



FEATURE ARTICLE

A stem-boring moth drives detritus production in SW Atlantic marshes

Alejandro D. Canepuccia^{1,2,*}, Diana Montemayor^{1,2}, Jesus Pascual^{1,2},
Juan L. Farina³, Oscar O. Iribarne^{1,2}

¹Laboratorio de Ecología, Universidad Nacional de Mar del Plata, CC 573 Correo Central, B7600WAG, Mar del Plata, Argentina

²Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina

³Museo de Ciencias Naturales Lorenzo Scaglia, Área Entomología, Mar del Plata, Argentina

ABSTRACT: Boundary habitats are frequently hot-spots for the production and flow of organic matter (OM) and exert strong effects on ecological processes in the habitats which they link. Salt marshes, which are boundary habitats occurring between the land and the sea, are important sources of OM for coastal habitats. Primary productivity and tides are among the main causes of OM production and export from salt marshes. By field sampling and experiments we found that the stem-boring moth *Haimbachia* sp. nov. substantially increases the production of detritus in salt marshes along the SW Atlantic coastline. The larvae of this moth enhance the natural mortality of *Spartina alterniflora* and *S. densiflora* by feeding inside the basal and middle portions of the stem tissue. The attacks of the moth larvae produce dead and debilitated stems that are more easily broken and transported by the tides than non-attacked stems. Because the moth-attack frequencies will vary geographically in response to variation in the physical environment, the amount of OM flow between habitats will also vary, resulting in a positive relationship between moth-attack frequencies and OM production on a regional scale. Our field and experimental results show that herbivory by this moth and tidal transport could be the main determinants of the production of *Spartina* macrodetritus in these marshes. A key finding based on this previously undescribed interaction is that biological interactions (i.e. the effects of herbivores) can change the permeability of boundary habitats by altering the OM flow between terrestrial and aquatic ecosystems.

KEY WORDS: Boundary habitats · Herbivory · *Haimbachia* sp. nov. · *Spartina* · Organic-matter flow

Resale or republication not permitted without written consent of the publisher



Larva of stem-borer moth *Haimbachia* sp. nov., whose feeding activity can drive detritus production in tidal *Spartina* marshes.

Image: A. D. Canepuccia, J. L. Farina

INTRODUCTION

Boundary habitats, which are located between 2 different types of ecosystems, are ubiquitous across a wide range of ecological systems (e.g. Cadenasso et al. 2003). Although boundary habitats share characteristics with neighbouring habitats, they also have their own unique characteristics that are defined by the strength of their interactions with their neighbour habitats (e.g. Holland 1988, Traut 2005). Boundary habitats are frequently production hotspots (e.g. Mitsch & Gosselink 1993), and depending on their permeability (Stamps et al. 1987, Lopez-Barrera et al. 2007), they can regulate the flux of organic matter between habitats (e.g. nutrients, detritus and species; Mitsch & Gosselink 1993, Traut 2005). These charac-

teristics of boundary habitats produce strong direct and indirect effects on the distribution of organisms and on the ecological processes that interconnect natural systems (Levin et al. 2001, Cadenasso et al. 2003, Hoffman et al. 2008). Despite their ecological importance (e.g. Holland 1988, Cadenasso et al. 2003, Arrigoni et al. 2008), relatively little is known about the ecological processes that mediate the rates of the flow of energy and materials between boundary habitats and their neighbours.

Tidal marshes are boundary habitats that exhibit the attributes of both terrestrial and aquatic ecosystems. These marshes occur along the coastlines from mid- to high latitudes and are among the most productive systems worldwide (e.g. Mitsch & Gosselink 1993, Valiela et al. 2004). Most of the primary productivity of tidal marshes is returned to the environment as dead organic matter (e.g. Cebrian 1999) and is periodically transported by the tides (e.g. Childers et al. 2000). Thus, marshes are important for the production and flux of organic matter to neighbouring ecosystems. This flux of organic matter can even subsidise coastal oceanic productivity (the 'outwelling hypothesis': Teal 1962, Childers et al. 2000, Valiela et al. 2004). The degree of export is highly variable among marshes, and the factors that modulate this variability have constituted a matter of considerable debate. In marshes, the phenology of plants determines the timing of tissue death and the amount of detritus production (this tissue is added to the detrital pathway; Hardisky & Reimold 1977), whereas physical forces (e.g. tidal flooding) transport detritus between ecosystems. Thus, the productivity of marsh plants is strongly linked with energy flow to the ecosystems connected to the marsh (e.g. Childers et al. 2000, Odum 2000). As a result, given similar marsh areas, those with higher tidal amplitudes will produce and export greater amounts of plant detritus. However, the importance of herbivores to the structure of the marsh environment (e.g. Silliman et al. 2005, Jefferies et al. 2006) must also be considered. Physical variables alone may not be sufficient to explain the characteristics and dynamics of the organic material generated by primary producers.

