores on the productivity and distribution of the cordgrass *Spartina densiflora* along an intertidal stress gradient, in a Southwestern Atlantic salt marsh. We characterized abiotic stresses (salinity, ammonium concentration, and anoxia) and manipulated nutrients and the presence of the herbivorous crab *Neohelice* (*Chasmagnathus*) *granulata*, at different tidal heights with a factorial experiment. Abiotic stress increased at both ends of the tidal gradient. Salinity and anoxia were highest at the upper and lower edge of the intertidal, respectively. Nutrients and herbivory interacted to control cordgrass biomass, but their relative importance varied with environmental context. Herbivory increased at lower tidal heights to the point that cordgrass transplants onto bare mud substrate were entirely consumed unless crabs were excluded, while nutrients were most important where abiotic stress was reduced. Our results show how the impact of herbivores and nutrients on plant productivity can be dependent on environmental conditions and that the lower intertidal limits of marsh plants can be controlled by herbivory.

Keywords Herbivory · *Neohelice granulata* · Nutrients · *Spartina densiflora* · Tidal stress gradient

Introduction

Whether primary production in ecosystems is controlled by bottom-up (nutrients or physical factors) or top-down forces (herbivores and their predators; see Hunter and Price 1992; Power 1992) has been a long-standing debate in ecology. Evidence has supported both theories (top-down: Terborgh et al. 2001; Silliman et al. 2005; Halpern et al. 2006; Myers et al. 2007; bottom-up: Valiela et al. 1976; Peterson et al. 1993; Nixon and Buckley 2002; White 2007), but until recently the relative roles of these factors were debated rather than synthesized (Hunter and Price 1992). Over the last decade, however, a growing number of studies have revealed that control of ecosystem productivity is an interaction of both forces, not the product of a single force

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J. Alberti (✉) · A. Méndez Casariego · P. Daleo ·
E. Fanjul · O. Iribarne
Laboratorio de Ecología, Departamento de Biología (FCEyN),
Universidad Nacional de Mar del Plata, CC 573 Correo Central,
B7600WAG Mar del Plata, Argentina
e-mail: jalberti@mdp.edu.ar

J. Alberti · A. Méndez Casariego · P. Daleo · E. Fanjul · O. Iribarne
Consejo Nacional de Investigaciones Científicas y
Técnicas (CONICET), Rivadavia 1917,
CP C1033AAJ Ciudad de Buenos Aires, Argentina

B. Silliman
Department of Biology,
University of Florida, Gainesville, FL 32611, USA

M. Bertness
Department of Ecology and Evolutionary Biology,
Brown University, Providence, RI, USA

(Moran and Scheidler 2002; Russell and Connell 2005; Burkepile and Hay 2006).

Community organization models (Menge and Sutherland 1976, 1987) have hypothesized that the strength of biological interactions, like herbivory and competition, diminish with increasing physical stresses. Numerous studies have shown that physical stress influences consumers (Gough and Grace 1998; Harley 2003; Silliman et al. 2005), and may also affect nutrient uptake (Linthurst and Seneca 1981; van Katwijk et al. 1999; Emery et al. 2001). For example, the impact of consumers on salt marsh plants may depend on the type of stress, herbivore and plants studied (Goranson et al. 2004). In general, however, little research has examined how abiotic factors can interact with nutrient availability and herbivores to affect plant productivity (Dudt and Shure 1994; Feller 1995) and zonation patterns in communities (Louda 1989).

Understanding processes underlying zonation patterns has long been a key focus in ecology. Darwin (1859) pointed out that physical factors usually vary gradually while species boundaries tend to be comparatively abrupt, and he ascribed these patterns to the interaction of biotic (predation and competition) and abiotic factors. Current models of species zonation, in marine (Bertness and Leonard 1997) and terrestrial systems (Callaway et al. 2002), postulate that negative biotic interactions increase in importance towards the most benign extreme of the environmental gradient, while positive biotic interactions and physiological tolerance dominate towards the harsh abiotic extreme. Intertidal systems usually show marked abiotic stress gradients and, along this gradient, herbivory, nutrients and physical factors can strongly influence plant distributions. In rocky shore systems, herbivory can set the lower (Lubchenco 1980) and upper limit (Underwood 1980; Cubit 1984) of algal distribution. Physical factors cause similar results, especially with upper limits (Connell 1972), while nutrients can indirectly raise the lower limit (Kautsky et al. 1986). Generalizations from empirical studies on rocky shores postulate that the upper limits of species distributions are mostly controlled by abiotic stress and positive interactions while lower limits are mostly controlled by competition and consumers (see Bertness and Leonard 1997). While experimental studies do not allow generalizations about the maintenance of plant zonation in mangroves (Ellison and Farnsworth 2001), there is evidence of strong effects of herbivores (Smith 1987; Clarke and Kerrigan 2002), abiotic stress (Clarke and Myerscough 1993; Castañeda-Moya et al. 2006) and nutrient availability (Feller et al. 2003). In salt marshes, interspecific competition generally controls the upper intertidal limits of plants (Bertness and Leonard 1997), abiotic stress generally controls the lower zonation limits of plants (Bertness 1991b; Castillo et al. 2000, but see Bockelmann and Neuhaus 1999), while nutrients, by affecting competition, modify boundaries between species (Levine et al. 1998; Daleo et al. 2008). Herbivores can modify marsh species distributions (Bertness 1984; Silliman et al. 2005), but there is little evidence that they control zonation patterns (but see Furbish and Albano 1994).

