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Increase of organic matter transport between marshes and tidal flats by the burrowing crab *Neohelice* (*Chasmagnathus*) *granulata* Dana in SW Atlantic salt marshes

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ABSTRACT

Marshes are considered exporters of organic material, with tides being one of the most studied transport mechanisms. However, animal movements can enhance this energy transport and even, in some cases, import energy to marshes by fecal deposition. In this work, we analyze if *Neohelice* (*Chasmagnathus*) *granulata*, an abundant intertidal burrowing crab that changes its diet between marsh (herbivorous) and tidal flat (deposit feeder) zones and moves between zones during the tidal cycle, enhance energy transfer between marshes and tidal flats by fecal deposition. Given that higher tidal levels increase these movements, two intertidal habitats with different tidal amplitudes were compared (Mar Chiquita Coastal lagoon 37° 40' S –MCCL, max 2 m and San Antonio Bay 40° 46' S –SAB, max 9 m). The seasonal and tidal movements between zones were studied using movement traps. Crabs moving towards each direction were kept in containers to calculate fecal production and the total organic matter (OM) release and OM% of their feces. With these data, a resampling technique was performed to compare with a 3 way ANOVA the net transport of feces seasonally, between zones, in both intertidals. The results showed that the movement of *N. granulata* enhances the exchange of OM among habitats by fecal deposition between marsh and tidal flats with seasonal variations in its importance. Fecal transport showed differences between locations being 10 times higher in winter and decreasing towards summer in MCCL, while the opposite trend was found in SAB. There were no differences in the OM deposited in each zone in SAB but in MCCL there was 45% more feces deposited in the marsh than in the tidal flat. The fecal OM% is higher in SAB than in MCCL suggesting that biodeposition in SAB, where it can reach 40%OM (surrounding sediment is lower than 2%) could be more important. The fecal production in MCCL is about 80% of the rate of detritus production in the marsh. In conclusion, fecal deposition is a very important input of energy in marsh zones, being crabs an important mechanism in transporting OM mainly towards the marsh zones.

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1. Introduction

Despite ecosystems usually viewed and described as “close” systems, the importance of cross-habitat linkages in ecosystem dynamics is now recognized (Polis et al., 2004). Subsidies of organisms or resources originated in one system, for example, can significantly affect the trophic dynamics of a recipient system (e.g. sea-to-land nutrient transport by seabirds; see Anderson and Polis, 1999; Ellis et al., 2006, steam-to-adjacent riparian areas migration of emergent insects, see Sabo and Power, 2002). All this evidence suggests that ignoring alloctonous inputs strongly reduces the ability to predict ecosystems structure and function. Thus a more in-depth study of cross habitat ecological flows is needed (see Polis et al., 2004).

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Coastal systems are productive zones that may act as receptors, producers and/or energy transformers (Jordan et al., 1991; Alongi, 1998; Hauxley and Valiela, 2004). Nevertheless, energy transfer from these systems to open water depends on physical (e.g. light, temperature, dissolved oxygen, and tidal fluxes) as well as biological factors (e.g. vegetation type, feeding modes) that dominate each community (Nixon, 1980; Nedwell et al., 1999; Teal and Howes, 2000). The importance of these areas is associated to high productivity of macrophytic communities (marshes, mangroves and seagrasses), and by the fact that these systems export a large fraction of their productivity by fluxes of organic detritus (e.g. Adam, 1990) supporting secondary production beyond their boundaries (e.g. Cebrian, 2002). Indeed organic detritus is one of the most important food sources in coastal areas, supporting, in some cases, large and complex food webs (Mann, 1972; Day et al., 1989; Valiela et al., 2000). Among these systems, marshes are one of the most important carbon exporters (Cebrian, 2002). Carbon is highly mobile in aquatic systems because

water acts as a vector for particulate and dissolved organic matter (Carr et al., 2003). However, in some marshes detritus is trapped and accumulated in adjacent sediments (Nixon, 1980) making carbon movement negligible (Dittel et al., 2000; Guest et al., 2006).

Organic matter export or transport between marshes and adjacent zones can be by physical (nearbed and bedload transport of organisms, detritus or other forms of organic matter by tidal fluxes, Hemminga et al., 1996) or biological processes (migration of organisms, Deegan and Garritt, 1997). Nevertheless, in a review comparing export from different types of coastal communities, there are no reports on export mediated by organisms that consume in the system but defecate out of it (see Cebrian, 2002). Animal movements can connect different types of habitats, enhancing the energy transfer between them (Irlandi and Crawford, 1997; Kneib, 1997). Nevertheless, this coupling has been generally focused on the “trophic relay” hypothesis (Kneib, 1997), which is consumption of nekton after their migration. The small nekton usually inhabits in marsh zones where they feed and grow, accumulating biomass until they migrate to adjacent areas, thus exporting the accumulated energy (Kneib, 1997). These movements operate at different temporal scales, ranging from tidal to ontogenetic changes. Tidal movements are often associated to spatial segregation between refuge and feeding habitats (Deegan et al., 2000). Several species utilize vegetated intertidal zones during high tide, remaining in deeper water during low tide (fishes: Weisberg and Lotrich, 1982; Minello and Zimmerman, 1983; Boesch and Turner, 1984; crabs: Fitz and Wiegert, 1991, both: Hettler, 1989). The energy obtained in the feeding zone, is then transferred to the refuge zone either by predation or by fecal deposition (Kneib, 2000). However, species that inhabit the “border” between habitats usually can feed and defecate, or be predated, in both zones, linking them with a bi-directional energy transfer (Deegan et al., 2000).

