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Direct and indirect effects of burrowing crab *Chasmagnathus granulatus* activities on erosion of southwest Atlantic *Sarcocornia*-dominated marshes

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Abstract

Using field measurements and field experiments, we investigated the effect of a dominant Southwest Atlantic intertidal burrowing crab, *Chasmagnathus granulatus*, on the inland growth of tidal creeks and creek genesis in salt marshes. By burrowing intensively on marsh sediments, this crab changed sediment physical parameters, such as penetrability, water content, and shear strength, which are related to sediment resistance to erosion. There were positive relationships between crab density and activities occurring in the creek heads and creek growth rates. Field experiments show that the presence and activity of *C. granulatus* and the presence of their burrows enhance the growth rates of tidal creeks, promoting marsh erosion. When crabs were present, these creeks grew faster than did creeks in which crabs were excluded. Furthermore, the interaction (disturbance and herbivory) between crabs and the dominant halophyte marsh plant, *Sarcocornia perennis*, generate circular depressions that accumulate standing water (salt pans), which in turn facilitates the creation of new creeks in the marsh surface, which evolve, to a greater extent, into fully functional tidal creeks because of colonization by crabs, which in turn further enhances creek growth rates. These direct and indirect effects of crabs on marsh erosion provide strong evidence of the importance of bioturbation and biological processes to the erosion and geomorphology of marshes.

Although it has been claimed that salt marshes protect shorelines from erosion (van Eerdt 1985; Adam 1990) and are important natural dissipators of tidal currents and waves (Möller and Spencer 2002), salt-marsh erosion has recently been reported (Allen 2000). Marshes can become more dissected by creeks, existing creeks may widen, and marshes can retreat laterally (Pethick 1992). Physical factors, such as wind action, wave energy, and high tides, are largely responsible for increased salt-marsh erosion rates (van der Wal and Pye 2004). However, biological factors that interact with physical forces (Talley et al. 2001; Hughes and Paramor 2004) can also play an important role in the erosion of salt marshes (Wolters et al. 2005). The activity of infaunal organisms can remove large surfaces from creek banks (e.g., crabs [Letzsch and Frey 1980]; polychaetes [Hughes 1999]). Herbivory by polychaetes, amphipods, and gastropods may negatively affect the establishment of pioneer plants, thus increasing sediment erodibility (Hughes 2001). Burrowing isopods could also reduce sediment stability and induce marsh erosion (Talley et al. 2001). These studies show that, via direct and indirect mechanisms, invertebrates that inhabit salt marshes may promote erosion. Thus, in reviewing those processes that

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affect salt-marsh erosion, biological processes must be considered alongside physical processes (Hughes and Paramor 2004; Paramor and Hughes 2004).

A common erosive mechanism in salt marshes is the growth of tidal creeks (Allen 2000). Many studies have investigated the hydrodynamic and transport processes inside channel networks (e.g., Davidson-Arnott et al. 2002), but only a few have attempted to understand the genesis and development of these creeks (i.e., Perillo et al. 1996; Allen 2000; Perillo et al. 2005). However, there is evidence that the genesis of tidal creeks could be influenced by both physical and biological factors (e.g., southwest Atlantic salt marshes [Perillo and Iribarne 2003*a*]; southeast England salt mashes [Hughes and Paramor 2004]). There is evidence that creeks, formed initially by water drained from the marsh, can be quickly colonized by invertebrates, and under certain circumstances, these invertebrates can accelerate erosion (Hughes 1999). Burrowing by animals has long been recognized to influence and alter the geotechnical properties of the sediment matrix in intertidal environments (e.g., Meadows and Meadows 1991; Murray et al. 2002). Furthermore, burrowing activities have been reported to weaken the mud and clay banks of salt marshes, thus rendering them more susceptible to erosion by wave action and creek flows. Within salt-marsh sediments, crabs form the most permanent (and active) burrow structures in several marshes worldwide (e.g., Bertness 1999; Bortolus and Iribarne 1999).

The vegetation of the salt marshes of the southwest Atlantic (from 28°S in the south of Brazil to 44°S in Argentina) is dominated by species of *Spartina* and *Sarcocornia* (Isacch et al. 2006). The burrowing crab *Chasmagnathus granulatus* is abundant (e.g., Iribarne et al. 1997) in tidal plains and salt marshes vegetated by species of *Spartina* and *Sarcocornia* (e.g., Iribarne et al. 1997; Bortolus and Iribarne 1999). The crabs build and maintain semipermanent, open burrows, and their activity oxygenates the marsh sediment, increases drainage, and alters mechanical sediment properties such as penetrability, shear strength, water content, and organic matter content (Botto and Iribarne 2000). Crabs are mainly deposit feeders when they inhabit mudflats, but they shift to herbivory on vascular halophytic vegetation when they inhabit vegetated marshes (Iribarne et al. 1997). While constructing and maintaining burrows, these organisms excavate large quantities (up to 5 kg m^{-2} d^{-1}) of sediment (Iribarne et al. 1997), which is deposited on the surface in mounds susceptible to erosion (Botto and Iribarne 2000). Crabs are widely distributed in both marsh and creek margins, reaching high burrow densities (up to 60 burrows m^{-2}; Iribarne et al. 1997). Some recent studies demonstrated that *C. granulatus* facilitate stream and creek formation in southwest Atlantic coastal wetlands (Perillo and Iribarne 2003*a*; Perillo et al. 2005). However, while studies indicate that their effect on salt-marsh erosion may be important, this effect has never been quantified.