Salt marshes are vegetated intertidal areas characterized by strong abiotic stress gradients (Bertness and Leonard 1997; Pennings and Bertness 2001), including salinity (Pennings and Callaway 1992) and anoxia (Howes et al. 1981). In general, salinity increases and anoxia decreases with marsh height (Pennings and Bertness 2001). Nitrogen availability (Valiela et al. 1976; Dai and Wiegert 1996) and herbivory (Silliman and Bortolus 2003; Jefferies et al. 2006) are also recognized as limiting factors for marsh plants. Another way herbivores, nutrients and physical factors can affect plant productivity is by affecting plant distributional boundaries (Levine et al. 1998; Silliman et al. 2005). Given the strong influence of both physical and biological control on marsh plants, marshes are good model systems with which to evaluate the relative importance of nutrients and consumers along abiotic stress gradients.

In the Southwestern (SW) Atlantic, salt marshes associated with freshwater inputs are dominated by the cordgrass *Spartina densiflora* (Isacch et al. 2006). *Spartina* spp. productivity is strongly limited by nutrients, since fertilization increases their biomass by nearly 50% (Daleo et al. 2008). In these marshes, the abundant burrowing, herbivorous crab *Neohelice* (*Chasmagnathus*) *granulata* (Iribarne et al. 2005) can diminish cordgrass biomass by up to 87% (Bortolus and Iribarne 1999). These crabs (~3 to 4 cm in carapace width) play an important role in the food web of these marshes, in terms of both biomass and interactions, reaching densities of up to 60 crabs m^{-2} (Iribarne et al. 1997), eating grass (Bortolus and Iribarne 1999; Alberti et al. 2007a) and other crabs (Daleo et al. 2003; Méndez Casariego et al. 2009), affecting benthic community structure (Escapa et al. 2004) and mediating predator–prey interactions (Escapa et al. 2004; Martinetto et al. 2005). Recent evidence suggests that the intensity of crab grazing increases by as much as 60% at lower elevations (Alberti et al. 2007a). This high grazing rate may contrast with current theoretical models of plant distribution limits suggesting that a biological factor (i.e., grazing) could be a strong limiting factor at lower elevations. Based on these observations, we tested the following hypotheses: (1) nutrients and herbivory interact to determine marsh plant biomass, but their relative contribution varies with abiotic stress along an intertidal gradient; and (2) herbivory can maintain the lower distributional limits of marsh plants.

Materials and methods

Study site

This study was carried out at the Mar Chiquita coastal lagoon (37°46′S, Argentina), a brackish lagoon (salinity 0.5– 34‰) with low-amplitude tides ($\leq$1 m) that has been intensively studied (see Iribarne 2001). Shoreline salt marshes in the lagoon are dominated by *Spartina densiflora* and *Sarcocornia perennis* (Isacch et al. 2006). The burrowing crab *N. granulata* is distributed in the tidal flats and marshes and is one of the most important macro-invertebrates of SW Atlantic salt marshes (Iribarne et al. 1997). We performed experiments in five areas covering most of the intertidal and a wide range of abiotic conditions. Given that each tidal height showed particular abiotic conditions we will refer to these areas as environmental contexts. Three of these environmental contexts were located in *S. densiflora* vegetation: the low marsh-mudflat edge (lower limit of marsh vegetation with an extension of more than 1,000 m parallel to the shore), the low marsh matrix (*S. densiflora* monoculture), and the intertidal border of *S. densiflora*, on the edge of hypersaline bare patches (mid marsh). The remaining two environmental contexts were located in lower elevation mudflats, 14 and 28 cm (in tidal elevation) below the lowest distribution of marsh vegetation. We chose the first mudflat tidal height because preliminary tests showed that transplants moved to that height survived when herbivory was prevented, and chose the second lower mudflat elevation to determine if they could tolerate a much lower elevation.

Environmental context

We obtained a snapshot of abiotic conditions at the study site, by measuring sediment salinity, ammonium concentration and anoxia in the five environmental contexts, in the summer (March 2008; when abiotic differences between environmental contexts are expected to be greatest; Bertness 1991a). Even though these single-date samples do not let us know the abiotic conditions operating during the whole experiment, they allow us to compare relative environmental conditions. Sediment salinity ($n = 5$ per environmental context) was obtained by collecting random sediment samples (5 cm diameter, 8 cm deep), which were weighed, dried to constant weight, mixed with a known volume of distilled water, measured by refractometry after 48 h, and then corrected by the initial sample water volume, to reflect the original concentration of salt. Ammonium concentration ($n = 5$ per environmental context) was measured in pore water by the indophenol blue method (Solórzano 1969). Sediment redox potential ($n = 8$ per environmental context) was measured in situ, 5 cm deep in each environmental context, with a combined platinum electrode with silver/silver chloride internal reference. Values were corrected with respect to a reference hydrogen electrode. The null hypotheses of no differences in salinity, in pore water ammonium concentration and in sediment redox potential (100 was summed to the raw data and then it was square-root transformed) between the five environmental contexts were evaluated with separate one-way ANOVAs (Zar 1999). Another potential factor influencing plant performance is herbivore density. Thus, we measured burrow density (an estimator of crab density; Iribarne et al. 1997) by counting the number of burrows in eight randomly distributed 1-m^2 quadrats per environmental context, and then compared burrow density between environmental contexts using a Kruskal–Wallis test followed by a non-parametric multiple comparison test (Conover 1980).

