

POSITIVE PLANT–ANIMAL INTERACTIONS IN THE HIGH MARSH OF AN ARGENTINEAN COASTAL LAGOON

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Abstract. Although plant–plant facilitations have been shown to be important structuring forces in salt marshes, less attention has been given to the potential role played by plant–animal facilitations in structuring these communities. We used a combination of sampling and field experiments to evaluate the effect of microenvironmental changes produced by plant cover on the distribution of the burrowing crab *Chasmagnathus granulata*, a dominant macroinvertebrate of high marshes of the southwestern Atlantic coast. Four questions were explored. Is there a relationship between the spatial distribution of *C. granulata* and the spatial distribution of rooted macrophytes or distance from the marsh edge? How important is plant cover for the establishment and survival of crabs in the high marsh? Does plant cover affect critical physical variables for crab establishment? How important are environmental conditions for the survival of crabs in the high marsh?

Surveys of the marsh surface showed that: (1) there was a strong relationship between the presence of plant cover and the spatial distribution of *Chasmagnathus granulata* in the high marsh, and (2) both mean crab size and burrow density decreased from the marsh edge to high-marsh levels. By shading the substrate, live plants and experimental plant mimics were found to be equally efficient at buffering high temperature, dehydration, and soil hardness in the high marsh. Experimental amelioration of these harsh physical conditions led to higher crab densities. Crab burrows also buffered harsh environmental conditions, diminishing surface air temperature from ~46°C to 23°C. Finally, tethering experiments showed that stressful heating in the high marsh is lethal for crabs, and that plant cover is crucial for the establishment and long-term success of crabs in the high marsh. No predation was observed in tethering experiments.

Our results suggest that plant cover is largely responsible for determining the spatial distribution of this dominant crab in the high marsh through facilitation. Thus, our work shows that plant–animal facilitations as well as plant–plant facilitations are important structuring forces in salt marsh communities.

Key words: Argentina; *Chasmagnathus granulata*; cordgrass; crabs; microenvironment; plant–animal interactions; positive interactions; *Salicornia ambigua*; salt marsh; *Spartina alterniflora*; *Spartina densiflora*; stress amelioration.

INTRODUCTION

Positive interactions (i.e., mutualism, facilitation, including direct and indirect, trophic and nontrophic relationships) are common in most ecosystems. However, until recently they were seldom included in discussions about the organization of natural communities (Bertness and Callaway 1994, Callaway 1996, Bertness and Leonard 1997). This was at least partly the result of the strong impact that studies of competitive interactions and their importance in structuring communities have had on the scientific community (Kareiva and Bertness 1997). Nevertheless, positive interactions appear to be more important in structuring communities than previously believed (Jones et al. 1997). Direct

positive interactions occur when neighbors modify physical or biotic conditions (Bertness and Callaway 1994). For example, the cordgrass *Spartina alterniflora* has been shown to facilitate the establishment of an entire cobble beach plant community by reducing physical disturbance by waves to tolerable levels (Bruno 2000). Similarly, salt marsh plants may ameliorate harsh and potentially limiting physical microenvironmental conditions, positively influencing the establishment of other organisms and indirectly affecting community structure (Bertness and Hacker 1994, Bertness 1999). Examples of positive interactions between plants and animals are less common in the literature, even though they are likely to be common (e.g., Nomm and Pennings 1998, Pennings and Bertness 2001).

In salt marshes, burrowing crabs often inhabit both mud flats and vegetated areas (Chapman 1977, Day et al. 1989, Adam 1993). The environmental conditions in the lower part of the marsh are generally less stressful for these organisms, which need water to avoid

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dehydration and to obtain oxygen. These macroinvertebrates, however, are also found in the high marsh, where environmental conditions can be quite stressful (Adam 1993, Bertness and Leonard 1997). Crabs are usually less abundant in the high marsh than in the low marsh, a pattern that is found both within and among species (e.g., Bertness and Miller 1984, Spivak et al. 1994). These patterns have been suggested to be related to high dehydration stress, breathing complications, and lower shelter availability, all of which vary with distance to the coastline (Spivak et al. 1994, Halperin et al. 1999). In high-marsh habitats, amelioration of physical stress by primary space-holder plants could potentially buffer neighbors from limiting stresses (Bertness and Callaway 1994, Bertness and Leonard 1997). In spite of the potential role of facilitation in influencing intertidal animal distributions, most studies have emphasized the importance of other mechanisms, such as physical limitations (e.g., Pennings and Callaway 1992, Pennings and Bertness 2001), competition (Connell 1961, Snow and Vince 1984), and predation (Paine 1966, Bortolus et al. 1998) in the structuring of both animal and plant intertidal communities.