Physical and biological processes have also been related to salt-pan formation and expansion (Perillo et al. 1996; Perillo and Iribarne 2003*b*). Although salt pans are common features in salt marshes, they are rarely related to creek formation (Perillo et al. 1996; Perillo and Iribarne 2003*a*). For example, salt marshes at the Bahía Blanca Estuary (Argentina, 38°50′S, and 62°30′W; Fig. 1) are dominated by *Spartina alterniflora* and *Sarcocornia perennis* (formerly known as *Salicornia ambigua*) (Isacch et al. 2006). A set of biological interactions between *C. granulatus* and *S. perennis* may induce the formation of salt pans in the marsh. *S. perennis* may facilitate marsh colonization by crabs, and when crabs reach high densities beneath plants they may disturb and promote die-back of plants as a result of sediment reworking. These salt pans are widely distributed over the marsh, occupying up to 50% of the marsh area (Minkoff et al. 2006). Clones of *S. perennis* are concentrated in a ring along the outer portion of the pan, with dead plants at the central part; vegetated borders and

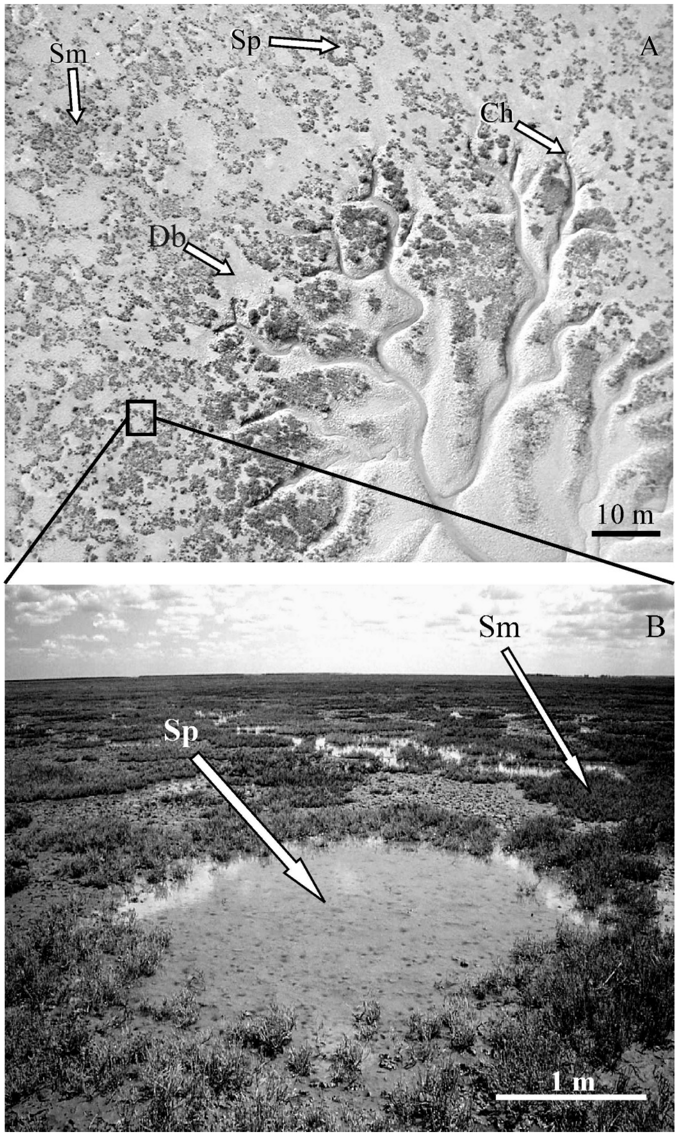

Fig. 1. Photographs of the salt marshes at Bahía Blanca Estuary: (A) Vertical air photograph showing the tidal creeks (Ch), salt pans (Sp), salt marsh (Sm), and creek drainage basins (Db) and (B) oblique photograph of a salt pan densely excavated by crabs and delimited by plants.

unvegetated centers of the salt pans are densely excavated by crabs, reaching densities of up to 70 burrows m^{-2} (Perillo and Iribarne 2003*a*). As a result of continuous reworking of sediments by crabs, the pans start to sink and accumulate water, even during low tides. These circular pans are continuously expanding in size and may eventually collapse and merge with adjacent pans, forming different configurations (Perillo and Iribarne 2003*a*). However, water trapped in the pans has the potential to drain to some nearby, preexistent creek if the substrate at the pan edge is removed (i.e., plant removal during storm tides, substrate loss). Thus, new flow areas are created in the marsh surface, and these areas continue to drain even during low tide because of the standing water accumulated in the salt pans.

In this context, the main goal of this work was to investigate the potential role of the burrowing crab *C. granulatus* in the erosion of salt marshes of southwest Atlantic estuaries. With this purpose, we address the following questions: (1) How are crabs spatially distributed in the salt marsh? (2) Are there differences in burrow architecture in different hydrodynamically defined sites of the marsh? (3) Which geotechnical parameters of the marsh sediment do crabs alter? (4) Can crab activities affect salt-marsh erosion by tidal creeks? (5) Can crabs indirectly (i.e., by salt-pan generation) affect tidal creek genesis in the marsh?

Materials and methods

Study site—The study was performed at the Bahía Blanca Estuary, an extensive habitat (2,300 km^2) affected by up to 4-m tides (Perillo and Piccolo 1999) and characterized by a series of major northwest–southeast tidal channels separated by extensive tidal flats, salt marshes, and islands, constituting a mesotidal coastal plain system (Perillo and Piccolo 1999; Perillo et al. 2005). The creek edges and laterals and most of the marsh area are dominated by the burrowing crab *C. granulatus* (e.g., Iribarne et al. 1997; Bortolus and Iribarne 1999). The salt marsh studied is characterized by dendritic networks of low-order creeks (Fig. 1A) and is vegetated by the halophyte *S. perennis*. This species interacts with crabs, generating ring-shaped patches (hereafter referred to as "salt pans"; Perillo and Iribarne 2003*a*) that accumulate standing water (Fig. 1B). These pans cover approximately 50% of the marsh surface (Minkoff et al. 2006).