Do nutrients and herbivory effects vary with the environmental context?

Effects on plant biomass

We performed an experiment to evaluate the direct and interactive effects of nutrients, herbivory and abiotic stress on *S. densiflora* production. The experiment had a fully factorial design (2 × 2 × 3): with and without herbivory (controls and exclosures), with and without nutrient addition, and in three marsh environmental contexts, spanning gradients in salinity and anoxic stress (low marsh-mudflat edge, low marsh matrix, middle marsh-hypersaline patch edge). The experiment ran from December 2005 to March 2008, and each treatment combination (12), was replicated 8 times (75 × 75 cm).

Crab-exclusion plots were surrounded by a 1-cm-plastic mesh fence 40 cm high. Gastropods (Canepuccia et al. 2007), and all other invertebrates in the marsh easily passed through the mesh (A. Canepuccia and O. Iribarne, unpublished data). Field observations showed that other invertebrate herbivores produce leaf wounds different than those of crabs. Even though vertebrate herbivores could be excluded by the cages, rodents forage at higher intertidal levels (A. Canepuccia and J. Alberti, unpublished data) and produce distinctive grazing marks, cutting stems a few centimeters aboveground (see Vicari et al. 2002), marks that were not observed in our experiment. Fish could also be excluded, but there are no herbivorous fish in this system (Cousseau et al. 2001). Nutrient addition treatments received 60 g ($\sim$100 g m^{-2}) of the slow-release pelletized fertilizer Ferticare (29% nitrogen, 5% phosphorus, 5% potassium) monthly. Fertilizer was spread into six artificial holes (5 cm deep, 1 cm diameter) evenly distributed in each plot that were then filled with mud. Experimental units located on edges between marsh and bare mudflat surfaces (low marsh-mudflat, marsh-hypersaline patches) were initially established to include 50% vegetation and 50% bare surface (75 × 37.5 cm of each) to quantify the effect of nutrients, herbivores and abiotic stress on the asexual colonization of bare areas (see below).

At the end of the experiment we collected a 20 × 20-cm sample of aboveground *S. densiflora* biomass from the center of the vegetated area in each replicate. Live stems were dried (50°C for 72 h), and weighed. The null hypothesis of no difference in the dry weight of *S. densiflora* (log-transformed), between environmental contexts, with and without crabs and nutrient addition was evaluated with a three-way ANOVA (environmental context, herbivory and nutrients as fixed factors), with Tukey tests for a posteriori contrasts. To test for exclosure artifacts, we compared controls, cage controls (three sided cages) and exclosures with one-way ANOVA for each environmental context; no cage effects were found (results are given in S1).

Effects on asexual colonization of bare surfaces

Since herbivores, nutrients and abiotic factors can affect plant productivity by affecting plant distributions (Levine et al. 1998; Silliman et al. 2005), we also monitored the asexual colonization of unvegetated mudflat surfaces in the above experiment. We marked the vegetation/mudflat limit in all low marsh-mudflat edge and marsh-hypersaline patch edge replicates. In each replicate, we marked five fixed points on the edge with plastic flags to detect edge movement. We quantified the average distance between the new position of the edge (i.e., after movement) and the flags per replicate and then compared edge movement, with and without crabs, and nutrient addition using a two-way ANOVA in each environmental context (herbivory and nutrients as fixed factors; marsh-mudflat edge data was square-root transformed, we added 1 to the raw data to avoid negative values). The two environmental contexts were analyzed separately because it was impossible to meet the assumption of homogeneity of variances in the three-way design. To detect potential artifacts due to exclosures, we compared controls, cage controls and exclosures using one-way ANOVA for each environmental context; no cage effects were found (results are given in S1).

