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Cordgrass canopy elicits weak effects on sediment properties and microphytobenthic abundance in a harsh environment

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ABSTRACT: The magnitude of the outcome of ecosystem engineering is context-dependent; as environmental stresses increase, habitat amelioration by ecosystem engineers becomes more relevant. Moreover, the individual- and population-level traits of ecosystem engineers can affect their ability to reduce environmental stress. On the Patagonian shores of Argentina (SW Atlantic, 41° S), the intertidal community is exposed to harsh conditions. We predicted that in this severe environment, variation in the above-ground structure of the smooth cordgrass *Spartina alterniflora* should buffer the physical stress on the substrate through shading and reduction of wind and water flow energy, ultimately affecting the sediment properties and microphytobenthic biomass. To test this hypothesis, we experimentally manipulated cordgrass density at the edge and inner marsh of a *S. alterniflora* meadow during both summer and winter. In summer, evaporation and temperature were higher in clipped plots, while in winter, evaporation varied across densities and location treatments, with higher sediment water content in the inner marsh. No effect of *S. alterniflora* density or location were observed on sediment organic matter or chl *a* concentration, and mean sediment grain size was always smaller inside the marsh. In summer, extracellular polymeric substance (EPS) content was higher in clipped plots inside the marsh, however this did not differ from the other density treatments at this location. Overall, shading had weak effects on sediment properties and microphytobenthic biomass, and most observed differences were attributable to grain size. We speculate that the harsh conditions of this system overwhelm the ecosystem engineering effects of *S. alterniflora*, probably because of its relatively small above-ground biomass.

KEY WORDS: Ecosystem engineering · Environmental stress · Patagonia · Salt marsh · *Spartina*

INTRODUCTION

Empirical evidence has established that biotic modification of the environment, in particular ecosystem engineering, is a widespread, non-trophic interaction, with both basic and applied relevance to the understanding of ecological communities (Jones et al. 2010, Linder et al. 2012). There is general agreement that the magnitude of the outcome of ecosystem engineering is context-dependent and

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will vary with the background environment, the limiting resources, and the ecosystem functions of interest. However, there is uncertainty about the conditions and extent to which these engineers can impact community and ecosystem processes (Crain & Bertness 2006, Wright & Jones 2006). Renewed interest in the outcomes of species interactions and their dependence on context and species traits has broadened our understanding of community organization, and improved our ability to predict community changes under different scenarios of climate change (Bulleri et al. 2014, Chamberlain et al. 2014).

Benthic ecosystem engineers such as seagrasses, macroalgae, reef-building filter feeders and cordgrasses are conspicuous in many coastal systems (e.g. Bouma et al. 2009). In salt marshes, species of the cordgrass genus *Spartina* spp. are considered important ecosystem engineers, and their effects on the local environment and community have been well documented (e.g. Bouma et al. 2005). Dense, monospecific stands of *Spartina* sp. reduce water velocity and turbulence, promoting the deposition of fine-grained, organic-rich particles (Leonard & Croft 2006). This increased sedimentation rate triggers changes in sediment characteristics which may lead to a reduction in macrofaunal densities and a shift in species composition (Neira et al. 2006). *Spartina* spp. plays a fundamental role in community organization by attenuating the energy of waves and stabilizing cobble sediments (Bruno 2000, Altieri et al. 2007). The *Spartina* canopy also reduces light intensity as stem density increases, buffering temperature stress on the substrate, soil hardness and dehydration (Bortolus et al. 2002, Lambrinos & Bando 2008), which can have a considerable effect on benthic microalgal communities, particularly in arid climates (Pinckney & Zingmark 1993, Whitcraft & Levin 2007). Moreover, the inhibition of microphytobenthos growth induced by shading has been proposed as a major mechanism for the reduction of epifaunal abundance under the *Spartina* canopy (see da Cunha Lana & Guiss 1992, Cutajar et al. 2012).

In salt marshes, benthic microalgae are ubiquitous in sediments both directly exposed to full sunlight and shaded by a vascular plant canopy (Sullivan & Currin 2000). This benthic microalgal community, which occupies the upper few millimetres of sediments and often forms dense mats or biofilms, is one of the most important primary producers in this system (Underwood 2010). The biofilms contribute to sediment stability through the production of extracellular polymeric substances (EPS), which form a sediment-binding mucus that affects motility, desiccation resistance, mediation of extracellular exchange and photosynthetic overflow (see Bellinger et al. 2005). During tidal emersion, microphytobenthic biofilms are exposed to high temperatures and irradiances, which can affect primary productivity as well as the production of EPS (Perkins et al. 2001). Shading by the vascular plant canopy appears to alter biomass production and controls the microphytobenthic composition (Sakamaki & Richardson 2009, Park et al. 2013).

Theory predicts that the impact and importance of ecosystem engineers will vary along gradients of physical stress. As environmental stress increases, habitat amelioration by engineers becomes more important, promoting high species diversity and abundance (Crain & Bertness 2006, Silliman et al. 2011). However, in some cases environmental stress may also affect the engineer. For instance, at a local scale, productivity of the smooth cordgrass *Spartina alterniflora* seems to be positively associated with higher amounts of precipitation (Morris & Haskin 1990), probably because this species develops better when exposed to freshwater input (Crain et al. 2004). In North American salt marshes, *S. alterniflora* productivity is also controlled by temperature and/or the length of the growing season along a latitudinal gradient (Kirwan et al. 2009). Furthermore, in Northern Patagonia salt marshes, *S. alterniflora* densities and heights are relatively low (80 stems m^{-2}, 25 cm tall; Daleo et al. 2009), and it has been experimentally demonstrated that climatic conditions can severely affect its performance at the southernmost limit of its distribution (Idaszkin & Bortolus 2011). However, most studies on *Spartina* spp. engineering come from North American coasts, where plants are generally taller and densities are higher. For instance, stem density varies from 150–270 stems m^{-2} and height ranges from 15–118 cm North Carolina (35° N; Leonard & Croft 2006), to 245–570 stems m^{-2} in Chesapeake Bay (37° N; Long & Burke 2007) and 530 stems m^{-2} and 75–90 cm height in Rhode Island (41° N; Irving & Bertness 2009). This is particularly relevant since trait variation of the engineer (e.g. size, height, density, biomass) can affect the degree of amelioration of environmental stress and may therefore substantially modify the strength of positive interactions (Bruno & Kennedy 2000, Firstater et al. 2011). Some previous studies have experimentally examined the interaction between *Spartina* spp. and the microphytobenthic community, but experiments in harsh environments are still lacking.