Between southern Brazil and northern Patagonia (Argentina), there are several salt marshes located in estuaries with large sediment discharges and brackish water conditions (Adam 1993). In these salt marshes, the low marsh is dominated by halophytic grasses, whereas high-marsh areas are dominated by halophytic and hyper-halophytic plant species (West 1977). *Spartina densiflora* B. and *S. alterniflora* L. are generally the dominant species in the low marsh (Mobberley 1956, Cabrera 1978, Davy and Costa 1992). Crabs are distributed throughout the intertidal zone, from mud flats to the high marsh (Olivier et al. 1972). Bare, unvegetated areas are generally found in the high marsh, but also occur in the low marsh. In the high marsh, small patches of *Spartina* occur along with the highly salt-tolerant *Salicornia ambigua* (West 1977, Davy and Costa 1992). The high marsh has salty, compact, dehydrated sediments in comparison with the low marsh (Mitsch and Gosselink 1993). As a result of increased water loss, the high-marsh soil has a superficial hard clay layer often covered by a conspicuous layer of salt (Bertness 1999, Bortolus and Iribarne 1999). These harsh physical conditions probably diminish the probability of survival for most crustaceans living in the intertidal zone (i.e., amphipods, isopods, and decapods).

Although crabs are common in these marshes, relatively high-elevation areas have microenvironmental conditions (e.g., sparse root mats and sandy soils) that do not favor burrow construction (Bertness and Miller 1984, Spivak et al. 1994). In addition, regular exposure to air during ebb tides can potentially limit crab mobility, because most intertidal decapods obtain oxygen from tidal waters. This is particularly important at the highest marsh elevations, where water arrives only dur-

ing extreme high tides or occasional floods. Extreme values in crucial variables like dehydration, superficial soil hardness, and high temperatures, all driven by the incidence of sunlight, could also negatively affect semiterrestrial crabs (Seiple 1979, Palmer 1995), as well as the associated flora and fauna (Bertness 1985, Bortolus and Iribarne 1999). The effect of temperature on the biology and ecology of these estuarine crabs, however, has not yet been investigated through field experiments (but see Nomann and Pennings 1998).

Marsh plants shade the soil surface, potentially helping to overcome stressful temperature conditions (Callaway 1995) that may limit crab intertidal distributions. High temperatures cause dehydration, protein denaturation, and cellular membrane damage; consequently, plant shading is likely to increase habitat availability for many marsh organisms (Boughey 1978, Bertness and Hacker 1994, Callaway 1995). Nevertheless, the impact of positive interactions on species distribution in salt marshes has only recently received attention (e.g., Bertness and Callaway 1994, Bertness and Yeh 1994, Hacker and Bertness 1996). In this paper, we evaluate the importance of microenvironmental changes generated by plant cover on the distribution of the burrowing crab *Chasmagnathus granulata*, the dominant macroinvertebrate of the high marsh of a coastal lagoon in Argentina. We examine four questions: (1) Is there a relationship between the spatial distribution of *C. granulata* and the spatial distribution of rooted macrophytes, or distance from the marsh edge? (2) How important is plant cover for the establishment and survival of crabs in the high marsh? (3) Does plant cover affect critical physical variables for crab establishment? (4) How important are environmental conditions for the survival of crabs in the high marsh?

METHODS

Study area

The study was performed in the Mar Chiquita coastal lagoon, Argentina (37°32' to 37°45' S, and 57°19' to 57°26' W), a large body (46 km²) of brackish water affected by low-amplitude tides (≤ 1 m; Spivak et al. 1994). The lagoon is characterized by mudflats and large surrounding areas of cordgrass, *Spartina densiflora* (Fasano et al. 1982) (see Plate 1, left). Creek banks are densely populated by the burrowing crab *Chasmagnathus granulata* (Olivier et al. 1972, Cabrera 1978) (see Plate 1, right), but crabs also live at lower densities in the high marsh, several hundred meters from the marsh edge (A. Bortolus, *personal observation*). Most of the sampling and all experiments described in this paper were performed at higher marsh levels (hereafter referred to as high marsh, ~ 50 m from the marsh edge; Bortolus and Iribarne 1997), which are only flooded by extraordinary tides and are dominated by *S. densiflora* and *Salicornia ambigua* (Olivier et al. 1972, Cabrera 1978).



PLATE 1. (Left) A typical Argentinean salt marsh at the Mar Chiquita coastal lagoon (Buenos Aires Province). *Spartina densiflora* dominates the low and medium area of the intertidal level of this community. (Right) A male adult burrowing crab *Chasmagnathus granulata*, the dominant macro-invertebrate in the Argentinean salt marshes. Its specific Latin name originated from the grains on its relatively large claws. Photography by A. Bortolus.