Nutrients and herbivory in transplants moved to the mudflat

Generally, the lower distributional limit of marsh plants is thought to be controlled by physiological tolerances to abiotic stress (Bertness 1991b; Castillo et al. 2000; Bertness and Leonard 1997); however, in SW Atlantic salt marshes, crab herbivory also increases with decreasing marsh height (Alberti et al. 2007a) and may set lower distribution limits. To test this, we conducted a third experiment to evaluate the role of nutrients and crab herbivory on the survival of *S. densiflora* transplants moved to two heights in the mudflat. This experiment had a 2 × 2 × 2 factorial design, and was performed using cordgrass transplants ($n = 8$ per treatment) moved into the mudflat 14 and 28 cm below the lowest limit of marsh vegetation, with and without herbivory (controls and exclosures), and with and without nutrient addition. Each transplant was extracted using a corer (10 cm diameter, 35 cm deep, which includes ~90% of *S. densiflora* belowground biomass; Daleo and Iribarne 2009) containing ~12 live *S. densiflora* stems, taken independently from the marsh-mudflat edge. Crab-exclusion cages were made of a 1-cm plastic mesh (60 × 60 × 60 cm). Nutrient addition treatments received 40 g (~100 g m^{-2}) of a slow-release pelletized fertilizer (29% nitrogen, 5% phosphorus, 5% potassium) monthly. The fertilizer was spread into four evenly distributed artificial holes (5 cm deep, 1 cm diameter) that were then filled with mud. To detect potential artifacts due to transplanting, we compared the number of live stems and the percent live between transplant controls (extracted and then put back in) and unmanipulated controls ($n = 6$ per group) using a *t*-test for unequal variances (Welch approximation t_c). The t_c is equal to the *t*-value when sample sizes are the same, but *df* decrease as the difference between variances of the two groups increases (Zar 1999).

After 2 months, we counted the number of live and dead stems per replicate (transplant), and then compared the number of live stems (square-root transformed) between environmental contexts, with and without nutrient addition, and crab exclosures with a three-way ANOVA (height, nutrients and herbivory as fixed factors). To test for exclosure artifacts, we compared controls, cage controls and exclosures with an ANOVA for each environmental context, and no cage effects were found (results are given in S1). The same procedure was used after a year, excluding the herbivory treatment since all cordgrass transplanted to the mudflat without cages was entirely eaten by the fourth month. Hence, we used a two-way ANOVA to compare means of square-root transformed data between treatments (height and nutrients as fixed factors). One year after the experiments began, transplants inside exclosures were more than 2 times larger than when they were transplanted, and the addition of nutrients only affected transplants 14 cm below the marsh-mudflat edge (see "Results"). Thus, we decided to use this mudflat height to run a second experiment (cages located in the low mudflat were removed, and those transplants were abandoned). To determine if these transplants were able to survive the herbivory found on the mudflat, and how nutrients affected their survival, we removed all exclosures from these transplants (both fertilized and unfertilized). Thus, these transplants grew for the first year without grazing pressure (caged) and expanded in size and distribution during that time. We counted the number of live stems per replicate, and the following year compared the square-root transformed means of live stems per transplant between treatments with and without nutrient addition, before and 1 year after removing exclosures, with repeated-measures ANOVA (note that we only used those units originally assigned to crab-exclusion treatments, as all original control treatments were already dead by the time we started this second experiment). To quantify differences before and after removing exclosures associated with herbivory, we scored the percent live leaves consumed per stem as an estimate of herbivory pressure (Rand 2002). We compared herbivory pressure with and without nutrients before removing exclosures and after a month with repeated-measures ANOVA on square-root transformed data.

Results

Environmental context

Soil salinity increased significantly with increasing tidal height. Salinity was lowest in the mudflat, the lowest elevation habitat, and twice as high on hypersaline patch edges, the highest elevation habitat ($F_{4,20} = 21.69$, $P < 0.001$; Fig. 1). Pore-water ammonium had the opposite pattern. Ammonium concentration was highest in the low mudflat, and lowest on hypersaline patch edges ($F_{4,20} = 11.57$, $P < 0{,}001$; Fig. 1). Like soil salinity, soil redox potential increased significantly with increasing tidal height ($F_{4,35} = 62.19$, $P < 0.001$; Fig. 1). Crab densities were highest at the low marsh-mudflat edge and at the low marsh matrix, while almost no crabs were found at the low mudflat ($H_{(4,n=40)} = 34.60$, $P < 0.001$; Fig. 1).

Do nutrients and herbivory effects vary with the environmental context?

Effects on plant biomass

Treatments with increased nutrients had 4.5 times more biomass than controls on the marsh-mudflat edge, 6.5 times in the low marsh matrix, and there were no differences in the middle marsh-hypersaline bare patch edge (S2; Fig. 2). Across all habitats crab herbivory removed nearly 20% of live *Spartina densiflora* biomass (S2; Fig. 2).

Effects on asexual colonization of bare surfaces

In the middle marsh (hypersaline patches), asexual colonization of bare areas was almost zero and was not affected by nutrients ($F_{1,28} = 1.55$, $P > 0.22$) or herbivory ($F_{1,28} = 1.14$, $P > 0.29$; Fig. 3). However, on the marsh-mudflat edge, excluding crabs and adding nutrients increased asexual cordgrass movement into the mudflat by 130% (interaction: $F_{1,28} = 7.4$, $P < 0.05$; Fig. 3).