Exposure to highly variable and often extreme conditions (e.g. UV radiation, desiccation, changes in temperature, salinity and hydrodynamic forces) can regulate the structure and functioning of the microphytobenthic community (Van Colen et al. 2014). On Argentinean Patagonian shores, dry trade winds and low amounts of rainfall cause high desiccation rates, producing extremely harsh conditions for the intertidal community (Bertness et al. 2006, Bazterrica et al. 2007). We therefore predicted that in this severe environment, variation in the aboveground structure of *S. alterniflora* should alter the buffering effects of the physical stress acting on the substrate through shading and reduction of wind and water flow energy, ultimately affecting the sediment properties and microphytobenthic community. To test this hypothesis, we performed an experiment in a northern Patagonian salt marsh (40° S), in which we manipulated *S. alterniflora* stem density. The climatic conditions in Patagonia vary considerably throughout the year; since this variation could alter the strength of the effects of ecosystem engineering (see Gutierrez et al. 2011), we replicated the experiment in both summer and winter.

MATERIALS AND METHODS

Study site

Experiments were performed in San Antonio Bay, northern Patagonia (Argentina; 40° 46′ S, 64° 54′ W). This 80 km^2 embayment is affected by a semidiurnal tidal regime (up to 9 m tidal amplitude), while the combination of low annual rainfall (~250 mm yr^{-1}) and absence of freshwater inflows to the Bay produce a hypersaline environment (Daleo et al. 2005, Garcia et al. 2010). The intertidal zone is characterized by extensive sandy pebble flats at lower tidal elevations, whereas at higher tidal elevations the smooth cordgrass *Spartina alterniflora* dominates the salt marsh, which covers ~2068 ha (Daleo et al. 2006, Isacch et al. 2006). This salt marsh is located close to the austral limit of *S. alterniflora* distribution (~42° S; Idaszkin & Bortolus 2011). Mean annual air temperature is 15.1°C, and extreme temperatures occur in July (austral winter; −7.7°C) and February (austral summer; 41.4°C). Relative humidity is 57 %, and mean annual wind speed is 18 km h^{-1}, reaching an average of 25 km h^{-1} in spring/summer (Lucas et al. 2005, Gonzalez et al. 2010, Genchi et al. 2011).

Aboveground structure of *S. alterniflora*

In November 2010, 20 plots (0.25 × 0.25 m) were randomly selected along the lower marsh edge. In 10 of those plots the number of stems were counted; in the other 10, average stem height (n = 5) was recorded. We followed the same procedure in another 20 plots, located 10 m inside the *Spartina* meadow. Differences in stem density and height between locations were examined with Student's *t*-tests.

Experiment

To test the effects of aboveground structure of *S. alterniflora* on sediment features and the abundance of benthic microalgae, we performed an experiment replicated during the austral summer (from November 2010 to February 2011) and winter (from May to July 2011). Since changes in sediment characteristics produced by *S. alterniflora* appear to be related to distance to the meadow edge (Neira et al. 2006), we established 33 plots (1.5 × 1.5 m) in the lower marsh edge and 33 parallel plots 10 m inside the *S. alterniflora* marsh (hereafter referred to as edge and interior, respectively). Plots were assigned to each of 3 treatments: (1) *S. alterniflora* removal (S–), where stems were clipped to ground level without disturbing the sediment; (2) density enhancement (S+), where stem density was augmented by 50 % by adding plastic stem mimics; and (3) control (C), where density was undisturbed. *Spartina*-like plant mimics were made with plastic cable ties (30 cm long × 0.5 cm wide) driven 4 to 10 cm into the ground. These mimics proved to be similar in stiffness to *Spartina* spp. stems and have been successfully used to study stem biomechanical effects on hydrodynamics (see Bouma et al. 2005, Peralta et al. 2008).

Over the course of the experiment, we measured plot evaporation rate by placing a cylindrical plastic container filled with 50 ml of water (evaporation surface: 26.6 cm^2) in the center of 10 plots of each treatment (5 at each location) during low tide. Containers were collected just before incoming tide and the final volume was measured. Evaporation was expressed as volume of water loss per hour (ml h^{-1}). We also measured sediment surface temperature of all plots with a portable temperature probe. Both measurements were replicated on 3 d during each season; there was no difference among days, so data were pooled for analysis.

At the end of the experiments (109 d in summer and 117 d in winter), we collected 2 sediment cores (10 cm diameter, 3 cm deep) from each plot to measure water content (WC), organic matter content (OMC) and sediment grain size; 2 other sediment cores (2.7 cm diameter, 1 cm deep) were collected to analyze chl *a* and EPS content. Samples were frozen and stored at −20°C until analysis.

WC in the sediment was determined by weight loss after oven drying (70°C, 72 h), and a subsample was analyzed for total OMC by calcination (500°C, 5 h). Sediment grain size distribution was estimated by dry sieving (Folk 1974), and grain size was expressed as phi (ϕ; Folk & Ward 1957). Sediment pigments were extracted in 90% acetone, and chl *a* biomass, an indicator of total microalgal load (e.g. Cartaxana et al. 2006), was measured spectrophotometrically in accordance with Lorenzen (1967).

Colloidal-EPS and carbohydrate fractions (sensu Smith & Underwood 1998) were determined in the top 1 cm of sediment. The samples were weighed, mixed with 35 ml of saline (25‰), and extracted twice at 20°C for 15 min. Samples were centrifuged at 3500 × *g* for 15 min after extractions, and both supernatants containing colloidal-S carbohydrate fraction were combined (Underwood et al. 1995). Colloidal-S carbohydrate fraction was measured in 1 ml of supernatant as glucose equivalents by the phenol-sulfuric assay using a D-Glucose standard curve (Dubois et al. 1956). Colloidal-S fraction of EPS (Colloidal-EPS) was extracted from another 10 ml of supernatant by cold (4°C) overnight precipitation with 70% ethanol (final concentration; Underwood et al. 1995). Samples were centrifuged at 3500 × *g* for 25 min, the supernatant was discarded and the remaining pellet was re-dissolved in saline (25‰) solution to measure carbohydrate content. The phenol-sulfuric assay was used to determine the concentration of carbohydrate present as glucose equivalents (Dubois et al. 1956).