Distribution of Chasmagnathus granulata in relation to vegetation and distance to coastline

In order to evaluate the relationship between crab density and plant cover in the high marsh, we estimated crab densities in areas covered by *Spartina densiflora*, areas covered by *Salicornia ambigua*, and uncovered bare areas. Samples were taken in 20 haphazardly placed quadrats (50 × 50 cm) in each habitat type within the high marsh. In the low marsh, the relationship between crab density and *Spartina densiflora* cover was quantified in areas with and without plant cover ($n = 20$, 1 × 1 m each). To evaluate the relationship between crab size and distance from the marsh edge, we compared the mean crab size at low, medium, and high marsh (10 m, 15 m, and 40 m from the marsh edge, respectively). Ten traps were deployed at each level; after three days, crabs were counted and their maximum carapace width was measured with digital calipers (± 0.001 mm). Each trap was a cylindrical plastic box (15 cm diameter, 20 cm depth) buried in the sediment, with the upper part level with the sediment surface. The top of the trap was funnel shaped, with a 4 cm diameter entrance. Preliminary tests showed that once crabs were caught, they were unable to escape. Traps were deployed for three days.

To evaluate the relationship between distance from the marsh edge and crab density independently of plant cover, burrow densities (a good estimator of crab density; Iribarne et al. 1997) were quantified in 20 haphazardly chosen quadrats (1 m² each) in unvegetated areas within each marsh level. All sampling was conducted between December 1996 and February 1997 (summer months).

Importance of plant cover in establishment and maintenance of high-marsh crabs

The ability of crabs to construct burrows was used to examine whether crabs could colonize a particular

habitat. To evaluate the effect of plant cover on crab burrowing, we conducted an experiment from December 1997 to December 1999 by placing artificial covers in uncovered areas devoid of crab burrows within the high marsh. Three treatments were deployed: (1) plant mimics similar in shape to *Salicornia ambigua* (80 × 40 × 20 cm high) constructed of plastic and nylon mesh and pinned to the substrate ($n = 9$); (2) live *S. ambigua* constructed by cutting aboveground structures at ground level and placing them in natural positions, fastened by small wires ($n = 9$); and (3) bare areas without plant cover (80 × 40 cm; $n = 10$) delimited as controls. The treatments were inspected monthly, maintaining the proportion of live plant structures and replacing dead parts when needed. After two years, the number of crab burrows in all plots was counted.

To evaluate the effect of plant cover on the maintenance of established crab burrows, we started an experiment in December 1997 with two treatments: pruning, in which *Salicornia ambigua* patches (~80 × 40 cm; $n = 9$) were pruned at ground level; and control, with unmanipulated patches of *S. ambigua* with the same dimensions ($n = 5$). After two years, the number of crab burrows was counted, and the difference between the initial and final number of burrows in each replicate plot was compared.

All field experiments involving plant cover manipulations were conducted with *Salicornia ambigua* because their rugged and compact structure facilitated pruning and transplant. Preliminary attempts to use *Spartina* were unsuccessful and were abandoned. A light meter was used to assure that live plant and plant mimic treatments produced the same degree of shading.

Because it could be possible that crabs use plants for food as well as shelter, we examined whether crabs could consume *Salicornia* in a laboratory experiment. Previous work had shown that these crabs can eat *Spartina densiflora* (Bortolus and Iribarne 1999), so we

compared the ability of these crabs to eat these two plants. We confined 60 crabs in separate 10-L containers with estuarine water (5 cm depth) and a constant amount (~50 g) of either *S. ambigua* ($n = 30$ crabs) or *S. densiflora* ($n = 30$ crabs). Prior to the experiment, crabs were starved for 24 h until they stopped producing fecal pellets. After a week, the experiment was stopped. Plant damage and fecal pellet accumulation were used as indicators of plant consumption.

Importance of plants in affecting physical variables in high marsh

To examine the influence of plants on physical variables that are important to crabs, we quantified surface air temperature (0.5 cm above ground level), sediment water content and hardness, and evaporation in soil sediments. Diurnal variation of surface air temperature was estimated using alcohol thermometers (in degrees Celsius, $n = 10$). Air temperature 1.5 m above ground level was measured simultaneously, as a reference, and maximum and minimum temperatures were compared between treatments. All measurements were made during the Argentinean summer (December–March).

