



## Effect of crab bioturbation on organic matter processing in South West Atlantic intertidal sediments



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### ABSTRACT

Organic matter (OM) remineralization plays a key role in controlling the biogeochemistry of marine sediments. Through their burrowing activities, bioturbating macrofauna not only induces physical, chemical and biological modifications, which can affect microbial communities responsible for organic matter remineralization, but it could also directly affect the distribution and bioavailability of sedimentary organic matter. Through in situ experiments manipulating crab and burrow density in intertidal soft-bottoms, we assessed if crab-bioturbation affects benthic metabolism, and the amount, distribution, and bioavailability of sedimentary OM. Crab-bioturbation enhanced overall benthic metabolism and benthic flux of dissolved OM toward the water column at both mudflat and saltmarsh zones. Moreover, our results revealed that bioturbation also changes the quality, bioavailability and distribution of sedimentary OM in mudflats and saltmarshes. Overall, bioturbation enhanced the proportion of labile organic carbon of bioturbated sediments and homogenized the sediment column in terms of their proportion of labile organic carbon. However, crabs also generated biogenic structures (e.g., mounds) that could promote spatial heterogeneity of high nutritional-value OM. Bioturbation-induced changes on benthic metabolism and on OM availability would result in a reduction of the storage capacity of carbon in our intertidal systems. Previous works indicated that crab-burrows trap detritus and OM-rich sediments. Our results suggest that detritus are efficiently remineralized at bioturbated sediment, and finally they are quickly exported to the water column as CO<sub>2</sub> and DOC. Thus, crabs are modifying the OM processing at intertidal soft bottoms, and the ways in which carbon is exported to coastal waters.

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### 1. Introduction

Shallow coastal ecosystems (including marshes and mangroves, intertidal and subtidal sediments, tidal plains and seagrass beds) are distributed worldwide and though they represent less than 2% of the oceanic surface, they account for about 20% of the global marine primary production (Charpy-Roubaud and Sournia, 1990; Pedersen et al., 2004). Although some of the carbon fixed by plants is consumed by herbivores, most of the fixed carbon enters benthic detrital trophic pathway (e.g., Cebrian and Lartigue, 2004; Mann, 1988; Schlesinger, 1997). The carbon input into sediments can be as detrital particulate organic matter (OM) from plant dead tissues, but also as soluble organic secretions from primary producers (i.e., from roots of vascular plants, Hines et al., 1989; from exopolymeric secretions of microphytobenthos, Smith and Underwood, 2000). As a result, organic matter in marine sediments is composed of a mixture of labile and refractory organic compounds

(e.g., Burdige, 2006; Canfield et al., 2005). This sedimentary OM is converted back to inorganic carbon by hydrolysis/fermentation (involving dissolved organic carbon formation, DOC) and subsequent mineralization to CO<sub>2</sub> by heterotrophic microorganisms (Canfield, 1993; Kristensen and Holmer, 2001). Moreover, labile organic carbon (LOC), often measured as the sum of protein, carbohydrate and lipid carbon, has been reported as the fraction of organic carbon potentially available to benthic consumers (Fabiano et al., 1995). Thus, the geochemistry of marine sediments is controlled not only by the composition of the material initially deposited in the sediments (e.g., Fenchel et al., 1998), but also by the chemical, biological, and physical processes that affect this material after its deposition (processes commonly referred to as “early diagenesis”; sensu Berner, 1980; Burdige, 2006).

Benthic macrofauna affects microbial processes in sediments by their burrowing and feeding activities (e.g., Kristensen and Kostka, 2005; Pappaspyrou et al., 2006, 2010), and directly participates in sedimentary processes through OM metabolism coupled with aerobic respiration and metabolic excretions (Furukawa, 2005). By means of active or passive irrigation and sediment reworking, bioturbation injects

