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Effects of two estuarine intertidal polychaetes on infaunal assemblages and organic matter under contrasting crab bioturbation activity

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ABSTRACT

Polychaetes and burrowing crabs are widely distributed in intertidal soft bottom environments, playing an important role in structuring infaunal assemblages through trophic and non-trophic interactions such as bioturbation. In southwestern Atlantic (SWA; 37°40′S, 57°23′W) intertidal mudflats, the polychaetes *Laeonereis acuta* and *Neanthes succinea* coexist with the burrowing crab *Neohelice (Chasmagnathus) granulata. N. granulata* and *L. acuta* strongly modify the sediment characteristics at different spatial scales, changing the infaunal assemblages and probably affecting feeding mode of *N. succinea*, which could prey upon *L. acuta*. Here, we experimentally evaluated the effects of constant densities of *L. acuta* and *N. succinea* on the benthic species assemblages and sediment organic matter (OM) content in two contrasting scenarios of crab bioturbation: inside and outside crab beds. We found that (1) both polychaetes did not affect the mean density of other macrofaunal organisms neither the meiofauna in general, but *L. acuta* modifies the abundance of specific groups such as foraminiferans; (2) polychaetes produced changes in meiofaunal spatial distribution probably by adding habitat heterogeneity; and (3) no evidence of predation of *N. succinea* on *L. acuta* were observed. Additionally, the variable effects of polychaetes on chlorophyll *a*nd OM content showed that they were species-specific and also modified by crab bioturbation. Moreover, effects of crab bioturbation on primary producers, quality and content of OM, and on some macro and meiofaunal organisms were found. Our results suggest that the effects of *L. acuta* and *N. succinea* on benthic species and OM content are mostly species-specific and, with regard to food sources (OM content and microphytobenthic biomass), strongly modified by larger scale crab bioturbation.

1. Introduction

Intertidal soft bottom systems are world widely distributed and are recognized as essential sites that provide unique ecosystem services (Elliott and Whitfield, 2011), such as flood and storm protection or cycling of nutrients (Atkins et al., 2011). They are characterized by low species diversity with high abundance and biomass (Elliott and Whitfield, 2011) and sediments with large amounts of organic matter (Spohn et al., 2013). These ecosystems may account for the 20% of the global marine primary production (Pedersen et al., 2004), are important stop over sites for several species of shorebirds (e.g. Morrison and Ross, 1989) and feeding sites for fishes (e.g. Green et al., 2009). Therefore, these are key systems in coastal food webs (Zedler and Callaway, 2001).

Interactions between organisms and environmental factors are structuring forces inside communities (Pennings and Bertness, 2001; Widdows and Brinsley, 2002). These interactions determine species abundance and distribution through competition (e.g. Connell, 1961), predation (e.g. Paine, 1966) and/or ecosystem engineering (e.g. Jones et al., 1997). In soft sediments, predation among infaunal organisms modify preys assemblages (e.g. polychaetes: Caron et al., 2004; nemertines: Thiel and Reise, 1993), generating multiple trophic levels (Thrush, 1999 and references therein) and linking meiofauna with higher-level predators (fishes or birds; Ambrose Jr., 1984). However, the effects of infaunal predation are linked to the quantity and quality of organic matter (OM, Venturini et al., 2011) because only a small portion is available for organisms (e.g. Dell'Anno et al., 2000; Fanjul

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et al., 2015). Therefore, predation and other physical factors, determine the relationships between species and consumption rates (Snelgrove and Butman, 1994; Papaspyrou et al., 2010).

Bioturbation is a common process, exerted by different organisms at different intensities and different time and spatial scales (Murray et al., 2002; Citadin et al., 2016). In soft bottom intertidals, burrowing species are relevant because through bioturbation they modify physical (e.g. Natálio et al., 2017), chemical (e.g. Chapman and Tolhurst, 2007) and biological (e.g. Papaspyrou et al., 2006) characteristics of sediments. These organisms generate high levels of spatial heterogeneity that favor the development of different infaunal species assemblages (e.g. Escapa et al., 2004; Papaspyrou et al., 2006) with consequences in the food webs and species interactions (e.g. Alvarez et al., 2015). Polychaetes and crabs are important bioturbator organisms, abundant and widely distributed in intertidal soft bottom environments (Wang et al., 2010; Venturini et al., 2011). In habitats where they coexist, the effects of polychaetes (which are relatively small-scale bioturbators) could be affected by the intensity of crab burrowing (which are relatively large-scale bioturbators).

In the intertidal soft bottoms of the Southwestern Atlantic (SWA; 37°40′S, 57°23′W) the burrowing crab *Neohelice (Chasmagnathus) granulata* and the polychaetes *Laeonereis acuta* and *Neanthes succinea* coexist (Iribarne et al., 1997; Palomo et al., 2003, 2004). *N. granulata* (up to 8 cm carapace width; Luppi et al., 2002) generates large areas with high density of burrows (i.e. crab beds, > 100 burrows m^{-2}) which may reach up to 20 cm in surface opening diameter and 40 cm depth in mudflats (Iribarne et al., 1997; Alberti et al., 2015). The burrows increase habitat complexity and bioturbation affects the abundance and distribution of other species (e.g. fishes: Martinetto et al., 2005; polychaetes: Palomo et al., 2003; meiofaunal organisms: Escapa et al., 2004) and the sediment organic matter (OM) bioavailability and spatial distribution (Fanjul et al., 2015). The polychaete *L. acuta* is up to 6 cm length (Palomo and Iribarne, 2000), reaching densities up to 7400 ind m^{-2} (Botto and Iribarne, 1999) depending on sites, seasons and years (e.g. from 500 ind m^{-2}Palomo et al., 2003). In particular, the abundance of *L. acuta* is at least 2.5 times higher inside crab beds compared with similar areas outside crab beds (Botto and Iribarne, 2000). Biotubartion by *L. acuta* produces sediment mounds, which contain more OM than the surrounding sediments (Palomo and Iribarne, 2000).