Differences in sediment characteristics, chl *a* and EPS content were analyzed with 2-way ANOVAs, with location (edge and interior) and density treatment as main, fixed factors (Zar 1999). Summer temperature was the only dataset with heterogeneous variances (determined by Levene's tests). Variances could not be stabilized after different transformations; therefore analyses were done on untransformed data, but with a more conservative significance level ($\alpha = 0.01$) given the increased likelihood of a Type I error (Blockley & Chapman 2006). The assumption of normality was checked by visual inspection of residual plots.

RESULTS

Aboveground structure of *Spartina alterniflora*

The height and density of *Spartina alterniflora* stems were similar both at the edge and in the interior of the marsh (height: $t = 0.7$, df = 18, $p = 0.49$; density: $t = -0.31$, df = 18, $p = 0.76$). Total mean (±SD) height was 22.3 ± 1.3 cm and mean density was 355 ± 111 stems m^{-2}.

Experiment

Evaporation was higher in S– plots during the summer (Table 1, Fig. 1), but in winter the treatment ×

Table 1. Two-way ANOVAs on sediment properties and microphytobenthic biomass for the summer experiment, with *Spartina alterniflora* density treatment and location as main factors. *Significant at $p < 0.05$ ($p < 0.01$ for temperature). EPS: extracellular polymeric substances

Source	df	SS	MS	*F*	p
Evaporation rate					
Treatment	2	5.66	2.83	8.36	<0.001*
Location	1	0.26	0.26	0.77	0.38
Treatment × Location	2	0.01	0.006	0.02	0.98
Error	84	28.4	0.34		
Temperature					
Treatment	2	290.4	145.2	13.28	<0.001*
Location	1	0.2	0.2	0.02	0.89
Treatment × Location	2	14.5	7.3	0.66	0.51
Error	192	2098.5	10.9		
Water content					
Treatment	2	3.6	1.8	0.48	0.61
Location	1	2.61	2.61	0.7	0.4
Treatment × Location	2	1.01	0.5	0.13	0.87
Error	60	223.43	3.72		
Organic matter content					
Treatment	2	0	0	0.03	0.97
Location	1	0.02	0.02	1.56	0.22
Treatment × Location	2	0.01	0	0.46	0.63
Error	60	0.96	0.02		
Mean grain size					
Treatment	2	0	0	0.03	0.96
Location	1	0.81	0.81	8.59	0.004*
Treatment × Location	2	0.16	0.08	0.86	0.42
Error	60	5.68	0.09		
Chl *a* concentration					
Treatment	2	0.2	0.1	0.32	0.72
Location	1	0.03	0.03	0.1	0.74
Treatment × Location	2	1.13	0.56	1.81	0.17
Error	60	18.73	0.31		
EPS content					
Treatment	2	0.09	0.04	1.06	0.35
Location	1	0.71	0.71	17.49	<0.001*
Treatment × Location	6	0.28	0.14	3.45	0.03*
Error	60	2.43	0.04		

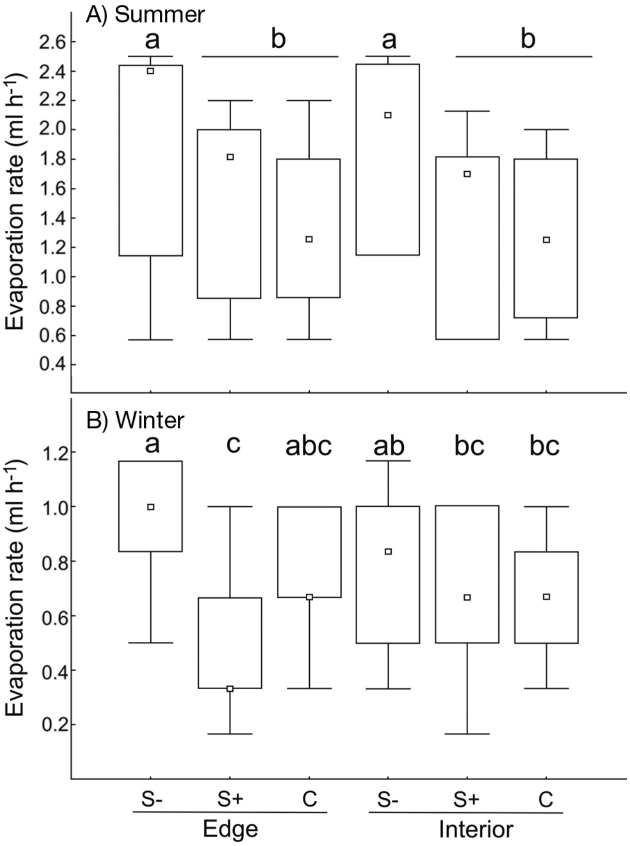

Fig. 1. Evaporation rate (median; box: 25th to 75th percentiles; whiskers: 5th to 95th percentiles) in *Spartina alterniflora* clipped plots (S–), plots with enhanced stem density (S+) and controls (C) during (A) summer and (B) winter. Different lowercase letters denote significant differences; note different *y*-axis scales

location interaction was significant (Table 2). We found the highest evaporation rate in S– plots; C plots at the edge, along with S+ and C in the interior had intermediate levels of evaporation, and the lowest evaporation rates were registered in S+ edge plots (Tukey's HSD test; see Fig. 1). We also found that during summer, sediment temperature was higher in the surface of S– plots (Table 1), whereas there was no difference in sediment temperature during winter (see Table 2, Fig. 2).

There was no difference in WC among plots in summer (Table 1), however in winter WC was higher in plots located in the interior (Table 2, Fig. 3). Regarding the OMC of the sediments, there was no difference among plots in summer (Table 1) or winter (Table 2, Fig. 4). Nevertheless, during both seasons mean grain size of plots located in the interior of the marsh was lower than at the edge (Tables 1 & 2, Fig. 5).

We observed similar chl *a* concentrations in all plots during both seasons (Tables 1 & 2, Fig. 6), but for EPS content the treatment × location interaction was significant in summer (Table 1). The highest colloidal-EPS content was observed in S– plots in the interior, and the lowest in plots located at the edge; S+ and C plots from the interior showed intermediate colloidal-EPS contents (Tukey's HSD test). We found no differences in colloidal-EPS content during winter (Table 2, Fig. 7).

