



Sediment dynamics modulated by burrowing crab activities in contrasting SW Atlantic intertidal habitats

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ABSTRACT

Biogenic bottom features, animal burrows and biological activities interact with the hydrodynamics of the sediment–water interface to produce altered patterns of sediment erosion, transport and deposition which have consequences for large-scale geomorphologic features. It has been suggested that depending on the hydrodynamic status of the habitat, the biological activity on the bottom may have a variety of effects. In some cases, different bioturbation activities by the same organism can result in different consequences. The burrowing crab *Neohelice granulata* is the most important bioturbator at SW Atlantic saltmarshes and tidal plains. Because of the great variety of habitats that this species may inhabit, it is possible to compare its bioturbation effects between zones dominated by different hydrodynamic conditions. Internal marsh microhabitats, tidal creeks bottoms and basins, and open mudflats were selected as contrasting zones for the comparison on a large saltmarsh at Bahía Blanca Estuary (Argentina). Crab burrows act as passive traps of sediment in all zones, because their entrances remain open during inundation periods at high tide. Mounds are generated when crabs remove sediments from the burrows to the surface and become distinctive features in all the zones. Two different mechanisms of sediment transport utilizing mounds as sediment sources were registered. In the first one, parts of fresh mound sediments were transported when exposed to water flow during flooding and ebbing tide, with higher mound erosion where currents were higher as compared to internal marsh habitats and open mudflats. In the second mechanism, mounds exposed to atmospheric influence during low tide became desiccated and cracked forming ellipsoidal blocks, which were then transported by currents in zones of intense water flow in the saltmarsh edge. Sedimentary dynamics varied between zones; crabs were promoting trapping of sediments in the internal saltmarsh ($380 \text{ g m}^{-2} \text{ day}^{-1}$) and open mudflats ($1.2 \text{ kg m}^{-2} \text{ day}^{-1}$), but were enhancing sediment removal in the saltmarsh edge (between 10 and $500 \text{ g m}^{-2} \text{ day}^{-1}$ in summer). The implication is that biologically mediated sedimentological changes could be different among microhabitats, potentially leading to contrasting geomorphologic effects within a particular ecosystem.

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1. Introduction

Biological activity has important effects in terrestrial, marine and intertidal sediment structure, either stabilizing or destabilizing these bottom environments (Meysman et al., 2006). For example, in marine and intertidal systems, meiofaunal organisms secrete mucus while feeding (e.g., Riemann and Schrage, 1983;

Klause, 1986), and other organisms produce organic coating in the walls of burrows which enhance sediment cohesion (e.g., Aller, 1983; Watling, 1991). These biostabilization processes largely influence intertidal sediment strength by increasing cohesion mainly through secretion of polymers (Dade et al., 1991; Paterson, 1997). Extracellular polymeric substances (EPS) excreted by microphytobenthic organisms can also increase sediment stabilization (Decho, 2000) by formation of biofilms. However, destabilization of cohesive sediments may be promoted by macrofaunal bioturbation, which directly affects sediment porosity and permeability (Widdows et al., 1998). In addition, invertebrates may consume microphytobenthic organisms thus indirectly promoting sediment destabilization (Daborn et al.,

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1993). Thus, different biological activities can stabilize or destabilize intertidal sediments significantly affecting sediment transport (e.g., Nowell et al., 1981; Wood and Widdows, 2002) and geomorphology (Murray et al., 2002).

Within biological processes, burrowing activity can affect sediment erosion, transport, and sedimentation patterns (e.g., Cadée, 2001). A burrow can be a temporary excavation made by an organism while it slides through sediment or while it settling from the water column (e.g., Jones and Jago, 1993). In both cases, construction of burrows significantly affects the structure of the sediment since the cohesive nature of the sediment matrix is broken during this process (Jumars and Nowell, 1984). Active burrowing species can increase the rates of erosion and the mobility of the sediment, particularly when occurring at high densities (Posey, 1987; Talley et al., 2001; Perillo et al., 2005). While constructing burrows, these organisms bring sediments to the surface where it will be available for transport by currents (Murray et al., 2002) and waves. However, intertidal decapods often construct open burrows with funnel-shaped entrances that facilitate trapping of organic matter and sediment (e.g., Nowell et al., 1981; Suchanek, 1983; Botto and Iribarne, 2000; Botto et al., 2006). Furthermore, it is expected that burrowing activity will have different consequences depending on the hydrodynamic conditions where the activity occurs (see Murray et al., 2002). Thus, in habitats where flow energy has low values, it is expected that burrowing animals will produce trapping of sediments; whereas in habitats with high flow energies the removal rates of sediments could be increased by burrowing activity.

In the SW Atlantic estuaries and embayments, both tidal flats and salt marshes vegetated by species of *Spartina* and *Sarcocornia* are dominated by the burrowing crab *Neohelice granulata* (e.g., Spivak et al., 1994; Iribarne et al., 1997; Bortolus and Iribarne, 1999; Iribarne et al., 2005). This crab species construct vertical burrows of up to 10 cm in diameter (Iribarne et al., 1997; Botto and Iribarne, 2000) that can reach up to 1 m depth in vegetated marshes (Iribarne et al., 1997) where crabs are herbivorous in contrast to tidal flats where crabs are mainly deposit feeders. The burrows remain open during high tide periods and generally remain full of water during low tide (Iribarne et al., 1997; Botto and Iribarne, 2000). Furthermore, these burrows act as passive traps of sediment and detritus in open mud flats (Botto and Iribarne, 2000; Botto et al., 2006). Depending on their plastic morphology (i.e., funnel-shaped entrances or tubular-shaped entrances), these burrows trap both suspended particles and bedload material respectively (Botto et al., 2006). The funnel-shaped entrances and the bed roughness generated by crabs are largely responsible for this effect (Botto et al., 2006). Crabs also remove a large quantity of sediment (up to 5 kg day⁻¹ m⁻², Iribarne et al., 1997) while constructing and maintaining burrows and the excavated sediment is deposited in the surface often forming mounds near burrow entrances (Botto and Iribarne, 2000). Recent studies showed that *Neohelice granulata* may facilitate tidal creek formation and further growth at SW Atlantic salt marshes (Perillo and Iribarne, 2003a; Perillo et al., 2005; Minkoff et al., 2006; Escapa et al., 2007), thus enhancing marsh erosion (Perillo and Iribarne, 2003b).