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oxygen and other electron acceptors into anoxic sediment (e.g., Daleo et al., 2008; Fanjul et al., 2007; Gribsholt et al., 2003; Kostka et al., 2002), and it rapidly transports organic substances (i.e., dissolved, particulate, and also compounds adsorbed into mineral particles) between oxic and anoxic surfaces (Aller, 1994; Fanjul et al., 2007). Organic matter at oxic surfaces are thus displaced toward deep sediment dominated by anaerobic bacteria, and in the opposite direction, relatively refractory substances in anoxic deep sediments are transported to aerobic microorganisms capable to degrade it (Kristensen and Holmer, 2001; Kristensen et al., 2012; Montague, 1982), usually increasing overall benthic community metabolism (Andersen et al., 1992; Fanjul et al., 2011; Kristensen, 1985). Moreover, since sorption of dissolved organic substances is a redox-dependent process (Chin et al., 1998; Komada et al., 2004), bioturbators could also impact on DOC accumulation and benthic flux by creating a redox-oscillating environment (Aller, 1994). Indeed there are evidences of differences in DOC flux between bioturbated and non-bioturbated sediments (e.g., Burdige and Homstead, 1994; Michaud et al., 2006). Thus, to identify the factors affecting transport processes, composition, reactivity, and distribution of sedimentary OM, it is critical to understand which processes are controlling mineralization, benthic metabolism and DOC export toward coastal waters.

South West (SW) Atlantic intertidal sediments are mostly pristine systems, which are intensely bioturbated by the burrowing crab *Neohelice (Chasmagnathus) granulata*. Bioturbation coefficients in these sediments are among the highest reported worldwide, with values around  $250 \text{ cm}^{-2} \text{ yr}^{-1}$  (Fanjul et al., 2007) and sediment reworking rates of up to  $5.9 \text{ kg dry sediment m}^{-2} \text{ d}^{-1}$  (Iribarne et al., 1997), values that are similar to those found for the ghost shrimp *Callinectes kraussi* (up to  $12 \text{ kg wet sediment m}^{-2} \text{ d}^{-1}$  Branch and Pringle, 1987; Kristensen et al., 2012). This burrowing crab, according to the reworking mode, is a “regenerative” bioturbator (sensu Solan and Wigham, 2005; Kristensen et al., 2012), and affects the whole intertidal ecosystem functioning. For example, crab-bioturbation favors plant growth (Daleo et al., 2007), modifies benthic community structure (Escapa et al., 2004), mediates predator–prey interactions (Escapa et al., 2004; Martinetto et al., 2005), and affects microalgal assemblages (Alvarez et al., 2013). Crab-bioturbation also affects carbon burial (Gutiérrez et al., 2006), enhances sediment oxygenation (Daleo et al., 2007), benthic metabolism (Fanjul et al., 2011) and nutrient benthic flux (Fanjul et al., 2011). Oxygen uptake increases from  $200 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$  in non-bioturbated zones up to  $6000 \mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$  in bioturbated zones (Fanjul et al., 2011). In marshes with low content of dissolved inorganic nitrogen ( $\sim 18 \mu\text{M}$ ), crabs favor dissolved inorganic nitrogen flux toward the sediment, increasing from  $-100 \mu\text{mol N m}^{-2} \text{ h}^{-1}$  at non-bioturbated sediments to  $-700 \mu\text{mol N m}^{-2} \text{ h}^{-1}$  at bioturbated sediments (Fanjul et al., 2011).

Recent studies suggested that the extensive crab-bed zones affect the particle movement and near-bottom fluid dynamic (Escapa et al., 2008), and burrows could locally increase the sedimentary OM content of such zones by passively trapping detritus and OM-rich sediments (Botto et al., 2006; Escapa et al., 2008; Montemayor et al., 2011). Indeed, crab activity produces important zones of macro-detritus retention that can enhance the amount of OM that is stored in saltmarshes (e.g., Botto et al., 2006; Gutiérrez et al., 2006). This could be particularly important in systems with low OM content, such as in many SW Atlantic intertidal soft bottoms (e.g., Mar Chiquita,  $37^\circ 45\text{S}$ : 3.8%; Bahía San Antonio,  $40^\circ 46\text{S}$ : 1.8%; Luppi et al., 2013). Although it is well known that saltmarsh sediments store large amounts of OM, little is known about OM quality in saltmarsh soils (Spohn et al., 2013), and about the spatial variability of this OM. We hypothesize that bioturbation by *N. granulata* impacts on OM processing affecting its availability (e.g., by enhancing the proportion of readily labile compounds to total organic matter) and also stimulating their remineralization rate (by enhancing OM and solute transport processes, and creating a redox-oscillating environment). Thus, the aim of this work is to evaluate the role of the burrowing crab *N. granulata* on the overall benthic metabolism and

benthic flux of dissolved organic substances (i.e., DOM, dissolved carbohydrates and proteins flux across the water-sediment interface), and on the amount, distribution, composition and reactivity of sedimentary OM at intertidal soft bottoms. For this purpose, we conducted field experiments manipulating bioturbation intensity.