Fecal pellets provide an important source of repackaged organic matter (Wotton and Malmqvist, 2001) particularly those from filter and deposit feeders which contain high organic content (see Kautsky and Sverker, 1987). These species select smaller particles rich in organic content covering them with a mucus matrix (e.g. Watling, 1988; Palomo and Iribarne, 2000; Wotton and Malmqvist, 2001). Typically, deposit feeders are in high densities and feed continuously for long periods of time assimilating little of the food ingested (Wotton and Malmqvist, 2001). Thus, deposit feeder feces are key organic matter sources given that the surrounding sediment has significant lower quality (Watling, 1988). Burrowing organisms have an additional impact by enhancing decomposition due to bioturbation activities (Aller and Aller, 1986) and also because burrows act like passive traps for sediment and detritus (e.g. Botto and Iribarne, 2000). Thus, if burrowing deposit feeders (with their physical effects of the burrows) also perform tidal movements between zones, they may have consequences on the organic transfer between habitats.

Estuary intertidals and embayments in the Southwestern Atlantic are characterized by extensive mudflats surrounded by salt marshes dominated by *Spartina* spp. (Isacch et al., 2006) and dominated by the activity of the burrowing grapsoid crab *Neohelice* (*Chasmagnathus*) *granulata* Dana (Boschi, 1964; Spivak et al., 1994; Iribarne et al., 1997). This crab species reaches 40 mm of carapace width (CW) and their physiological adaptations allow them to be water and air breather (Luquet et al., 1998; Halperin et al., 2000). This enables them to occupy the whole intertidal, from the uppermost parts of the salt marshes to the lowest tidal flat zones (Spivak et al., 1994). They are primarily deposit feeders in mud flats and herbivorous–detritivorous in the salt marsh (Iribarne et al., 1997; Bortolus and Iribarne, 1999; Botto et al., 2005). Herbivory by *N. granulata* can decrease the aerial biomass of *Spartina alterniflora* Brong. by up to 87% (Bortolus and Iribarne, 1999; Alberti et al., 2007), and a high proportion of *Spartina* production is trapped inside burrows (Botto et al., 2006). Burrows also trap small grains of sediment richer in organic matter (Iribarne et al., 1997). The material inside this type of burrows may become

enriched during decomposition by bacterial biota colonization (see Mann, 1988). Moreover the organic content could also be enhanced by fecal deposition because crabs remain inside burrows when the marsh is unflooded (Gutierrez et al., 2006), which has important consequences on the coastal sediments.

N. granulata usually performs tidal movements from mudflats to marshes (A. Méndez Casariego Pers. Obs.). Given that *N. granulata* changes its diet and densities between mudflat and marsh zones (Iribarne et al., 1997), crab movement between these zones could be an important mechanism of cross-habitat energy transfer. Given that these movements across the tidal range may depend on the tidal amplitude, it is also likely that tidal amplitude may enhance transport of OM by crabs. Upon the several variables that can affect habitat use by mobile species (Minello et al., 2003) the most important factor controlling access to marshes is flood duration, which gives the opportunity to these species to gain access for longer periods of time (Kneib, 2000). This may be affected by tidal ranges (Hollingsworth and Connolly, 2006) or by the position of the marsh edge across the intertidal (Kneib, 2000). As prolonged flooding enhances energy transfer, two intertidal areas with different tidal amplitudes but also with lower position of the marsh edge were compared. Thus, given this context the purpose of this paper is to analyze the energy transfer between the marsh and mudflat zones in two different intertidal habitats by the fecal deposition of *N. granulata*.

2. Materials and methods

2.1. Study site

The study was conducted at the San Antonio Bay (40° 46'S, 64° 50' W; thereafter SAB) and the Mar Chiquita coastal lagoon (37° 40'S, 57° 23'W; thereafter MCCL, both in Argentina) during winter, spring and summer of 2006 and 2007. SAB is located at the southern part of *N. granulata* distribution and presents a large intertidal area (~100 km²) with tidal amplitudes up to 9 m during spring tides (Schnack et al., 1996). It has unvegetated zones in the lower intertidal and marshes with a well-defined edge dominated by *S. alterniflora* at the mid-intertidal. Burrows of the crab *N. granulata* are found throughout the intertidal zone, in areas with and without vegetation. The MCCL (see Fig. 1) is a body of brackish water (46 km²) permanently connected to the sea with amplitudes up to 2 m (Reta et al., 2001). The main habitats around the lagoon are intertidal mudflats and large plains irregularly flooded (10 to 15 times per month) dominated by the cordgrass *S. densiflora* (Isacch et al., 2006). The crabs are distributed in both the *S. densiflora* salt marsh and the intertidal mudflats generating large burrowing beds (e.g. Spivak et al., 1994; Iribarne et al., 1997; Botto et al., 2005). Adults are preyed mainly by the American oystercatcher *Haematopus palliatus* (Daleo et al., 2005) and the Olrog's gull *Larus atlanticus* (Copello and Favero, 2001), while megalopae and recent settlers are preyed by fishes (Rivera Prisco et al., 2001).