Burrow density, spatial distribution, and architecture in the salt marsh—A field survey was performed with the purpose of determining the spatial distribution of crab burrows in different hydrodynamically defined sites of the salt-marsh environment. Sites selected were tidal creek heads (i.e., ends of tidal creeks in the marsh surface, hereafter called "Ch"), creek drainage basins (i.e., unvegetated areas in the marsh surface contiguous to creek heads, hereafter called "Db"), interior marsh (i.e., vegetated internal areas of the marsh, hereafter called "Sm"), salt pans (i.e., circular depressions in the internal marsh surface, hereafter called "Sp"). The different sites were visually identified (Fig. 1A). Burrow densities were surveyed by counting inside square quadrats (0.5 × 0.5 m) that were randomly located in all sites ($n = 10$ for each site); active burrows were also identified (i.e., burrows with recently removed sediment, prints, or presence of crabs) and recorded. This procedure was repeated seasonally for 2 yr (10 times from April 2002 to August 2004). The null hypothesis of no differences in mean burrow densities between sites and seasons was evaluated using two-way analysis of variance (ANOVA), with sites and seasons as fixed factors (Zar 1999). If a significant interaction was obtained, the main effects of fixed factors were not considered since this indicates lack of independence (Underwood 1997). In the case of significant differences with ANOVA, a posteriori multiple-comparison tests (Tukey test; Zar 1999) were used to identify significant differences. For all statistical analyses, monotonic transformations were used when assumptions were not satisfied (following the methods of Underwood [1997] and Zar [1999]). The requirements of data normality and homoscedasticity required by ANOVA and other parametric tests (i.e., the *t*-test) were tested with the Shapiro–Wilk (test for normality) and Bartlett's (test for homoscedasticity) tests before and after transforming data. We corrected all of the *p*-values of all Tukey tests for Type I error by applying the sequential Bonferroni technique. The Welch approximation t_c-test for unequal variances (Zar 1999) was used when the requirement of homoscedasticity was not met in the standard *t*-test (Zar 1999).

Two studies were performed to describe burrow architecture variables in the salt-marsh habitat. To determine the architecture of crab burrows in relation to their position in the salt marsh (i.e., Ch, Db, Sm, and Sp), 15 burrows for each site defined above were randomly selected and were then filled with expansible polyurethane foam and were left to harden for at least 3 h. The casts of burrows were then extracted, and the maximum length and width of individual burrows, burrow openings, number of connections, and total volume (by water displacement) were estimated from these casts. The null hypothesis of no difference in burrow architecture variables between sites was evaluated using ANOVA (Zar 1999). Finally, to determine the interconnection between burrows, ten 1-m^2 quadrats were randomly located on the surface of each site; the total number of burrows within the squares was then registered. In the central part of each unit, one burrow entrance was filled with a solution of rhodamine dissolved in filtered estuarine water (3 liters for each square). After 10 min, the number of burrows with evidence of rhodamine was counted, and the percentage of interconnection between burrows was calculated as the number of burrows with traces of rhodamine as a proportion of the total number of burrows in the plot. Thus, a value of 100% indicates that all burrows in the plots were interconnected. Differences in mean percentages of burrow interconnections between sites were evaluated using ANOVA (Zar 1999).

Effects of burrows on the physical properties of the sediment—Sediment physical properties could be modified by the activity of organisms (e.g., bioturbators), and some of these properties could affect the resistance of the sediment to erosion (e.g., Widdows et al. 2000). *C. granulatus* promotes changes in physical properties of low intertidal sediments (Botto and Iribarne 2000). In those areas, the sediment excavated has higher penetrability, lower shear strength, and higher water content than does sediment without crabs. Given these results, it is also expected that *C. granulatus* affects sediment structure and quality at the marsh edge where heads of tidal creeks are present.

To evaluate the effect of crab activities on marsh sediment properties, we measured penetrability, shear strength, percolation rate, water content, and organic matter content. We randomly selected zones of the salt marsh between 1 and 2 m from the heads of the creeks and noted the presence or absence of crabs. A total of 20 samples or readings were obtained from each zone (with and without crabs). Penetrability was measured using a hand penetrometer and was calculated as the pressure (kg cm^{-2}) necessary to compress the spring of a piston that was forced into the sediment to a standard depth (head of the penetrometer was a flat cylinder, 25 mm in diameter). A Torvane shear-strength meter was used to measure resistance to torsion (i.e., the amount of torsional force needed to shear the top 1 cm of sediment). Percolation rates were measured with an open-ended, graduated, acrylic cylinder (5-cm diameter, 600-mL volume) that was inserted 2 cm into the sediment and then filled with filtered estuarine water. The volume of water draining into the substrate per unit of time was then recorded during a 10-min period. Randomly located sediment samples (corers of 5-cm diameter, 20-cm depth) were collected at each zone. Wet weight was determined using an analytical balance (precision, 0.0001 g), and after drying in a stove (60°C) to constant weight, the sample's dry weight was determined. The difference between wet and dry weights was then considered to indicate water content. In order to determine percent combustible organic matter, a subsample (10 g) was obtained from the original cores and then sieved thought a 2-mm mesh (separating out roots and rhizomes). These sediments were incinerated (at 550°C for 8 h) and weighed to obtain percentage of ash-free dry weight (AFDW) as a measure of organic matter content. The null hypothesis of no differences in the mean values of these variables between zones with and without crabs was evaluated using *t*-tests (Zar 1999).

Additionally, a field experiment was performed in the marsh to evaluate the hypothesis that crabs are actually affecting sediment properties. Twenty quadrats (1 m^2) were marked in areas without burrows at the marsh edge surface. Artificial burrows were excavated (60 burrows per plot with homogeneous distribution) on half of those plots using a plastic corer (60-mm diameter, 50-cm depth), and crabs were added to each artificial burrow. The permanence of crabs in artificial burrows was periodically assayed and maintained (*see* Iribarne et al. 2005). The rest of the plots were not excavated and served as controls that were maintained without crabs or burrows. After 1 yr, sediment properties were measured in treatment and control plots. Paired *t*-tests (Zar 1999) were used to evaluate the null hypothesis of no difference in sediment properties between crab-inhabited and control plots.