DISCUSSION

In physically harsh habitats, slight alterations in physical parameters can create hospitable habitats for organisms that would otherwise have been unable to tolerate such limiting physical conditions (Crain & Bertness 2006). In Argentinean Patagonia, salt marshes

Table 2. Two-way ANOVAs on sediment properties and microphytobenthic biomass for the winter experiment, with *Spartina alterniflora* density treatment and location as main factors. *p < 0.05. EPS: extracellular polymeric substances

Source	df	SS	MS	*F*	p
Evaporation rate					
Treatment	2	1.09	0.54	10.72	<0.001*
Location	1	0.01	0.01	0.21	0.64
Treatment × Location	2	0.35	0.17	3.98	0.02*
Error	84	4.26	0.05		
Temperature					
Treatment	2	82.25	41.13	2.43	0.09
Location	1	0.28	0.28	0.02	0.9
Treatment × Location	2	0.4	0.2	0.01	0.99
Error	192	3245.02	16.9		
Water content					
Treatment	2	1.79	0.9	0.13	0.88
Location	1	35.78	35.78	5.11	0.02*
Treatment × Location	2	5.06	2.53	0.36	0.7
Error	60	420.17	7		
Organic matter content					
Treatment	2	0.01	0	0.2	0.81
Location	1	0.06	0.06	1.97	0.16
Treatment × Location	2	0.1	0.05	1.58	0.21
Error	60	2	0.03		
Mean grain size					
Treatment	2	0.08	0.04	0.04	0.96
Location	1	9.97	9.97	4.92	0.03*
Treatment × Location	2	2.11	1.05	0.99	0.38
Error	60	63.76	1.06		
Chl *a* concentration					
Treatment	2	1.46	0.73	1.94	0.15
Location	1	0	0	0	0.95
Treatment × Location	2	0.62	0.31	0.82	0.44
Error	60	22.53	0.37		
EPS content					
Treatment	2	0.08	0.04	1.88	0.16
Location	1	0	0	0.02	0.89
Treatment × Location	6	0.08	0.04	1.85	0.16
Error	60	1.29	0.02		

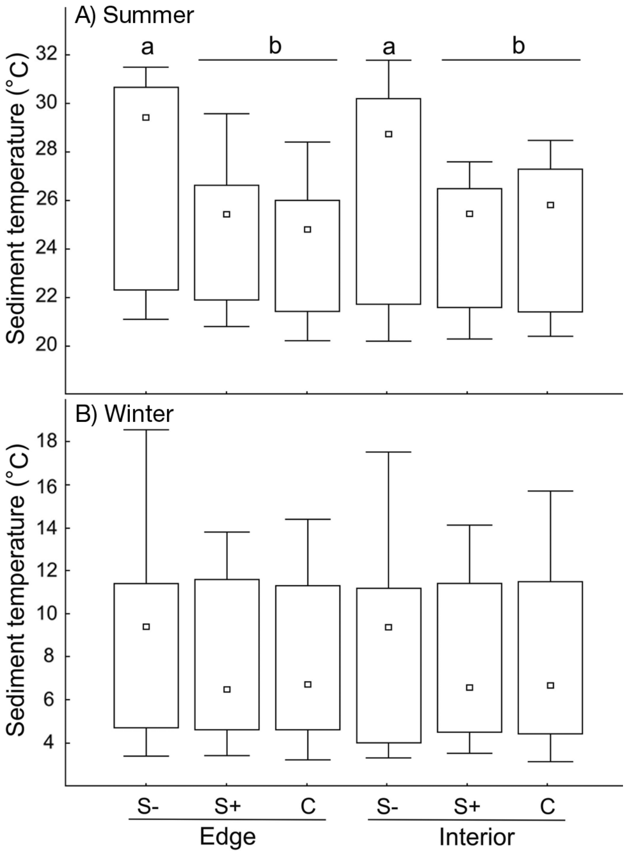

Fig. 2. Sediment temperature (median; box: 25th to 75th percentiles; whiskers: 5th to 95th percentiles) in *Spartina alterniflora* clipped plots (S−), plots with enhanced stem density (S+) and controls (C) during (A) summer and (B) winter. Different lowercase letters denote significant differences; note different *y*-axis scales

are exposed to relatively severe environmental conditions. However, our experimental manipulation of *Spartina alterniflora* density had little impact on sediment properties or on the microphytobenthic biomass.

While stem heights and densities were greater than previously reported for this area (Daleo et al. 2009), we found that *S. alterniflora* was short and moderately dense, with a stem density and height range in the lowest limits of other studies of *S. alterniflora* engineering (Leonard & Croft 2006, Long & Burke 2007, Irving & Bertness 2009). As expected, evaporation and temperature were higher in clipped plots during the summer. In winter this pattern disappeared; the evaporation rate in clipped plots matched that of controls and temperature did not differ between plots. Previous studies on macrophytes in salt marshes have shown that both live and plant-mimic canopies buffer high temperatures, dehydration and soil hardness (see Bortolus et al. 2002, Lambrinos & Bando 2008). Our results showed that in summer, when heat and radiant energy were highest, the temperature increased on the sediment surface, increasing the evaporation rate, while in winter, abiotic factors other than irradiation seem to control sediment de-watering. Such factors (i.e. wind velocity or air moisture) seem not to be buffered by the *S. alterniflora* canopy.

The differences in evaporation and temperature among treatments were not reflected in sediment WC, which was higher in all plots of the marsh interior in winter, regardless of the treatment. In general, fine sediment contains more water than coarse sediment, likely because of its lower rate of de-watering (see Perkins et al. 2003, Cartaxana et al. 2006). Here, the relatively finer sediment in the marsh interior retained more water in winter when evaporation was low, while the harsher conditions in summer entailed higher de-watering rates regardless of grain size, reducing water content to less than half of the winter amount.