2.2. Crab densities

Given that fecal production, activity and/or movement of crabs are density dependent, in each zone (marsh and mudflat) of SAB and MCCL, density was calculated seasonally by collecting all crabs present inside plots (50×50 cm, n=10). Plots were selected randomly from each zone (see Fig. 1) and compared with a three way ANOVA (data was log-transformed to achieve homoscedasticity) with LSD test for a posteriori comparisons (Zar, 1999).

2.3. Activity patterns

Activity patterns can be affected by short and long term variations in abiotic factors (daily and seasonal respectively, Craig and Crowder, 2002). To detect short term crab activity patterns 20 pitfall traps were

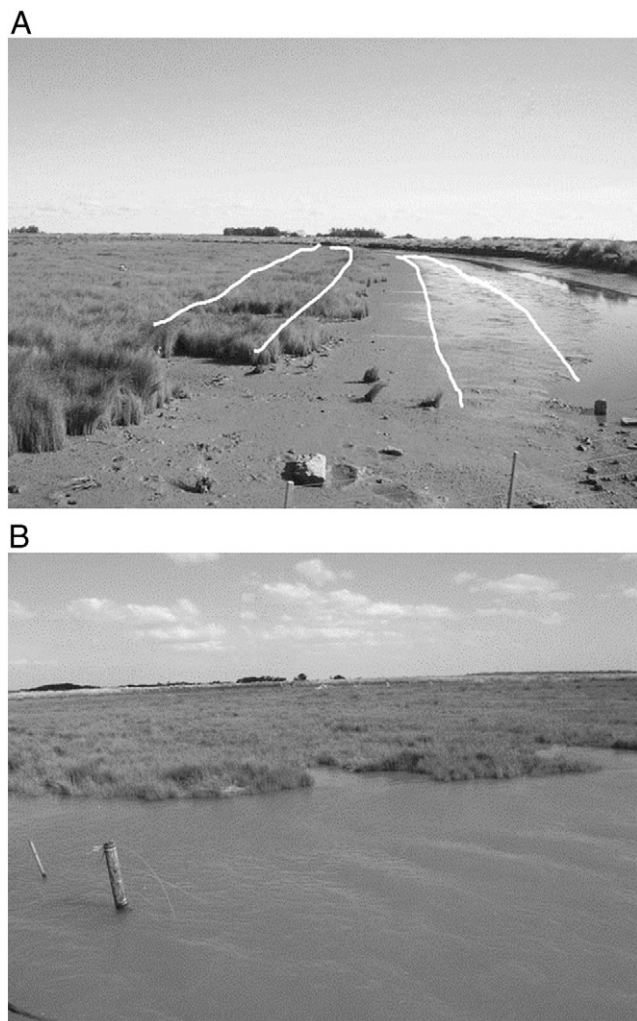


Fig. 1. MCCL (Mar Chiquita coastal lagoon) at low (A) and high (B) tides. White lines indicate the limits where marsh and mudflat zones were sampled.

placed parallel to the shore in the marsh, the mud flat and the edge between both areas. They were used to have an index of crab activity in each of the three areas. Each pitfall trap consisted in 5-liters empty bottle (20 cm diameter, 17 cm height) buried into the ground to surface level. The top of the bottles was removed and replaced with funnels to ease crab trapping and to prevent crabs from escaping once caught. Crabs were collected every 6 h during 8 tidal cycles in order to cover different tidal amplitudes with ebbing and flowing tides and different conditions (temperature, time of day, and weather). The total number of crabs collected in a trap was used as an estimation of activity.

To analyze if short term differences in activity is influenced by tidal condition (ebbing vs. flooding), t-test for dependent samples (Zar, 1999, each pitfall trap compared between ebbing and flooding) were performed between total number of crabs collected at the ebbing and flooding tides for each season (winter, spring and autumn) level and each zone (mudflat, marsh and mudflat/marsh edge) in both intertidals (SAB and MCCL).

To analyze if there are differences in activity patterns between the mudflat and the marsh, and due to possible differences in activity depending on tides, only the ebbing tides were taken into account. Total trapped crabs collected between the flooding and ebbing tides were summed per season and were compared using one way ANOVAs (one per each season, log-transformed to achieve homoscedasticity), with LSD test for a posteriori comparisons (Zar, 1999).

2.4. Movement patterns

To evaluate movements of crabs between marsh and mudflat, 10 movement traps were placed parallel to the shore, between the mud flat and the marsh. Each trap consisted in a drift fence, 1.5 m long, 30 cm high, 1 mm mesh size, vertically buried into the sediment with a zigzag shape to detect bi-directional movement. In each vertex 2 pitfall traps (described above) were placed one in each side of the mesh collecting the crabs that were moving down to the mudflat and the ones that were moving upward to the marsh zone. The crabs were collected every 6 h (at low tide and at high tide) during 8 tidal cycles at ebbing and flooding tides. Given the design of the movement trap the crabs collected moving down and upward are dependent because they are placed in the same fence, thus the average number of crabs moving upwards vs. downwards was compared using t-tests for dependent samples (Zar, 1999, separately for season).