Relationship between crab activities and creek elongation—If the bioturbation activity modifies physical properties of marsh sediments, it would be expected to increase erodibility and thus affect tidal creek growth patterns. To evaluate the relationship between crab excavation activities and the growth of tidal creeks, we randomly chose 50 heads of tidal creeks. Linear inland growth (i.e., elongation) of tidal creeks was recorded monthly for 2 yr (from March 2002 to April 2004). Reference stakes were placed around the creek heads. A differential GPS and theodolite topographical survey was performed to determine the positions of the reference stakes. A 50-cm–long (4-mm–diameter) steel rod was inserted into the substrate at the edge of the creek head. Every month the distance from the steel rod to the reference stakes was determined. In the case of head retreat, the steel rod was removed and placed in the new position, again determined in relation to the reference stakes. Tidal creek growth rates were then calculated and expressed as landward growth by month. Burrows densities were recorded monthly from each creek head at which growth measures were done; percentage of active burrows was also recorded, as previously described. The relationships of tidal creek growth rates (cm yr^{-1}) to mean burrow densities and total number of active burrows were evaluated using linear regression models (Zar 1999).

Erosion experiments—A field experiment was performed from September 2002 to August 2004 to evaluate if the presence of crabs in the heads of tidal creeks could affect creek growth rates. We used a crab exclusion–inclusion experimental approach to quantify these effects. A set of 20 plastic-wire cages (1-cm mesh, 60 × 60 cm wide and 50 cm tall) were placed in 20 randomly selected drainage basins of tidal creeks. Half of the cages were pushed 10 cm into the substrate to exclude crabs and were maintained without crabs and burrows during the experiment, while the rest of the cages were placed in the substrate with openings in the cage base to permit crab colonization and were used as control cages. Creek growth was measured monthly for both treatments using the methodology described above; at the end of the experiment creek growth rate and total growth (cm) were calculated. The null hypotheses of no differences in mean creek growth rates and total growth in heads of creeks with and without crabs were evaluated using one-tailed *t*-tests (Zar 1999).

Biologically generated salt pans (i.e., result of crab–*Sarcocornia* interaction; Perillo and Iribarne 2003*b*) may serve as water reservoirs during low tides. However, initiation of new creek heads may depend on availability of water flows draining from the marsh surface to the creeks. Thus, salt pans may be responsible for the formation of new creek heads and their extension at the marsh edge, given that the retained water may drain to a nearby creek (e.g., with vegetation die-back or sediment removal from the salt-pan edge). This pattern is commonly observed in salt marshes of the Bahía Blanca Estuary (pers. obs.). To test this hypothesis, an experimental manipulation was carried out in the salt marsh. Twenty randomly selected salt pans were artificially drained to the nearest creek edge. Artificial drainage was generated by removing the two superficial centimeters (20-cm width) of the substrate from the pan edge to the creek edge. Plastic mesh cages (1-cm mesh) were installed in these artificially generated drainage zones. Half of these cages were pushed into the sediment in order to exclude crab colonization, while the rest of the cages were placed in the substrate with openings in the cage base to allow crab colonization and were used as control drainage zones. In each experimental unit, crab burrows were counted every month to determine the percentage of active burrows. Erosion of the artificially drained zones was also monitored monthly as deepening of the created grooves and inland growth of new creek heads if they appeared. The null hypotheses of no differences in mean creek growth rates and total growth in artificially generated drainage zones with and without crabs were evaluated using *t*-tests (Zar 1999).

Results

Burrow density, spatial distribution, and architecture in the salt marsh—Burrow density was higher in salt-marsh edge sites (i.e., creek heads and drainage basins) than in interior salt-marsh sites (i.e., salt marsh and salt pans) during the year (two-way ANOVA interaction: $F_{9,464}$ = 2.82, p = 0.003; Fig. 2A). The main effects of season and salt-marsh site were not considered since the significant interaction between these factors indicates that they are not independent (Underwood 1997). Crab densities decreased during autumn, reaching their lowest values in winter, and this pattern was less accentuated for creek-head sites, which maintained high burrow densities even during winter (Fig. 2A). In the salt-marsh sites, crab burrow densities did not vary significantly during the year and for all seasons showed lower values than the other sites (Fig. 2A). The percentage of active burrows also showed differences between sites and seasons (two-way ANOVA interaction: $F_{9,464}$ = 2.18, p = 0.002; Fig. 2B). For all sites that showed significant differences among seasons, burrow activity showed the highest values during summer. Creek heads and drainage basins showed high percentages of active burrows over the whole year; however, maxima for both sites were registered during summer (Fig. 2B).

Burrow architecture varied significantly between sites. Burrow lengths were longer in salt-marsh and salt-pan than in creek-head and drainage-basin sites, where the shortest lengths were registered (ANOVA: $F_{3,56}$ = 3.80, p = 0.014; Fig. 3A). The maximum width of crab burrows also showed higher values in salt marshes and salt pans than in creek heads and drainage basins (ANOVA: $F_{3,56}$ = 3.28, p = 0.027; Fig. 3B). The smallest burrow widths were registered on the drainage-basin sites. Total volumes of burrows established in salt-marsh and salt-pan sites were higher than those of burrows present on creek heads and drainage basins (ANOVA: $F_{3,56}$ = 4.75, p = 0.03; Fig. 3C). Burrows constructed on the marsh-edge sites (creek heads and drainage basins) had higher numbers of connections with neighboring burrows than burrows occurring at salt-marsh and salt-pan sites (ANOVA: $F_{3,56}$ = 17.0, $p = 5 \times 10^{-6}$; Fig. 3D). Similarly, rhodamine assay showed that percentages of interconnected burrows were higher in the creek heads ($\bar{x}$ = 76.5%, standard deviation [SD] = 29.9%) than in the other sites, reaching their lowest values in salt-pan sites ($\bar{x}$ = 30.7%, SD = 17.7%; ANOVA: $F_{2,27}$ = 3.76, p = 0.036).

