Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.

(This is a sample cover image for this issue. The actual cover is not yet available at this time.)

This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

http://www.elsevier.com/copyright

Author's personal copy

Journal of Experimental Marine Biology and Ecology 440 (2013) 216–224

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Cascading top-down effects on estuarine intertidal meiofaunal and algal assemblages

M. Fernanda Alvarez [a,*], K. Soledad Esquius [b], Mariana Addino [a], Juan Alberti [a], Oscar Iribarne [a], Florencia Botto [a]

[a] Laboratorio de Ecología, Instituto de Investigaciones Marinas y Costeras (IIMyC) Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), FCEyN, Universidad Nacional de Mar del Plata, CC 573 Correo Central, B7600WAG, Mar del Plata, Argentina
[b] Laboratorio de Limnología, Instituto de Investigaciones Marinas y Costeras (IIMyC) Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), FCEyN, Universidad Nacional de Mar del Plata, CC 573 Correo Central, B7600WAG, Mar del Plata, Argentina

ARTICLE INFO

Article history:
Received 18 May 2012
Received in revised form 28 November 2012
Accepted 30 December 2012
Available online xxxx

Keywords:
Crabs
Interactions
Microalgal assemblage
Mudflats
Snails
Top-down effects

ABSTRACT

Interactions between organisms are important determinants of species distributions and abundances. Due to the high complexity of interactions between species in natural systems, the outcome of a given interaction can affect others, finally modifying community composition. In South-Western Atlantic intertidal mudflats, the zonation of the burrowing crab *Neohelice* (*Chasmagnathus*) *granulata* and the intertidal snail *Heleobia australis* rarely overlaps, suggesting that both species might have negative interactions; and, given that both species have different foraging strategies, these negative interactions can have top-down impacts on community composition. Zonation patterns of both species showed that snails are more abundant in areas without crab burrows, and field experiments revealed that snail density correlated with a reduction in crab density and that when crabs were excluded, snails were able to colonize those higher intertidal areas. Bioturbation and not competition seems to drive that pattern, given that crabs have no effects on microalgae, but negatively affect infaunal organisms such as copepods, flagellates, nauplli larvae and snails. Conversely, snails negatively affect algal assemblages, specifically cyanobacteria, chlorophytes, and euglenophytes, although diatoms, the most abundant group, was not modified. Our results show that crab–snail competition disrupts snail herbivory upon microalgae by limiting the area over which algal consumption occurs and highlight the complex web of interactions that frequently regulates community structure in natural systems.

© 2013 Elsevier B.V. All rights reserved.

1. Introduction

Predation and competition can strongly influence community structure (e.g. Schoener, 1983; Wilson, 1991) and ecosystem properties and functions (e.g. diversity, Schmitz, 2006; invasibility, Stachowicz et al., 2002). For instance, predation can regulate diversity, species abundances and community structure in a variety of marine systems, including salt marshes (e.g. Silliman and Bertness, 2002) and, mud and sand flats (e.g. Armitage and Fong, 2006). Similarly, competition can regulate the structure of communities by also changing abundances and distributions of species (e.g. Schoener, 1983) and affecting individual growth and emigration (Moksnes, 2004). In general, competition is asymmetric and results from the differential sizes or abilities of species (see Young, 2004 and cites therein). However, besides competition and predation, ecosystem engineers can also affect community structure directly or indirectly by modulating the availability of resources to other species. Thus, both, trophic and non-trophic interactions are major community structuring forces (e.g. de Ruiter et al., 2005).

Soft bottom intertidal areas are characterized by high primary production (e.g. Valiela et al., 2000), where benthic microalgae are often dominated by diatoms (Paterson and Hagerthey, 2001), and are responsible for up to 50% of the carbon assimilated by consumers of intertidal estuarine sediments (Sullivan and Currin, 2000). These habitats can provide unique ecosystem services providing essential feeding sites for migratory shorebirds (e.g. Morrison and Ross, 1989) and nursery grounds for fishes (Green et al., 2009). Microphytobenthos is also an essential food resource for a variety of species (James-Pirri et al., 2001) being an important link of energy in the estuarine food webs (Riera, 2010).

These soft bottom systems are frequently inhabited by herbivores and/or bioturbators (e.g. Pillay et al., 2007) that can have profound impacts on community and ecosystem dynamics (Hagerthey et al., 2002). In fact, top-down control from grazers can be considered a major perturbation to estuarine mudflats diatom assemblages (Cadée, 2001). In particular, the impacts of invertebrates like snails and crabs have been widely documented. For example, hydrobioid snails frequently found inhabiting coastal environments (e.g. Lillebo et al., 1999), often drastically reduce microalgal populations (Coles, 1979) and affect benthic community structure (Kelaher et al., 2003). Moreover, due to their

* Corresponding author. Tel.: +54 223 4753554; fax: +54 223 4753150.
E-mail addresses: mfalvare@mdp.edu.ar (M.F. Alvarez), kesquius@mdp.edu.ar (K.S. Esquius), maddino@mdp.edu.ar (M. Addino), jalberti@mdp.edu.ar (J. Alberti), osiriba@mdp.edu.ar (O. Iribarne), fbotto@mdp.edu.ar (F. Botto).

0022-0981/$ – see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.jembe.2012.12.015

Author's personal copy

feeding strategies these snails may be considered ecosystem engineers. *Hydrobia ulvae* can horizontally mix the surface sediment layer (Cadée, 2001), and *Littoraria* sp. snails effectively displaces another detritivore via mucus cues and alterations in the shade canopy (Lee and Silliman, 2006) acting as an allogenic ecosystem engineer (*sensu* Jones et al., 1994). Crabs can also exert strong control over benthic communities *via* grazing and bioturbation. For example, grapsid crabs can strongly affect benthic assemblages due to their feeding and burrowing activities (e.g. Botto and Iribarne, 1999), and grazing by fiddler crabs can reduce microalgal abundances up to 60% in surface sediments (Ribeiro and Iribarne, 2011). Moreover, through bioturbation, crabs may also reduce meiofaunal density and affect community composition (e.g. *Uca* sp. Ólafsson and Ndaro, 1997; *Carcinus* sp. Schratzberger and Warwick, 1999).

In SW Atlantic estuaries (between southern Brazil and northern Argentinean Patagonia), higher intertidal areas are occupied by marsh plants while mudflats extend on lower intertidal areas (Isacch et al., 2006). The burrowing crab *Neohelice* (formerly *Chasmagnathus*) *granulata* is one of the most abundant intertidal macroinvertebrate species, being an important herbivore and bioturbator (e.g. Alberti et al., 2011; Iribarne et al., 1997). On the mudflats, this crab is mainly a deposit feeder that builds semi-permanent burrows and removes up to 5.9 kg m^{-2} d^{-1} of sediment (Iribarne et al., 1997) altering the physico-chemical characteristics and dynamics of the area (see Botto and Iribarne, 2000). The mudflats are also inhabited by the Hydrobioid mud snail *Heleobia australis* (usually<7 mm total shell length) (De Francesco and Isla, 2003). This is also a deposit feeder and grazer on microphytobenthos (Falniowski, 1987) that inhabits mudflats from Rio de Janeiro (22° 54′ 10″ S), Brazil, to the northern Argentinean Patagonia (40° 84′ 59″ S) (Aguirre and Farinati, 2000).