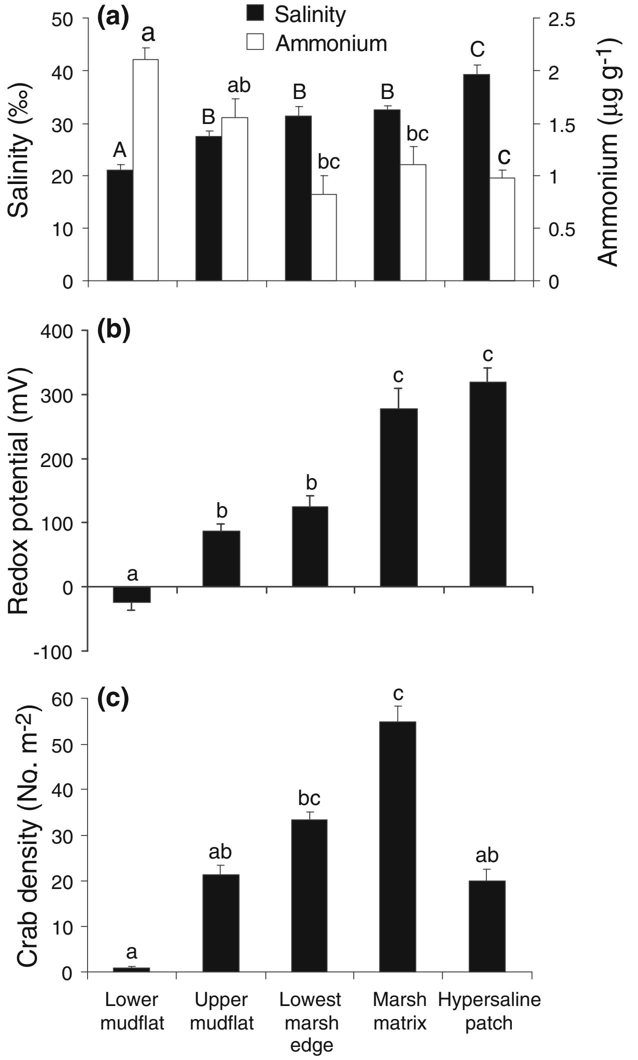

Fig. 1 Variation in environmental conditions across sites where experiments were conducted: **a** salinity and ammonium, **b** redox potential, **c** crab density. Elevations above mean low tide (m): 0.42 (*Lower mudflat*), 0.56 (*Upper mudflat*), 0.70 (*Marsh-mudflat edge*), 0.80 (*Marsh matrix*), 0.92 (*Hypersaline patch*). *Letters* indicate significant differences ($P < 0.05$) among environmental contexts, for a given abiotic factor. *Bars* are mean + SE

Nutrients and herbivory in transplants moved to the mudflat

After 2 months, nutrient addition increased the number of live stems per transplant by 35%, regardless of crab exclusion and or location (i.e., 14 or 28 cm below the lower limit of the marsh; S3; Fig. 4). The impact of crab herbivory diminished with increasing height; the number of stems was

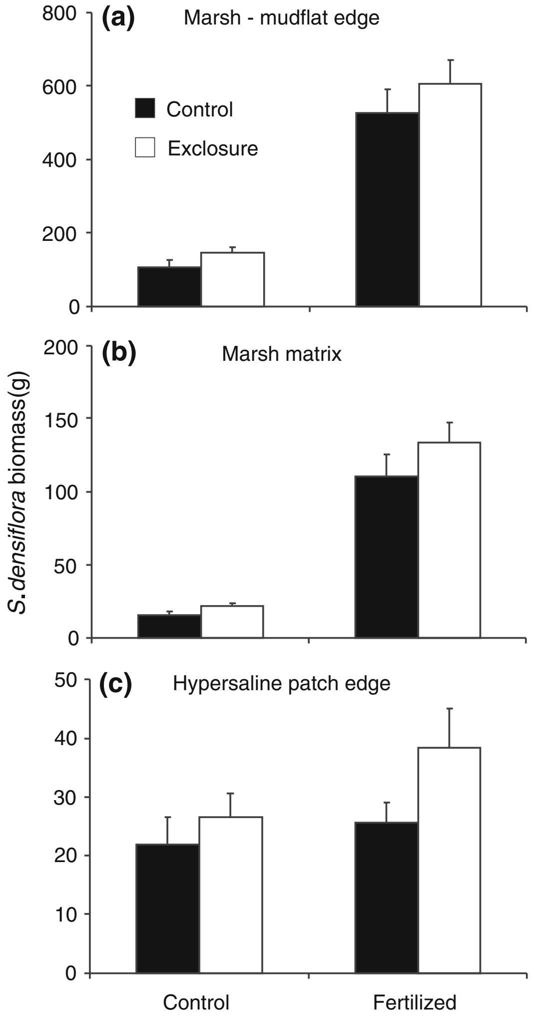

Fig. 2 *Spartina densiflora* live biomass in the experiment manipulating crab presence and nutrient availability in three different marsh heights: **a** marsh-mudflat edge, **b** marsh matrix, and **c** hypersaline patch edge. Statistical results are given in S2

reduced by 60% at the low mudflat, and 10% at the upper mudflat (S3; Fig. 4). We found no artifacts due to transplanting (number live stems, $t_c = 0.92$, $df = 6$, $P > 0.39$; percent live stems, $t_c = 1.77$, $df = 5$, $P > 0.13$). All transplants without crab exclosures were entirely consumed in 4 months, and hence, were not further considered. For caged transplants, after the first year, there was no nutrient effect at the lowest height; these treatments showed the same number of stems per transplant as fertilized treatments at the upper height, which were 6 times larger than controls (interaction: $F_{1,28} = 15.11$, $P < 0.001$; Fig. 5). At that time we removed exclosures from the upper height, and by the next month, herbivory (% of consumed leaves per stem) had more than doubled ($F_{1,14} = 18.17$, $P < 0.001$), regardless of nutrients ($F_{1,14} = 2.98$, $P > 0.1$). After a year, 97% of the newly exposed transplants had been consumed (interaction: $F_{1,14} = 30.88$, $P < 0.001$; Fig. 6; S4).