Thus, to compare the effects that burrowing activities by *Neohelice granulata* has on sediment dynamics in contrasting intertidal habitats (i.e., with different hydrological status) is the main goal of this study. With this purpose we (1) evaluate the distribution, architecture and density of crab burrows in different intertidal habitats inhabited by crabs, (2) quantify the trapping of sediments by burrows in the different habitats, (3) quantify the amount of sediment which is transported due to crab activities, and (4) estimate the balance between sediment trapped and transported due to crab activity in the different habitats.

2. Materials and methods

2.1. Study area

The study was performed at the Bahía Blanca Estuary, a large embayment habitat (2300 km²) affected by up to 4 m semidiurnal tides (Perillo and Piccolo, 1991) and characterized by a series of major NW–SE tidal channels separated by extensive tidal flats, saltmarshes, and islands constituting a mesotidal coastal plain system (Perillo and Piccolo, 1999; Perillo et al., 2005; Fig. 1). Salt marshes are mostly dominated by species of *Spartina* (mainly *Spartina densiflora* and *Spartina alterniflora*) and by *Sarcocornia perennis* (formerly known as *Salicornia ambigua*) as in the majority of the SW Atlantic estuaries (Isacch et al., 2006). Open mudflats, streamside (i.e., creeks ends that dissect the marsh surface) and banks of tidal creeks and most of the inner marsh area are dominated by the burrowing crab *Neohelice granulata* (Iribarne et al., 1997; Bortolus and Iribarne, 1999; Botto et al., 2006). To contrast the effect of crab activities on the sedimentary dynamics in microhabitats subject to different hydrodynamic conditions, four types of habitats were characterized in terms of current velocity using a hand current meter (the current meter was located 10 cm above the bottom level, precision 0.5 cm s⁻¹), 20 independent readings were carried out during the first hour of the ebbing phase of neap tides in each habitat. Thus, the habitats selected were: open mudflats (current velocity during neap tides: $x = 10 \text{ cm s}^{-1}$, SD (standard deviation) = 3 cm s⁻¹, $n = 20$; thereafter called “mudflat”), inner saltmarsh ($x = 8 \text{ cm s}^{-1}$, SD = 3.5 cm s⁻¹, $n = 20$; thereafter called “saltmarsh”), tidal creek bottoms (between one and three meters downstream from the creek head; $x = 40 \text{ cm s}^{-1}$, SD = 8 cm s⁻¹, $n = 20$; thereafter called “creek”), and creek tidal basins (unvegetated areas of the saltmarsh surface that drains toward creeks; $x = 34 \text{ cm s}^{-1}$, SD = 15 cm s⁻¹, $n = 20$; thereafter called “basin”).

2.2. Density and distribution of crab burrows in the intertidal

Field surveys were performed with the purpose of determining the spatial distribution of crab burrows in the different hydrodynamically-defined habitats described above (i.e. “mudflat”, “saltmarsh”, “creek”, “basin”). Burrow densities and size distribution were surveyed using quadrats (0.5 × 0.5 m side) which were randomly allocated in all sites ($n = 20$ samples in each site), counting burrows inside the squares and measuring their diameters. Active burrows were also identified (i.e. burrows with recently removed sediment, prints, or presence of crabs) and recorded. We conducted this sampling during January 2003 (southern hemisphere summer) and repeated in August 2003 (winter), January 2004, and August 2004. These sampling dates were selected to contrast the summer when crabs are very active versus the winter when crabs are mainly inactive (see Section 3), although the burrows often persist during the winter season. The null hypothesis of no differences in burrow density between habitats and seasons was evaluated with Two-way ANOVA, taking habitat and season as fixed factors (Zar, 1999). Main effects were not considered and reported for the two-way ANOVAs when significant interaction between factors was detected, since it indicates that the factors are not independent (see Underwood, 1997), we carried out an *a posteriori* planned comparisons between means in the case of significant interaction effect (Underwood, 1997). For all statistical analyses, monotonic transformations were used when assumptions were not satisfied (following Underwood, 1997; Zar, 1999). The requirements of data normality and homoscedasticity required by ANOVA were tested with the Shapiro–Wilk (test for normality) and Bartlett’s test (test for homoscedasticity) before and after transforming data. We corrected all *p*-values of all Tukey tests for Type I

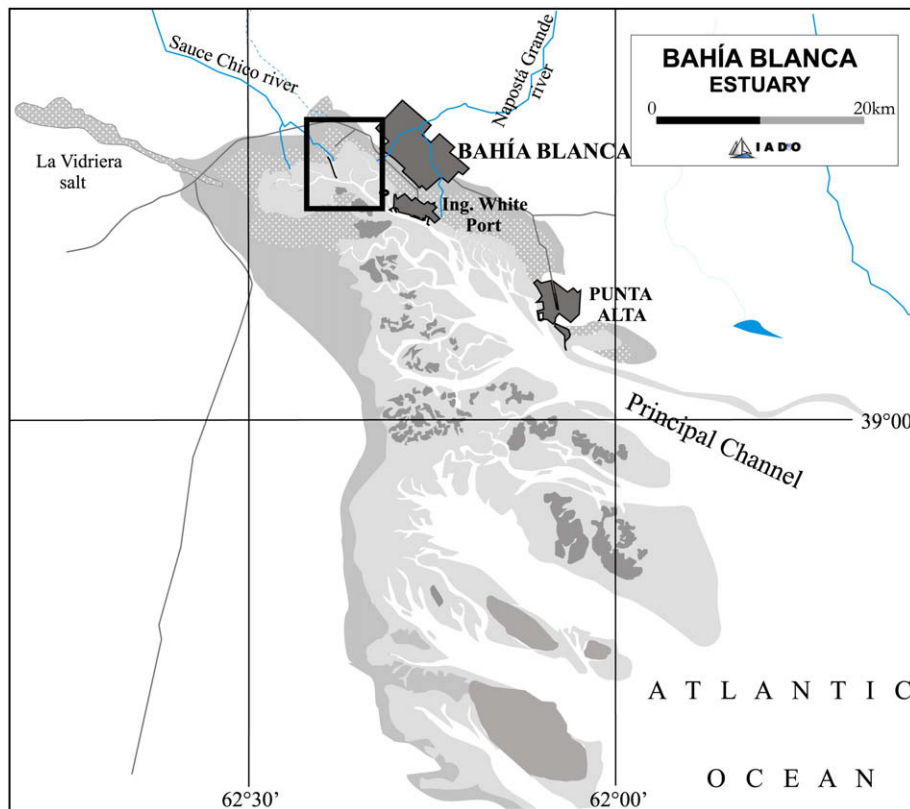


Fig. 1. Map of the study area located in the Bahía Blanca Estuary, Argentina.

error by applying the sequential Bonferroni technique. Size frequency distribution of burrows was evaluated between habitats with Kolmogoroff–Smirnov test (Zar, 1999). Burrow architecture was also evaluated for each habitat; we characterized the burrows inside sample units in two main categories: funnel-shaped entrance burrows (i.e. funnel shape aspect ratio <1 , as funnel depth/entrance diameter) and tubular-shaped burrows (Aspect ratio >1 ; *sensu* Botto et al., 2006). The null hypothesis of no difference in the percentage of burrows with funnel-shaped entrances between habitats was evaluated with ANOVA (Zar, 1999).