However it is uncommon to find high crab and snail densities at the same intertidal height. Even though crabs use the entire intertidal area, crab burrows are rare at lower mudflat areas (Méndez Casariego et al., 2011), where snails are most abundant. Thus, this zonation pattern may be driven by differential tolerance to abiotic factors (e.g. crabs build considerably less burrows in low intertidal, Iribarne et al., 2005; snails depend on desiccation and wave exposure, Canepuccia et al., 2007 and references therein) and not to predation pressure, given that one species of gulls, the Olrog's gull (*Larus atlanticus*) mainly preys on crabs (Copello and Favero, 2001), but given their low abundance their impact is negligible (Favero et al., 2001). There may also be negative interactions between them. In this context, we hypothesized that crabs could be displacing snails through bioturbation (as they do with other infaunal species; see Escapa et al., 2004) at the edge between the area mostly occupied by crabs (higher mudflat) and the one mostly occupied by snails (lower mudflat). We believe that the upper zonation limit of snails might be ultimately controlled by abiotic factors (such as inundation period and salinity; e.g. Fenchel, 1975), but at least on a small temporal or spatial scale, crabs could be preventing snails from reaching that upper level. Additionally, although there is no information about *H. australis* foraging strategies, we hypothesized that the effects they produce on microalgae are similar to the ones reported for other similar species (i.e. *Hydrobia ulvae*, Hagerthey et al., 2002), mainly affecting microalgae assemblages by foraging and horizontal sediment mixing (Cadée, 2001).

In consequence, given that both species have different foraging and bioturbation strategies, we expect that the single presence of one of these two species as well as their potential interaction will produce different effects on the algal and infaunal assemblage. The objectives of this work were (1) to evaluate if the burrowing crab *N. granulata* displaces the mud snail *H. australis*, and (2) to evaluate if this interaction modifies the infaunal and algal assemblage and their interactions in benthic food webs. We hypothesized that (1) *N. granulata* crab negatively affects snail densities; and (2) that this interaction modifies the top-down effects of snails on the benthic assemblages by changing the composition and abundances of microalgae and infaunal organisms.

2. Materials and methods

2.1. Study site

The study was conducted at the Mar Chiquita coastal lagoon (Argentina, 37° 32′S and 57° 19′W; a UNESCO Man and the Biosphere Reserve) between 2010 and 2011. This is a 46 km^2 shallow embayment of brackish water (salinity 2 to 35) permanently connected to the sea and affected by a microtidal regime (~1 m; Reta et al., 2001), and characterized by mudflats irregularly flooded surrounded by *Spartina densiflora* marshes (Isacch et al., 2006). *Neohelice granulata* crabs are distributed in both the *S. densiflora* salt marsh and the intertidal mudflats generating large burrowing beds (Iribarne et al., 1997), while *H. australis* distribution in these lagoon is restricted to mudflats of the estuary influenced by tides (De Francesco and Isla, 2003).

In particular, our study was conducted on a tidal channel that is connected to the outlet of the lagoon into the sea. Crab densities are spatially and temporally variable, with very few crabs at the low mudflat throughout the year, while the highest densities are found on the high mudflat and the low marsh, particularly during summer and fall (Méndez Casariego et al., 2011). *Heleobia australis* densities follow an opposite pattern, being highest at the low mudflat. At intermediate mudflat heights (~18 cm AMLW), there are many areas with crabs and a few areas (separated by several meters) without crabs that, on the contrary, respectively exhibit very low and high snail densities. At this intertidal height, we performed our samplings and experiments on a 400 m long and 3 m wide fringe.

2.2. Crabs and the zonation patterns of snails

To evaluate if there is a negative relationship between crab and snail densities, we registered the number of snails in areas with and without crab burrows, in 19 different sampling dates evenly distributed between August and February. All samples were taken at the edge between the low mudflat, dominated by snails, and the upper one, dominated by crabs and selecting inside them areas with and without high densities of crab burrows. On each date samples (n = 7) were obtained from areas with and without crab burrows and in two moments: just before the tides reached the sampling area, and one hour later (12 cm under water approximately). This was done just in case the relationship between crabs and snails would be affected by tidal immersion. The density of snails was registered on each sample (20 × 20 cm). Then, a t_c-test (corrected *t*-test for unequal variances which is equal to *t*-test if variances are the same; Welch approximation; Zar, 1999) was performed between plots with and without crab burrows, for each sampling date and flooding condition. Moreover, to avoid the probability of committing a Type I error, we correct the p-value with a Bonferroni procedure (e.g. Quinn and Keough, 2002).

2.3. Effects of crabs on snail densities

Based the negative relationship between crabs and snails observed on the results from the previous section (see Results), and considering that there is no evidence that crabs prey on microphytobenthos (D'Incao et al., 1990; Iribarne et al., 1997), we hypothesized that crabs displace snails through ecosystem engineering activities and not due to food competition. Crabs can affect snails as an indirect effect of burrow building and maintenance or through the disturbance generated by their movements on the surface. A mound of sediment is frequently found on one side of the crab burrow entrance (Iribarne et al., 1997), which affects infaunal organisms (e.g. Botto and Iribarne, 1999); while the opposite side of the entrance remains mostly undisturbed. To evaluate if crab bioturbation affects snail densities, we randomly chose (once) 10 active crab burrows and registered the number of snails (20 cm × 20 cm plot) in the mound generated by crabs and in the opposite site. To evaluate if the disturbance created by crab walking (tracks)

Author's personal copy

affects the abundance of snails, the density of snails was randomly sampled once in ten 20×20 cm areas with crab tracks (i.e. areas with several traces of crabs) and ten adjacent areas without tracks. Neither of both selected areas exhibited signs of mounds or burrows. In both cases, the null hypotheses of no differences in snail densities between areas with or without mounds and with or without tracks were analyzed with *t*-tests for dependent samples (Zar, 1999).

2.4. Effects of crabs and snails on infaunal and microalgal assemblages, and organic matter content

Given that crab and/or snail activities can have top-down effects on the infaunal assemblages, an exclusion experiment was performed to evaluate the effect produced on the infaunal community by these two species. Six treatments (n = 10 per treatment) were performed: (1) snail exclusion (2 replicates were lost due to unwanted crab disturbance), (2) snail-cage control, (3) crab exclusion (1 replicate was lost due to unwanted crab disturbance), (4) crab-cage control, (5) undisturbed control for snails, and (6) undisturbed control for crabs. Snail exclusions were performed using plastic mesh cages (30×30×40 cm, 2 mm mesh opening) buried 10 cm into the sediment. These cages prevented the entrance of both, snails and crabs, and we removed all snails or crabs from the cages. Crab exclusions were also performed using plastic mesh cages (50×50×70 cm, 1 cm mesh opening, which inhibits crab entrance but allows free movement of snails). Snail-cage control and crab-cage controls were similar to their respective exclusions but with three instead of four sides allowing free movement of either species. Given that these two species are segregated in the mudflat (snails occupy the lower level while crabs occupy the mid-upper intertidal; see Study site), the replicates were randomly distributed along the edge between both zonations where areas dominated by one or the other species can be found. For this reason, we established two types of open undisturbed areas (i.e. without manipulation; 50×50 cm) as undisturbed controls, each type belonging to the area dominated by one of these two species. Following Byers (2000) we rubbed the sediment surface of each experimental unit by hand to homogenize any initial spatial variability in epipelic algal densities. The experiment ran for 15 days during the early autumn (March–April), because this is the season when crabs are more active (e.g. Méndez Casariego et al., 2011). The duration of the experiment was decided based on the short life cycles, the high turnover rates and the quick response after disturbance of the studied organisms (i.e. meiofauna and microalgae) (see Coull, 1999; Pillay et al., 2009). During the experiment, the exclusion treatments were daily controlled and snails or crabs were manually removed each time they were found where they should be excluded.