Stem-boring insects are common marsh herbivores worldwide (e.g. Stiling & Strong 1984, White et al. 2005, Canepuccia et al. 2010a). On the coasts of the SW Atlantic, the stem-boring moth *Haimbachia* sp. nov. is an herbivore specific to the *Spartina* plant. The abundance of this species decreases towards higher latitudes (Canepuccia et al. 2010a). Larvae overwinter inside *Spartina* stems, with only one larva per stem (A. D. C. pers. obs.). The larva feeds on a

large portion of the basal and middle central stem tissue and discards food waste and faeces through a conspicuous vent hole (Fig. 1). In the spring/summer, the moth imagoes emerge through this hole. Infested stems have lost much of their central tissue because of the feeding activities of the moth larvae. Therefore, they may be much more fragile than undamaged stems. The damaged stems may then easily be broken (Fig. 1) by tidal currents, which would increase the production of detritus in *Spartina* marshes. Invertebrates are important in detritus decomposition during decay (Graça et al. 2000, Zimmer et al. 2004). However, no study has examined the indirect effects of herbivores, such as stem-boring insects on the amount of detritus produced in marshes. We tested the hypotheses that stem-boring insects could modulate marsh detritus production by increasing the rate at which *Spartina* stems break. The broken stems would then be incorporated into the detrital pathway and thereby contribute additional detritus to neighbouring marine communities.

This study investigated the possible modification of detritus production by the moth *Haimbachia* sp. nov. across a wide geographic range of SW Atlantic marsh

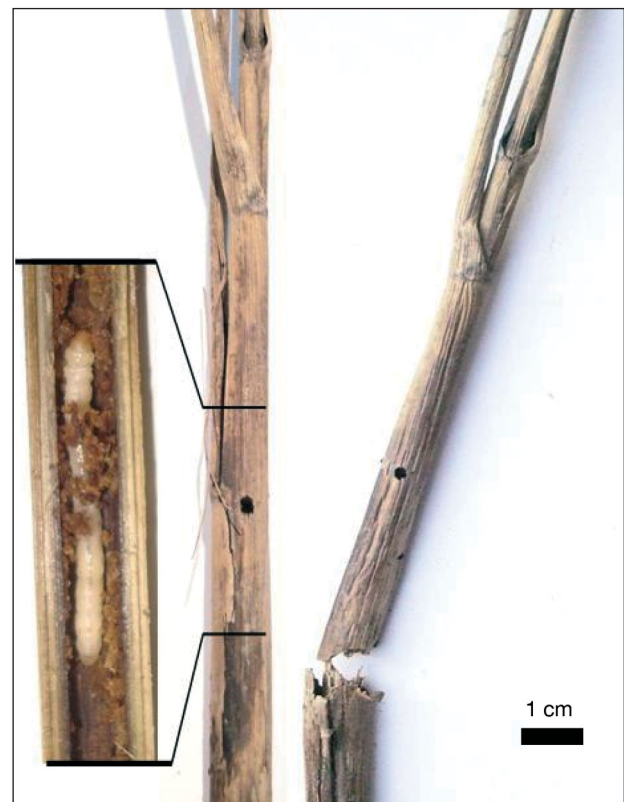


Fig. 1. *Spartina alterniflora*. Stem attacked by *Haimbachia* sp. nov. larvae. Left: close-up of a feeding larva inside a hollowed. Right: the same stem broken after the adult moth emerged

habitats exposed to different tidal amplitudes. In particular, we evaluated the following: (1) the frequencies of attack by the larvae of *Haimbachia* sp. nov. on *Spartina* spp. stems across different seasons in 6 marshes along 5° of latitude of the Argentine SW Atlantic coastline; (2) the likelihood that attack by larvae of *Haimbachia* sp. nov. increases the fragility of stems, leading to breakage and subsequent removal by tidal currents; and (3) the possible relationships between moth attack frequencies and marsh macrodetritus production in representative marshes of the Argentinean SW Atlantic coastline.

MATERIALS AND METHODS

Study area

The study was conducted in 6 marshes, including some of the most extensive SW Atlantic marshes (Isacch et al. 2006; Fig. 2). At lower elevations, these marshes are dominated by *Spartina alterniflora*, while *S. densiflora* dominated the higher marsh elevations. The marshes are exposed to tidal amplitudes that range from a mean of 0.75 m in northern areas to a mean of 6.44 m in the south (Isacch et al. 2006).

Frequencies of attack by moth larvae across season

To estimate the frequencies of attack by *Haimbachia* sp. nov. larvae (hereafter 'moth larvae') on *Spartina alterniflora* and *S. densiflora*, we cut all mature stems from the plants in 10 randomly selected square plots (25 × 25 cm) in the center of the spatial distribution of each *Spartina* species at each study site during each season for 1 yr. Since there is only one larva per stem, the frequency of attacked stems is an estimator of larval densities. All mature stems were taken to the laboratory for analysis. We did not include the older stems (e.g. dry and degraded stems or those without leaves). The use of these stems might have resulted in an overestimation of the rate of attack because stems attacked in the previous larval cycle could have been counted. The presence of a geometrically regular hole in the attacked stems makes them easily identifiable (Fig. 1). To estimate the frequencies of attack by moths, the stems were cut longitudinally and classified as attacked stems (i.e. stems with larvae or signs of larvae: a hole, tunnel or sawdust) or non-attacked stems (i.e. stems without larvae or signs of larvae). We then estimated the frequencies of attack by the moth as the ratio

between the number of attacked stems and the total number of stems in each quadrat for each *Spartina* species. A Tukey's HSD test following an analysis of variance (ANOVA; Zar 1999) was used to evaluate the null hypothesis of no differences among marshes in the proportions of attacked stems.