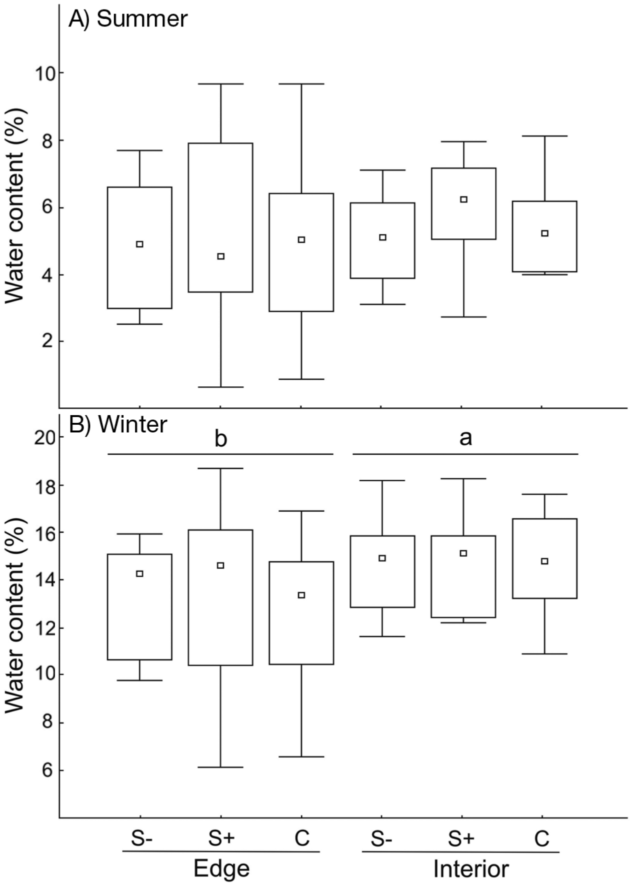

Fig. 3. Water content (median; box: 25th to 75th percentiles; whiskers: 5th to 95th percentiles) in *Spartina alterniflora* clipped plots (S−), plots with enhanced stem density (S+) and controls (C) during (A) summer and (B) winter. Different lowercase letters denote significant differences; note different *y*-axis scales

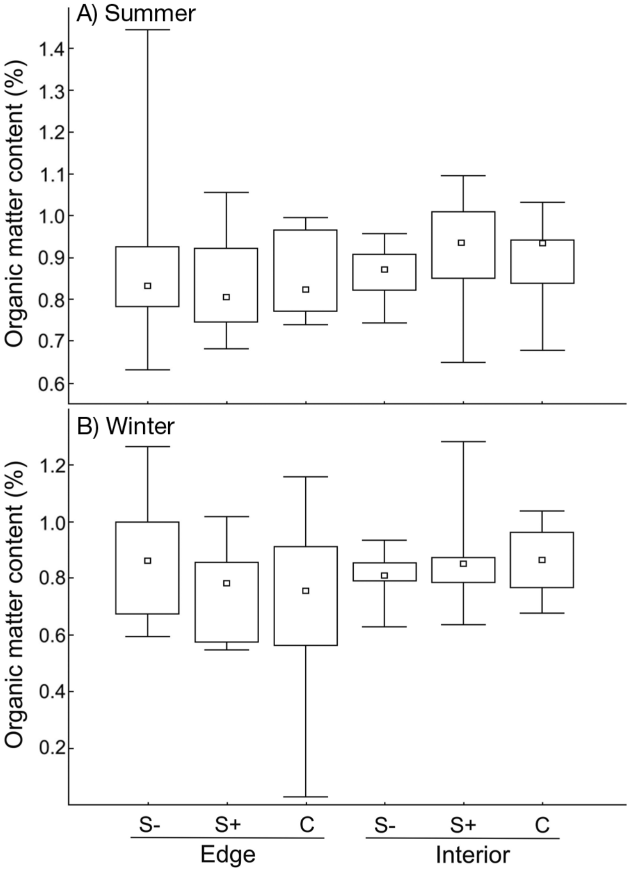

Fig. 4. Organic matter content (median; box: 25th to 75th percentiles; whiskers: 5th to 95th percentiles) in *Spartina alterniflora* clipped plots (S–), plots with enhanced stem density (S+) and controls (C) during (A) summer and (B) winter

The sediment in our study area consisted of medium and coarse sand, but as mentioned above, mean grain size was always lower in the interior of the marsh than at the edge. This pattern has been well-described and seems to be widespread. In general, in tide-dominated systems, sediments tend to become finer towards the land (see Yang et al. 2008). Moreover, the presence of vegetation considerably attenuates hydrodynamics, inducing the deposition and trapping of fine-grained suspended sediment (e.g. Bouma et al. 2005, Yang et al. 2008). Sediment type is one of the main factors involved in the control of microphytobenthic abundance in salt marshes, where lower microalgal biomass is usually found on non-cohesive silts and sands compared to that on fine cohesive sediments (Perkins et al. 2003, Coelho et al. 2009). Sands tend to have lower nutrient concentrations and are more frequently resuspended (Underwood 2010). The overall low microalgal biomass found at San Antonio Bay may therefore be a consequence of the relatively large grain size observed in this salt marsh.

Previous studies have shown that by controlling the amount of light reaching the sediment surface, canopy forming plants can influence microphytobenthic biomass and taxonomic diversity (e.g. Sullivan 1981, Whitcraft & Levin 2007). Surprisingly, we found no differences in microalgal biomass between clipped and shaded plots. Simplified mimics of *Spartina* have proven to be useful for examining the effects of shoot density and stiffness on hydrodynamic forces in other studies (Bouma et al. 2005, Peralta et al. 2008), but since we did not measure irradiance under the canopy, it is possible that light was not effectively attenuated by increasing stem density. However, biotic interactions may explain the similar microphytobenthic biomass observed at control, clipped and shaded plots. For instance, studies on invasive *Spartina* in California, USA, reported higher diversities and densities of invertebrates in the sediments of unvegetated tidal flats relative to *Spartina* patches (Neira et al. 2006), while in the latter there was a

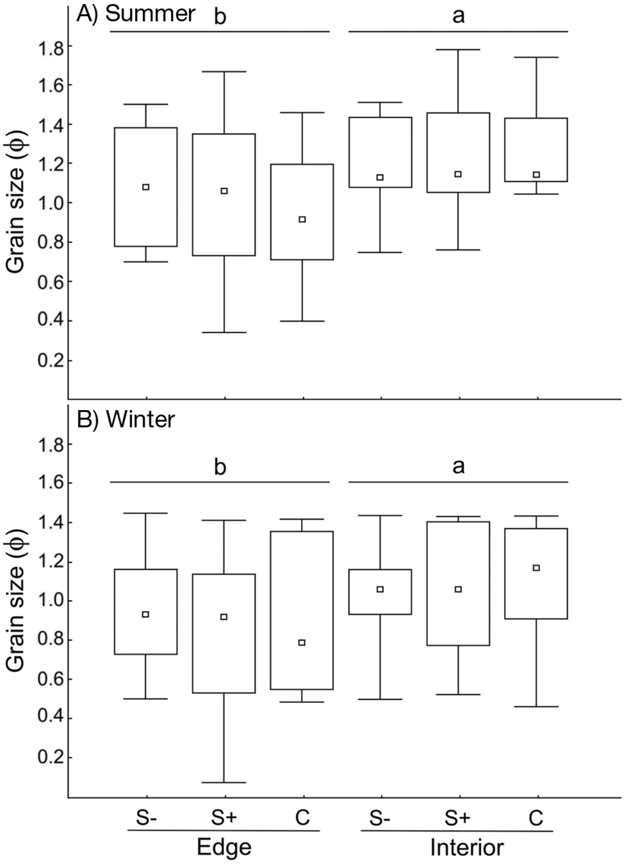

Fig. 5. Mean grain size (median; box: 25th to 75th percentiles; whiskers: 5th to 95th percentiles) in *Spartina alterniflora* clipped plots (S–), plots with enhanced stem density (S+) and controls (C) during (A) summer and (B) winter. Different lowercase letters denote significant differences