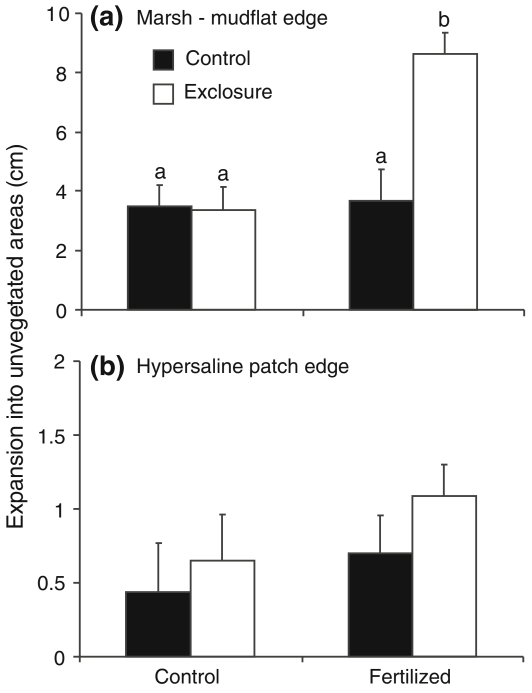

Fig. 3 *S. densiflora* asexual colonization in **a** mudflat in the low marsh and **b** hypersaline bare patches in the middle marsh in an experiment manipulating crab presence and nutrient availability. *Letters* denote significant differences between treatments

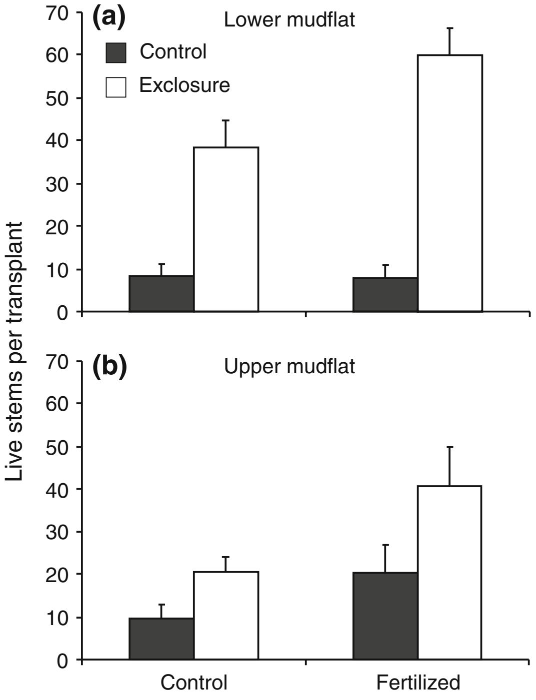

Fig. 4 Number of live stems per *S. densiflora* transplant moved to the **a** lower (28 cm below the marsh-mudflat edge) and **b** upper mudflat (14 cm below the marsh-mudflat edge), in an experiment manipulating crab presence and nutrient availability. Statistical results are given in S3

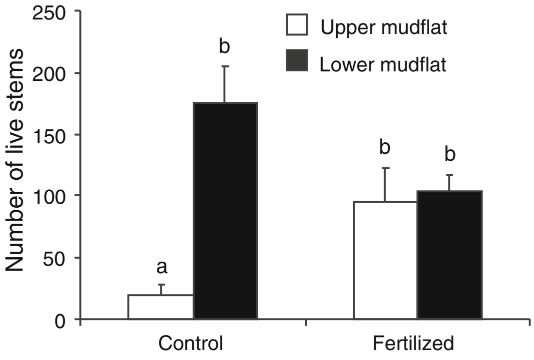

Fig. 5 Number of live *S. densiflora* stems in transplants moved to the upper (14 cm below the marsh-mudflat edge) and lower mudflat (28 cm below the marsh-mudflat edge) after 1 year growing inside exclosures, with and without nutrient addition. *Letters* indicate significant differences ($P < 0.05$) among treatments