2.3. Effect of burrows of *Neohelice granulata* on the trapping of sediment

Burrows of *Neohelice granulata* remain open during high tide periods. To evaluate the effect of individual burrows on the trapping of sediment at sites under different hydrodynamic conditions, we deployed burrow mimics at each habitat described above (“saltmarsh”, “creek”, “basin”, and “mudflat”). Five funnel-shaped burrow mimics were placed in the substrate at each habitat type (entrances of funnel-shaped mimics were 10 cm in diameter with 5 cm of funnel depth, aspect ratio = 0.5). In addition, five tubular-shaped burrow mimics (funnels of 5 cm in diameter and 20 cm depth, aspect ratio = 4) were inserted in the substrate at each habitat type. These mimics were constructed using PVC funnels for the two different diameters, this funnels were inserted in the substrate to reach the surface level. At the end of each funnel, a PVC tube (4 cm diameter, 30 cm depth) was inserted to collect trapped sediment. All mimics were deployed during low tide and filled with filtered estuarine water to avoid sedimentation by incoming water (see Botto et al., 2006). The sediment collected in the mimics was sampled after 2 tidal cycles (i.e. ~24 h) and the experiment was repeated on 5 consecutive tidal cycles in January 2003 and other

five occasions in August 2003 (5 tidal cycles each time). Sediment trapped on the mimics was then dried at 60 °C until constant weight (i.e. ~5 days) and weighed. The null hypothesis of no differences in the sediment mass trapped between different habitats and type of mimic was evaluated using a two-way ANOVA (Zar, 1999) per season.

Sediment trapped by burrows per square meter and tidal cycle (g m^{-2} tidal cycle $^{-1}$) was also calculated as

$$TST_i = ST_i * BD_i \quad (1)$$

where TST is the total sediment trapped (g m^{-2} tidal cycle $^{-1}$), i represents burrow type (i.e., tubular or funnel), ST_i is sediment trapped in a single tidal cycle for each burrow type (g burrow^{-1} tidal cycle $^{-1}$); BD_i are density of tubular or funnel burrows (burrows m^{-2}). To solve equation (1) for each burrow type we used a resampling method (Manly, 1998) that independently resample data of these measured variables for each microhabitat and season without replacement. This procedure allows different combinations of the equation terms that reflect the natural variability of these patterns. The null hypothesis of no differences in the sediment trapped between different habitats and type of burrows was evaluated using a two-way ANOVA (Zar, 1999) per season.

2.4. Sediment removal rate

The sediment removed by crabs would be available to transport, since crabs deposit this material on the surface. Thus, if different quantities of sediment are being deposited in the different habitats it could lead to changes in the availability of sediment to erosion. To explore this possibility the amount of sediment removed per day was evaluated for each burrow category (i.e. funnel- and tubular-shaped) in all habitat types. Twenty burrows for each category were randomly selected and marked (10 cm steel stakes, 1 mm in

diameter) for each habitat type. The sediment deposited near the burrow entrance was then collected (during low tide) and weighed after drying at 60 °C until constant weight. This procedure was repeated for each burrow during three tidal cycles in January 2003 and repeated in August 2003. Sediment removal rate was then calculated (i.e. dry weight burrow⁻¹ tidal cycle⁻¹) and mean values were compared between habitats and seasons using two-way ANOVA (Zar, 1999) for both burrow categories.

Sediment removal rates per square meter and tidal cycle (g m⁻² tidal cycle⁻¹) were also calculated as

$$SRR_i = SRI * ABD_i \quad (2)$$

where *SRR* is the sediment removal rate (g m⁻² tidal cycle⁻¹), *SRI* is the sediment removed in a single tidal cycle for each burrow type (g burrow⁻¹ tidal cycle⁻¹) and *ABDi* are density of tubular or funnel active burrows (burrows m⁻²). To solve the equation (2) for each burrow type we used a resampling method (Manly, 1998) independently with data of these measured variables for each microhabitat and season without replacement. The null hypothesis of no differences in the sediment removal rates between different habitats and seasons was evaluated using a two-way ANOVA (Zar, 1999) for each burrow category.

2.5. Sediment transported from mounds

The sediment removed by crabs is deposited near the burrow entrance, and then is exposed to erosion by water flow. Due to this, we conducted field experiments to evaluate the proportion of this sediment removed by crab (i.e., mound generation) activity that was transported by currents. At each habitat 20 fresh mounds were selected (similar mounds of 15 cm in diameter and 5 cm height), and half (10) of these mounds were collected and processed to obtain dry weights of mounds that were not exposed to water flows. The crabs corresponding to the other 10 mounds (i.e., crab that inhabit the burrow associated to each mound) were extracted, and crab exclusion cages were installed surrounding the mound (40 cm in diameter) to avoid crabs to enter inside them (cages were constructed with 1 cm plastic mesh inserted 5 cm into the substrate, 20 cm tall). The mounds excluded inside the cages were collected after two complete tidal cycles and were dried and weighed as described above. This experiment was conducted in January 2003 and repeated in August 2003. The difference between dry weights of mounds exposed to tidal currents and not-exposed was calculated and represented the amount of sediment lost by mound erosion. The null hypothesis of no differences between mean dry weight of mounds exposed and not-exposed to tidal currents and habitats was evaluated using two-way ANOVA (Zar, 1999) for each season.