Stem breakage and removal by tides

We collected random adult stems with and without moth attack (25 replicates for each group and each plant species) at the San Clemente site to test the hypothesis that moth larvae modify the resistance of the stems to breakage by tidal currents. The resistance of a stem was estimated as the tension required to break the stem by applying a perpendicular force to an average section using a dynamometer (precision = 2 g). We used a *t*-test (Zar 1999) to compare the tension needed to break attacked and non-attacked stems for each plant species. In addition, we collected adult stems with and without moth attack for each *Spartina* species to test whether attacked stems are more easily broken or removed by tides. Stems were collected at the San Clemente site and individually placed (50 replicates for each treatment and

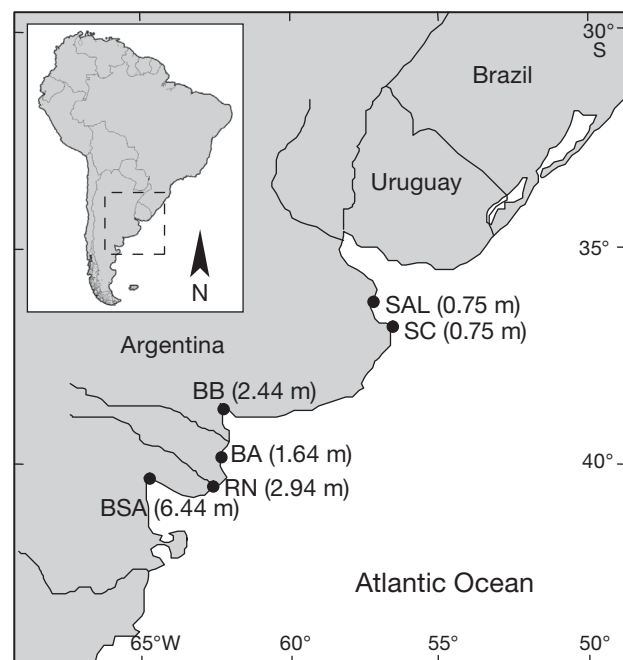


Fig. 2. Marshes sampled along the SW Atlantic coast. SAL: mouth of El Salado river (36° 18' S); SC: San Clemente (36° 22' S); BB: Bahía Blanca (38° 41' S); BA: Bahía Anegada (39° 48' S); RN: mouth of Rio Negro river (41° 00' S); and BSA: Bahía San Antonio (40° 42' S). The mean tidal amplitudes are given in parentheses

each plant species) in a vertical position on a piece of 0.15 m × 0.15 m plastic mesh. The stem was attached to the mesh with epoxy resin. Each stem, with its mesh base, was buried 4 cm deep in marsh substrate. The stems were placed 1 m apart and exposed to the same tidal currents for 7 d. We used the χ^2 test (Zar 1999) to evaluate the null hypothesis that attack by moth larvae did not influence the numbers of stems lost during tidal exposure.

Relationship between moth attack frequencies and marsh detritus production

To estimate the production of macrodetritus that can be exported by tides, we seasonally collected the macrodetritus (hereafter 'detritus') found after tides of intermediate amplitude (see Fig. 2). This kind of tide is the most frequent throughout the year and reflects expected average effects. We avoided sampling after storms and high spring tides when detritus production and export may increase (e.g. Weinstein & Kreeger 2000) due to transport of detritus from other marsh areas. Detritus was collected at 10 transects (1 m long each) along the drift line, separated by 10 m). The entire amount of material accumulated in the drift line was collected at each station. The detritus was cut longitudinally and classified as attacked (i.e. with evidence of attack by larvae: a hole, tunnel or sawdust) or non-attacked (i.e. without such evidence). Because the detritus consisted primarily of fragments of the middle basal sections and bits of the upper sections of stems, we used the number of basal sections as an estimator of the number of initial stems. We then estimated the stem number and the dry weight (after drying for 48 h at 65°C) for both detritus groups (attacked and non-attacked). For each *Spartina* species, we used a simple Pearson's correlation analysis (Zar 1999) to test for relationships between the average value of the total number of stems in the detritus (and the total dry weight of the stems) and the following variables for the marshes studied and for each season: (1) tidal amplitude; (2) stem density; (3) dry stem density; (4) area covered by each *Spartina* species (obtained from Isacch et al. 2006); and (5) average frequency of moth attacks on *Spartina* spp. To determine whether stems attacked by moth larvae contributed more to the detritus pathway than non-attacked stems, we used a *t*-test (Zar 1999) to compare the moth attack frequencies in each *Spartina* species with the frequencies of detritus showing moth attack signs in the detritus pool for each season and each marsh site.

RESULTS

Frequencies of attack by moth larvae across season

The analysis of 3919 *Spartina alterniflora* and 9916 *S. densiflora* stems showed that the rate of attack by moth larvae varied between plant species and among marsh sites and seasons. For all marshes, the moth attack frequencies were higher for *S. alterniflora* than for *S. densiflora* (*t*-test, $p < 0.05$; Fig. 3, Table 1). Also, the northern marshes (the mouth of El Salado River and San Clemente; Fig. 2) showed a greater proportion of attacked stems than the marshes located to the south (Bahía Blanca, Bahía Anegada, the mouth of Rio Negro River, and Bahía San Antonio; Tukey's HSD, $p < 0.05$; Fig. 3). Finally, the highest attack frequency occurred during winter and decreased by the summer, when most of the larvae had emerged as imagoes (Fig. 3).