At the end of the experiment, one sediment sample per plot (2 cm diameter and 2 cm depth) was taken and sieved through a 62 μm mesh to analyze meiofauna. Organisms were preserved in formalin 5% and stained with Rose Bengal to facilitate their visualization. Then, they were counted under binocular microscope (40×) and identified to the major taxa, given that there is only slight information about the taxonomy of meiofauna in this area. Also, one sediment sample per plot (10 cm diameter and 10 cm depth; following Botto and Iribarne, 1999) was taken and sieved through a 500 μm mesh to analyze macrofauna. The retained organisms were identified to species level and counted under binocular microscope (20×). The density of crabs on each plot was estimated by counting active burrows into each experimental unit (Iribarne et al., 2005). After all samples were obtained, the first two centimeters of the sediment were collected from each experimental unit and sieved to estimate snail density. Only live organisms were counted (those that still have the operculum) and attributed to the only species that inhabit this area (De Francesco and Isla, 2003).

Moreover, to analyze if burrowing crabs and snails affect the abundance and distribution of primary producers, one sediment sample per plot (2 cm diameter and 2 cm depth) was obtained and the epipelic algal biomass was estimated as the *a*, *b*, *c* and *total* chlorophyll concentration. Samples were conserved in darkness until arriving to the laboratory, where they were frozen (−18 °C) until processed. Chlorophyll was determined through extraction of pigments from the sediment (using acetone 90%) and estimated with spectrophotometric analysis (Jeffrey and Humphrey, 1975). The null hypothesis of no difference in chlorophyll concentrations (an estimator of primary production) between treatments was performed using one-way ANOVAs (one for each chlorophyll type; Zar, 1999). In some cases, measuring chlorophyll concentration can underestimate the impact on the microalgal assemblage (e.g. Cibic et al., 2007) given that the relative abundance of species or groups can change without translating into changes in chlorophyll concentration; with important implications for trophic webs. Then, to evaluate if snails or crabs modify microalgal assemblages, one sample of sediment (2 cm diameter and 1 cm depth) was taken from half of the replicates and the abundance of different microalgal groups (cyanobacteria, chlorophytes, euglenophytes and diatoms) was measured. Samples were preserved in a mixture of distilled water, alcohol and formalin solution (6:3:1; Prescott, 1962). Algae were identified following commonly used keys (e.g. cyanobacteria, Guarrera et al., 1972; Komárek and Anagnostidis, 2005; chlorophytes, Hindák, 1990; euglenophytes, Tell and Conforti, 1986; and diatoms Cox, 1996). Algal counts were performed in a 0.5 ml Sedgwick–Rafter chamber under an optic microscope (McAlice, 1971). Species abundances were expressed as the number of individual cm^{-2}, considering only those with chloroplast remains.

To compare meiofaunal and microalgal assemblages between treatments, multivariate and univariate analyses were performed. Bray–Curtis similarity matrix using fourth root transformed data were calculated and non-metric Multidimensional Scaling (nMDS) ordinations were used to provide visual representations of similarities between samples (Clarke and Warwick, 2001). The differences in meiofaunal and microalgal assemblages among treatments were evaluated using one-way analysis of similarities (ANOSIM). The percentage contribution of each taxon to patterns of dissimilarity was examined using SIMPER (Clarke, 1993), and those taxa contributing at least 10% of dissimilarity were considered important differentiators (Bulleri, 2005). nMDS, SIMPER and ANOSIM analysis were performed using the PRIMER software (Clarke and Gorley, 2001). The abundances of each of these important differentiators were analyzed separately using one-way ANOVAs, followed by Tukey's post-hoc tests (Zar, 1999). Normality and homoscedasticity were evaluated using Shapiro–Wilk (Zar, 1999) and Cochran tests (Underwood, 1997). Common transformations were used when necessary.

Excavating and maintaining burrows by crabs can increase organic matter content (Botto and Iribarne, 2000). Similarly, the foraging activities of some mud snails could increase the sediment organic matter content (e.g. *A. globulus*, Pillay et al., 2009) and provide a sticky substrate for microalgae (Edwards and Davies, 2002). Thus, to evaluate if crabs and snails affect organic matter content in the sediments, one sediment sample (5 cm diameter, 5 cm depth) was taken from each experimental unit. Total organic matter content was estimated as the percentage of ash free dry weight (thereafter AFDW); ashes were obtained after incinerating samples at 550 °C for 6 h (Holme and McIntyre, 1971). The null hypothesis of no difference in percentage of organic matter content between treatments was analyzed with a one-way ANOVA.

3. Results

3.1. Crabs and the zonation patterns of snails

Even though *Heleobia australis* densities were highly variable (from 3500 to 30,000 individuals per square meter), t_c-test always showed higher snail densities in areas without crabs than in areas with crabs, on those samples not covered by water (highest $t_c = 22.18$, df = 12,

Author's personal copy

$p<0.001$; lowest $t_c=5.01$, df = 12, $p<0.001$). Only one date of sampling showed no differences in snail density between areas with and without crabs ($t_c=2.99$, df = 12, $p=0.01$). Similar results were observed in almost 85% of the dates (16 out of 19) when under water (highest $t_c=27.44$, df = 6.33, $p<0.001$; lowest $t_c=3.95$, df = 6.02, $p<0.001$), while there were no differences in snail abundances between areas with and without crabs on the three remaining dates ($t_c=-1.27$, df = 12, $p=0.22$; $t_c=-1.43$, df = 12, $p=0.17$; and $t_c=3.95$, df = 6.02, $p=0.002$).

4. Effects of crabs on snail densities

Snail densities were lower on the mounds ($t=-3.63$, df = 9, $p<0.01$) than on the opposite side of crab burrow entrances, and they were also lower in areas with than without crab tracks ($t=-2.92$, df = 9, $p<0.05$). However the highest differences in snail density were found in areas with and without crab mound showing that bioturbation is the main process that regulates snail's zonation.

4.1. Effects of crabs and snails on infaunal and microalgal assemblages, and organic matter content

The experimental exclusion of crabs and snails worked successfully, registering the lowest values in their respective exclusions (see Fig. 1).