Another common situation occurs when mounds are not exposed to water flow for several hours. In this case they become dehydrated and start to crack, forming ellipsoidal blocks (personal observation, Fig. 2). These blocks are often seen far from the burrow-occurring area where they were generated, which implies that they were transported. We evaluated this additional erosion mechanism. The density of blocks was determined at each habitat, counting inside of randomly distributed 0.5 m side squares (*n* = 20 for each habitat). Twenty blocks were collected from each habitat and processed as described above to obtain dry weights. To determine if mound-generated blocks were being transported by currents we marked the position of 10 blocks from each habitat. A small colored stake (5 cm tall, 0.5 mm diameter) was inserted in the substrate (only a portion of 0.5 cm of the stakes were left beyond the sediment surface to avoid significant interactions with flow patterns) adjacent to the block to register the starting point, and a colored needle (1.5 cm tall, 0.3 mm diameter) was pushed

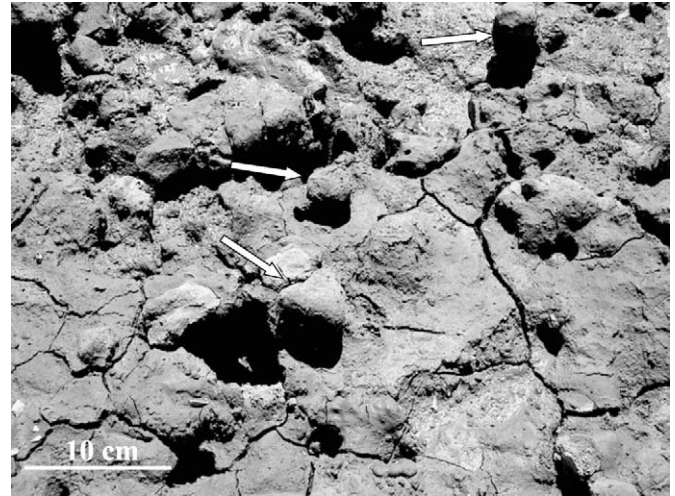


Fig. 2. Photograph of the saltmarsh substrate showing sediment blocks generated by crab mounds desiccation.

into the block; each block and their starting point were marked with the same color in order to individualize blocks. After a tidal cycle the marked blocks were located, the proportion of blocks that suffered transport were registered and the distance to the stake was measured if this was the case. This procedure was repeated during four complete tidal cycles in February 2003 and another four tidal cycles during August 2003. The null hypotheses of no difference in the proportion of blocks that suffered transport and the mean displacement from original mounds between habitats were evaluated using ANOVA (Zar, 1999).

2.6. Balance between trapping and removal of sediment due to crab activity

The balance between sediment trapping into burrows or transported from mounds was estimated for each microhabitat where crabs occur and for the two contrasting seasons (i.e., summer and winter), by combining equations (1) and (2) as follows:

$$SB_j = (TSTt + TSTf)_j - (SRRt + SRRf)_j * pSE_j \quad (3)$$

where *SB* is the sedimentary balance, *j* represents the combinations of microhabitat and seasons (i.e., eight combinations), *TSTt* and *TSTf* are the total sediment trapped for tubular- and funnel-shaped burrows, respectively, *SSRt* and *SRRf* are the sediment removal rates for tubular- and funnel-shaped burrows, respectively, and *pSE* is the proportion of sediment that was transported from mounds by currents (see Section 2.5). All these variables were resampled and randomly combined to solve (3) independently for each microhabitat, season and year. Thus, the *SB* (g m⁻² tidal cycle⁻¹) was compared between habitats and years seasons using Two-way ANOVA.

3. Results

3.1. Density and distribution of crab burrows in the intertidal

Burrow densities were different when compared between habitats (ANOVA: $F_{3,312} = 51.39$, $p < 0.01$). They were higher in the inner saltmarsh habitats and at mudflats (these two habitats always had the same burrow density, Fig. 3A) than in drainage basins and tidal creeks, where the lowest densities were registered (Fig. 3A). Burrow densities decreased in winter in all habitats analyzed

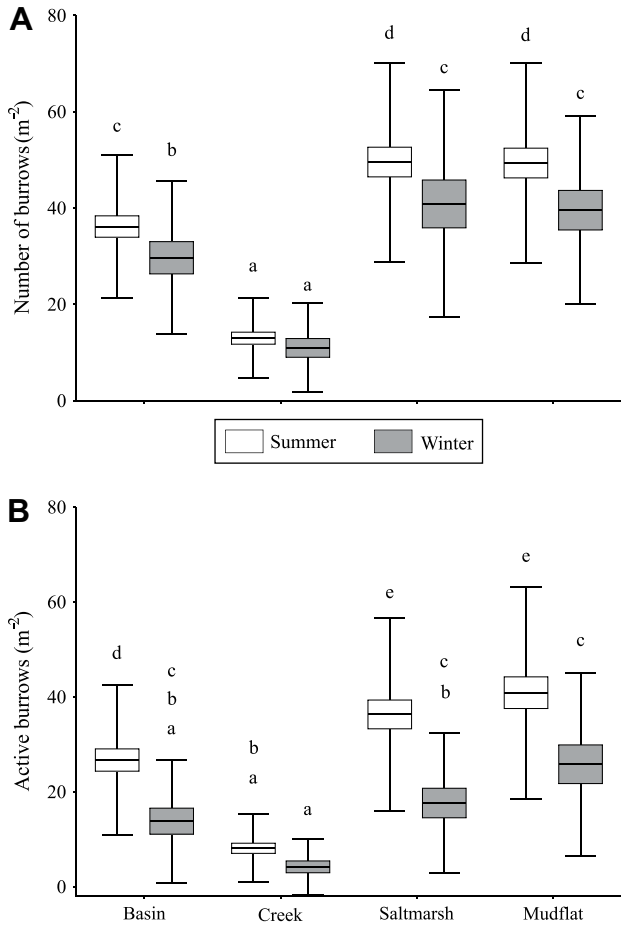


Fig. 3. (A) *Neohelice granulata* density expressed as number of burrows (burrows m⁻²) for the different microhabitats and year seasons. (B) Crab activity expressed as number of active burrows for the different microhabitats and year seasons. Here and thereafter box plots are constructed with limits of boxes being the standard error, lines outside boxes represent standard deviation, lines inside boxes are means. Different letters above the boxes denote significant differences (Tukey test after ANOVA, $\alpha = 0.05$) between groups of data.