On the other hand, the biology and ecology of the polychaete *N. succinea* is less known. In SWA mudflats, *N. succinea* can reach up to 8 cm length (Elías, 2002) and has densities between 47 ind m^{-2} (Botto and Iribarne, 1999) and 255 ind m^{-2} (Martinetto et al., 2005, 2011). Despite *N. succcinea* inhabits brackish-water areas building galleries in intertidal sediments (Rioja, 1946), its bioturbation effects on OM are unknown. This species is a typical surface deposit-feeder (Fauchald and Jumars, 1979) but, depending on the habitat, it can be carnivorous (Pardo and Dauer, 2003) controlling the abundances of other polychaetes and possibly feeding on *L. acuta* (Gutiérrez et al., 2000). In fact, inside crab beds, this polychaete changes its trophic positions showing a diet enriched ^{13}C (Botto et al., 2005). Together, *L. acuta* and *N. succinea* constitute the main prey items for higher trophic level organisms in these areas (e.g. silverside: Martinetto et al., 2005 and birds: Botto et al., 1998) and are the principal constitutive taxon of macrofauna.

In intertidal soft bottoms of the SWA, the crab *N. granulata,* as mentioned above, by increasing OM total content and OM bioavailability and spatial distribution, increases abundances and change feeding behaviour of polychaetes inside crab beds. Thus, the objectives of this work were to evaluate the effects of the polychaetes *L. acuta* and *N. succinea* on the benthic species assemblage and the quality and content of OM in two contrasting scenarios: with and without crab bioturbation. We hypothesize that (a) *L. acuta* and *N. succinea* bioturbation have negative effects on meiofaunal densities, OM quality and content and microphytobenthic biomass (estimated on chlorophyll content); (b) *N. succinea* reduce *L. acuta* density, and this effect is exacerbated outside crab beds where OM is lower than inside crab beds; and (c) the outcome of these interactions (polychaetes-meiofauna-primary producers) is different inside than outside crab beds.

2. Materials and methods

2.1. Study site

The study was performed in a tidal flat area at Mar Chiquita Coastal Lagoon (37° 40′ S, 57° 23′ W; Argentina), a Man and the Biosphere Reserve from UNESCO, during November–December 2008 and January–February 2009. The coastal lagoon is a body of brackish water (46 km^2) with low tidal amplitude (≤1 m) permanently connected to the sea (Reta et al., 2001) with a wide salinity range (2 to 35; Spivak et al., 1994). The intertidal zone is characterized by mudflats surrounded by a large *Spartina densiflora* salt marsh area (Isacch et al., 2006). The present study was made in open intertidal mudflats, which are the only habitats flooded daily by tides. In the same intertidal level (15 cm over mean lower low water, MLLW), we identified two sites inhabited by high densities of crab burrows and thus strongly bioturbated (hereafter "CB+") and two sites not bioturbated by crabs, but with some occasionally isolated crab burrows during the warm season (hereafter "CB−" Fig. 1). The two sites of each type were similar in terms of hydrodynamic conditions and general characteristics, and also in the effects generated by active crab bioturbation on sedimentary characteristics in the case of CB+ (Iribarne et al., 1997; Botto and Iribarne, 2000).

2.2. Effects of Laeonereis acuta and Neanthes succinea on benthic assemblages and OM content

To evaluate the effects of the polychaetes *Laeonereis acuta* and *Neanthes succinea* on the benthic assemblage (i.e., macrofauna, meiofauna, and microphytobenthos), sediment organic matter quality (labile organic carbon, "LOC") and sediment organic matter ("OM") content, in two contrasting scenarios of crab bioturbation, two field experiments

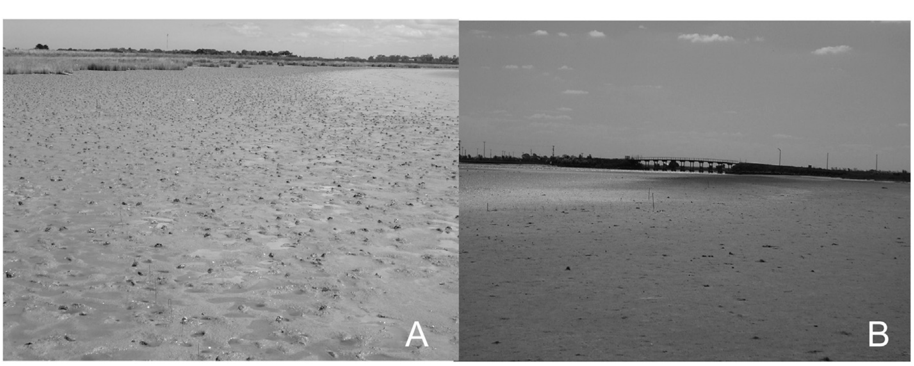

Fig. 1. Sites where experiments were deployed: (A) crab beds sites is shown; the caves are conspicuous and cover the whole intertidal area between the cordgrass and the sub tidal line. Next to the caves, there are mounds of reworked sediment. (B) outside crab beds site is shown, caves are scarce and scattered in the intertidal. Photo credit: (A) Paulina Martinetto and (B) M. Fernanda Alvarez.