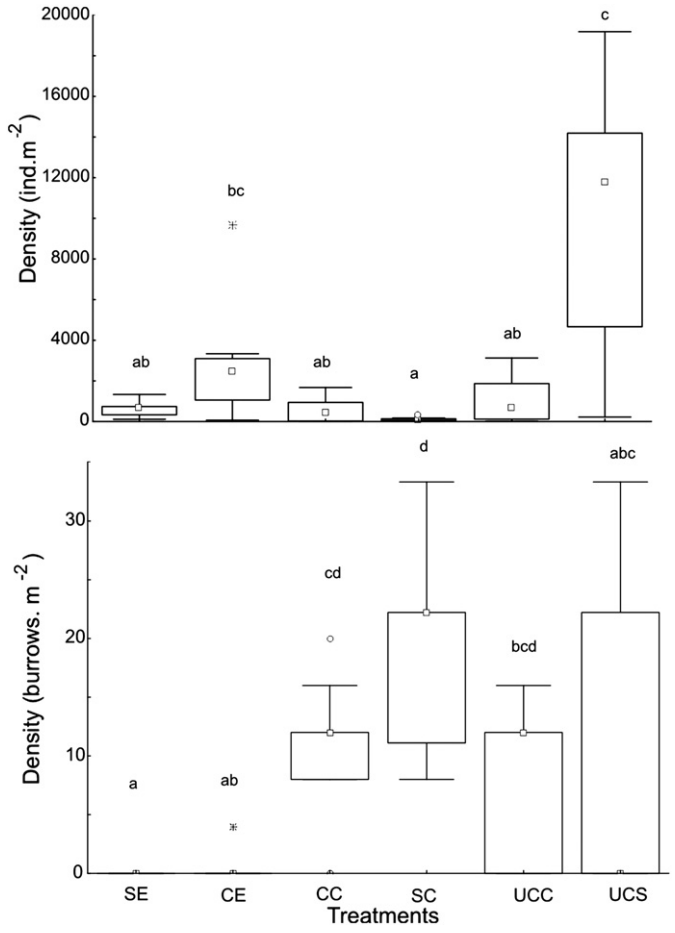

Fig. 1. Density of *Heleobia australis* (upper panel) and of crab burrows (lower panel) across the different treatments. In this and the following figures, symbols within boxes denote the median, boxes denote 25 and 75 percentiles (50% of data) and circles outside boxes are outliers. All data are presented prior to transformations. Different letters illustrate differences between treatments: (SE) snail exclusion, (CE) crab exclusion, (CC) crab cage control, (SC) snail cage control, (UCC) undisturbed control for crabs, (UCS) undisturbed control for snails.

Highest snail densities were observed in those treatments with lowest crab densities (undisturbed control for snails and crab exclusion; $\log_2$ transformed; $F_{5,50}=11.73$; $p<0.01$; Fig. 1). However, as a side effect, *Nehoelice granulata* crabs made burrows within both cage controls (because they are attracted to strange objects) and therefore, highest densities of active crab burrows were registered in snail- and crab-cage controls (square root transformed; $F_{5,51}=8.96$; $p<0.01$; Fig. 1). This result was analyzed considering that those treatments have higher crab densities than undisturbed controls for crabs and thus, potential crab effects could be exaggerated.

Meiofaunal organisms found during the experiment were ostracods, nematodes, foraminiferans, harpactocoid copepods, nauplii larvae, small *Laeonereis acuta* polychaete, polychaetes of the family Ctenodrillidae, and flagellates. The analysis of similarity revealed differences in meiofaunal assemblages between treatments ($R=0.081$; $p<0.05$; Fig. 2). Pairwise comparisons showed effect of crabs on infaunal assemblages, as there were dissimilarities between treatments with lower densities of active crab burrows (both exclusions) and those with higher densities (cage controls and undisturbed control for crabs; Table 1). However, there was no evident effect of snails on infaunal assemblages as, for example, there were no differences between snail exclusion and undisturbed control for snails (treatments with contrasting snail densities; Table 1).

Based on SIMPER results, five groups could be explaining the dissimilarities between treatments (nematodes, harpacticoid copepods, flagellates, nauplii larvae and ostracods). Harpacticoid copepods (square root transformed; $F_{5,50}=4.59$; $p<0.01$), nauplii larvae (square root transformed; $F_{5,50}=2.75$; $p<0.05$), and flagellates (fourth-root transformed; $F_{5,50}=4.57$; $p<0.01$) showed higher densities on those treatments with the lowest crab densities (both exclusions), and particularly when both, snails and crabs, were excluded (Fig. 3). For three groups mentioned, the highest variances were observed in both exclusions. ANOVA analyses revealed no differences between treatments for the remaining groups, nematodes ($F_{5,50}=0.64$; $p=0.66$) and ostracods (square root transformed; $F_{5,50}=1.06$; $p=0.39$). Only one macrofaunal species was found, the *Laeonereis acuta* polychaete, which showed no differences in density between treatments ($F_{5,51}=0.23$; $p=0.94$).

Chlorophyll *b* concentration was 50% higher on snail-cage controls than on snail exclusions (fourth root transformed, $F_{5,51}=2.93$; $p<0.05$; Fig. 4), the treatments with the highest and lowest crab densities but similar and low snail densities. However, there were no differences in chl *a*, *c* and *total* (respectively, $F_{5,51}=0.34$; $p=0.88$; $F_{5,51}=1.4$; $p=0.23$ and $F_{5,51}=0.36$; $p=0.87$; Fig. 4).

When we analyzed the microalgal assemblages, we found 47 different taxa, corresponding mostly to four major groups: cyanobacteria (4 taxa, 8.5%), chlorophytes (10 taxa, 21.3%), euglenophytes (1 taxa, 2.2%) and diatoms (32 taxa, 68%). Total algal densities (ind.cm^{-2}) did not respond clearly to snails or crabs as the highest densities were found on both exclusions (lowest densities of crabs on both, but high snail densities only in crab exclusions), and the lowest on undisturbed controls for snails (highest densities of snails but low crab densities; square root transformed; $F_{5,24}=4.84$, $p<0.01$; compare Figs. 1 and 5). Variance was higher in both cage exclusion (i.e. SE and CE) and in areas bioturbated by crabs (i.e. UCC), showing that the absence of predators (crab and low density of snails) or heterogeneous areas (as crab beds) could offers patches between crab burrows more favorable to algae.

The analysis of similarity revealed differences in microalgal assemblages between treatments ($R=0.34$; $p<0.01$; Fig. 6), and pairwise tests showed a larger effect of snails than crabs; snail exclusions (without snails) were different from crab exclusions (intermediate snail densities) and undisturbed control of snail (high snail densities); and were only similar to undisturbed control for crabs (low snail densities). Crab exclusions were only different from undisturbed control for snails (highest snail densities; Table 2). SIMPER results suggest that each

Author's personal copy

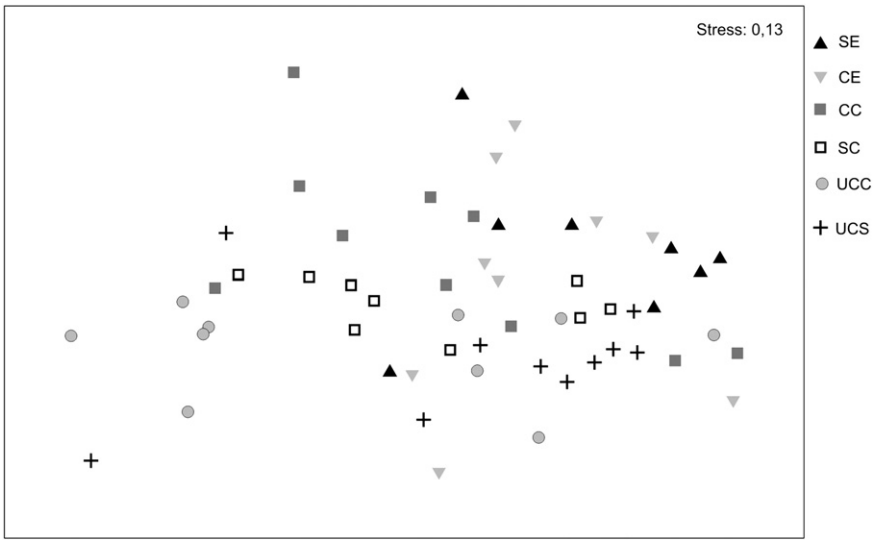

Fig. 2. Non-metric multidimensional scaling (nMDS) plot comparing fourth-root transformed data of meiofaunal groups between treatments.

microalgal group (cyanobacteria, chlorophytes, euglenophytes and diatoms) could be contributing to the dissimilarities between treatments.