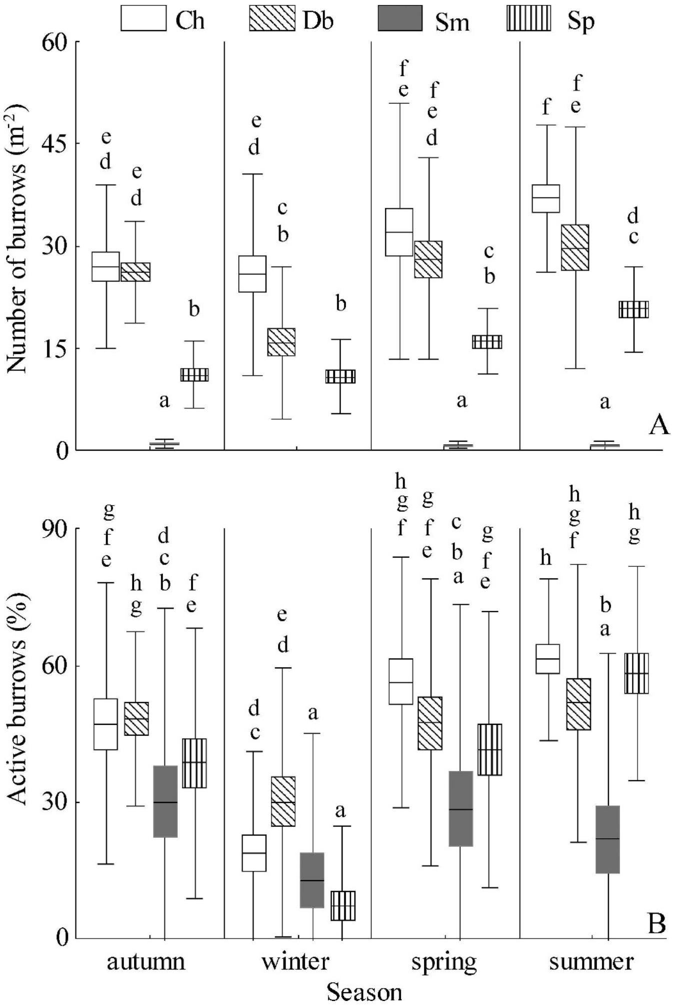

Fig. 2. (A) Number of crab burrows and (B) percentage of active burrows within a 1-m^2 sampling unit in creek heads (Ch), creek drainage basins (Db), internal salt marsh (Sm), and salt pans (Sp) during the year. Lines inside boxes are mean values, box limits are standard errors of the mean, and error bars represent nonoutlier ranges. Different letters denote significant differences (p < 0.05) between groups of data (ANOVA interaction effects).

Effects of burrows on the physical properties of the sediment—Both direct measurements and experimental manipulations demonstrated effects of *C. granulatus* burrowing activities on salt-marsh sediment properties. Penetrability was higher (i.e., lower pressure necessary to penetrate the sediment) in naturally crab-inhabited zones than in zones without crabs (t_c = −7.97; df = 38; $p = 1 \times 10^{-9}$; Fig. 4A). In addition, the experiment of crab inclusion showed that crabs could change sediment penetrability. When they were included, the mean force

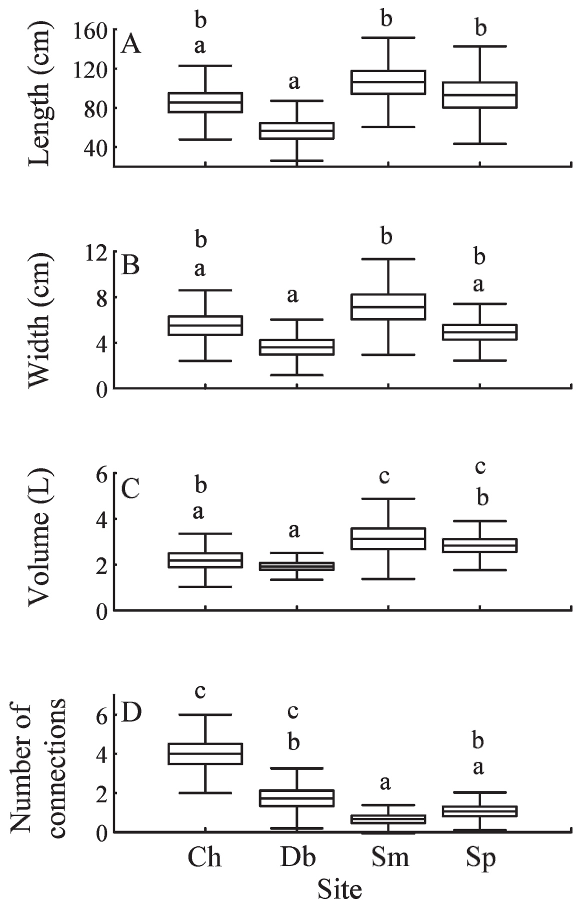

Fig. 3. Burrow morphometric variables measured in polyurethane casts; different panels represent (A) burrow length, (B) width of the burrow entrance, (C) total volume of burrows, and (D) number of connections with adjacent burrows for creek heads (Ch), creek drainage basins (Db), internal salt marsh (Sm), and salt pans (Sp). Lines inside boxes are mean values, box limits are standard errors of the mean, and error bars represent nonoutlier ranges. Different letters denote significant differences ($p < 0.05$) between sites.