The water content of surface soil sediments was evaluated by drying soil sample cores (diameter 28 mm, depth 6 mm) at 75°C until they reached a constant mass. Water evaporation at the soil surface in areas with and without plants was estimated using graduated glass tubes (volume 6 mL, evaporation surface 16.45 mm²) initially filled with a constant volume of water, and comparing the water volume remaining after 12 h. Surface soil hardness was measured as the pressure (expressed in Newtons per square centimeter) necessary to compress a penetrometer (diameter 2 cm) into the sediment to a standard depth (see Brown and McLachlan 1990). Because this value decreases with increasing penetrability, low numbers indicate soft sediments and high numbers indicate harder sediments. For all variables (i.e., temperature, water content, evaporation, and soil hardness) measurements were taken two years after the experimental plots were established (December 1997) during a randomly chosen summer day.

To evaluate the effect of plant cover on the physical environment, we measured surface air temperature, surface soil hardness, and water evaporation in the vegetation manipulation plots (live cover, mimics, and bare areas) described previously ($n = 9$ in all cases). Surface air temperature was recorded hourly from each replicate plot. Surface soil hardness and evaporation were estimated, as previously described from each experimental plot. To evaluate the capacity of crab burrows to buffer critical air temperature and water evaporation rates, these variables were also estimated inside crab burrows (10 cm depth from ground level), in the same plots, by placing thermometers and glass tubes inside burrows.

To evaluate the relationship between natural plant

cover and crab activity during peak daytime temperatures, we estimated the percentage of active crab burrows at the highest temperature hour of the randomly chosen day (approximately at 1400 hours) in areas with and without plant cover. We randomly chose 50 burrows from each type of area and the percentage of active burrows was quantified. Burrows with recent removal of sediment were considered as active, and burrows with no recent sediment removal were considered inactive (see Iribarne et al. 1997).

Influence of microenvironmental conditions on crab survival

To evaluate the effect of microenvironmental conditions in the high marsh on crab survival, we performed tethering experiments. Crabs were tethered with a nylon thread (0.5 mm diameter, ~20 cm long) to a small wire stake. The treatments were: (1) areas with natural plant cover, and (2) bare areas 5 m from plant cover. Preliminary observations showed that tethering crabs did not interfere with their locomotion or burrowing activities. Burrows were not available to tethered crabs in either treatment. Treatments were replicated 10 times and replicates were separated by ≥ 5 m to maximize replicate dispersion (see Hulbert 1984). Tethering experiments were carried out following the recommendations suggested by Peterson and Black (1994), Barbeau and Scheibling (1994), and Aronson and Heck (1995). Tethered crabs were observed every 15 min and the percentage of dead crabs from areas with and without cover were compared. The experiment was terminated when all crabs from uncovered areas had died. The experiment was done in both the afternoon and at night using different crabs each time to examine the importance of daytime thermal conditions in influencing physical stresses on these crabs. Two people from nearby fixed points observed the tethered crabs every 15 min during a 4-h period using binoculars (8 \times) to distinguish whether death was due to physical stress or predation.

Data analysis

The null hypotheses of no differences in variables between areas with and without plant cover were evaluated with a Welch-approximation *t* test (Zar 1999). The null hypotheses of no differences in any variable between the start and the end of a given experiment were evaluated by using a paired *t* test, following the recommendations of Zar (1999). When variances were not homogeneous (*F* test), differences in mean values were evaluated with a nonparametric test (Zar 1999). The null hypothesis of no difference between more than two variables was evaluated with ANOVA. Proportions were analyzed by using a binomial test (*P* test; Zar 1999). The null hypotheses of no difference in superficial soil hardness and water content between treatments were separately evaluated by using ANOVA. An a posteriori Tukey test was used to identify differences

FIG. 1. Photograph showing overlapping spatial distributions of *Chasmagnathus granulata* burrows and *Salicornia* cover in the high marsh. The area outlined by a dashed white line shows where plant cover was recently removed. The arrow points to one of the many burrows (~15) in the area where plants had been.



among treatment means, and the acceptance level for significance was 0.05 (Zar 1999). The null hypothesis of no difference for any variable measured over time was tested by using a repeated-measures ANOVA.

RESULTS

Distribution of Chasmagnathus granulata in relation to vegetation and distance to coastline