## 2. Material and methods

### 2.1. Study area

The study was conducted between September 2008 and March 2009, in the southern part of the Samborombom bay ( $36^\circ 22' \text{ S}$ ,  $56^\circ 45' \text{ W}$ , southern mouth of La Plata River, Argentina), a natural protected area affected by low amplitude ( $< 1.4 \text{ m}$ ) semidiurnal tides and characterized by large intertidal areas inhabited by burrowing crabs (Daleo et al., 2007; Luppi et al., 2013). *N. granulata*, a large-sized burrowing crab (up to 40 mm carapace width; Spivak et al., 1994) occurs in the whole intertidal (Iribarne et al., 1997), from low mudflats to high saltmarshes composed of *Spartina alterniflora* at the low zone, and *Spartina densiflora* at the high zone (Isacch et al., 2006). Crabs are mostly deposit feeders in mudflats, and herbivorous–detritivorous in saltmarshes (Bortolus and Iribarne, 1999; Botto et al., 2005; Iribarne et al., 1997). *N. granulata* excavates semipermanent burrows generating extensive burrowing beds commonly with up to 60 burrows  $\text{m}^{-2}$  (Botto and Iribarne, 2000; Iribarne et al., 1997), which cover up to 80% of the intertidal areas of SW Atlantic estuaries and bays (Botto et al., 2006; Iribarne et al., 2005). This crab is active over a wide range of environmental conditions (Luppi et al., 2013). Crabs leave burrows but stay near burrow entrances during low-tide, and show more intense activity during high tide periods (Luppi et al., 2013). This natural system allows us to evaluate the biogeochemical functioning in areas where crab densities are among the few remaining examples of present densities closely similar to those of the ancient population baselines (Fanjul et al., 2007), that have now largely been reduced in other systems (e.g., Wang et al., 2010).

### 2.2. Experimental design

To evaluate the effect of *N. granulata* on benthic metabolism and benthic flux of dissolved organic substances (i.e., flux of dissolved substances across the water-sediment interface), and on sedimentary OM quality and bioavailability, we conducted a series of field experiments manipulating bioturbation intensity in a *S. alterniflora* saltmarsh and bare intertidal mudflat (see Fig. 1). Each experiment had three treatments (6 replicates each one): (1) unoccupied burrows (thereafter B treatment); (2) inclusion of adult crabs *N. granulata* in burrows (thereafter B + C treatment); and (3) exclusion of crabs and burrows used as control (thereafter NBC). Plastic mesh boxes (0.75 cm mesh opening; 0.4 m height, 0.5 m diameter; Fig. 1a and b) with a cover of the same mesh (treatment NBC) or without cover (treatments B and B + C) were used to delimit each experimental unit (see the use of similar boxes in Fanjul et al., 2007; Thomas and Blum, 2010; Needham et al., 2011). Experimental units were deployed in natural sediments without crab bioturbation. Cylindrical holes (3.5 cm in diameter and 40 cm in depth) were excavated in soil at B and B + C treatments in order to reach 30 holes  $\text{m}^{-2}$ , which was a density similar to natural burrow densities (i.e., mean natural density: 29.6 burrows  $\text{m}^{-2}$ ; SD: 6.1; Fanjul et al., 2011). Then, one adult crab was added to each hole in B and B + C treatments, and in a few days the crabs colonized, maintained and often expanded the holes transforming it into burrows (see Fanjul et al., 2007; Iribarne et al., 2005; Thomas and Blum, 2010). The experimental units were periodically monitored to check that crabs did not colonize NBC treatments (i.e., closed boxes, see Fig. 1). After 2 months of their inclusion, the crabs inhabiting boxes corresponding to treatment B were removed by hand, and the plastic mesh covers were attached to those boxes to inhibit further crab colonization. By this

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