Effects of attack by moth larvae on stem breakage and removal by tides

The breakage of stems attacked by moth larvae required less tension (*Spartina alterniflora*: mean = 45.1 g, SD = 16.2 g; *S. densiflora*: mean = 26.9 g, SD = 15.04 g) than the breakage of non-attacked stems (*S. alterniflora*: mean = 101.8 g, SD = 26.7 g, $t_{48} = 9.1$, $p = 0.017$; *S. densiflora*: mean = 124.6 g; SD = 54.9 g; $t_{48} = 8.5$, $p < 0.001$). This result is consistent with experiments showing that attacked stems fixed to a base buried in marsh substrate were broken more frequently by tidal currents (*S. alterniflora*: 74%, *S. densiflora*: 52%) than non-attacked stems (*S. alterniflora*: 32%, $\chi^2 = 16.06$, $p < 0.01$; *S. densiflora*: 4%, $\chi^2 = 25.70$, $p < 0.01$).

Relationship between moth attack frequencies and marsh detritus production

The detritus produced by marshes after tides of intermediate amplitudes varied among sites and seasons. The northern marshes showed larger detritus production than the southern marshes (Tukey's HSD, $p < 0.05$, Fig. 3). A negative relationship was found between dry stem densities and detritus production for *Spartina alterniflora* in winter ($r^2 = 0.68$, $p = 0.042$). No relationships were found between the tidal amplitudes, stem densities (for each *Spartina* species), the area covered by each plant and the detritus production from each *Spartina* for any season ($p > 0.05$). However, the detritus production was higher during

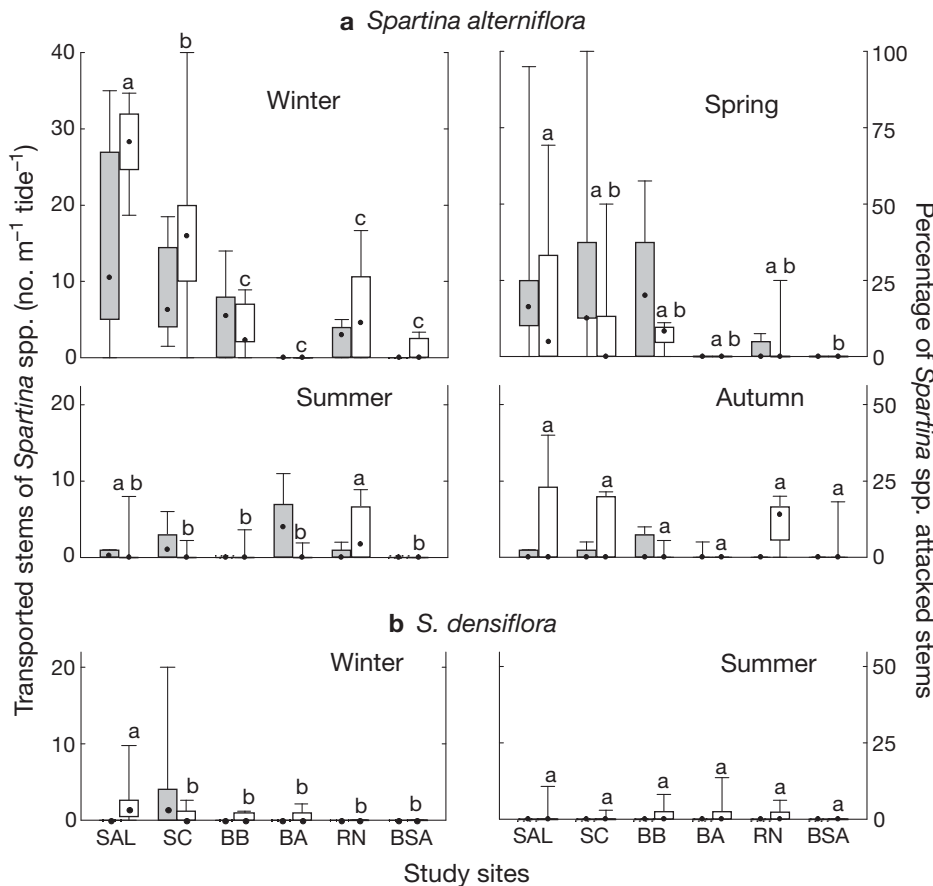


Fig. 3. (a) *Spartina alterniflora* and (b) *S. densiflora*. Grey boxes: number of dead stems of *Spartina* spp. transported after average tidal amplitude; white boxes: attack frequencies by moth larvae in standing *Spartina* spp. stems for each study marsh. Samples were performed seasonally across 6 SW Atlantic coastal marshes (see Fig. 2). Limits of the boxes represent 25th and 75th percentiles; vertical lines show the minimum and maximum values and black points inside the boxes represent median values (n = 10). Different lowercase letters denote significant differences between sites for a given season at p < 0.05 with Tukey's HSD test. There was no *S. densiflora* detritus production in autumn and spring, and frequencies of moth larva attack were zero

winter (at the time of the highest moth attack frequencies) and decreased during summer, when a new moth cycle was beginning and the attack frequencies were the lowest (Tukey's HSD, see Fig. 3). Indeed, when the attack frequencies by moth larvae were higher (winter and spring), we found positive relationships between the average moth attack frequencies and the average number of stems in detritus for *S. alterniflora* (winter: $r^2 = 0.92$, $p = 0.0027$, Fig. 3;

spring: $r^2 = 0.67$, $p = 0.047$, Fig. 3) and between the attack frequencies and the average dry weight of total detritus production for *S. alterniflora* (winter: $r^2 = 0.81$, $p = 0.014$; spring: $r^2 = 0.94$, $p = 0.0014$) across the study sites. However, during summer and autumn, when the attack frequencies and detritus production were low, there was no relationship between the average moth attack frequencies and the average number of stems in detritus for *S. alterniflora* (summer: $r^2 = 0.03$,