In the high marsh, crab density showed no difference between areas covered by *Spartina densiflora* (61 ± 17.8 crabs/m², all values expressed as $\bar{X} \pm 1$ SD) and *Salicornia ambigua* (62 ± 21.6 crabs/m²), but was significantly lower in areas without plant cover (0.2 ± 0.4 crab/m², $F_{2,62} = 42.9$, $P < 0.05$; Tukey $P < 0.05$). In the low marsh, areas with (57.4 ± 14.9 crabs/m²), and without *S. densiflora* cover (52.1 ± 8.1 crabs/m²) showed no differences in crab density ($t = 0.93$, $df = 1$, $P > 0.05$). When unvegetated areas were included in the estimation (i.e., considering covered as well as uncovered areas), crab density was lower in the high marsh than in the other two marsh levels ($F_{2,27} = 461.3$, $P < 0.05$; Tukey $P < 0.05$). When plant cover (either *Spartina* or *Salicornia*) was pruned, the high degree of spatial overlap between crab burrows and plant canopies was obvious (Fig. 1). Similarly, the number of crabs trapped in pitfall traps was lower in the high marsh (11.3 ± 3 individuals/trap, $n = 10$) than in medium or low marsh (medium, 25 ± 12.6 individuals/trap; low, 23.2 ± 15 individuals/trap; $F_{2,28} = 4.5$, $P < 0.05$; Tukey $P = 0.05$). Average crab size was significantly higher at the low marsh level (28 ± 3.9 mm, $n = 100$) than at medium or high elevations (medium, 26 ± 3.9 mm, $n = 100$; high, 27 ± 1.7 mm, $n = 20$; $F_{2,298} = 11.3$, $P < 0.001$; Tukey $P < 0.05$). There was also a wider range of crab sizes in low marsh than in the other two levels (Fig. 2).

Importance of plant cover in establishment and maintenance of crabs in high marsh

The number of crab burrows was higher in plant plots (7.4 ± 1.3 burrows) than in plant mimic plots ($5.7 \pm$

1.1 burrows; $t = 3.1$, $df = 16$, $P < 0.05$). No burrows were found in uncovered control plots. At the end of the cover experiment, the establishment of burrows in covered plots was significant (start vs. end of the experiment, $t_{mimic} = 15.2$, $t_{live} = 16.7$, $df = 16$, $P < 0.05$). Crabs established themselves approximately at the same time (early summer) below both kinds of cover.

Control plots in the pruning experiment showed no differences between the initial and final number of burrows (16 ± 2.9 burrows; $t = 1.8$, $df = 8$, $P > 0.05$), but the final number of crabs in the pruning treatment (9 ± 3.3 crabs; $t = 2.7$, $df = 8$, $P < 0.05$) was significantly lower than the initial number of crabs (12.4 ± 3.3 crabs).

Crabs consumed *Salicornia ambigua* in 76.7% of the containers, and *Spartina densiflora* in 70% of them ($P < 0.05$). Both plant species showed high tissue damage,

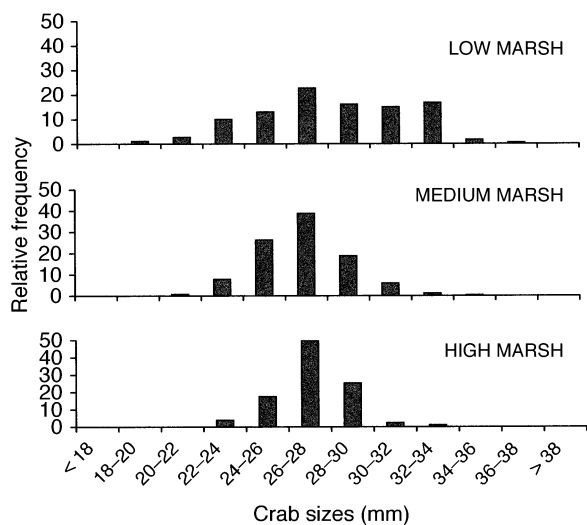


FIG. 2. Size distribution of *Chasmagnathus granulata* crabs at low ($n = 182$), medium ($n = 257$), and high ($n = 104$) marsh levels.

TABLE 1. Results of the repeated-measures ANOVA for the effect of vegetation treatment on air temperature, soil water content and soil hardness.

Variable and sources	Effect		Error		F	P
	df	MS	df	MS		
Air temperature						
Treatment	2	489.21	9	9.38	52.1	<0.0001
Time	20	183.08	180	1.62	112.71	<0.0001
Treatment × Time	40	28.44	180	1.62	17.51	<0.0001
Soil water content						
Treatment	2	0.82	12	0.01	57.28	<0.0001
Time	5	0.13	60	0.02	4.71	<0.001
Treatment × Time	10	0.05	60	0.02	1.76	0.08
Soil hardness						
Treatment	2	2501.7	12	355.53	7.03	<0.01
Time	5	368.9	60	45.9	8.03	<0.0001
Treatment × Time	10	64.53	60	45.9	1.4	0.19

and green fecal pellets were observed within all of the containers in both experiments.