The analysis of each migroalgal group separately revealed that chlorophytes (natural logarithm transformed; $F_{5,24} = 11.89$ $p<0.01$; Fig. 7), cyanobacteria (square root transformed; $F_{5,24} = 3.99$ $p<0.05$; Fig. 7) and euglenophyte densities (natural logarithm transformed; $F_{5,24} = 3.06$ $p<0.05$; Fig. 7) were affected by a combination of both snails and crabs, but diatom densities were not ($F_{5,24} = 1.49$; $p = 0.22$; Fig. 7). Density of chlorophytes on the undisturbed control for snails was only similar to snail exclusion, being lower than the four other treatments. Cyanobacteria densities followed almost the same pattern as total algae density (lowest values on undisturbed control for snails and both cage controls). Density of euglenophytes on crab exclusions was eight times higher than on undisturbed control for snails. Following the similar pattern of total algae density, variances for chlorophytes, cyanobacteria and euglenophytes were higher in areas bioturbated by crabs, suggesting that inside crab beds the density of algae groups is not homogenous; possibly they are growing in small zones inside a heterogeneous matrix of burrows, mound and bare sediment. In addition, there were no differences in organic matter content between treatments ($F_{5,51} = 0.56$; $p = 0.72$).

Table 1
Pairwise of ANOSIM tests comparing meiofaunal assemblages between treatments. (SE) snail exclusion, (CE) crab exclusion, (CC) crab cage control, (SC) snail cage control, (NCC) natural control for crabs, (NCS) natural control for snails. Global $R = 0.085$,* $p<0.05$.

Groups	R Statistic
SE, CE	−0.047
SE, CC	0.109*
SE, SC	0.296*
SE, NCC	0.26*
SE, NCS	0.063
CE, CC	0.055
CE, SC	0.127*
CE, NCC	0.217*
CE, NCS	0.075
CC, SC	−0.067
CC, NCC	0.057
CC, NCS	0.1*
SC, NCC	0.007
SC, NCS	0.107*
NCC, NCS	0.045

5. Discussion

Our results showed that when they coexist, crabs (*Neohelice granulata*) reduce snail (*Heleobia australis*) densities, and given that crabs occupy higher mudflat areas, our results suggest that crabs are excluding snails from the higher intertidal areas. The displacement by crabs correlated with a reduction in snail density likely due to bioturbation activity and not by food competition, given that bioturbated areas (undisturbed controls for crabs) showed comparatively high microalgal densities. This negative crab–snail interaction has marked effects on the benthic community, given that each of these two species affect the infaunal and microalgal community in different ways. For example, snails modified cyanobacteria, chlorophytes, and euglenophytes abundances through bioturbation and/or herbivory. In addition, the presence of both species modifies infaunal communities.

Our experimental results showed that crabs acting as key bioturbators, negatively affect the abundances of snails, leading most of them to occupy lower intertidal levels. Crabs displace snails, not by food competition because crabs neither negatively affected the overall amount of microalgae nor their assemblages. In addition, stable isotope analysis showed that the main food resources for them are live leaves or detritus of *Spartina* spp. and not the microalgae, even for those crabs living in the mudflat (Botto et al., 2005). Other studies have shown that intertidal crabs, by increasing snail burial, can effectively reduce the time spent by snails on foraging (e.g. Armitage and Fong, 2006). In our case, and given that a few snails were found buried, alternative mechanisms involved in this displacement could be physico-chemical changes in the sediment produced by crab burrows (Botto and Iribarne, 2000), reductions in the area available for foraging produced by the mounds associated with crab burrows, or the disturbance generated by crab walking (see Results). However, crabs could also have indirect positive effects on cyanobacteria, chlorophytes and total algae density, but only at intermediate densities, given that in areas moderately bioturbated by crabs (undisturbed control for crabs), snail abundances are reduced and those algal groups reach high abundances; in areas with highest crab densities (cage controls), densities of those same algae were lowest. This pattern highlights the previously mentioned characteristics of ecosystem engineers: the same organism can benefit some species and negatively affect others.

Author's personal copy

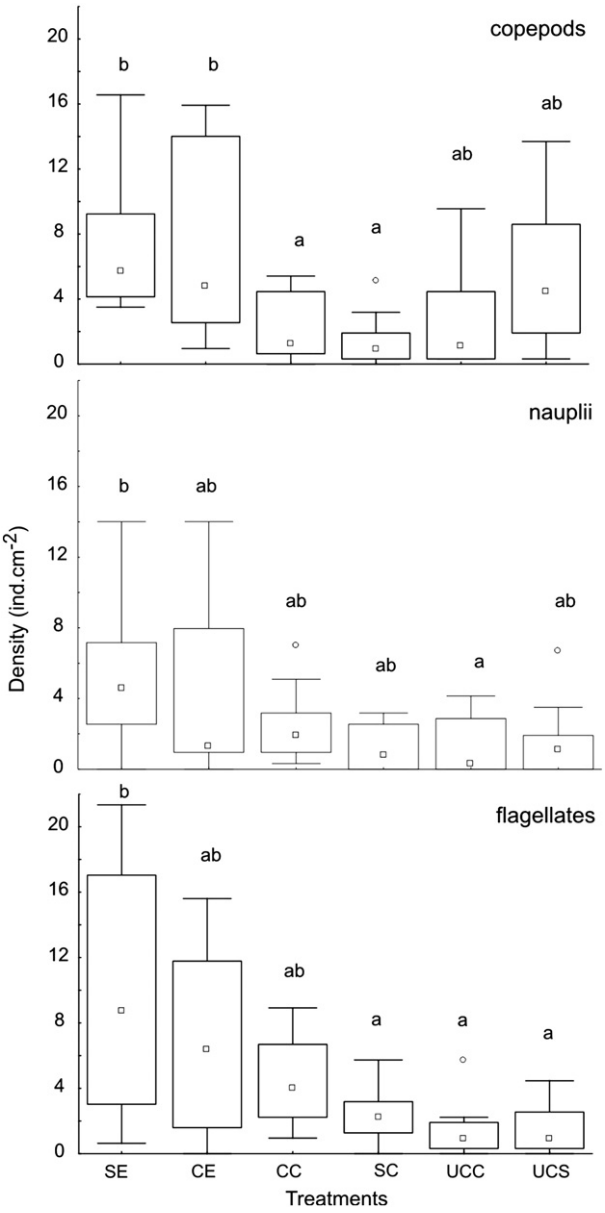

Fig. 3. Densities of copepods, nauplii larvae and flagellates across the different treatments.