Table 1. *Spartina alterniflora* and *S. densiflora*. Mean (SD) of the percentages of detritus (Det.) and standing plant (Stan-pl) with tracks of moth larvae attack. Data from 6 marshes throughout the SW Atlantic coast (see Fig. 2). Dashes indicate no detritus found. Win.: winter, Spr.: spring, Sum.: summer, Aut.: Autumn. Asterisks indicate significant differences between Det. and Stan-pl (t -test, $p < 0.05$)

	El Salado		San Clemente		Bahía Blanca		Bahía Anegada		Rio Negro		San Antonio	
	Det.	Stan-pl	Det.	Stan-pl	Det.	Stan-pl	Det.	Stan-pl	Det.	Stan-pl	Det.	Stan-pl
<i>S. alterniflora</i>												
Win.	90.4 (10.7)	69.6 (12.9)*	83.5 (19.9)	43.6 (36.4)*	70.9 (13.9)	9.1 (7.5)*	-	0.0 (0.0)	77.6 (21.7)	15.1 (16.9)*	-	2.3 (3.7)
Spr.	98.6 (2.9)	17.8 (24.9)*	82.5 (22.3)	7.8 (15.9)*	69.4 (10.1)	0.0 (0.0)*	-	0.0 (0.0)	70.8 (20.0)	4.5 (9.6)*	-	0.0 (0.0)
Sum.	40.0 (54.8)	2.0 (6.3)*	77.8 (40.4)	0.6 (1.9)*	-	0.9 (2.9)*	55.8 (35.6)	1.0 (2.0)*	66.7 (28.9)	8.0 (9.29)*	-	0.0 (0.0)
Aut.	75.0 (50.0)	11.2 (15.5)*	66.7 (28.9)	8.3 (10.5)*	77.1 (15.8)	1.0 (2.1)*	50 (28.9)	0.0 (0.0)	-	19.9 (13.5)*	-	3.3 (6.9)
<i>S. densiflora</i>												
Win.	-	5.7 (7.3)	44.71 (31.8)	2.0 (2.6)*	-	0.9 (1.3)	-	1.1 (1.9)	-	0.0 (0.0)	-	0.0 (0.0)
Sum.	-	2.0 (4.1)	-	0.4 (1.0)	-	1.8 (3.0)	-	2.3 (5.1)	-	1.6 (2.5)	-	0.0 (0.0)

$p = 0.73$, autumn: $r^2 = 0.11$, $p = 0.52$; Fig. 3) or between the average moth attack frequencies and the average dry weight of total detritus production for *S. alterniflora* (summer: $r^2 = 0.11$, $p = 0.52$, autumn: $r^2 = 0.02$, $p = 0.77$). Moreover, the frequencies of *S. alterniflora* stems showing evidence of moth attack were higher in detritus than in standing plants (Table 1). Finally, the amounts of *S. densiflora* detritus were consistently lower than the amounts of *S. alterniflora* detritus, and the production of *S. densiflora* detritus was not related to the moth attack frequencies (Fig. 3).

DISCUSSION

Marshes are highly productive ecosystems that intimately link land and water through the fluxes of organic matter (Teal 1962, Childers et al. 2000, Mitsch & Gosselink 1993). Marsh productivity makes a very important contribution to aquatic food webs (the 'outwelling hypothesis': Teal 1962, Childers et al. 2000, Valiela et al. 2004) and constitutes one of the most important influences on the ecological integrity of both systems. This key interaction of marshes with their neighbouring ecosystems has usually been attributed to the plant community, marsh productivity, microbial activity and/or to abiotic vectors such as tidal currents and runoff (Childers et al. 2000, Odum 2000). This study provides a novel example of the way in which biological interactions (i.e. herbivores) drive detritus production in *Spartina* marshes and change the flow of energy between terrestrial and aquatic ecosystems. Throughout the SW Atlantic marshes, the feeding of the larvae of the moth *Haimbachia* sp. nov. on *Spartina* species increases detritus production by increasing the stems' fragility and vulnerability to tidal advection. This process creates a positive relationship between the frequencies of moth attack and the production of detritus by *Spartina* spp. on a regional scale. Thus, moth attack frequencies, coupled with the action of tidal flooding, can drive the production of detritus by *Spartina* species and the flux of detritus across the SW Atlantic marshes.

Given that the number of marsh plants may be related to the amount of detritus production through plant senescence (e.g. Childers et al. 2000, Odum 2000), we expected that large marsh size (e.g. Bahia Anegada, see Isacch et al. 2006) or marshes with higher plant densities (mainly dry stem densities, e.g. Bahia San Antonio) would produce more plant detritus. However, marsh size, stem densities, and dry stem densities do not fully explain the production of

detritus. Some herbivores can indirectly modify the quantity of detritus production by primary producers. For example, many tree-feeding insects induce premature foliar abscission (Karban & Baldwin 1997, Chapman et al. 2006, Kominoski et al. 2008) which also can provide substantial allochthonous subsidies to streams (e.g. Kominoski et al. 2008). The destructive feeding habits of some herbivorous vertebrates, such as the coypu *Myocastor coypus* and the wild boar *Sus scrofa*, can also increase the quantity of detritus produced by grasses (Ford & Grace 1998). Our study shows that the moth *Haimbachia* sp. nov. can produce similar effects in SW Atlantic marshes. *Haimbachia* sp. nov. is a common herbivore in SW Atlantic marshes (Canepuccia et al. 2010a). As a result of the damage caused by the feeding of the moth larvae, *Spartina* spp. stems lose a large amount of their central tissue, become more fragile, and are more easily broken by tidal turbulence. Tidal water enters *Spartina* stands daily, breaking the debilitated stems and exporting them to the coastal waters. This process increases the input of detritus to aquatic systems. In addition, the herbivore-produced detritus may have different nutrient quality because the detritus has not completely senesced (e.g. Chapman et al. 2003, 2006, Wardle & Bardgett 2004, Kominoski et al. 2008). Thus, each detritus type (produced by moth or by senesced plants) would have different effects on the aquatic food web.