(ANOVA: $F_{1,312} = 31.67, p < 0.01$, Fig. 3A); this winter reduction in burrow densities was observed in all habitats, with the exception of creeks where Tukey test demonstrated no significant differences (Fig. 3A), since interaction effects between habitats and seasons were not significant (ANOVA interaction: $F_{3,312} = 2.05, p > 0.05$). The number of active burrows varied between habitats and seasons (ANOVA interaction: $F_{3,312} = 8.96, p < 0.01$, Fig. 3B). The number of active burrows was higher in saltmarsh and mudflats than in basins and creeks, and the number decreased during the winter season, but this decrease was more pronounced for saltmarsh habitats (Fig. 3B). Size frequency distribution of burrow entrances also varied between habitats, burrows had bigger entrances in open mudflats than in the other habitats (Kolmogoroff–Smirnov test: $p < 0.05$; mudflat: $x = 10.2$ cm, $SD = 3.4, n = 305$; creek: $x = 6.5$ cm, $SD = 2.9, n = 298$; saltmarsh: $x = 6.2$ cm, $SD = 3.2, n = 312$; basins: $x = 6.1$ cm, $SD = 2.5, n = 322$). Percentage of burrows with funnel-shaped entrances was higher in open mudflats (funnel-shaped: $x = 35.2$ burrows, $SD = 17.1$; tubular-shaped: $x = 13.5$ burrows, $SD = 10.8$) and creeks (funnel-shaped: $x = 8.5$ burrows, $SD = 4.8$; tubular-shaped: $x = 5.1$ burrows, $SD = 4$) than in basins (funnel-shaped: $x = 16.1$ burrows, $SD = 8.2$; tubular-shaped: $x = 22.1$ burrows, $SD = 5.5$) and inner saltmarsh habitats (funnel-shaped: $x = 15.1$ burrows, $SD = 9.3$; tubular-shaped: $x = 34.5$ burrows, $SD = 12.3$), where most burrows were tubular-shaped (ANOVA: $F_{1,146} = 147.4, p < 0.01$).

3.2. Effect of burrows of *Neohelice granulata* on the trapping of sediment

The sediment trapping rate (dry weight day⁻¹) during the high tide for individual mimics of burrows was higher for funnel than tubular-shaped mimics in all habitats (ANOVA interaction: $F_{3,192} = 4.62, p < 0.05$, Fig. 4A). Funnel-shaped mimics trapped more sediment in creek and mudflat habitats than in saltmarsh and basins habitats, where they showed the lowest trapping rates (Fig. 4A). In contrast, tubular-shaped mimics trapped the same amount of sediment in all habitats (Fig. 4A). When these data were expressed by square meter (i.e., equation (1)), funnel-shaped burrows showed higher sediment trapping rates than tubular-shaped burrows at mudflat, creeks, and basins; but in saltmarsh habitats, the total amount of sediment trapped per square meter did not differ between burrow shapes (ANOVA interaction: $F_{3,192} = 69.42, p < 0.01$, Fig. 4B).

3.3. Sediment removal rate

The sediment removal rate of individual funnel-shaped burrows was higher at basin and creek habitats than at saltmarsh and mudflats during summer and there were no differences in winter seasons (ANOVA interaction: $F_{3,232} = 3.32, p < 0.05$, Fig. 5A). In addition, for this type of burrows the amount of sediment removed by crabs was higher in summer

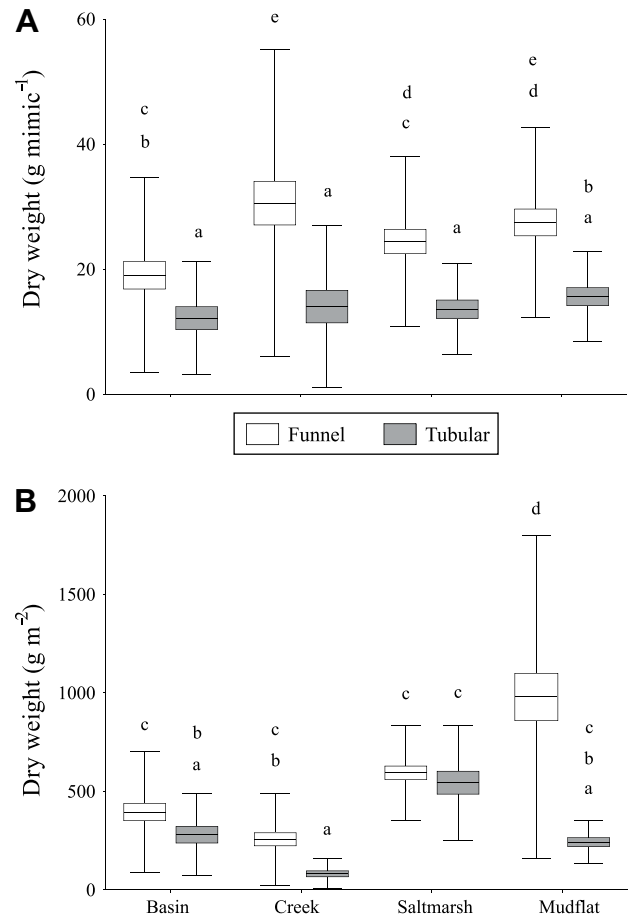


Fig. 4. (A) Mass of sediment trapped into individual burrow mimics (tidal cycle⁻¹) for funnel and tubular-shaped mimics in the different microhabitats. (B) Sediment trapping rate (g dry sediment m⁻² tidal cycle⁻¹) into burrow mimics for funnel and tubular-shaped mimics in the different microhabitats.