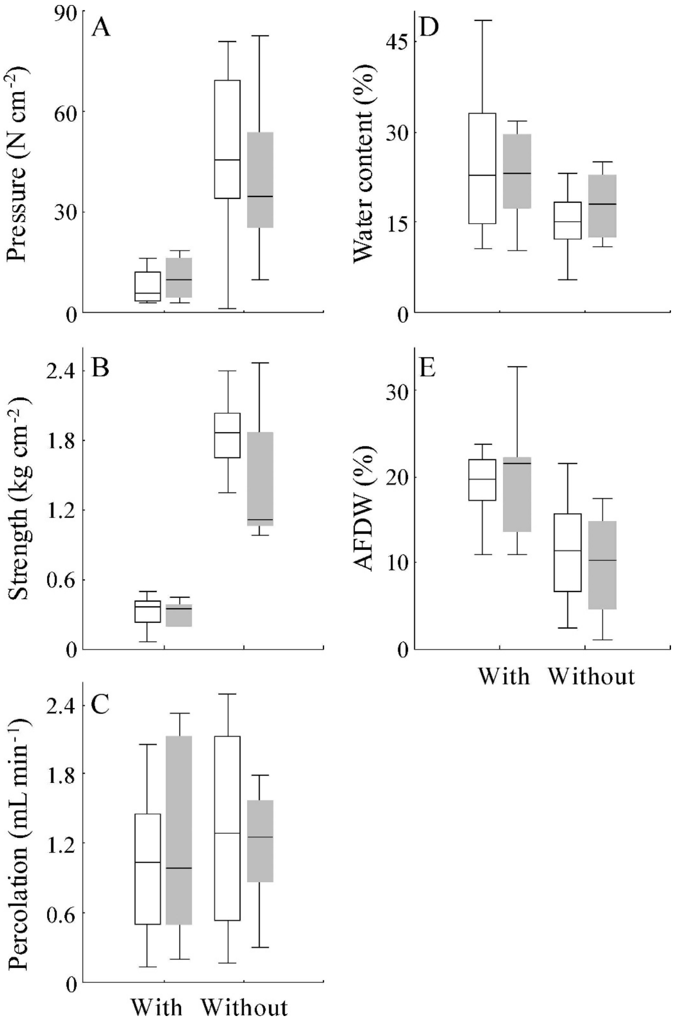

Fig. 4. Open boxes represent sediment geotechnical properties in natural sites with presence and absence of crabs, and closed boxes show sediment geotechnical properties in experimental units for treatments of crab inclusion and control plots (i.e., crab exclusion). Different panels represent (A) the pressure necessary to penetrate the sediment, (B) the sediment shear strength, (C) the percolation rate, (D) the sediment water content, and (E) the ash-free dry weight of sediments. In all cases boxes contain 50% of data (percentile 25–75), and vertical bars include the minima and maxima; lines inside boxes indicate the medians.

required to penetrate the sediments was reduced to less than 20% of that in control areas ($t_c = -3.74$; df = 18; $p = 0.0014$; Fig. 4A). Sediment shear strength was 3.9–5.0 times higher in zones without crabs than in those with crabs ($t_c = -20.65$; df = 38; $p = 3 \times 10^{-22}$; Fig. 4B). Similarly, after 1 yr of experimentation shear strength was lower in treatments of crab inclusion than in control areas without crabs ($t_c = -6.28$; df = 18; $p = 6 \times 10^{-5}$; Fig. 4B). Percolation rates varied significantly neither between zones with and without crabs ($t_c = -1.64$; df = 38; $p = 0.12$; Fig. 4C) nor between inclusion treatments and controls ($t_c = 0.25$; df = 18; $p = 0.8$; Fig. 4C). Sediment water content and AFDW were higher in zones with crabs than in those without crabs (water content: $t_c = 3.02$; df = 38; $p = 0.004$; AFDW: $t_c = 5.27$; df = 38; $p = 6 \times 10^{-5}$; Fig. 4D,E). Although water content did not differ significantly between crab inclusion treatments and controls ($t_c = 1.8$; df = 18; $p = 0.07$), AFDW was different between treatments after 1 yr ($t_c = 3.7$; df = 18; $p = 0.0014$).

Relationship between crab activities and creek elongation—A positive relationship was found between mean burrow density and creek growth rates ($r^2 = 0.49$; b = 0.68; $\mathrm{SD_b} = 0.13$; $F_{1,28} = 27.02$; $p = 1.5 \times 10^{-5}$; Fig. 5A). In addition, there was a positive relationship between percentage of active burrows and creek growth rates (b = 0.53; $\mathrm{SD_b} = 0.10$; $F_{1,28} = 24.32$; $p = 3.3 \times 10^{-5}$; Fig. 5B); in this case, the variation in the percentage of active burrows could explain 46% ($r^2 = 0.46$) of the variation of tidal creek growth rates.

Erosion experiments—The first experiment revealed a strong effect of crab presence and activity on creek growth rates and the consequent erosion of existing marsh structures. Creek growth rates (cm month^{-1}) were higher

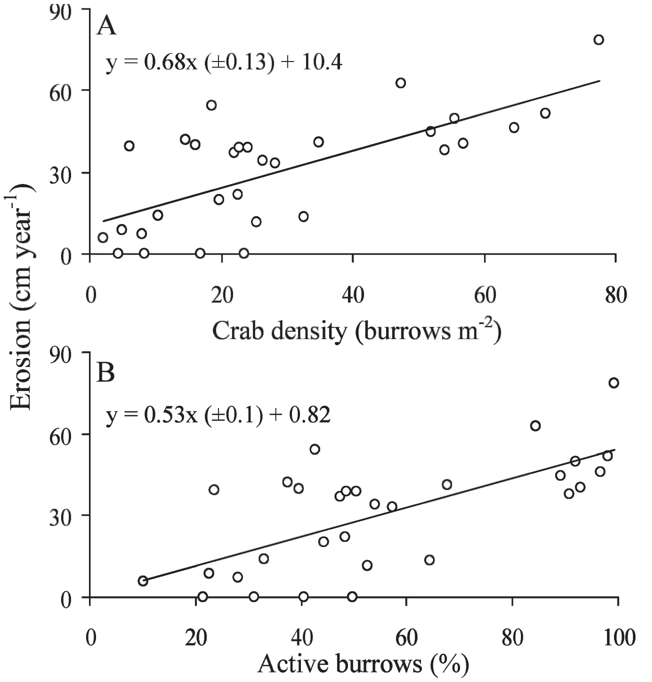

Fig. 5. Relationship between tidal creek growth rate and (A) burrow densities in creek heads and (B) percentage of active burrows in the same sites.