2.5. Stomach content

Given that *N. granulata* is a deposit feeder in mud flats and herbivorous–detritivorous in vegetated salt marshes (Iribarne et al., 1997), the production of feces may vary in quality or quantity between habitats due to differences in consumption rate or quality of food consumed (Thongtham and Kristensen, 2005). Thus, to analyze if there are differences in diet between zones, crabs from each zone (SAB, n = 94 and MCCL, n = 106) were collected and foregut contents were examined under a binocular dissecting microscope. Frequency of occurrence (FO) was calculated for each food item by dividing the number of crabs in the sample whose foregut contained a given prey by the total number of crabs in the sample with food in their stomachs. Food item proportions were compared between habitats using test for proportions (Zar, 1999).

2.6. Feces production and movement

To calculate the feces transported by crabs between zones, the crabs trapped with the movement traps were used in order to ensure that they were eating in one zone and moving to the other zone. Each crab was placed alone in plastic containers for 3 h to collect their feces. Dry weight of these feces was calculated after drying at 70 °C up to constant weight. Feces total organic matter (TOM) was calculated as the difference between dry weight and ash-free dry weight after combustion at 500 °C for 8 h, and the organic matter percent (OM%) of the individual feces. Samples were collected during winter, spring and autumn. For each season, dry weight and TOM produced per day and OM% transported in each direction was compared with t-tests for dependent samples (see above, Zar, 1999).

To have an estimation of the total feces transported by *N. granulata* due to their movements with high tides, randomization and resampling (a computer-based method that obtains estimates of the mean and standard deviation of particular variables using random combinations of relevant field measures, Manly, 1998) was used considering the number of crabs moving between marsh and mudflat zones and fecal production during 6 h, which is the average time of flooding or ebbing tides. To associate fecal production to each replicate of the movement traps, fecal production values were resampled with reposition to obtain the same number of crabs that were found in the movement traps. These values were summed obtaining a single fecal production per movement trap replicate. This value was recalculated 100 times for each replicate and the average of these iterations was used to compare the fecal transport between marsh and mudflat zones between seasons and sites with a 3 way ANOVA (site: SAB and MCCL), with movement direction (to the marsh or mudflat) and season (winter, spring and summer) as factors (Zar, 1999, root square transformed to meet the assumption of homoscedasticity).

3. Results

3.1. Crab densities

Density of crabs was more than 3 times higher in MCCL marsh than in SAB mudflats independently of the type or zone (Table 1, Fig. 2). Marsh zones generally showed higher densities except for spring in MCCL (LSD test in Fig. 2).

3.2. Activity patterns

In both sites *N. granulata* activity was tide-dependent. Crabs were always more active during high tide (independently, which is confirmed by the differences in the number of crabs trapped during ebbing compared with flooding tides) (Tables 2 and 3). In winter crabs in the SAB showed very low activity and only during high tides (see Table 2) with values 20 times higher for the mudflat with the ebbing than with the flooding tides. In spring and summer these differences were higher in the marsh zone, being 10 and 4 times higher with the ebbing tides in spring and summer respectively. In the mudflat and marsh/mudflat edge, the activity was 10 times higher in winter, 5 in spring and 2 in summer (see Table 2). In MCCL crabs showed no differences in activity in summer (see Table 3). In winter crab activity was 20 times higher in the mudflat, 10 in the mudflat/marsh edge, and 3 in the marsh. In spring, marsh/mudflat edge showed 3 times and marsh 4 times higher activity with high tides (see Table 3).

Crab activity in the different tidal levels (marsh/mudflat) showed no differences in winter (SAB, ANOVA: $F = 2.07$; $df = 2, 237$; $p = 0.12$; MCCL, ANOVA: $F = 0.78$; $df = 2, 177$; $p = 0.5$). In spring there were differences in both zones (SAB: ANOVA: $F = 23.4$; $df = 2, 234$; $p < 0.0001$; MCCL: $F = 34.1$; $df = 2, 197$; $p < 0.0001$). In SAB crab activity was highest in the marsh (LSD $p < 0.0001$), and in MCCL was higher both in the marsh and marsh/mudflat edge than in the mudflat (LSD $p < 0.0001$). The summer showed the opposite trend: the lowest activity was found in the marsh zone in both estuaries (SAB: $F = 24.05$; $df = 2, 189$; $p < 0.0001$; LSD $p < 0.00001$; MCCL: $F = 37.5$; $df = 2, 237$; $p < 0.0001$; LSD $p < 0.00001$).

3.3. Movement patterns

Movement traps in general showed no differences in movement direction between marsh and mudflat zones during tidal cycles (see Figs. 3 and 4) with only a few exceptions: in SAB in one ebbing tide in spring with more crabs moving to the marsh ($t = 2.47$; $p = 0.01$) and one ebbing tide in summer moving to the mudflat ($t = 2.4$; $p = 0.01$; Fig. 3) and in MCCL more crabs moved to the mudflat in one ebbing tide in winter ($t = 3$; $p = 0.01$; Fig. 4).

Table 1

N. granulata densities. Results of the three way ANOVA comparing A: both zones (SAB and MCCL), B: intertidal zones (marsh and mudflat) and C: seasons (winter, spring and summer).