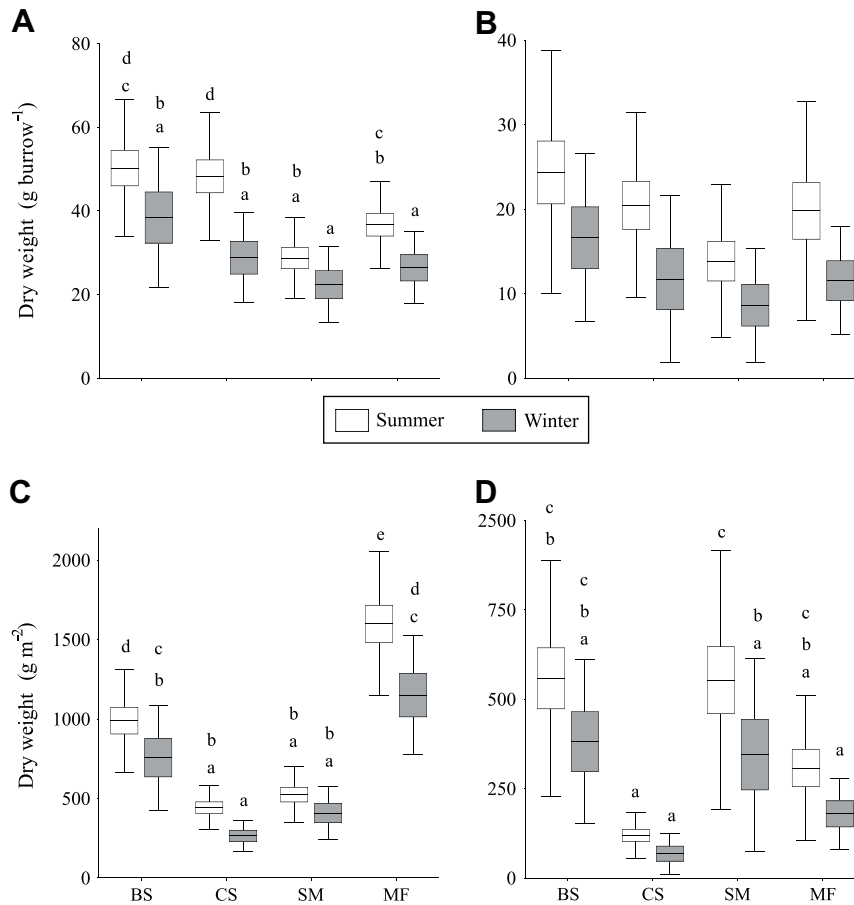


Fig. 5. Sediment removal rate for individual burrows in creek tidal basins (BS), creek bottoms (CS), inner part of saltmarsh (SM), and open mudflats (MF); estimated for: (A) funnel-shaped burrows and (B) tubular shaped burrows. (C) and (D) show sediment removal rates ($\text{g dry sediment m}^{-2} \text{ tidal cycle}^{-1}$) for funnel and tubular-shaped burrows respectively.

than in winter for all habitats except in saltmarshes (Fig. 5A). However, the sediment removal rate of tubular-shaped burrows did not differ between habitats (ANOVA: $F_{3,192} = 2.01$, $p > 0.05$, Fig. 5B) but was higher during summer than in winter for basins and creeks habitats (ANOVA: $F_{1,192} = 25.46$, $p < 0.05$, Fig. 5B).

Sediment removal rates ($\text{g m}^{-2} \text{ tidal cycle}^{-1}$) for funnel-shaped burrows were higher in the mudflat than in the basin habitats and both were higher than rates registered in creek and saltmarsh habitats. For funnel-shaped burrows occurring in the same habitat, the rates were always higher in summer than in winter (ANOVA interaction: $F_{3,232} = 4.3$, $p < 0.01$, Fig. 5C), but the winter reduction in removal rates was not the same for the different habitats (Fig. 5C). A similar pattern was obtained for sediment removal rates of tubular-shaped burrows, the rates were higher in summer than in winter periods for all habitat type (ANOVA: $F_{1,236} = 18.01$, $p < 0.01$, Fig. 5D), and the winter reduction of this values were the same for all habitats. However, for this type of burrow, the higher rates were registered in saltmarsh and basin habitats (ANOVA: $F_{3,236} = 10.19$, $p < 0.01$, Fig. 5D), given the higher proportion of tubular-shaped burrows that occurred at these environments. When pooled (i.e. funnel and tubular-shaped burrow removal rates) using summer data, the two components show higher remotion rates for mudflat and basin habitats (mudflat: $x = 2.4 \text{ kg m}^{-2} \text{ day}^{-1}$, $SD = 1.1$, $n = 30$; basin: $x = 1.9$, $SD = 1.3$, $n = 30$) than at saltmarsh and creek habitats (saltmarsh: $x = 1.4 \text{ kg m}^{-2} \text{ day}^{-1}$, $SD = 1.0$, $n = 30$; creek: $x = 0.8$, $SD = 0.34$, $n = 30$; ANOVA: $F_{3,236} = 27.96$, $p < 0.01$).

3.4. Sediment transported from mounds

During summer, the dry weight of mounds that were not exposed was significantly larger than dry weight of mounds exposed to water currents in the basin and creek habitats, and there were no differences within mudflat and saltmarsh habitats (ANOVA interaction: $F_{3,152} = 4.57$, $p < 0.05$, Fig. 6A). Furthermore, mean weights of not-exposed mounds collected did not differ between habitats (Fig. 6A). Total amount of sediment removed from mounds exposed to currents was higher in creeks (61% of exposed sediment was removed after one tidal cycle) and basins (46%) than at saltmarsh (12%) and mudflat habitats (13%). Winter and summer showed the same pattern (Fig. 6B): basin and creek habitats showed the higher differences between mounds exposed and not exposed to flow (ANOVA interaction: $F_{3,152} = 3.53$, $p < 0.05$, Fig. 6B), but in this case, the percentages of removed sediment increased during summer for all habitats (creek = 74%, basin = 71%, saltmarsh = 24%, mudflat = 25%).

The density of blocks generated by mound desiccation was different between habitats (ANOVA: $F_{3,76} = 22.61$, $p < 0.01$). Basin habitats showed higher block density ($x = 80 \text{ blocks m}^{-2}$, $SD = 30$, $n = 20$) than creek habitats ($x = 58.5$, $SD = 18$, $n = 20$) and the lowest densities were registered at saltmarsh and mudflat habitats (saltmarsh: $x = 36.2$, $SD = 12$, $n = 20$; mudflat: $x = 39.3$, $SD = 6$, $n = 20$). Dry weight of those blocks also differed between habitats (ANOVA: $F_{3,76} = 3.68$, $p < 0.05$). The blocks were larger in saltmarsh habitats ($x = 20.9 \text{ g block}^{-1}$, $SD = 7.98$, $n = 20$) than in the other habitats (basin: $x = 16.5$, $SD = 5.1$, $n = 20$; creek: $x = 14.2$, $SD = 4.9$, $n = 20$; mudflat: $x = 16.9$, $SD = 5.3$, $n = 20$). The net displacement