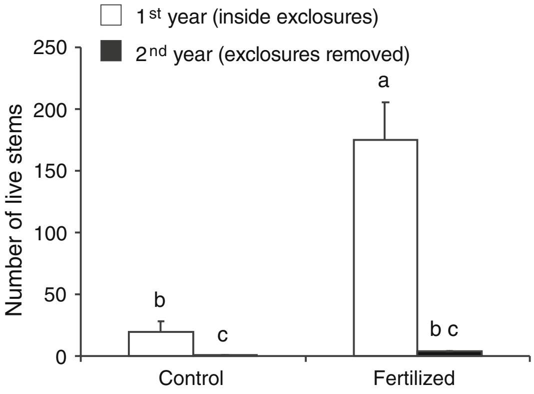

Fig. 6 Number of live *S. densiflora* stems in transplants moved to the upper mudflat (14 cm below the marsh-mudflat edge), with and without nutrient addition, and growing for the first year inside exclosures and the second year without exclosures. Statistical results are given in S4. *Letters* indicate significant differences ($P < 0.05$) among treatments

Discussion

Our results show that nutrients and herbivores interact to control *Spartina densiflora* primary production and asexual colonization of unvegetated areas, but that their relative importance is context dependent, varying across the intertidal stress gradient. The maximum effect of nutrient addition occurred at intermediate elevations. Nutrients did not affect primary production at low or high elevations, where anoxia and high salinities, respectively were potentially limiting. In contrast, the importance of herbivory increased with decreasing elevation, to intensities capable of controlling colonization and survival on the low intertidal mudflat. Thus, our results highlight that herbivory can be important under stressful conditions, when herbivores and plants are not limited by the same abiotic stresses, and that the lower limit of marsh plants can be controlled by herbivory.

Environmental context mediates top-down and bottom-up control

There has been a long debate about whether natural communities are controlled by top-down or bottom-up forces (see Hunter and Price 1992; Power 1992). During the last two decades, however, evidence has emerged showing that top-down and bottom-up control are coupled (Moran and Scheidler 2002; Russell and Connell 2005; Burkepile and Hay 2006). In some cases, nutrient supply can trigger top-down control, in systems where it is otherwise unimportant (Bertness et al. 2008; Sala et al. 2008). In our edge movement experiments, herbivory was only evident when plots were fertilized. Potential causes of this pattern include increased consumption of enriched marsh plants (Vince et al. 1981; Silliman and Zieman 2001), or immigration of herbivores into the fertilized plots (suggested by Hillebrand 2002). Maximum edge movement was <10 cm (in this system, *S. densiflora* growth is very slow; see Alberti et al. 2008) but over time and without herbivory, plants should be able to occupy much lower tidal heights.

It is also known that herbivores and nutrients can produce variable results, depending on the abiotic stress [herbivory (Harley 2003; Silliman et al. 2005); nutrients (Linthurst and Seneca 1981; van Katwijk et al. 1999)]. While there are studies considering interactions between herbivores, nutrients and abiotic stress (Dudt and Shure 1994; Feller 1995), few have directly evaluated the context dependency of the balance between nutrient and consumer effects (see Burkepile and Hay 2006). Here we found that the balance between the positive effect of nutrients and the negative effect of herbivory on cordgrass productivity varies depending on abiotic conditions. In the high intertidal where salinity was maximum and anoxia minimum, neither herbivory nor nutrients played a role as important as in other environmental contexts. At intermediate heights with intermediate salinity and anoxia, nutrients produced major changes in cordgrass biomass, while herbivores were of greater importance at the lowest tidal heights with maximum anoxia and nutrient availability. The high impact of crab herbivory in the low intertidal is expected, because *Neohelice granulata* grazing increases when it is submerged (Alberti et al. 2007b). It is not surprising that crab densities were not related to the impact of crab herbivory as it has been shown that within a given marsh, there is no correlation between crab density and crab herbivory (Alberti et al. 2007a), probably due to high crab mobility and the fact that they prefer to graze while underwater (Alberti et al. 2007b). Salinity and anoxia diminish the positive effects of nutrient enrichment on *Spartina alterniflora* (Linthurst and Seneca 1981); hence, it is not surprising that the greatest impact of nutrient addition was at intermediate heights where neither of these variables was maximum.

Underlying abiotic conditions can also explain differences in the performance of caged transplants in the high and low mudflat. The performance of unfertilized transplants was best at the lowest height, consistent with maximum nutrient availability. Conversely, nutrient addition did not have a significant effect at the lowest height, probably due to other limiting factors (like low access to carbon dioxide, light availability, or increased anoxia due to increased submersion). Indeed, highest anoxia occurred at that tidal height, and it can limit the effect of increased nutrients (Linthurst and Seneca 1981).

Biological interactions and stress factors

Environmental stress models predict that the importance of negative biological interactions (competition, predation) diminishes with increasing abiotic stress (Menge and Sutherland 1976, 1987) and that the importance of positive interactions increases with abiotic stress (Bertness and Hacker 1994; Bertness and Leonard 1997). These predictions have received support from different environments (Bertness et al. 1999; Huckle et al. 2000; Pugnaire and Luque 2001). Menge and Farrell (1989), however, found only partial support for these predictions for negative biological interactions (competition, predation), concluding that the model is probably restricted to habitats in which variation in interaction web structure responds primarily to environmental stress. Thus, there are habitats where a factor that is a stressor for a given trophic level is not a stressor for other trophic levels.

