



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 Garrit, 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

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