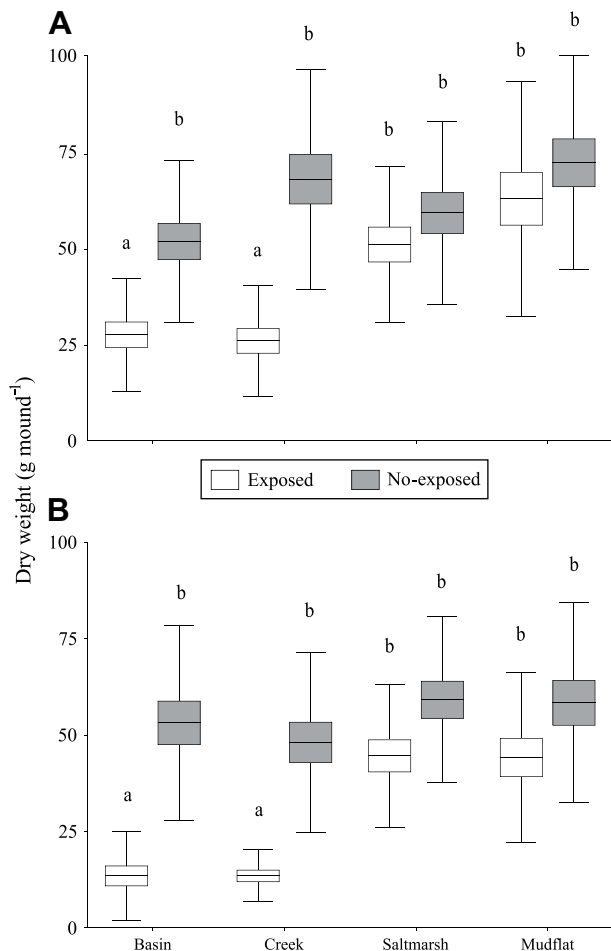


Fig. 6. Dry weight of mound sediments exposed and not exposed to water flow during (A) summer and (B) winter seasons and for the different microhabitats.

of sediment blocks showed higher values for basin and creek habitats (summer values; basin: $x = 6.9$ cm, $SD = 3.9$, $n = 40$; creek: $x = 8.9$, $SD = 6.1$, $n = 20$) than for saltmarsh and mudflat habitats (saltmarsh: $x = 0.3$ cm, $SD = 0.48$, $n = 20$; mudflat: $x = 0.67$, $SD = 0.5$, $n = 20$; ANOVA: $F_{3,312} = 167.9$, $p < 0.01$). Net displacement did not differ when comparing summer and winter data (ANOVA: $F_{1,312} = 2.45$, $p > 0.05$). Percentage of marked blocks that were transported by currents was also different between habitats (basin: $x = 96\%$, $SD = 5$, $n = 4$; creek: $x = 97$, $SD = 4.1$, $n = 4$; saltmarsh: $x = 45$, $SD = 14.1$, $n = 4$; mudflat: $x = 77$, $SD = 15$, $n = 4$; ANOVA: $F_{3,28} = 38.49$, $p < 0.05$).

3.5. Balance between trapping and remotion of sediment due to crab activity

The sediment deposited into burrows or transported from biogenic mounds varied among crab-inhabited microhabitats and between seasons (ANOVA interaction: $F_{3,152} = 26.05$, $p < 0.05$, Fig. 7). In the inner parts of saltmarshes ("Saltmarsh") and in the open mudflats, the balance on sediment dynamics was always positive (Fig. 7). Approximately 380 g of dry sediment m^{-2} were being deposited into crab burrows every day in the saltmarsh and 1200 g were deposited in burrows occurring at mudflats. In contrast, tidal creek bottoms ("Creek") and tidal creek basins ("Basin") had negative balance values during summer, indicating that the crabs are promoting transport of sediment from burrows, those negative values indicate that the erosion of biogenic mounds

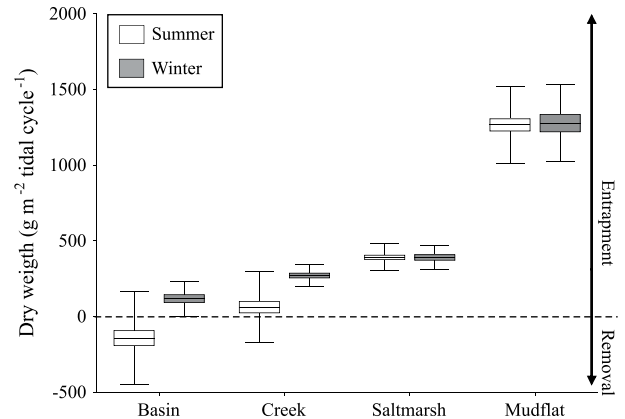


Fig. 7. Sedimentary balance due to crab activity, expressed as dry weight of sediment entrapped (positive values) or transported (negative values) per tidal cycle, during summer and winter seasons.

is higher than the entrapment of sediment into burrows. Between 10 and 500 g dry sediment $m^{-2} day^{-1}$ were transported from mounds in creek bottoms and basins during those year seasons. However, this pattern shifted during winter for these habitats, high amounts of sediment are being trapped into burrows in relation to the sediment that was exported from mounds, thus producing positive values on this balance (Fig. 7).

4. Discussion

Our results show that burrows and burrowing activity of *Neohelice granulata* have strong effects on the sediment dynamics. This species inhabits all intertidal microhabitats analyzed in this study, and burrow architecture varied among habitats. The burrows act as passive traps of sediments, but depending on their density and architecture, lead to different trapping rates in different intertidal habitats. At the same time, the burrowing activity of this crab exposes sediments to water flows, primarily due to the generation of biogenic mounds. Even though these mounds were present in all intertidal microhabitats, they were differentially transported between them. The resulting effect of this crab species on the sedimentary balance also varies among habitats: at saltmarsh edge sites (i.e. small tidal creeks and creek tidal basins), the crabs enhance transport of sediments, but at zones with low current speeds (i.e. inner part of saltmarshes and open mudflats) the crabs promote trapping of sediments into burrows.

Previous studies have demonstrated the role of burrows constructed by invertebrates as passive traps of sediments (e.g. Nowell et al., 1981; Botto and Iribarne, 2000; Botto et al., 2006). Particularly, burrows of *Neohelice granulata* have been shown to play this role (i.e. passive trapping of sediment) at SW Atlantic mudflats (Botto and Iribarne, 2000; Botto et al., 2006). Our results extend these findings to the rest of intertidal zones that *N. granulata* inhabits. Funnel-shaped burrow entrances were more frequent in low intertidal zones (open mudflats and creek bottoms), and the entrapment of sediment for this type of entrance was twice as large as that of tubular entrances. Plasticity in the feeding methods of this crab is likely responsible for this pattern. This species is a deposit feeder when inhabiting mudflats (Iribarne et al., 1997) and funnel-shaped burrow entrances that efficiently trap organic-reached sediments and detritus from the water column (Botto et al., 2006) may enhance the deposit feeding activity (Iribarne et al., 1997). Indeed, tubular-shaped burrow entrances were most frequent within saltmarshes, where the deposit feeding activity is mainly replaced by herbivory on live stems and leaves of vascular plants (Iribarne et al., 1997; Bortolus and Iribarne, 1999).