Effect	df	MS	F	p
A	1	1.2	78.3	<0.0001
B	1	1.4	92.7	<0.0001
C	2	0.02	1.12	0.3
A×B	1	0.009	0.58	0.4
A×C	2	0.01	0.84	0.4
B×C	2	0.08	5.7	<0.005
A×B×C	2	0.001	0.09	0.9
Error	108	0.01		

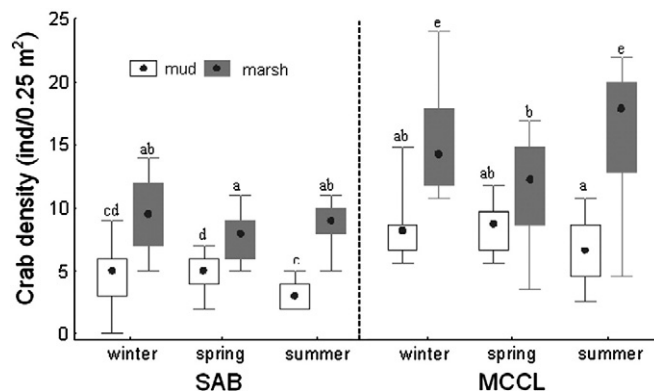


Fig. 2. Differences in *N. granulata* densities between SAB (San Antonio bay) and MCCL, marsh and mudflat zones and seasons. Different letters indicate significant differences (LSD test).

3.4. Stomach content

No differences were found in the proportion of *Spartina* spp. ingested between sites (FO MCCL = 0.46; FO SAB = 0.41; $p = 0.5$). The proportion of mud was higher in MCCL than in SAB (FO = 0.6; FO = 0.04 respectively, $p < 0.001$), while the proportion of crabs was higher in SAB than in MCCL (FO = 0.42; FO = 0.25 respectively, $p = 0.04$). Crabs in MCCL showed a higher proportion of empty stomachs than in SAB (FO MCCL = 0.45; FO SAB = 0.29; $p = 0.02$).

3.5. Feces production and movement

For the individual estimations, in winter, the few crabs trapped in SAB did not produce feces, in MCCL the crabs moving to the marsh produced more feces than the crabs moving towards mudflat zone ($t = 3.47$; $df = 36$; $p = 0.001$; Fig. 5). In spring and for the two sites, SAB and MCCL, total dry weight of feces produced by day showed no differences between crabs moving towards different directions (SAB $t = 1.58$; $df = 41$; $p = 0.12$; Fig. 6) (MCCL $t = 1.84$; $df = 30$; $p = 0.07$; Fig. 5). The same results were found in summer with no differences in SAB ($t = 0.9$; $df = 43$; $p = 0.37$; Fig. 5) nor in MCCL ($t = 0.74$; $df = 23$; $p = 0.46$; Fig. 5).

The only difference found in TOM was in winter in MCCL ($t = 2.02$; $df = 26$; $p = 0.02$). Crabs moving to the marsh produce more organic matter because they produce more feces. Nevertheless, the OM% was higher in crabs moving from the marsh to the mudflat ($t = 3.1$; $df = 32$; $p = 0.001$). In the spring of SAB no differences were found for TOM ($t = 1.33$; $p = 0.19$) nor for OM% ($t = 1.4$; $df = 41$; $p = 0.16$). The same results were found for MCCL (TOM: $t = 1.85$, $p = 0.07$; OM%:

Table 2

t Test results comparing *N. granulata* activity after high (ebbing) and low (flooding) tides in San Antonio bay estimated by number of crabs collected per trap. *** indicates $p < 0.0001$.

	×ebbing	×flooding	t	df	p
<i>Winter</i>					
Mudflat	5.83	0.3	10.7	79	***
Edge	3.25	0.2	9.6	79	***
Marsh	3	0.3	10.8	79	***
<i>Spring</i>					
Mudflat	5	1	9.8	79	***
Edge	5.4	2.6	6.7	79	***
Marsh	1.3	1.4	13.1	79	***
<i>Summer</i>					
Mudflat	10.8	4.3	7	47	***
Edge	18.5	6.5	8.5	71	***
Marsh	8.5	2.3	10.7	71	***

Table 3
t Test results comparing *N. granulata* activity after high (ebbing) and low (flooding) tides in Mar Chiquita estimated by number of crabs collected per trap. *** indicates $p < 0.0001$; * $p < 0.05$.

	×ebbing	×flooding	t	df	p
<i>Winter</i>					
Mudflat	8.5	0.4	5.4	59	***
Edge	4.1	0.4	4.6	59	***
Marsh	1.8	0.5	4.4	59	***
<i>Spring</i>					
Mudflat	0.8	0.3	2.3	59	*
Edge	3	0.9	5.6	59	***
Marsh	6.8	1.6	6.4	79	***
<i>Summer</i>					
Mudflat	0.3	0.2	0.6	79	0.5
Edge	0.3	1.2	1.1	79	0.3
Marsh	2.3	1.7	2.4	79	*

$t = 1.41$, $df = 30$, $p = 0.17$). No differences were found in summer (SAB TOM: $t = 0.6$, $p = 0.5$; OM%: $t = 0.28$, $df = 43$, $p = 0.77$; MCCL TOM: $t = 0.2$, $p = 0.8$; OM%: $t = 1.6$, $df = 23$, $p = 0.12$, all results in Figs. 5 and 6).