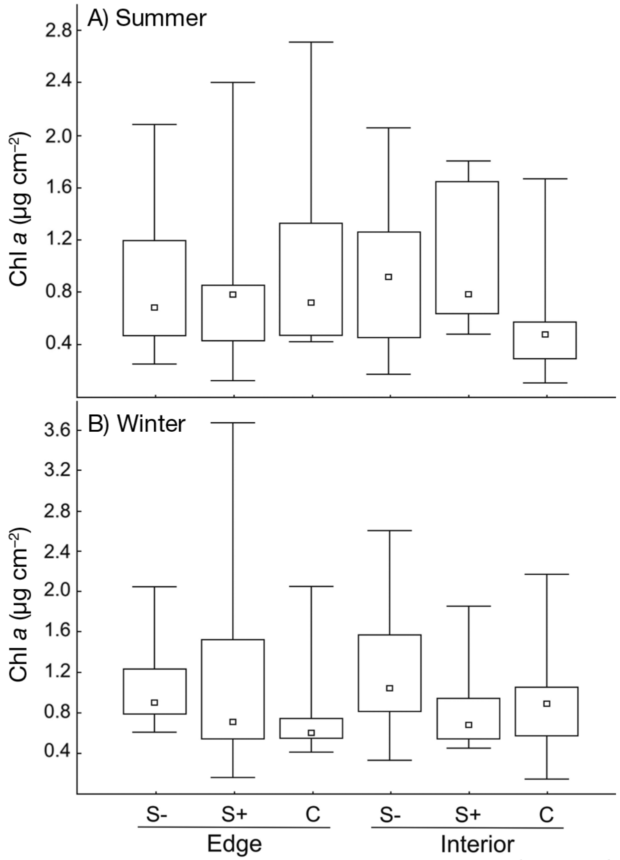

Fig. 6. Chl *a* concentration (median; box: 25th to 75th percentiles; whiskers: 5th to 95th percentiles) in *Spartina alterniflora* clipped plots (S–), plots with enhanced stem density (S+) and controls (C) during (A) summer and (B) winter

trophic shift from an algal-based to a detritus-based food web, likely as a result of bottom-up processes related to the decreased availability of algae and increase in detritus (Levin et al. 2006). Grazing pressure, possibly due to different abundances of amphipods and snails, may thus be more intense in exposed areas, balancing the positive effects of light availability on microphytobenthic biomass. Moreover, since we did not study taxonomic composition, we may have missed possible changes in the microalgal assemblage produced by shading (Defew et al. 2004, Whitcraft & Levin 2007).

Unlike microalgal biomass, we found that EPS concentration varied in summer, when concentrations were higher inside the meadow at clipped plots. In many soft sediment intertidal zones, microalgal biomass (i.e. chl *a*) is closely correlated with the concentration of colloidal-EPS (see Bellinger et al. 2005); this is particularly true for cohesive sediments (Underwood & Smith 1998). Moreover, the concentration of EPS depends on both light and sediment grain size. EPS production is coupled with photosynthesis, which is stimulated by light and is higher in fine sediment than in coarser sediment (de Brouwer & Stal 2001, Stal 2010). In our experiment, the clipped plots in the marsh interior had these conditions. However, since higher light availability did not enhance EPS at the edge of the marsh, it seems that grain size rather than shading by macrophytes is the main driving factor affecting EPS content.

According to the hypothesis of increasing importance of ecosystem engineering at higher levels of environmental stress (Crain & Bertness 2006), salt marsh plants are predicted to have strong effects on benthic ecosystems in arid regions (Whitcraft & Levin 2007). However, we found that in northern Patagonia, shading by plants has only a minor effect on sediment features and benthic microalgae biomass. Since changes in some sediment properties can take several years to accumulate (see Craft et al. 2003), longer-term studies are needed. We speculate that the harsh conditions of this system overwhelm the

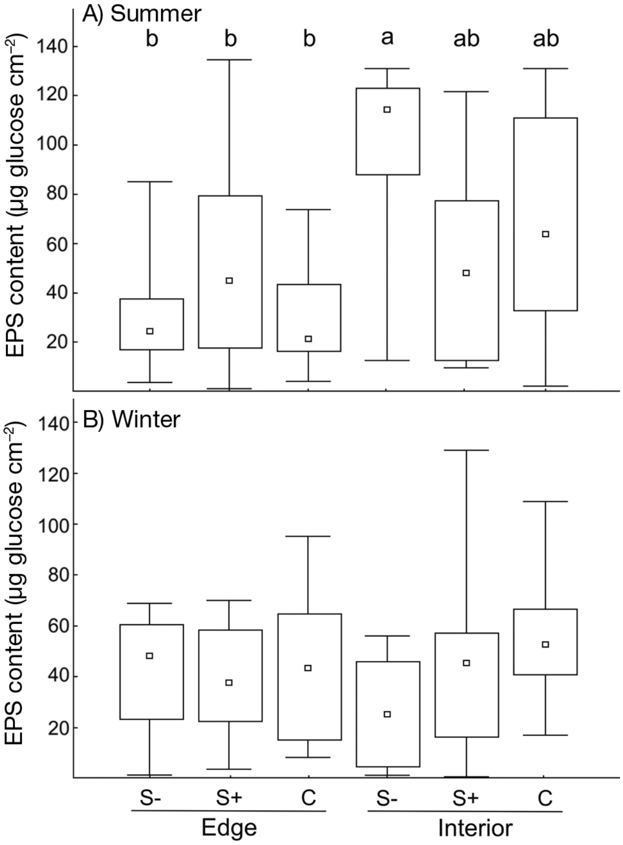

Fig. 7. Extracellular polymeric substance (EPS) content (median; box: 25th to 75th percentiles; whiskers: 5th to 95th percentiles) in *Spartina alterniflora* clipped plots (S–), plots with enhanced stem density (S+) and controls (C) during (A) summer and (B) winter. Different lowercase letters denote significant differences

engineering effects of *Spartina*, likely because of its relatively small aboveground biomass. This study represents a contribution towards a greater understanding of ecosystem engineering in harsh environments, and is relevant to improving our ability to predict community changes.