Most of the detritus found in this study occurred in the drift lines. Detritus was very rarely found between the plant stems (i.e. in the sampling quadrats). These results suggested that most detritus is transported by the tides. Given that differences in export between communities may be related to differences in the intensity of horizontal advection (Cebrian 1999), we expected that the southern marshes, having a higher tidal amplitude, would show greater breakage of stems and would produce and export more plant detritus. However, the tidal range does not fully explain the production and export of detritus. Our results show that biological interactions may mask these environmental effects. In fact, on a regional scale, after most of the larvae had emerged as moths, the production of detritus was positively related to the moth attack frequencies. This relationship was detected despite the high variance in tidal height among the sampled sites (Isacch et al. 2006; see Fig. 2). In the summer, however, when the moths begin a new life cycle, detritus production decreased and became unrelated to moth attack frequencies. In addition, the densities of dry stems were higher in winter at those sites with lower moth attack frequen-

cies (the same sites having less detritus production), perhaps because dry and non-attacked (and therefore relatively undamaged) stems could remain standing longer than attacked stems and could therefore accumulate in the marsh. In fact, our experimental results demonstrate that attacked stems are more fragile and more frequently removed by the tides than non-attacked ones. Moreover, evidence of moth attack was more frequent in detritus than in standing plants. This result strongly suggests that attacked stems are the main contributors to the detritus pool. In SW Atlantic coastal marshes, *Spartina* spp. do not die in winter and continue to grow all year (the stems live longer than 1 yr: Vera et al. 2009). Thus, herbivory by the moths can alter not only the amount but also the timing and the quality of the detritus input to aquatic systems.

During the study period, most of the detritus collected was from *Spartina alterniflora* rather than from *S. densiflora*. A possible explanation of this result is that plants located in the lower marsh are more likely to be advected than those located in the higher marsh (e.g. Taylor & Allanson 1995, Bouchard & Lefeuvre 2000). During most tides, water floods the low *S. alterniflora* area (Isacch et al. 2006). The area is thus exposed to water advection. However, the higher marsh, dominated by *S. densiflora*, is only flooded during storms and spring tides (Isacch et al. 2006). The differences in detritus production between *Spartina* species could also result because the frequency of moth attacks is higher on *S. alterniflora* than on *S. densiflora* (Canepuccia et al. 2010a, this study). This difference in attack pattern may result from species-specific differences between the plants (e.g. plant palatability) influencing herbivore preference (e.g. Goranson et al. 2004). It could also result from differences in physical stress across the tidal gradient. Plants that grow at higher tidal elevations are usually exposed to limiting hypersaline soil conditions. These conditions result from pore water evaporation and low nutrient availability, and they can have profound impacts on plant performance (Bertness et al. 1992, Goranson et al. 2004) and on the consumers of the plants (Moon & Stiling 2002, Rand 2002). Both mechanisms (plant palatability or a stress gradient) could explain the observed difference in moth attack frequencies between plant species and the between-species differences in detritus production.

The frequencies of attack by the moth larvae also changed at a regional scale, generally decreasing with increases in latitude. Changes in soil salinity could be responsible for local differences, and they could also explain differences among sites in the attacks by

moth larvae. The marshes in the northern part of the study area are subject to greater freshwater influence because of the proximity of the La Plata River estuary. They also receive higher rainfall that gradually decreased to the south sites. The average rainfall is 950 mm at the mouth of the El Salado river, which is in the northern area, whereas the average rainfall at Bahía San Antonio, in the south, is 248 mm (Isacch et al. 2006; see Fig. 2). High rainfall and the proximity to freshwater can reduce salt stress in marsh substrates (Canepuccia et al. 2010b). The attributes of plants usually changes in relation to physical environmental gradients within habitats (e.g. Hemminga & van Soelen 1988, Goranson et al. 2004) and on a geographic scale (e.g. changes in productivity, palatability, defensive capacity, Bolser & Hay 1996, Pennings et al. 2001, Salgado & Pennings 2005). These variations may result in changes in abundance of herbivores (e.g. Pennings et al. 2009) and their feeding pressure (e.g. Pennings & Silliman 2005, Pennings et al. 2009) altering the plant–herbivore relationship (e.g. Bolser & Hay 1996, Pennings et al. 2009). In fact, the abundance and diversity of herbivores that feed in salt marshes is lower than in freshwater ones (e.g. Odum 1988, Greenberg et al. 2006, Canepuccia et al. 2010b), and our results suggest a similar distributional pattern of abundance for this moth species across a salinity gradient in the SW Atlantic marshes. As a consequence, although the northern marshes are exposed to lower tidal amplitudes, these marshes show higher moth attack frequencies and higher detritus production. In fact, the levels of moth attack (and detritus production) decrease towards the southern marshes but increase again in marshes influenced by freshwater at the mouth of the Rio Negro river (see Fig. 2).