in control cages than in crab exclusion cages ($\bar{x}_{\mathrm{control}}$ = 3.18 cm month^{-1}, SD = 1.47; $\bar{x}_{\mathrm{exclusion}}$ = 0.34 cm month^{-1}, SD = 0.36; t_c = 5.94; df = 10; p = 0.00014). Furthermore, at the end of the experiment, creeks ended in crab exclusion cages showed lower total creek elongation (landward growth) than did control, crab-inhabited cages ($\bar{x}_{\mathrm{control}}$ = 79.9 cm, SD = 37.5; $\bar{x}_{\mathrm{exclusion}}$ = 8 cm, SD = 8.69; t_c = 5.99; df = 10; p = 0.00013).

New tidal creek heads appeared when salt pans were drained to existing creek edges. In control treatments, crabs rapidly started to colonize the artificially generated drainage zones. Rates of crab colonization were on the order of 11 burrows m^{-2} month^{-1} (SD = 5, n = 10), and they reached final densities of up to 90 burrows m^{-2} in this treatment. New, fully functional tidal creek heads were registered in control treatments after the first summer; 90% of the replicates developed new heads. Artificially drained zones became deeper ($\bar{x}$ = 2.6 cm month^{-1}, SD = 0.85 cm month^{-1}, n = 10) at the natural creek edge and increased their length inland ($\bar{x}$ = 5.2 cm month^{-1}, SD = 1.94 cm month^{-1}, n = 10). However, in crab-exclusion drainage zones, creek heads appeared after 19 months only in 30% of the cases (n = 10) and extended inland at lower rates than in control treatments ($\bar{x}$ = 0.33 cm month^{-1}, SD = 0.1 cm month^{-1}; t_c = 8.4, df = 9, $p = 2.1 \times 10^{-5}$). At the end of the experiment, control zones (i.e., those with crabs) were capable of developing real tributaries of up to 1.5 m in length ($\bar{x}$ = 1.10 m, SD = 0.3 m, n = 10).

Discussion

Our results show that the crab *C. granulatus* is widely distributed in *Sarcocornia*-dominated salt marshes. *C. granulatus* appears to have specific microhabitat preferences for salt-marsh edges and drainage basins in tidal creeks. Furthermore, burrow architecture differs between microhabitats, and burrowing activities modify sediment geotechnical properties. Erosion of the salt marsh mediated by tidal creek growth was accelerated as a result of crab burrowing activities. In addition, direct effects of crabs on creek growth rates and indirect effects of crab activities on creek generation were experimentally demonstrated.

C. granulatus burrows are present in *Sarcocornia*-dominated salt marshes, as in southwest Atlantic tidal flats and *Spartina*-dominated salt marshes (Iribarne et al. 1997). However, there are some differences in their local distribution over these marsh types. Burrow densities were higher in the salt-marsh edge (i.e., tidal creek banks and heads and drainage basins) than in the internal salt-marsh microhabitats. Burrows occur just below *Sarcocornia* canopy areas (i.e., substrate area underneath plant aerial structures) and inner parts of salt pans in the internal salt-marsh area. Thus, crab-burrow spatial distributions become patchier in *Sarcocornia* than in *Spartina* marshes; in these *Spartina* marshes the burrows are also associated with plant canopies, but in this case the vegetation is less patchy than in the case of *Sarcocornia*, which results in a more uniform burrow distribution over the marsh surface. Some difficulties arise when assessing which characteristics of these habitats (e.g., hydrodynamic conditions, tidal height, marsh-edge morphology, and plant distribution) are causing these contrasts. However, plants facilitate crab colonization and burrowing of the marsh by buffering stress conditions and keeping sediment moist (Bortolus et al. 2002). Desiccation can be a fundamental factor in the survival of this species (Bortolus et al. 2002). When crabs abandon their burrows they can die quickly within days from high temperatures during summer (up to 40°C at the soil level in the estuary; Beigt et al. 2003). Sites preferred by crabs are more frequently flooded than is the internal salt marsh; potential for desiccation seems to be the reason for this difference. Furthermore, our observations indicate that crabs prefer sites such as tidal creek heads and drainage basins, where water continues flowing even during low tides and accumulates after rainy days.

Burrow architecture differed between salt-marsh sites influenced by different hydrodynamic conditions. Burrows of up to 1 m in length were found in internal salt-marsh areas, while burrows reached only 60 cm at marsh-edge sites. Similarly, *C. granulatus* constructs deeper burrows in *Spartina*-dominated marshes than in open mudflats (Iribarne et al. 1997), showing that crabs change the depth of their burrows in order to reach phreatic water levels (Bortolus and Iribarne 1999). Burrow volume was higher in internal salt-marsh sites than in salt-marsh edges. Thus, it is reasonable to think that the large differences in burrow depth between these sites may explain this pattern in burrow volume (Iribarne et al. 1997). The internal salt marsh studied is fully flooded only about 40 times per year (Minkoff et al. 2006); thus, burrows of greater depths and volumes allow more water retention during low tides. As do other crustaceans, *C. granulatus* needs to renew respiratory water lost by evapotranspirative cooling and feeding.

Burrows may provide relief from both hot and cold ambient temperatures (Powers and Cole 1976). Burrows also show numerous connections at the salt-marsh edge; maximal burrow densities found here indicate an increased probability of connection with adjacent burrows. This spatial configuration would allow the generation of pressure-driven flows through burrows. Flows through burrows have been documented for other crustacean species (Allanson et al. 1991). For *C. granulatus*, there is evidence that in high-density burrow settings the lateral burrows made by the crab recruits induce a dynamic groundwater flow and the formation of tidal rills when the phreatic water intersects a sloping sediment surface (i.e., channel flank), and even tidal grooves and gullies as the percolates are concentrated by crab burrows (Perillo et al. 2005). Thus, these burrow settings may concentrate groundwater flows coming from the upper marsh and promote the formation of tidal streams in the channel banks.