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LITERATURE CITED

Altieri AH, Silliman BR, Bertness MD (2007) Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. Am Nat 169:195–206

Bazterrica MC, Silliman BR, Hidalgo FJ, Crain CM, Bertness MD (2007) Limpet grazing on a physically stressful Patagonian rocky shore. J Exp Mar Biol Ecol 353:22–34

Bellinger BJ, Abdullahi AS, Gretz MR, Underwood GJC (2005) Biofilm polymers: relationship between carbohydrate biopolymers from estuarine mudflats and unialgal cultures of benthic diatoms. Aquat Microb Ecol 38: 169–180

Bertness MD, Crain CM, Silliman BR, Bazterrica MC, Reyna MV, Hildago F, Farina JK (2006) The community structure of western Atlantic Patagonian rocky shores. Ecol Monogr 76:439–460

Blockley DJ, Chapman MG (2006) Recruitment determines differences between assemblages on shaded or unshaded seawalls. Mar Ecol Prog Ser 327:27–36

Bortolus A, Schwindt E, Iribarne O (2002) Positive plant-animal interactions in the high marsh of an Argentinean coastal lagoon. Ecology 83:733–742

Bouma TJ, de Vries MB, Low E, Peralta G, Tánczos IC, van de Koppel J, Herman PMJ (2005) Trade-offs related to ecosystem engineering: a case study on stiffness of emerging macrophytes. Ecology 86:2187–2199

Bouma TJ, Olenin S, Reise K, Ysebaert T (2009) Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. Helgol Mar Res 63:95–106

Bruno JF (2000) Facilitation of cobble beach plant communities through habitat modification by *Spartina alterniflora.* Ecology 81:1179–1192

Bruno JF, Kennedy CW (2000) Patch-size dependent habitat modification and facilitation on New England cobble beaches by *Spartina alterniflora*. Oecologia 122:98–108

Bulleri F, Xiao S, Maggi E, Benedetti-Cecchi L (2014) Intensity and temporal variability as components of stress gradients: implications for the balance between competition and facilitation. Oikos 123:47–55

Cartaxana P, Mendes CR, van Leeuwe MA, Brotas V (2006) Comparative study on microphytobenthic pigments of muddy and sandy intertidal sediments of the Tagus estuary. Estuar Coast Shelf Sci 66:225–230

Chamberlain SA, Bronstein JL, Rudgers JA (2014) How context dependent are species interactions? Ecol Lett 17: 881–890

Coelho H, Vieira S, Serodio J (2009) Effects of desiccation on the photosynthetic activity of intertidal microphytobenthos biofilms as studied by optical methods. J Exp Mar Biol Ecol 381:98–104

Craft C, Megonigal P, Broome S, Stevenson J and others (2003) The pace of ecosystem development of constructed *Spartina alterniflora* marshes. Ecol Appl 13: 1417–1432

Crain CM, Bertness MD (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. Bioscience 56:211–218

Crain CM, Silliman BR, Bertness SL, Bertness MD (2004) Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology 85:2539–2549

Cutajar J, Shimeta J, Nugegoda D (2012) Impacts of the invasive grass *Spartina anglica* on benthic macrofaunal assemblages in a temperate Australian saltmarsh. Mar Ecol Prog Ser 464:107–120

da Cunha Lana PC, Guiss C (1992) Macrofauna–plant-biomass interactions in a euhaline salt marsh in Paranaguá Bay (SE Brazil). Mar Ecol Prog Ser 80:57–64

Daleo P, Escapa M, Isacch JP, Ribeiro P, Iribarne O (2005) Trophic facilitation by the oystercatcher *Haematopus palliatus* Temminick on the scavenger snail *Buccinanops globulosum* Kiener in a Patagonian bay. J Exp Mar Biol Ecol 325:27–34

Daleo P, Escapa M, Alberti J, Iribarne O (2006) Negative effects of an autogenic ecosystem engineer: interactions between coralline turf and an ephemeral green alga. Mar Ecol Prog Ser 315:67–73

Daleo P, Silliman B, Alberti J, Escapa M, Canepuccia A, Peña N, Iribarne O (2009) Grazer facilitation of fungal infection and the control of plant growth in southwestern Atlantic salt marshes. J Ecol 97:781–787

de Brouwer JFC, Stal LJ (2001) Short-term dynamics in microphytobenthos distribution and associated extracellular carbohydrates in surface sediments of an intertidal mudflat. Mar Ecol Prog Ser 218:33–44

Defew EC, Perkins RG, Paterson DM (2004) The influence of light and temperature interactions on a natural estuarine microphytobenthic assemblage. Biofilms 1:21–30

Dubois M, Gilles KA, Hamilton JK, Rebers PA, Smith F (1956) Colorimetric method for determination of sugars and related substances. Anal Chem 28:350–356

Firstater FN, Hidalgo FJ, Lomovasky BJ, Ramos E, Gamero P, Iribarne OO (2011) Habitat structure is more important than nutrient supply in modifying mussel bed assemblage in an upwelling area of the Peruvian coast. Helgol Mar Res 65:187–196

Folk RL (1974) Petrology of sedimentary rocks. Hemphill Publishing, Austin, TX

Folk RL, Ward WC (1957) Brazos River bar: a study in the significance of grain size parameters. J Sediment Res 27: 3–26

Garcia GO, Isacch JP, Gomez Laich A, Albano M and others (2010) Foraging behavior and diet of American oystercatchers in a Patagonian intertidal area affected by nutrient loading. Emu 110:146–154

Genchi SA, Carbone ME, Piccolo MC, Perillo GME (2011) Hydrologic response of the drainage basins that intersect Las Grutas town, Argentina. Investig Geogr 75:23–36

Gonzalez R, Narvarte M, Verona C (2010) Principios, lineamientos generales y procedimientos para la elaboracion, adopcion, implementacion, evaluacion y revision de los Planes de Manejo Ecosistemico para la pesca maritima de captura en el Golfo San Matias. ECOPES (Iniciativa para un Ecosistema Pesquero Sustentable). Instituto de Biología Marina y Pesquera Almirante Storni, Universidad Nacional del Comahue, San Antonio Oeste