Boundary habitats are widely distributed in ecological systems and are key modulators of the flow of organic matter between habitats (e.g. Cadenasso et al. 2003). However, studies that analyse the mechanisms that produce and modulate this flow are needed (Cadenasso et al. 2003, Arrigoni et al. 2008), especially on a broad geographic scale. Our work represents a novel example of biological interactions that can drive the flow of energy between the land and the ocean. The relative importance of the biological interaction, however, is likely to vary both spatially (e.g. Hemminga & van Soelen 1988, Goranson et al. 2004) and as a function of geographical variation in the physical environment (Thompson 1988, Bertness & Ewanchuk 2002, Pennings & Silliman 2005, Pennings et al. 2009). As the biological interactions vary, the flow between habitats can also

vary geographically. Thus, the physical, environment-driven variation in the strength and nature of biological interactions (e.g. Bertness & Ewanchuk 2002, Pennings et al. 2009) could also be a characteristic of the interactions between habitats. Understanding the regulation of the energy flow between habitats by physical or biological variables is fundamental for developing more general knowledge of the function and the distinctive biological features of boundary habitats. Given that marshes may fuel aquatic food webs (Teal 1962, Childers et al. 2000, Valiela et al. 2004), the challenge lies in understanding the factors that modulate the strength of these linkages (e.g. Cadenasso et al. 2003, Arrigoni et al. 2008). Because stem borers occur commonly in marshes worldwide, our study suggests that this largely unexamined interaction needs to be recognised in order to improve understanding of the dynamics of energy flow between the land and the ocean.

Acknowledgements. We are very grateful to Dr. M. A. Solis (Systematic Entomology Laboratory, Agricultural Research Service, US Department of Agriculture, Beltsville), who kindly identified the moth, and M. S. Fanjul, R. Osman, and 3 anonymous reviewers for their valuable suggestions and corrections on early versions of the manuscript. This project was supported by grants from the Universidad Nacional de Mar del Plata, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and the Agencia Nacional de Promoción Científica y Tecnológica (all to O.I.). J.P. and D.M. were supported by scholarships from the Comisión de Investigaciones Científicas and CONICET (Argentina).

LITERATURE CITED

- Arrigoni A, Findlay S, Fischer D, Tockner K (2008) Predicting carbon and nutrient transformations in tidal freshwater wetlands of the Hudson River. *Ecosystems* (NY) 11: 790–802
- Bertness MD, Ewanchuk PJ (2002) Latitudinal and climate-driven variation in the strength and nature of biological interactions in New England salt marshes. *Oecologia* 132:392–401
- Bertness MD, Gough L, Shumway SW (1992) Salt tolerances and the distribution of fugitive salt marsh plants. *Ecology* 73:1842–1851
- Bolser RC, Hay ME (1996) Are tropical plants better defended? Palatability and defenses of temperate vs. tropical seaweeds. *Ecology* 77:2269–2286
- Bouchard V, Lefeuvre JC (2000) Primary production and macrodetritus dynamics in a European salt marsh: carbon and nitrogen budgets. *Aquat Bot* 67:23–42
- Cadenasso ML, Pickett STA, Weathers KC, Jones CG (2003) A framework for a theory of ecological boundaries. *Bioscience* 53:750–758
- Canepuccia AD, Alberti J, Daleo P, Pascual J, Farina JL, Iribarne OO (2010a) Ecosystem engineering by burrowing crabs increases cordgrass mortality caused by stem-boring insects. *Mar Ecol Prog Ser* 404:151–159
- Canepuccia AD, Alberti J, Pascual J, Alvarez G, Cebrian J, Iribarne OO (2010b) ENSO episodes modify plant/terrestrial-herbivore interactions in a southwestern Atlantic salt marsh. *J Exp Mar Biol Ecol* 396:42–47
- Cebrian J (1999) Patterns in the fate of production in plant communities. *Am Nat* 154:449–468
- Chapman SK, Hart SC, Cobb NS, Whitham TG, Koch GW (2003) Insect herbivory increases litter quality and decomposition: an extension of the acceleration hypothesis. *Ecology* 84:2867–2876
- Chapman SK, Schweitzer JA, Whitham TG, Powell M (2006) Herbivory differentially alters plant litter dynamics of evergreen and deciduous trees. *Oikos* 114:566–574
- Childers DL, Day JW, McKellar HN Jr (2000) Twenty more years of marsh and estuarine flux studies: revisiting Nixon (1980). In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Dordrecht, p 391–423
- Ford MA, Grace JB (1998) Effects of vertebrate herbivores on soil processes, plant biomass, litter accumulation and soil elevation changes in a coastal marsh. *J Ecol* 86: 974–982
- Goranson CE, Ho CK, Pennings SC (2004) Environmental gradients and herbivore feeding preferences in coastal salt marshes. *Oecologia* 140:591–600
- Graça MAS, Newell SY, Kneib RT (2000) Grazing rates of organic matter and living fungal biomass of decaying *Spartina alterniflora* by three species of salt marsh invertebrates. *Mar Biol* 136:281–289
- Greenberg R, Maldonado JE, Droegge S, McDonald MV (2006) Tidal marshes: a global perspective on the evolution and conservation of their terrestrial vertebrates. *Bioscience* 56:675–685
- Hardisky MA, Reimold RJ (1977) Salt marsh plant geratology. *Science* 198:612–614
- Hemminga MA, van Soelen J (1988) Estuarine gradients and the growth and development of *Agapanthia villosoviridescens* (Coleoptera), a stem-borer of the salt marsh halophyte *Aster tripolium*. *Oecologia* 77:307–312
- Hoffman JC, Bronk DA, Olney JE (2008) Organic matter sources supporting lower food web production in the tidal freshwater portion of the York River Estuary, Virginia. *Estuaries Coasts* 31:898–911
- Holland MM (1988) SCOPE/MAB technical consultations on landscape boundaries: a report of a SCOPE/MAB workshop on ecotones. *Biol Int (Spec Issue)* 17:47–106
- Isacch JP, Costa CSB, Rodriguez-Gallego L, Conde D, Escapa M, Gagliardini DA, Iribarne OO (2006) Distribution of salt marsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. *J Biogeogr* 33:888–900
- Jefferies RL, Jano AP, Abraham KF (2006) A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *J Ecol* 94:234–242
- Karban R, Baldwin IT (1997) Induced responses to herbivory. University of Chicago Press, Chicago
- Kominoski JS, Pringle CM, Ball BA (2008) Invasive woolly adelgid appears to drive seasonal hemlock and carcass inputs to a detritus-based stream. *Verh Internat Verein Limnol* 30:109–112
- Levin LA, Boesch DF, Covich A, Dahm C and others (2001) The function of marine critical transition zones and the importance of sediment biodiversity. *Ecosystems* 4: 430–451