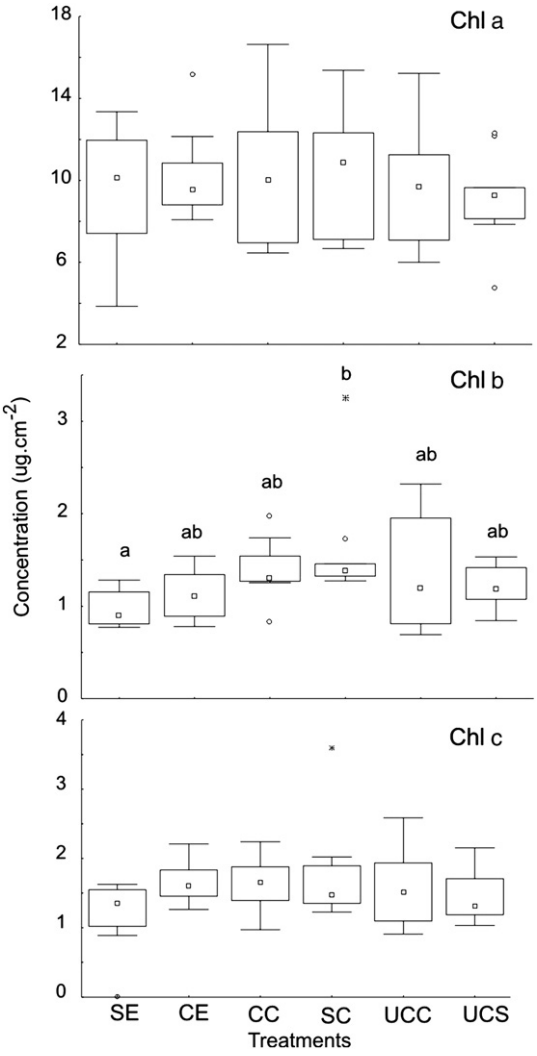

Fig. 4. Concentration of *a*, *b*, and *c* chlorophyll across the different treatments.

Several works have shown the top-down effects of herbivorous snails on abundances and diversity of species (e.g. Kelaher et al., 2003; Mak and Williams, 1999); however, few studies have examined the impacts of bioturbators on these herbivores and whether those effects cascade down to lower trophic levels (Armitage and Fong, 2006; Hagerthey et al., 2002). In line with other works (e.g. Armitage and Fong, 2006), our results revealed that only specific infaunal organisms, such as flagellates, copepods, and nauplii larvae were affected by both, crabs and snails. Previous results revealed that the bioturbation produced by *N. granulata* crabs affects the meiofaunal community structure, particularly ostracods, copepods and turbellarians (Cruz Rosa and Bemvenuti, 2005), and even the abundances of nematodes on the mounds around crab burrows (Botto and Iribarne, 1999). However, results from other systems showed that grazing by snails (e.g. *Assiminea globulus*, Pillay et al., 2009; *Terebralia palustrus*, Carlen and Ólafsson, 2002) can decrease total meiofaunal density, especially harpacticoid copepods because they are more susceptible to grazing.

Although our work shows that snails and crabs negatively affect the density of flagellates, copepods and nauplii larvae, these results cannot be exclusively attributed to crab and snail grazing. Both species, and particularly crabs, actively bioturbate the sediment, and consequently, bioturbation cannot be excluded as mechanism that modify infaunal

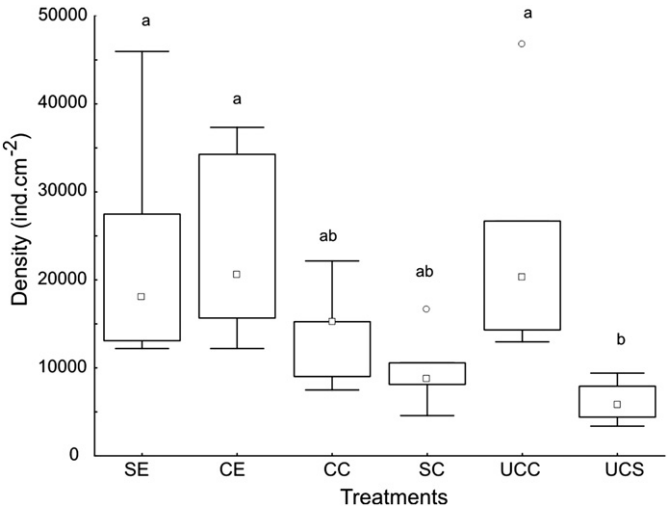

Fig. 5. Density (ind.cm^{-2}) of microalgae across the different treatments.

Author's personal copy

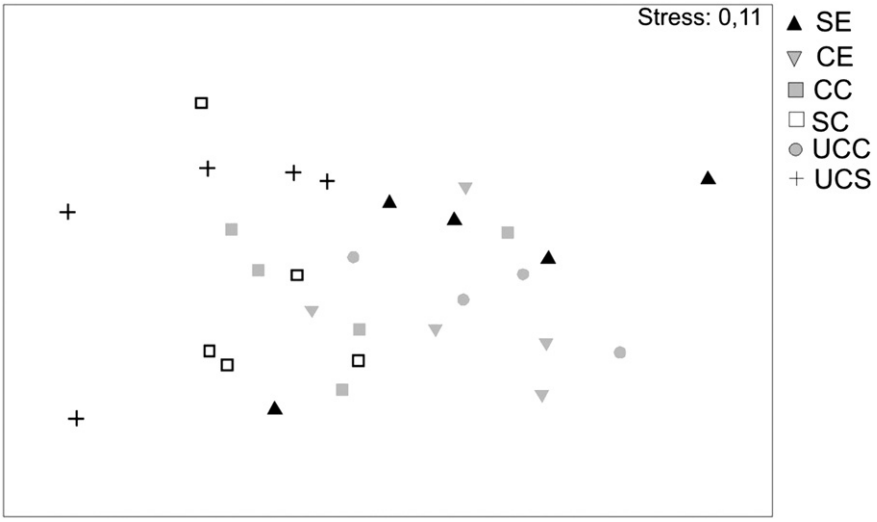

Fig. 6. Non-metric multidimensional scaling (nMDS) plot comparing fourth-root transformed data of microalgal groups between treatments.

abundances. Even more, given the complexity of possible interactions in our study system, it is likely that copepods positively selected experimental units with higher total algal density (snail and crab exclusions) considering that several studies have reported that copepods actively migrate (Hicks and Coull, 1983), are good swimmers (Palmer, 1988) and forage on benthic microalgae (De Troch et al., 2008). Thus, a combination of food availability (i.e. microalgae) and safer areas (i.e. low level of bioturbation or predation) may determine the density and diversity of some groups.

However, the negative effects of bioturbation and predation that snails and crabs might have on the benthic community would likely be different based on their different foraging strategies and bioturbation activities, as well as their different densities and sizes. Snails possibly forage mixing the first centimeter of sediment (e.g. *Hydrobia ulvae*, Cadée, 2001) affecting meiofaunal and algal assemblages (e.g. Pillay et al., 2009; this work). Given that they are conspicuous and very abundant, their effects might be important for microalgae and organisms that prey upon them. On the other hand, crabs build large and deep burrows (up to 0.33 m depth in mudflats) that strongly affect the sediment (Iribarne et al., 1997), but between burrows the sediment is slightly bioturbated, generating small scale patches with and without disturbance inside crab beds. Thus, the presence of either crabs or snails modify the benthic assemblage in different ways, depending on the species involved, and thus, the negative interaction between the two modifies top-down forces. Even more, there might also be temporal variations associated to seasonal variations in the activity of both species. For example, the effects we found of crabs on the benthic community are likely the most important given that the experiment was performed when crabs were most active.