An analogous situation occurs for positive interactions and stress identity and intensity. For example, in dry environments where soil moisture is a critical stressor, species that reduce stress (increase soil moisture) can have strong positive effects on other species. But in more humid environments, light availability becomes the limiting stressor and thus, even though the species that increases soil moisture is still present, its effects on the other species are null or negative because soil moisture is no longer the limiting stressor (see Holmgren et al. 1997).

Many salt marshes have opposing abiotic stress gradients, with anoxia decreasing and salinity increasing with marsh height (Pennings and Bertness 2001; Pennings and Callaway 1992). Thus, one may be expected to find decreasing importance of negative biotic interactions at both extremes of the tidal gradient. Our results only partially support this prediction. At the upper extreme (maximum salinity), herbivory did not play an important role, but in the lower extreme, where anoxia was maximum, the impact of herbivory was also maximum. Long flooding periods promote soil anoxia, which is a stressor for marsh plants (Linthurst and Seneca 1981; Bertness 1991b; Gough and Grace 1998; Castillo et al. 2000), but flooding also promotes crab herbivory (Alberti et al. 2007b). Thus, there is a decoupling of stress at different trophic levels, violating the underlying assumptions of environmental stress models (Menge and Sutherland 1976, 1987). Our study highlights the importance of taking into account the context dependency of most stressors that typically vary among species and environmental and biological contexts.

Biotic and abiotic interactions affecting zonation in intertidal communities

Many processes influence species zonation including: (1) varying physiological tolerance to abiotic stress, (2) differential dispersal, (3) interspecific competition, and (4) predation pressure (see Louda 1989). The relative importance and interactions of these processes are environmentally dependent. In mangroves, for example, predation (Smith 1987; Clarke and Kerrigan 2002), dispersal (Sousa et al. 2007), interspecific competition and abiotic stress (Clarke and Myerscough 1993) can set zonation patterns, but most evidence suggest that species distribution limits are set by interactions among these factors, that vary among species and sites (Duke et al. 1998; Ellison and Farnsworth 2001).

There are some general processes that operate to set zonation patterns in other intertidal systems. The paradigm emerging from studies in salt marshes and rocky shores is that competitively dominant species monopolize physically benign habitats and displace competitive subordinates to physically harsh habitats, where abiotic conditions preclude competitive dominance (Bertness and Leonard 1997). In these systems, species distributions are controlled by physiological tolerances to potentially limiting abiotic stresses [rocky shores (Connell 1972); marshes (Pennings and Callaway 1992)], but positive interactions generally expand these boundaries by ameliorating stress intensity (Bertness and Leonard 1997). Thus, physical factors and positive interactions control lower distributional limits in salt marshes (Bertness 1991b; Bertness and Leonard 1997; Castillo et al. 2000), and the upper boundaries in rocky shores (Connell 1972; Bertness and Leonard 1997).

These generalizations, however, are context dependent. Underwood and Denley (1984) suggested that recruitment limitation may often overshadow these generalizations. Underwood (1980) and Cubit (1984) found that herbivores could be more important than physical factors setting the upper distribution limits of algae on rocky shores. Our results show a similar situation in a salt marsh. Crab herbivory became so intense at low tidal heights that only transplants protected from crab herbivory could survive, revealing that *S. densiflora* tolerates more extreme abiotic conditions than its natural distribution shows and that herbivory can set the lower distribution limit of marsh plants.

While our generalizations must be made carefully since we did not replicate these experiments in other marshes, we believe that similar results can be expected for other SW Atlantic salt marshes, as crab herbivory on *Spartina* spp. is extremely common and crab herbivory is typically most intense in the low marsh on the edge of mudflats (Alberti et al. 2007a). It is also important to mention that using transplants can lead to the overestimation of the importance of herbivory, as it was shown that the impact of crab grazing increases as *S. densiflora* patch size decreases (Alberti et al. 2008). Nonetheless, we believe that our results are not artifacts. In another experiment, 1-m^2 *S. densiflora* transplants (more than 100 times larger than ours) moved to the mudflat grew vigorously for more than 2 years inside exclosures, but when the exclosures were removed all died in less than 2 years (E. Fanjul, unpublished data).

In conclusion, our results highlight the importance of nutrients for marsh plants' productivity (Valiela et al. 1976; Dai and Wiegert 1996), and contribute to growing evidence that herbivores can play a major role in controlling the abundance, distribution and productivity of marsh plants (Silliman et al. 2005; Jefferies et al. 2006). Most importantly, our results show that the relative importance of these two mechanisms of control are dependent on environmental context and suggest that herbivores can control the low intertidal distribution and extent of cordgrass on SW Atlantic marshes (plants were able to survive when growing at least 28 cm lower than in their natural distribution, but only in the absence of crab herbivory). Since vegetated marshes provide important ecosystem services including nursery grounds for estuarine nekton (Rozas and Minello 1998), biochemical filtering that diminishes nutrients and pollutants (Bertness et al. 2004), and shoreline buffers to erosion and storm damage (Pennings and Bertness 2001), limiting the abundance and distribution of cordgrass crabs could affect coastal ecosystem functioning.

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