Given that the proportion of these two burrow architectures and that burrow densities vary between studied microhabitats, the total amount of sediment trapped per unit area changed in the different microhabitats. The mudflats had relatively high burrow densities with a high proportion of funnel-shaped entrances, thus leading to high efficiency in the trapping of sediments. Inner parts of saltmarshes also showed high rates of sediment entrapping, but at this microhabitat the mechanism appeared to be different. Tubular-shaped burrows are most common over the marsh surface, but in this case the occurrence of plants may aid in the trapping process. There is strong evidence on the role of marsh vegetation in the deposition of sediments transported with the flow (Frey and Basan, 1985; Leonard and Luther, 1995; Leonard and Croft, 2006). Thus, high burrow densities together with plant-enhanced deposition may account for those large rates of sediment trapping in inner saltmarsh burrows. As expected, sites mostly unvegetated and with lower burrow densities (i.e. creek bottoms and creek tidal basins) showed the lowest values of sediment trapping rates per unit of area. Bed roughness may also offer a plausible explanation for this contrasting pattern; indeed bed roughness could enhance the deposition of sediment into burrows (Yager et al., 1993). *Neohelice granulata* increased bed roughness when constructing and maintaining their burrows given that they transport subsurface sediments to the surface forming sediment mounds (Botto and Iribarne, 2000). This crab-generated roughness is often smoothed by currents in creek bottoms and basins, where the lowest rates of sediment trapping were recorded. While some combination of these processes is probably occurring, it seems that these crab burrows are efficient sediment traps (this study; Botto et al., 2006) and the trapping pattern is highly dependent on burrow density and architecture, and possible bed roughness. Furthermore, the trapping of sediments in burrows is continuous because the burrows persist during all seasons. On the other hand, the mounds themselves could act as barriers for sediment being transported by the currents, producing low turbulence zones over the burrow mouths and allowing sediment deposition. Flow dynamics around crab mounds is a next step in our investigation.

Biogenic mounds generated by bioturbator species are thought to have some resistance to erosion (Murray et al., 2002). Some studies have argued that microbial colonization of mound sediment may promote its resistance to erosion (e.g., Rhoads and Young, 1970; Meadows and Tufail, 1986; Levinton, 2001). However, our results show that mounds generated by *Neohelice granulata* are eroded by currents in high current speed microhabitats (i.e., creek bottoms and basins), while in low current speed microhabitats the erosion of mounds was much lower. As with other bioturbator species, this crab removes large amounts of sediment (this study; Iribarne et al., 1997; Botto and Iribarne, 2000), affecting a large proportion of the bioturbated bed (up to 80%, Iribarne et al., 2005). Thus, it is expected to affect microbial colonization of mounds because of their lack of stability and continuous reworking (see Smith et al., 1996). Furthermore, large areas excavated by *N. granulata* have enhanced water content during low tide (Botto and Iribarne, 2000; Escapa et al., 2004). This constitutes an alternative explanation for mound erosion because sediment having high water content is more easily entrained by currents than sediments with low water content (Aller and Dodge, 1974).

We also reported a previously undescribed mechanism of erosion: desiccated mounds generate blocks that are then transported by currents. This process, to our knowledge, has never been described before. However, the transport and erosion of cohesive sediment are usually linked to desiccation processes (i.e. desiccated polygons) and to high current speeds (see Metha, 1986). Perillo and Sequeira (1989) describe this process as very common in the Bahía Blanca Estuary as most intertidal sediments are old delta material being exposed. At saltmarsh edge microhabitats, we registered high

transport rates for these ellipsoidal blocks, while at mudflats and inner parts of saltmarshes these blocks were not moved by currents. Creek bottoms and creek basins concentrate tidal currents mainly during ebb, thus generating strong unidirectional flows characterized by high current speeds (up to 50 cm s^{-1}). These currents are able to move and transport the blocks generated by crabs. In contrast, the currents that are generated in the saltmarsh and mudflats could not be sufficient to move those blocks.

Our small-scale (i.e. burrow scale) analysis demonstrates that the activity of an organism can result in different consequences, depending primarily on the hydrodynamic conditions of the affected area. There is strong evidence of the interplay between biological and physical processes in determining the erodibility of cohesive sediments (e.g., Amos et al., 1998; Widdows et al., 1998, 2000). These studies demonstrate that different benthic organisms can, interacting with local physical processes, affect a wide variety of sedimentological parameters (see Murray et al., 2002). However, there is less evidence on the role of different activities by the same organism on these parameters. For instance, the mud-burrowing crustacean *Corophium volutator* stabilizes estuarine sediment by de-watering of excavated sediment (Meadows and Tait, 1989); however, active resuspension by the same species may lead to sediment transport (Daborn et al., 1993; de Deckere et al., 2000). In our case, the effect of biological activity on the sedimentary processes was largely modulated by physical conditions that dominate the area where the activity impacts. However, the effect of biological activity on sedimentary dynamics may also depend on spatial-temporal variations on those activities. Burrow density and burrowing intensity vary among microhabitats and year seasons, which may shift these dynamics, enhancing sediment trapping into burrows during winter to favor sediment transport from mounds during summer (i.e. for saltmarsh edge sites). There is evidence that temporal variations in the density of the bivalve *Macoma balthica* in the Humber estuary (UK) lead to changes in sediment erosion/accretion rates over intertidal mudflats (Widdows et al., 2000). Furthermore, long-term temporal changes in benthic communities are expected to shift the sediment properties and mobility (Beukema, 1990; Beukema et al., 1998). Moreover, it may occur over large geographical scales (Widdows et al., 2000; Murray et al., 2002). At a landscape level, the activity of *Neohelice granulata* could produce a negative sediment balance at saltmarsh edge sites. The geomorphologic outcome of those negative balances is the facilitation of inland creek growth (Escapa et al., 2007) and the development of enhanced dendritic creek networks in *Sarcocornia*-dominated marshes (see Minkoff et al., 2006).

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