Table 2
Pairwise of ANOSIM tests comparing microalgal assemblages between treatments. Global R = 0.34, * $p<0.05$, ** $p<0.01$.

Groups	R Statistic
NCS, SC	0.328
NCS, NCC	0.604**
NCS, CC	0.552**
NCS, SE	0.516**
NCS, CE	0.748**
NCC, SC	0.308
NCC, CC	0.22
NCC, SE	0.176
NCC, CE	−0.088
SC, CC	−0.024
SC, SE	0.464*
SC, CE	0.24
CC, SE	0.376*
CC, CE	0.188
SE, CE	0.572*

Microphytobenthos are the preferred food items for deposit-feeding benthic infauna, those include mud snails, crustaceans, many polychaete, and organisms of other phyla (Miller et al., 1996). For example, diatoms are the main food source for *Hydrobia totteni* (Bianchi and Levinton, 1984), and microalgae and algal filaments are significant components of the diet of *Littoraria scabra* (Alfaro, 2008) and *Heleobia ulvae* (Riera, 2010). Thus, our work is in line with previous studies (e.g. Armitage et al., 2009 and cites therein) where the grazing by snails reduces microphytobenthos abundances and affects microalgal assemblages. Our results show that *H. australis* negatively affects the total algal density and the abundances of cyanobacteria. Although chlorophytes and euglenophytes were positively affected by snails, this effect was observed only at moderate snail densities (crab exclusion). Intermediate levels of grazing by herbivores may stimulate the microphytobenthos production by increasing nutrient availability and depth of the photic zone by thinning the microalgal overstory (Pinckney et al., 2003) or by "cropping" older cells (Pillay et al., 2009); and these have been well documented in marine and freshwater ecosystems (e.g. Worm et al., 2002). In these ecosystems, microalgae are an important component of primary production that support higher trophic levels; for example benthic microalgae are an essential food source for nematodes and polychaetes, and are also an important part of the diet for fish (Botto et al., 2005) which transfer a significant amount of energy outside estuaries (e.g. Kneib, 1997). In this context, our results become highly relevant showing how the snails modify the benthic assemblage by changing the relative species composition and abundances.

In conclusion, our sampling and experimental results show that, through bioturbation, the crab *N. granulata* negatively affects snail abundances, probably preventing them to reach higher mudflat areas. Moreover, this work shows that the negative interaction between crabs and snails has important top-down consequences on the infaunal and microalgal assemblages, given that crab bioturbation limits the area over which herbivore (snail) – algae interactions occur. Microphytobenthos play key roles in marine soft-bottom ecosystems (Lei et al., 2010), and many of these systems are inhabited by grazer snails that feed upon microalgae (Lever and Valiela, 2005) as well as by bioturbators. Thus, our study highlights the importance

Author's personal copy

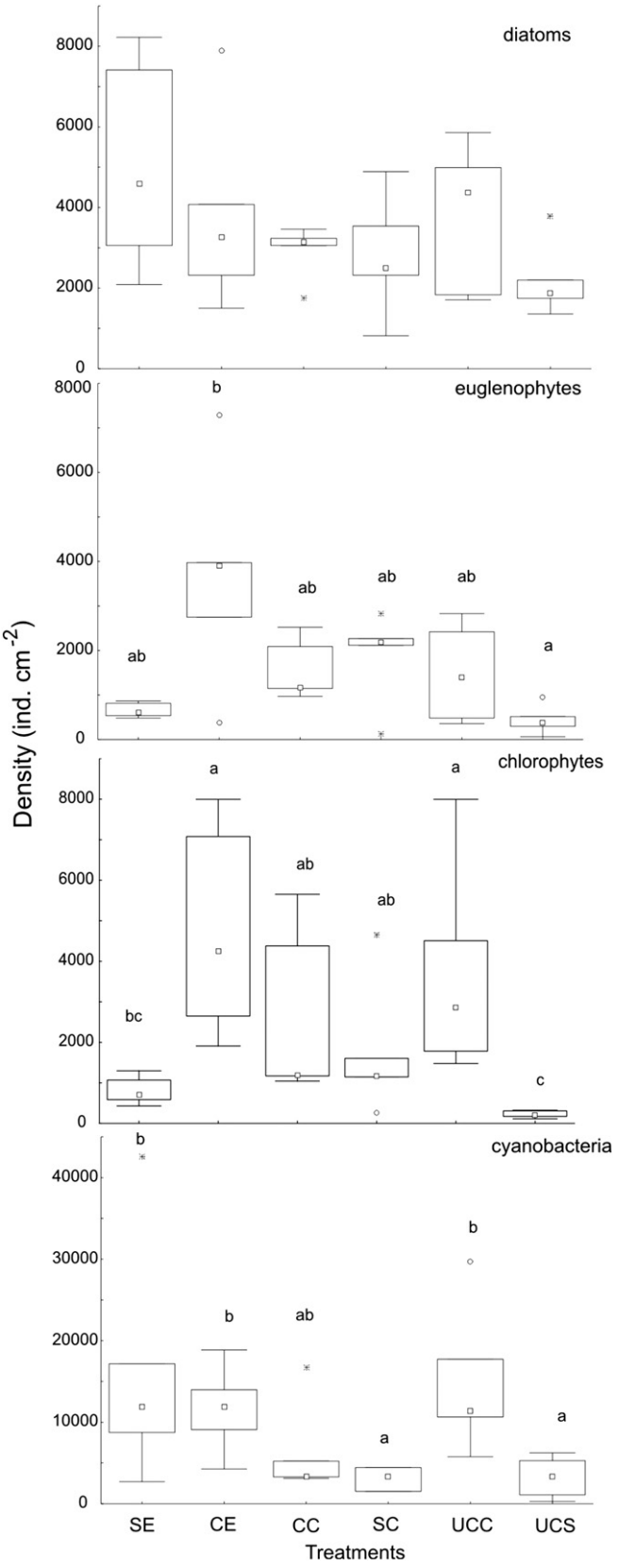

Fig. 7. Density (ind.cm^{-2}) of diatoms, euglenophytes, chlorophytes and cyanobacteria across the different treatments.

of considering the role of both trophic and non-trophic interactions as potential forces controlling the structure of microphytobenthos assemblages on a multi-species context.

Acknowledgements

We thank A. Méndez Casariego, D. Montemayor, G. Alvarez, F. Firstater, M. Bruschetti and G. Panisse for help in the field; to the Editor and two anonymous reviewers for their comments which greatly improved the manuscript. This project was supported by Universidad Nacional de Mar del Plata, ANPCyT and CONICET (all granted to O.I.). M.F.A. and M.A. were supported by doctoral scholarships from CONICET. This is part of Doctoral thesis of M.F.A. **[ST]**

References

Aguirre, M.L., Farinati, E.A., 2000. Aspectos sistemáticos, de distribución y paleoambientales de *Littoridina australis* (D'Orbigny, 1835) (Mesogastropoda) en el cuaternario marino de Argentina (Sudamérica). Geobios 33, 569–597.