Importance of plants in affecting physical variables in high marsh

The effect of plant cover on air temperature at 1.5 cm above the marsh substrate depended on time (Table 1). Air temperature at the surface was highest at 1400 hours (Fig. 3A). At this time, the highest temperature was found in uncovered areas ($43.1 \pm 1.3^\circ\text{C}$), while the lowest values were found 10 cm deep in the crab burrows in areas with cover ($23 \pm 1.5^\circ\text{C}$), and without cover ($23.2 \pm 2.1^\circ\text{C}$, $n = 9$; $F_{2,24} = 120.6$, $P < 0.05$; Tukey $P < 0.05$; Fig. 3B).

The effect of plant cover on water content of the marsh substrate was not dependent on time (Table 1), but the lowest values were generally found in uncovered areas (Fig. 3C). Water evaporation was significantly higher in uncovered areas (0.06 ± 0.01 mL evaporated from tubes after 12 h) compared to covered areas, where no evaporation was registered.

The effect of plant cover on superficial soil hardness was not dependent on time (Table 1, Fig. 3), but this variable was usually higher in uncovered than in covered areas (Fig. 3D, Table 1). There were no differences in any variable when samples from 10 cm inside crab burrows were compared between different treatment plots. The percentage of active burrows in the high marsh was an order of magnitude higher in covered areas (84%) than in uncovered areas (8%, $P < 0.05$).

Influence of microenvironmental conditions for survival of crabs

No crabs survived the diurnal tethering experiment in treatments without plant cover. All crabs died within 1 h after the experiment started, and new crab burrows were not detected. On the other hand, all tethered crabs in covered areas survived. These crabs were wet and moved when touched, whereas crabs from uncovered

areas looked dry and were inactive until they died. At the end of the experiment, all dead crabs were found intact and tied to the tether. All crabs in experiments conducted during the evening and night, both in covered and uncovered areas, survived. No new burrows were observed during these experiments, but some of the crabs were found buried in surface sediments. No predation on crabs was observed during tethering experiments, despite the presence of several shorebirds, Lapwings (*Vanellus chilensis*), and mice close to the experimental plots.

DISCUSSION

The main conclusion of this paper is that positive interactions between plants and animals can have important consequences for the structure and dynamics of marsh communities. In particular, in the high marsh community of Mar Chiquita coastal lagoon (Argentina), the amelioration of harsh physical conditions by plants plays an important role in dictating the abundance and distribution patterns of the numerically dominant crab, *Chasmagnathus granulata*.

Is distribution of C. granulata related to distribution of vegetation or distance from the marsh edge?

Our results show a strong relationship between plant cover and the spatial distribution of the dominant macroinvertebrate *Chasmagnathus granulata* in the high marsh. The spatial distribution of these crabs in the high marsh strongly overlapped the distribution of both *Spartina densiflora* and *Salicornia ambigua*. In high-marsh habitats specifically, the density of crabs below plants was about two times higher than the density of crabs found on bare substrate without plants present. These results suggest that environmental conditions are more stressful on bare than on vegetated substrate, and that crabs avoid bare areas by aggregating below plants. However, we found no relationship between crabs and plant cover in the low marsh, where crabs established