In SAB production of feces was higher in spring than in summer ($t = 2.2$, $p = 0.03$). TOM showed no differences between seasons ($t = 1.6$, $p = 0.1$) and the OM% was higher in summer than in spring ($t = 2.15$, all $df = 83$, $p = 0.03$). In MCCL the lowest production of feces was found in winter compared with spring and summer (ANOVA:

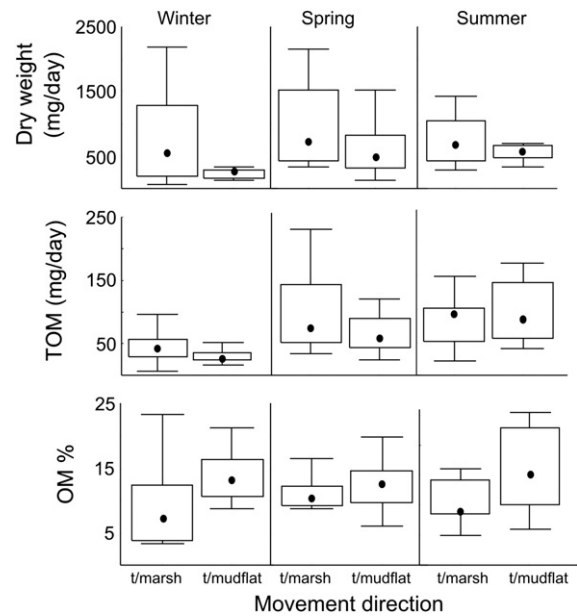


Fig. 4. Fecal production mg d^{-1} , total organic matter (OM) and fecal OM% moving to the marsh or to the mudflat in MCCL.

$F = 3.98$, $df = 2$, 92 ; $p = 0.02$; LSD test $p < 0.03$) as same as the TOM ($F = 23.4$, $df = 2$, 92 ; $p = 0.02$). No differences were found in the OM% of feces between seasons ($F = 1.3$, $df = 2$, 92 ; $p = 0.3$, Fig. 7).

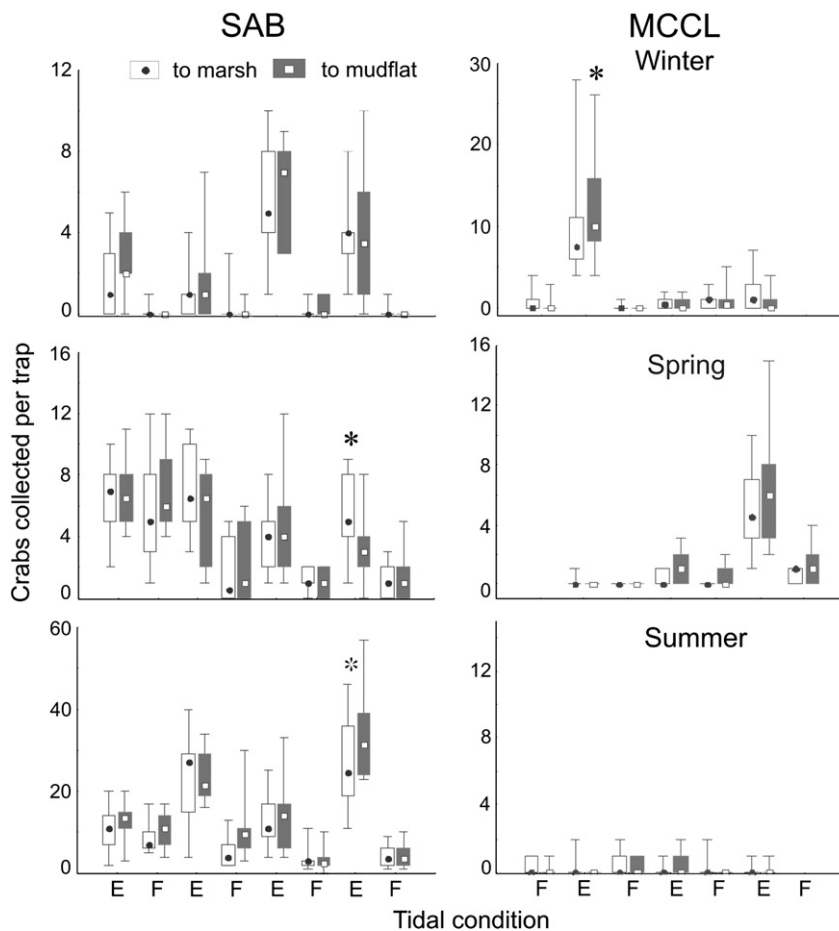


Fig. 3. Number of crabs collected per pitfall in SAB and MCCL at 4 consecutive tidal cycles with ebbing (E) or flooding (F) tides. Asterisk shows the differences between moving direction to the marsh or to the mudflat at one tide. Here and thereafter, box plots are constructed with limits of boxes being the 75th and 25th percentiles, lines represent 10th and 90th percentiles and square inside boxes are medians.