Our results show that burrowing by *C. granulatus* affects sediment geotechnical properties that are important in defining sediment erodibility (Meadows and Meadows 1991). These results are common effects of burrowing invertebrates (Levinton 1995; Paramor and Hughes 2004). There are animals that directly affect sediment characteristics, mainly bioturbators that are sediment destabilizers (Meadows and Meadows 1991; Widdows et al. 2000). Zones inhabited by *C. granulatus* showed high penetrability and low shear strength. Experimental results imply that these physical characteristics are direct effects on sediment characteristics by crab sediment reworking. The activity of burrow construction may disrupt the cohesive nature of the sediment matrix (Jumars and Nowell 1984). However, it is also possible that at least part of the effect of crabs on the sediment physical properties is indirect (e.g., Daborn et al. 1993) in that they affect microalgal and bacteria colonization and survival because of continuous sediment reworking by burrowing. Microorganism biofilms, the major agents–producing organic matrix that binds the sediment (Austen et al. 1999), may lead to an increase in sediment resistance to erosion (Austen et al. 1999). If this were the case, *C. granulatus* could be indirectly promoting sediment instability by reducing microphytobenthic abundance.

There is mounting evidence that an increase in salt-marsh sediment erosion is caused by invertebrates (Letzsch and Frey 1980; Talley et al. 2001; Paramor and Hughes 2004). However, recent work highlights the lack of information on the relative contributions of physical and biological processes to the initiation and maintenance of creeks in salt marshes (Wolters et al. 2005), even when creek elongation plays a major role in salt-marsh erosion (Paramor and Hughes 2004). Experimental field studies are particularly rare in the literature (Wolters et al. 2005). Our experimental results show that, independently of physical processes, burrowing crabs are actually affecting the growth of tidal creeks and enhancing marsh erosion. Even when physical processes are ultimately responsible for creek elongation (i.e., surface-ebb flows, groundwater flows), the activity of those burrowing crabs that inhabit salt-marsh edge areas could increase creek elongation by more than a 20-fold measure. Modification of sediment properties by *C. granulatus* appears to be largely responsible for these effects. Our results show that sediments inhabited by crabs have a higher water content and are softer, as indicated by decreases in both forces required for penetration; they may be more easily eroded by ebb currents and wind-induced wave activity. Furthermore, the continuous sediment reworking during burrow excavation and maintenance loosens sediment that is then removed by water motion and tidal currents. Thus, both sediment properties' alteration and sediment exposure to currents and waves could produce a net increase in landward creek elongation. Moreover, burrows are more persistent structures in the marsh edge than are the crabs themselves, so it is expected that erosion continues despite low crab activities, as happens during winter.

There is little evidence explaining how salt-marsh creeks are formed and develop. Recent reviews of such environments comment on their characteristics and function (Pethick 1992; Allen 2000; Mitsch and Gosselink 2000), but they seldom discuss their genesis. However, it has been suggested that the presence of hummocks formed via sediment retention by plants of the genus *Glyceria* (*Puccinellia*) may be a mechanism of channel formation in marshes (Yapp et al. 1917). A concept that seems to be generally accepted is that most channels found in salt marshes are inherited from the former tidal flat. However, formation of channels by interconnection of salt pans and later connection to preexistent channels has been recently described (Perillo et al. 1996). As previously hypothesized (Perillo and Iribarne 2003*a*), our results demonstrate that *C. granulatus* may indirectly generate new tidal creeks in the marsh surface. Salt pans are generated in the marsh surface as a result of the interaction between *C. granulatus* and *S. perennis* (Perillo and Iribarne 2003), and in turn these pans generate water flows in the marsh surface (Escapa pers. obs.). Our results show that once flows are generated, burrowing crabs rapidly colonize the flow zone and enhance erosion. The result is the formation of new, fully functional tidal creeks as branches of preexistent creeks. Most information on the genesis or growth of tidal creeks (i.e., Chapman 1960; Perillo et al. 1996) considers channels to be formed mainly by physical factors. Few studies (e.g., Chapman 1960; Garofalo 1980) have related the influence of biological processes (i.e., growth of salt-marsh vegetation) to the development of tidal creeks. Thus, our finding is also interesting because tidal creek genesis could be related to biological processes (i.e., crab–plant interactions), thereby constituting another example of how organisms play a major role in creek development and salt-marsh geomorphology.

Marshes in Argentina cover a relatively minor portion of the coastline (Perillo and Iribarne 2003*b*; Isacch et al. 2006). Estimates of the vulnerability of the coast to sea-level rise (i.e., Diez et al. 2007) predict that only a few of these environments will be seriously damaged. In particular, the Bahía Blanca Estuary will be inundated for most of the tidal period even during neap conditions. The estuary as a whole has little resilience to withstand sea-level rise, since there is almost no sediment input from the tributary rivers or from the adjacent inner shelf (Perillo and Piccolo 1999; Melo et al. 2003). The estuary is reworking its own sediments, accumulated as a delta during the Late Pleistocene–Early Holocene period, and they are exported to the inner shelf, as the whole estuary is ebb dominated (Perillo and Piccolo 1999). Tidal creeks are advancing in the entire estuary as part of the erosional state of the environment, and the mechanism described here is accelerating marsh dissection by creeks. Thus, crab activities and their interaction with plants are actually promoting creek inland growth. In summary, our results show that bioturbation activity exerted by crabs (i.e., construction and maintenance of burrows) controls salt-marsh geomorphology and has direct effects on salt-marsh erosion, as a result of the acceleration of the growth of tidal creeks, and indirect effects (i.e., mediated by salt-pan genesis) because of the potential to initiate new creeks in the marsh surface.

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