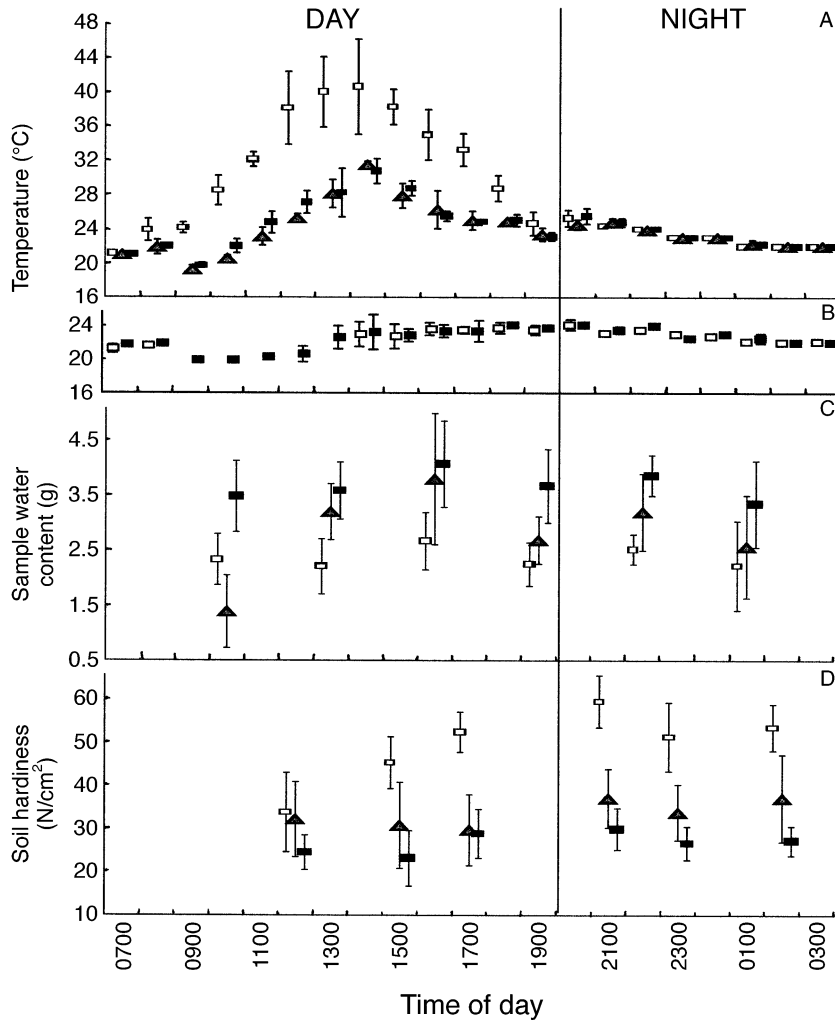


FIG. 3. Environmental variables inside and outside crab burrows, in relation to the nature of cover. Temperature variation during 24 h in the high marsh after a 2-yr period within experimental areas is shown for different treatments: (A) at the surface without cover (empty squares), with live plant cover (triangles), and with inert cover (black squares); (B) 10 cm below ground, inside crab burrows with and without live cover (black squares and open squares, respectively). (C) Soil water content and (D) superficial soil hardness (measured in Newtons, N) during 24 h in the high marsh after a 2-year period among experimental areas without cover (open squares), with live plant cover (triangles), and with inert cover (black squares). Values are means \pm 1 SD.

in both vegetated and unvegetated areas. This contrasting pattern strongly suggests that stressful temperature and dehydration are not important factors controlling the establishment and permanence of crabs in the low marsh.

In New England (USA), the black rush (*Juncus gerardi* Loisel) creates a hospitable environment for the marsh elder (*Iva frutescens* L.), extending its distribution to habitats in which it normally does not have the morphological or physiological plasticity to endure (Hacker and Bertness 1995). Algal canopies also have been shown to strongly enhance the recruitment, growth, and survival of the associated organisms in rocky intertidal communities (Bertness 1999). Similarly, our survey results indicate that plant cover buff-

ers crabs from stressful limiting physical conditions in the high marsh of Mar Chiquita lagoon. These findings strongly suggest that plant-animal facilitations as well as plant-plant facilitations are important structuring forces in salt marsh communities.

As previously described (Spivak et al. 1994), the size and density of crabs diminished from low to high marsh. For marine organisms, temperature and dehydration stress generally increase with tidal height and exposure to terrestrial conditions (Pennings and Bertness 2001). Most likely, the observed decrease in crab size and density with increasing distance from the marsh edge is the result of increased environmental stress at higher intertidal elevations.

How important is plant cover for establishment and survival of crabs in high marsh?

Crabs burrowed below both live plants and plant mimics, but did not burrow in bare substrate without cover. Burrowing below plant mimics, however, was slightly lower than below live plants. Given that crabs eat *Salicornia* plants, it is possible that crabs establishing burrows below plant mimics were obtaining food from nearby live plants, which agrees with the higher number of crab burrows established under live covers than under plant mimics. Nevertheless, plant mimics did enhance crab burrowing in comparison to unvegetated, bare substrate, suggesting that the alleviation of physical stress is the most important service provided to crabs by these plants. Roots and rhizomes were not a limiting factor for *Chasmagnathus granulata* establishment. The fact that crabs established below both live plants and plant mimics at approximately the same time suggests that cover quality (i.e., edible vs. inert) is not crucial for the initial selection of a microhabitat. In this study, however, plant cover drove the spatial distribution of crabs in the high marsh, mainly by increasing food and reducing physical stress in high-marsh habitats. Thus, plant cover could be amplifying the spatial distribution of crabs in the high marsh, increasing their local expansion and relaxing possible density-dependent negative interactions (e.g., cannibalism and competition) that may be important in the lower marsh.

When natural plant cover was experimentally removed, the number of crab burrows diminished, but a high percentage of burrows remained after two years. The longevity of active burrows after plant cover was removed suggests that once burrows are constructed, they probably buffer harsh conditions, and that crab survival becomes somewhat independent of plant cover. Burrows can connect with the water table, ensuring oxygen supply (Bortolus and Iribarne 1999), and can act as nutrient traps (Iribarne et al. 1997), providing excellent refuges under stressful conditions.

Does plant cover affect critical physical variables for crab establishment?