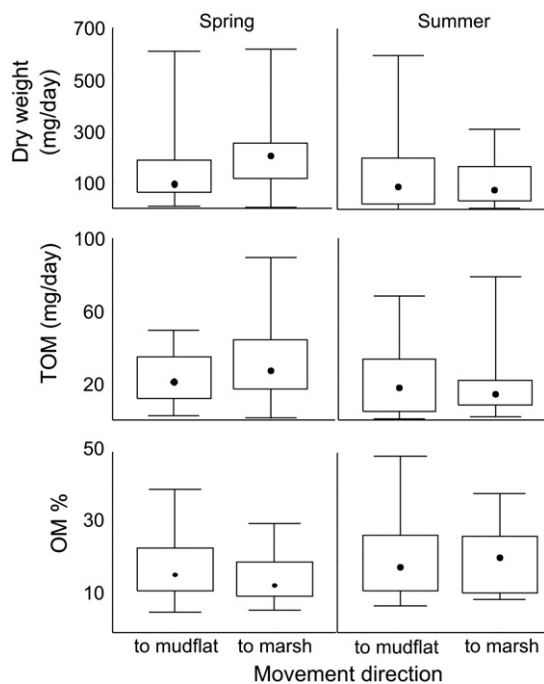


Fig. 5. Fecal production mg d^{-1} , total organic matter (OM) and fecal OM% moving to the marsh or to the mudflat in SAB.

With the above results based on individual performances in fecal production, a resample procedure was performed taking into account the number of crabs moving between zones in order to calculate the net transport of feces. This fecal transport between marsh and mudflat

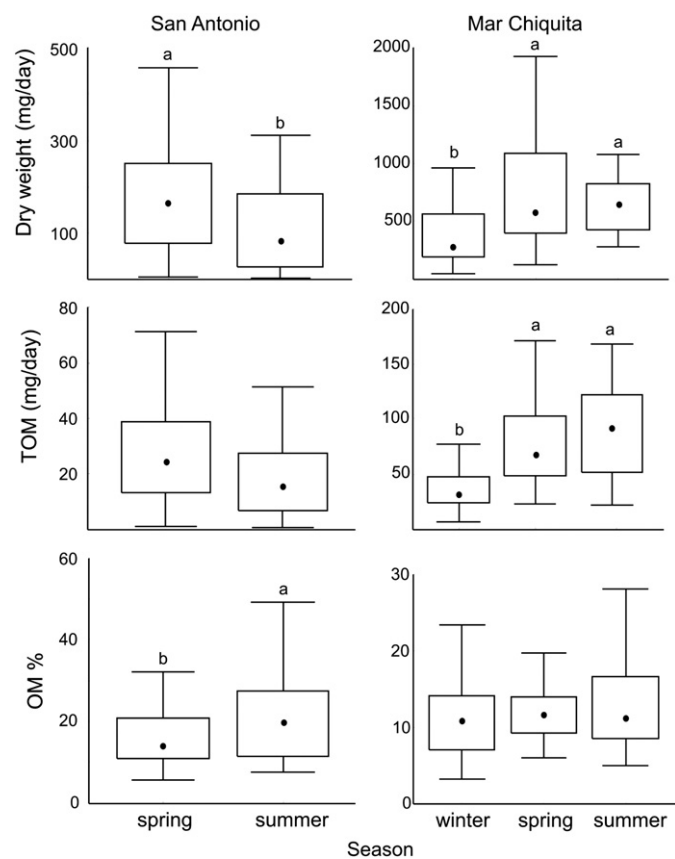


Fig. 6. Seasonal comparisons of fecal production (dry weight), organic matter (OM) and OM% in the marsh and mudflat in both coastal zones.

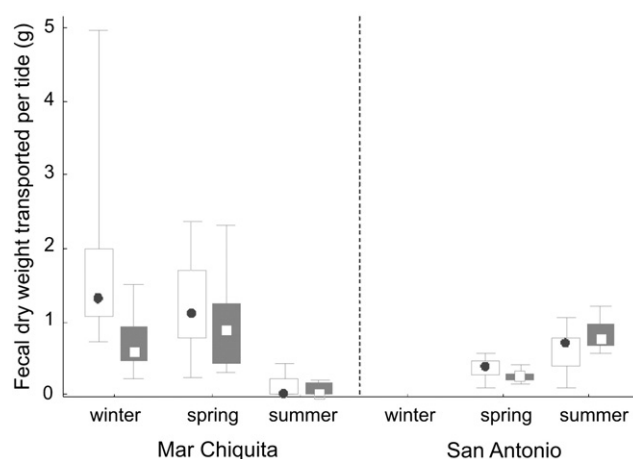


Fig. 7. Fecal dry weight transported by *N. granulata* to the mudflat (white boxes) and to the marsh (grey boxes) during 6 h (from flowing to ebbing tides) 1 m of marsh border (the longitude occupied by the movement traps).

showed no interaction effect between the 3 factors combined (site, season and movement direction; Table 4, Fig. 7). The highest transport was found in winter in MCCL which was 10 times higher than in summer, while there was the opposite trend in SAB (Table 4, Fig. 7). The movement direction depended on the site. There were no differences on movement direction at SAB, while in MCCL there were 45% more crabs moving to the marsh than to the tidal flat (Fig. 7).

4. Discussion

Our results show that crabs act as cross-habitat linkages through fecal deposition that may generate an important input of energy in marsh zones. This input varies temporarily because *N. granulata* activity is tide dependent and there were also differences in activity between seasons, sites or coastal areas. No differences were found in movement direction of crabs between marsh and mudflat zones. Given that there were differences in the diet composition (higher proportion of crabs in SAB, suggesting higher cannibalism), OM of fecal pellets were higher in SAB than in MCCL. The resampling analysis showed that there is an exchange of organic matter among habitats because of the movement of *N. granulata* and fecal deposition between marsh and tidal flats and this movement is higher in MCCL than in SAB. Nevertheless, these differences between both coastal zones depend on the season.