- Lopez-Barrera F, Manson RH, Gonzalez-Espinosa M, Newton AC (2007) Effects of varying forest edge permeability on seed dispersal in a neotropical montane forest. *Landscape Ecol* 22:189–203
- Mitsch WJ, Gosselink JG (1993) *Wetlands*, 2nd edn. John Wiley & Sons, New York, NY
- Moon DC, Stiling P (2002) The effects of salinity and nutrients on a tritrophic salt marsh system. *Ecology* 83: 2465–2476
- Odum WE (1988) Comparative ecology of tidal freshwater and salt marshes. *Annu Rev Ecol Syst* 19:147–176
- Odum EP (2000) Tidal marshes as outwelling/pulsing systems. In: Weinstein MP, Kreeger DA (eds) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Dordrecht, p 3–7
- Pennings SC, Silliman BR (2005) Linking biogeography and community ecology: latitudinal variation in plant–herbivore interaction strength. *Ecology* 86:2310–2319
- Pennings SC, Siska EL, Bertness MD (2001) Latitudinal differences in plant palatability in Atlantic coast salt marshes. *Ecology* 82:1344–1359
- Pennings SC, Ho CK, Salgado CS, Wieski K, Dave N, Kunza AE, Wason EL (2009) Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. *Ecology* 90: 183–195
- Rand TA (2002) Variation in insect herbivory across a salt marsh tidal gradient influences plant survival and distribution. *Oecologia* 132:549–558
- Salgado CS, Pennings SC (2005) Latitudinal variation in palatability of salt-marsh plants: are differences constitutive? *Ecology* 86:1571–1579
- Silliman BR, van de Koppel J, Bertness MD, Stanton L, Mendelsohn I (2005) Drought, snails, and large-scale dieoff of southern US salt marshes. *Science* 310: 1803–1806
- Stamps JA, Buechner M, Krishnan VV (1987) The effects of edge permeability and habitat geometry on emigration from patches of habitat. *Am Nat* 129:533–552
- Stiling PD, Strong DR (1984) Experimental density manipulation of stem-boring insects: some evidence for interspecific competition. *Ecology* 65:1683–1685
- Taylor DI, Allanson BR (1995) Organic carbon fluxes between a high marsh and estuary, and the inapplicability of the outwelling hypothesis. *Mar Ecol Prog Ser* 120: 263–270
- Teal JM (1962) Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43:614–624
- Thompson JN (1988) Variation in interspecific interactions. *Annu Rev Ecol Syst* 19:65–87
- Traut BH (2005) The role of coastal ecotones: a case study of the salt marsh/upland transition zone in California. *J Ecol* 93:279–290
- Valiela I, Rutecki D, Fox S (2004) Salt marshes: biological controls of food webs in a diminishing environment. *J Exp Mar Biol Ecol* 300:131–159
- Vera F, Gutierrez JL, Ribeiro PD (2009) Aerial and detritus production of the cordgrass *Spartina densiflora* in a southwestern Atlantic salt marsh. *Botany* 87:482–491
- Wardle DA, Bardgett RD (2004) Indirect effects of invertebrate herbivory on the decomposer subsystem. In: Weisser WW, Siemann E (eds) *Insects and ecosystem function*. Springer, Heidelberg, p 53–69
- Weinstein MP, Kreeger DA (2000) *Concepts and controversies in tidal marsh ecology*. Kluwer Academic Publishers, Dordrecht
- White WH, Adamski D, Fine G, Richard EP Jr (2005) Stem-borers associated with smooth cord grass, *Spartina alterniflora* (Poaceae), in a nursery habitat. *Fla Entomol* 88:390–394
- Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice-Hall, Englewood Cliffs, NJ
- Zimmer M, Pennings SC, Buck TL, Carefoot TH (2004) Salt marsh litter and detritivores: a closer look at redundancy. *Estuaries* 27:753–769

Editorial responsibility: Richard Osman, Edgewater, Maryland, USA

*Submitted: June 24, 2011; Accepted: October 3, 2011
Proofs received from author(s): November 4, 2011*