Gutierrez JL, Jones CG, Byers JE, Arkema KK and others (2011) Physical ecosystem engineers and the functioning of estuaries and coasts. In: Heip CHR, Philippart CJM, Middelburg JJ (eds) Treatise on estuarine and coastal science, Vol 7. Functioning of ecosystems at the land-ocean interface. Academic Press, London, p 53–81

Idaszkin YL, Bortolus A (2011) Does low temperature prevent *Spartina alterniflora* from expanding toward the austral-most salt marshes? Plant Ecol 212:553–561

Irving AD, Bertness MD (2009) Trait-dependent modification of facilitation on cobble beaches. Ecology 90: 3042–3050

Isacch JP, Costa CSB, Rodriguez-Gallego L, Conde D, Escapa M, Gagliardini DA, Iribarne OO (2006) Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. J Biogeogr 33:888–900

Jones CG, Gutiérrez JL, Byers JE, Crooks JA, Lambrinos JG, Talley TS (2010) A framework for understanding physical ecosystem engineering by organisms. Oikos 119: 1862–1869

Kirwan ML, Guntenspergen GR, Morris JT (2009) Latitudinal trends in *Spartina alterniflora* productivity and the response of coastal marshes to global change. Glob Change Biol 15:1982–1989

Lambrinos JG, Bando KJ (2008) Habitat modification inhibits conspecific seedling recruitment in populations of an invasive ecosystem engineer. Biol Invasions 10: 729–741

Leonard LA, Croft AL (2006) The effect of standing biomass on flow velocity and turbulence in *Spartina alterniflora* canopies. Estuar Coast Shelf Sci 69:325–336

Levin LA, Neira C, Grosholz ED (2006) Invasive cordgrass modifies wetland trophic function. Ecology 87:419–432

Linder HP, Bykova O, Dyke J, Etienne RS and others (2012) Biotic modifiers, environmental modulation and species distribution models. J Biogeogr 39:2179–2190

Long WC, Burke RP (2007) Habitat size, flora, and fauna: interactions in a tidal saltwater marsh. J Exp Mar Biol Ecol 353:80–88

Lorenzen CJ (1967) Determination of chlorophyll and pheopigments: spectrophotometric equations. Limnol Oceanogr 12:343–346

Lucas AJ, Guerrero RA, Mianzan HW, Acha EM, Lasta CA (2005) Coastal oceanographic regimes of the northern Argentine continental shelf (34–43° S). Estuar Coast Shelf Sci 65:405–420

Morris JT, Haskin B (1990) A 5-yr record of aerial primary production and stand characteristics of *Spartina alterniflora*. Ecology 71:2209–2217

Neira C, Grosholz ED, Levin LA, Blake R (2006) Mechanisms generating modification of benthos following tidal flat invasion by *Spartina* hybrid. Ecol Appl 16:1391–1404

Park HJ, Choy EJ, Kang CK (2013) Spatial and temporal variations of microphytobenthos on the common reed *Phragmites australis* bed in a marine protected area of Yeoja Bay, Korea. Wetlands 33:737–745

Peralta G, van Duren LA, Morris EP, Bouma TJ (2008) Consequences of shoot density and stiffness for ecosystem engineering by benthic macrophytes in flow dominated areas: a hydrodynamic flume study. Mar Ecol Prog Ser 368:103–115

Perkins RG, Underwood GJC, Brotas V, Snow GC, Jesus B, Ribeiro L (2001) Responses of microphytobenthos to light: primary production and carbohydrate allocation over an emersion period. Mar Ecol Prog Ser 223:101–112

Perkins RG, Honeywill C, Consalvey M, Austin HA, Tolhurst TJ, Paterson DM (2003) Changes in microphytobenthic chlorophyll *a* and EPS resulting from sediment compaction due to de-watering: opposing patterns in concentration and content. Cont Shelf Res 23:575–586

Pinckney J, Zingmark RG (1993) Photophysiological responses of intertidal benthic microalgal communities to in situ light environments: methodological considerations. Limnol Oceanogr 38:1373–1383

Sakamaki T, Richardson JS (2009) Dietary responses of tidal flat macrobenthos to reduction of benthic microalgae: a test for potential use of allochthonous organic matter. Mar Ecol Prog Ser 386:107–113

Silliman BR, Bertness MD, Altieri AH, Griffin JN and others (2011) Whole-community facilitation regulates biodiversity on Patagonian rocky shores. PLoS One 6:e24502

Smith DJD, Underwood GJC (1998) Exopolymer production by intertidal epipelic diatoms. Limnol Oceanogr 43: 1578–1591

Stal LJ (2010) Microphytobenthos as a biogeomorphological force in intertidal sediment stabilization. Ecol Eng 36: 236–245

Sullivan MJ (1981) Effects of canopy removal and nitrogen enrichment on a *Distichlis spicata*-edaphic diatom complex. Estuar Coast Shelf Sci 13:119–129

Sullivan MJ, Currin CA (2000) Community structure and functional dynamics of benthic microalgae in salt marshes. In: Weinstein MP, Kreeger DA (eds) Concepts and controversies in tidal marsh ecology. Kluwer Academic Publishers, Dordrecht, p 81–106

Underwood GJC (2010) Microphytobenthos and phytoplankton in the Severn estuary, UK: present situation and possible consequences of a tidal energy barrage. Mar Pollut Bull 61:83–91

Underwood GJC, Smith DJ (1998) Predicting epipelic diatom exopolymer concentrations in intertidal sediments from sediment chlorophyll *a*. Microb Ecol 35: 116–125

Underwood GJC, Paterson DM, Parkes RJR (1995) The measurement of microbial carbohydrate exopolymers from intertidal sediments. Limnol Oceanogr 40: 1243–1253

Van Colen C, Underwood GJ, Serôdio J, Paterson DM (2014) Ecology of intertidal microbial biofilms: mechanisms, patterns and future research needs. J Sea Res 92:2–5

Whitcraft CR, Levin LA (2007) Regulation of benthic algal and animal communities by salt marsh plants: impact of shading. Ecology 88:904–917

Wright JP, Jones CG (2006) The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. Bioscience 56:203–209

Yang SL, Li H, Ysebaert T, Bouma TJ and others (2008) Spatial and temporal variations in sediment grain size in tidal wetlands, Yangtze Delta: on the role of physical and biotic controls. Estuar Coast Shelf Sci 77:657–671

Zar JH (1999) Biostatistical analysis. Prentice Hall, Upper Saddle River, NJ

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