Our results show that both live and plant mimic cover buffered high temperature, dehydration, and soil hardness, and that this process favored the establishment of crabs. Temperature and dehydration stress often regulate the distribution and survival of intertidal organisms (Nomann and Pennings 1998, Bertness 1999). However, positive interactions usually diminish physical stresses, favoring the survival of the organisms that live there (Hay 1981, Callaway 1995). Vegetated and unvegetated areas may differ in reflectivity, heat capacity, heat conductance, and the amount of heat lost through evaporation (Bazzaz 1998). Plant cover tends to condense water as well as diminish evaporation below it by shading the understory (Callaway 1995). Giv-

en that the accumulation of dehydrated clay sediments and their compactness could hamper crab-burrowing in uncovered areas (Bortolus and Iribarne 1999; this paper), our results suggest that plant cover allows crabs to colonize high-marsh areas.

The burrows of *Chasmagnathus granulata* also buffered harsh temperature and dehydration conditions. The strong differences in temperature and water evaporation between surface level and 10 cm below ground level (i.e., $\sim 20^\circ\text{C}$ lower, and no detectable evaporation inside burrows), suggest that burrows buffer crabs from lethal values of these variables. Without plant or plant mimic shading, crabs died before being able to dig a burrow as a refuge. Once burrows were constructed, however, crabs could obtain refuge from high temperatures and dehydration independently of the cover above them. However, we found that most burrows in bare, unvegetated areas were inactive, which suggests that they are not good habitats compared to vegetated areas.

How important are environmental conditions for survival of crabs in high marsh?

Stressful heating conditions in response to high temperatures negatively affect semiterrestrial crabs (Seiple 1979). Our results indicate that stressful heating conditions in high-marsh areas during warm periods are potentially lethal for *Chasmagnathus granulata*.

Tethering techniques have been criticized because they can generate artifacts that may vary among treatments (Aronson and Heck 1995). For example, tethering may have differential effects on predation rate (e.g., Barbeau and Scheibling 1994, Zimmer-Faust et al. 1994). In this paper, however, tethering was used to evaluate and compare the mortality of crabs between different treatments, not to estimate natural predation rates. In our experiments, there was no predation on crabs before they died. In our daytime tethering experiments, crabs died in < 1 h, whereas during the afternoon or night (i.e., lower stress period), all crabs survived. During the experiments in which crabs died, they were not preyed upon. Crabs were also not eaten during the afternoon or nocturnal experiments, when potential predators (e.g., raptors, mice, and weasels) were more active. Potential predators of crabs include endemic species that are active all year long (e.g., *Polyborus plancus*, Crested Caracara; *Milvago chimango*, Chimango Caracara; *Athene cunicularia*, Burrowing Owl). The tethering experiments were performed within the breeding season of these potential predators. Given that feeding activity is usually more intense during breeding periods, our results may be showing the highest predatory effect of the year. This result suggests that predation (including cannibalism) is weak in the high marsh. Temperature stress is likely to be the main factor regulating crab survival in the high marsh, and plant cover modulates this physical factor. Therefore, plant cover appears to be the main factor regulating the

establishment and permanence of crabs in the high marsh, especially during warm periods.

Positive interactions in intertidal communities

Although community structure was, for several decades, considered to be primarily a result of negative interactions, accumulating evidence shows that a combination of positive and negative interactions may be responsible for structuring most communities (e.g., Bertness and Yeh 1994, Hacker and Bertness 1996, Holmgren et al. 1997, Callaway and Walker 1997). Although facilitation and mutualism may occur more frequently than negative interactions in many ecosystems, they generally are not seriously considered in discussions of the processes responsible for community structure (Jones et al. 1997).

A strong pattern of association between plants and crabs was described in the middle marshes of New England (USA) salt marshes, but the proposed mechanism was that *Spartina alterniflora* facilitates fiddler crab burrowing by stabilizing substratum (Bertness 1985). Nomann and Pennings (1998) also found a similar pattern of association between plants and crabs within the high marsh of Georgia (USA), but the proposed mechanism was again different, suggesting that crabs associated with plants to avoid predators. However, these authors did not conduct tethering experiments in different habitats to evaluate survival, and they may have overlooked positive effects of vegetation on crab survival. More recently, Bertness (1999) documented that amelioration of physical conditions by algal canopies has strong positive effects in rocky intertidal communities by enhancing the recruitment, growth, and survival of intertidal organisms. We found that in high marshes of the Mar Chiquita coastal lagoon (Argentina), plant cover drives the spatial distribution of the dominant macroinvertebrate through facilitation, by buffering crabs from harsh, stressful environmental conditions. Thus, positive interactions can have large effects on animal distributions in intertidal communities, and the importance of these effects should no longer be ignored in discussions of intertidal community ecology.

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