Sediments inhabited by *N. granulata* are characterized by having more organic matter than nearby areas without crabs (Botto and Iribarne, 2000; Escapa et al., 2004; Botto et al., 2006). This is likely to be a consequence of the organic matter trapped within crab burrows (Botto and Iribarne, 2000). Moreover, in these zones there are higher densities and better body conditions of deposit feeders, such as

Table 4

3 way ANOVA results (estuary, season and transport direction) comparing the amount of feces moving in 6 h (time between flow and ebbing tides) between marsh and mudflats zones. *** indicates $p < 0.0001$; ** $p < 0.005$; * $p < 0.05$.

Factor	df	F	p
estuary (A)	1	44.4	***
season (B)	2	12.1	***
direction (C)	1	4.8	*
AxB	2	126.3	***
AxC	1	8.2	**
BxC	2	3.8	*
AxBxC	2	2.2	0.1
Error	108		

polychaetes (Palomo et al., 2004). Nevertheless, it could also be related to biodeposition. In vegetated zones biodeposition may have important consequences in decomposition and incorporation of primary production in the system (Cebrian, 1999). Considering crab densities in SAB, deposition in marsh habitats through feces production is of more than 3 times higher in the marsh than in the tidal flat (5 and 1.4 g m⁻² d⁻¹ respectively), with a higher OM (16%) than the surrounding sediment (marsh sediments: 1.8%, mudflat sediment: 0.9%; Bas et al., 2005). Biodeposition in this zone could generate the differences found in organic matter between zones. Detritus production calculated for the same marsh at MCCL (Vera et al., 2009) ranged between 2 and 6 g m⁻² d⁻¹, even if the rate of fecal production is overestimated, it is about 80% of the detritus production.

The comparisons between sediment trapped through passive deposition inside burrows in MCCL (Botto et al., 2005; Gutierrez et al., 2006) with the results showed in this work, suggest that the cross habitat link generated by crab movement and deposition can be very important. Burrows in the marsh zone can trap in average 173 g m⁻² d⁻¹ of dry sediment (5% OM, Gutierrez et al., 2006). The results of this work suggest that 50% of this trapped material could be due to fecal deposition (90 g m⁻² d⁻¹). In the mudflat, instead, bedload transport can incorporate 2000 g m⁻² d⁻¹ (Botto et al., 2005) into burrows, being only 5% of these amount possible feces of *N. granulata* (120 g m⁻² d⁻¹), which suggests that biological transport is more important in the marsh than in the mudflat.

Differences found in organic matter content in feces between MCCL and SAB could be the result of differences in nutritional values (Miller and Roman, 2008). Organic matter of feces in MCCL represented 12% of feces total weight, while in SAB organic matter is in average 20%. Because organic matter is lower in SAB than in MCCL (Bas et al., 2005), the low quality could lead to enhance cannibalism in the former estuary (see Polis, 1981). Studies of stomach contents of adults in both sites showed a higher proportion of crab pieces in SAB than in MCCL. Cannibalism is generally caused by nutritional deficits, as an additional source of essential components to the diet when food quality is low (Wolcott and O'Connor, 1992; Anger, 1995). Thus, the lower quality of SAB sediments could be triggering higher cannibalism, and then highest organic content of feces in SAB, which enhances the importance of biodeposition.

The horizontal movement of energy and nutrients from salt marshes to adjacent areas has been mainly attributed to the migration and consumption of nekton (Kneib, 1997). This energy transfer can operate at different temporal scales. Nevertheless, tidal or diel migrations are generally associated with a spatial separation of foraging and refuge areas (Deegan et al., 2000). Energy obtained in the foraging place is then exported to the refuge zone through mortality or by fecal deposition. In this case, *N. granulata* is capable of being deposit feeder or herbivorous. Therefore salt marshes as well as mudflats are feeding areas, linking these two zones in a two way transfer of energy. Moreover, estimations in fishes foraging in marshes and then exporting energy as animal tissue to deeper habitats in other systems support the conclusion that fecal deposition should not be overlooked. For example, Deegan (1993) found that 0.1 g DW m⁻² d⁻¹ was exported as fish biomass (5–10% of the primary productivity of the area). Kneib and Stiven (1978) found that fishes provide a monthly average wet weight of 20 g for each meter of marsh edge sampled (0.7 g d⁻¹) to other commercial species as food. Moreover Cicchetti and Díaz (2000) found that 0.2 g DW m⁻² d⁻¹ was removed from the marsh primarily by *Callinectes sapidus* tissue. The values found in this work by *N. granulata* showed that in average they transport 1 g for each meter of marsh per tide, (5 more times than *C. sapidus*) while the deposition ranged from 17.5 to 120 g DW m⁻² d⁻¹. These values are larger than the values exported by the species describe above.

Even when it is well recognized the effects caused by the increased loading of nutrients in coastal systems, moderated inputs of nutrients

have received much less attention (see Posey et al., 2002, 2006). Most of the previous literature highlights the importance of marshes as exporters, both by physical or biological agents, but in this work we found that biodeposition may have an important contribution into the marsh system. This highly abundant mobile crab connects different habitats enhancing the interaction between habitats that function together. The results from this study may have direct application in the planning process for salt marsh and mudflat preservation projects.

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