Alberti, J., Cebrian, J., Méndez Casariego, A., Canepuccia, A., Escapa, M., Iribarne, O., 2011. Effects of nutrient enrichment and crab herbivory on a SW Atlantic salt marsh productivity. J. Exp. Mar. Biol. Ecol. 405, 99–104.

Alfaro, A.C., 2008. Diet of *Littoraria scabra*, while vertically migrating on mangrove trees: Gut content, fatty acid, and stable isotope analyses. Estuar. Coast. Shelf Sci. 79, 718–726.

Armitage, A.R., Fong, P., 2006. Predation and physical disturbance by crabs reduce the relative impacts of nutrients in a tidal mudflat. Mar. Ecol. Prog. Ser. 313, 205–213.

Armitage, A.R., Gonzalez, V., Fong, P., 2009. Decoupling of nutrient and grazer impacts on a benthic estuarine diatom assemblage. Estuar. Coast. Shelf Sci. 84, 375–382.

Bianchi, T.S., Levinton, J.S., 1984. The importance of microalgae, bacteria and particulate organic matter in the somatic growth of *Hydrobia totteni*. J. Mar. Res. 42, 431–443.

Botto, F., Iribarne, O., 1999. Effects of the burrowing crab *Chasmagnathus granulatus* (Dana) on the benthic community of a SW Atlantic costal lagoon. J. Exp. Mar. Biol. Ecol. 41, 263–284.

Botto, F., Iribarne, O., 2000. Contrasting effects of two burrowing crabs (*Chasmagnathus granulata* and *Uca uruguayensis*) on sediment composition and transport in estuarine environments. Estuar. Coast. Shelf Sci. 51, 141–151.

Botto, F., Valiela, I., Iribarne, O., Martinetto, P., Alberti, J., 2005. Impact of burrowing crabs on C and N sources, control, and transformations in sediments and food webs of SW Atlantic estuaries. Mar. Ecol. Prog. Ser. 293, 155–164.

Bulleri, F., 2005. Role of recruitment in causing differences between intertidal assemblages on seawalls and rocky shores. Mar. Ecol. Prog. Ser. 287, 53–65.

Byers, J.E., 2000. Competition between two estuarine snails: implications for invasions of exotic species. Ecology 81, 1225–1239.

Cadée, G.C., 2001. Sediment dynamics by bioturbating organisms. In: Reise, K. (Ed.), Ecological comparisons of sedimentary shores. : Ecological studies, 151. Springer-Verlag, Berlin, pp. 127–148.

Canepuccia, A., Escapa, M., Daleo, P., Alberti, J., Botto, F., Iribarne, O., 2007. Positive interactions of the smooth cordgrass *Spartina alterniflora* on the mud snail *Heleobia australis*, in South Western Atlantic salt marshes. J. Exp. Mar. Biol. Ecol. 353, 180–190.

Carlen, A., Ólafsson, E., 2002. The effects of the gastropod *Terebralia palustris* on infaunal communities in a tropical tidal mud-flat in East Africa. Wetlands Ecol. Manage. 10, 303–311.

Cibic, T., Blasutto, O., Hancke, K., Johnsen, G., 2007. Microphytobenthic species composition, pigment concentration and primary production in sublittoral sediments of the Trondheimsfjord (Norway). J. Phycol. 43, 1126–1137.

Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. Aust. J. Ecol. 18, 117–143.

Clarke, K.R., Gorley, R.N., 2001. PRIMER v5. User Manual/Tutorial. PRIMER-E, Plymouth.

Clarke, K.R., Warwick, D.R.M., 2001. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. PRIMER-E, Plymouth, U.K.

Coles, S.M., 1979. Benthic microalgal populations on intertidal sediments and their role as precursors to saltmarsh development. In: Jeffries, R.L., Davey, A.J. (Eds.), Ecological Processes in Coastal Environments. Blackwell Scientific Publications, Oxford, pp. 25–42.

Copello, S., Favero, M., 2001. Foraging ecology of Olrog's Gull *Larus atlanticus* in Mar Chiquita Lagoon (Buenos Aires, Argentina): are there age-related differences? Bird Conserv. Int. 11, 175–188.

Coull, B.C., 1999. Role of meiofauna in estuarine soft-bottom habitats. Aust. J. Ecol. 24, 327–343.

Cox, E.J., 1996. Identification of Freshwater Diatoms from Live Material. Chapman & Hall, Londres.

Cruz Rosa, L., Bemvenuti, C.E., 2005. Effects of the burrowing crab *Chasmagnathus granulata* (Dana) on meiofauna of estuarine intertidal habitats of Patos Lagoon, Southern Brazil. Braz. Arch. Biol. Technol. 48, 267–274.

De Francesco, C.G., Isla, F.I., 2003. Distribution and abundance of hydrobiid sails in a mixed estuary and a coastal lagoon, Argentina. Estuaries 26, 790–797.

de Ruiter, P.C., Wolters, V., Moore, J.C., Winemiller, K.O., 2005. Food web ecology: playing jenga and beyond. Science 309, 68–70.

De Troch, M., Chepurnov, V.A., Vincx, M., Ólafsson, E., 2008. The effect of *Fucus vesiculosus* on the grazing of harpacticoid copepods on diatom biofilms. J. Sea Res. 60, 139–143.

D'Incao, F., Rufino, M.L., Sllva, K.G., Braga, A.C., 1990. Habito alimentar do cangrejo *Chasmagnathus granulata* Dana, 1851 na barra de Rio Grande, RS (Decapoda, Grapsidae). Atlantica 1, 85–93.

Edwards, M., Davies, M.S., 2002. Functional and ecological aspects of the mucus trails of the intertidal prosobranch gastropod *Littorina littorea*. Mar. Ecol. Prog. Ser. 239, 129–137.

Author's personal copy

Escapa, M., Iribarne, O., Navarro, D., 2004. Effects of the intertidal burrowing crab *Chasmagnathus granulatus* on infaunal zonation patterns, tidal behavior, and risk of mortality. Estuaries 27, 120–131.
Falniowski, E., 1987. Hydrobioidea of poland (Prosobranchia: gastropoda). Folia Malacologica, 1.
Favero, M., Bachmann, S., Copello, S., Mariano-Jelicich, R., Silva, M.P., Ghys, M., Khatchikian, C., Mauco, L., 2001. Aves marinas del sudeste bonaerense. In: Iribarne, O. (Ed.), Reserva de biosfera Mar Chiquita: características físicas, biológicas y ecológicas. Editorial Martín, Mar del Plata, pp. 251–267.
Fenchel, T., 1975. Character displacement and coexistence in mud snails (Hydrobiidae). Oecologia 20, 19–32.
Green, B.C., Smith, D.J., Earley, S.E., Hepburn, L.J., Underwood, G.J.C., 2009. Seasonal changes in community composition and trophic structure of fish populations of five salt marshes along the Essex coastline, United Kingdom. Estuar. Coast. Shelf Sci. 85, 247–256.
Guarrera, S.A., Malacalza, L., López, F., 1972. Fitoplancton de las aguas superficiales de la provincia de Buenos Aires. II. Complejo Lagunar Salada Grande, Encadenadas del Oeste y Encadenadas del Sur. Rev. Mus. La Plata Nueva Ser. Secc. Bot. 12 (67), 161–219.
Hagerthey, S.E., Defew, E.C., Paterson, D.M., 2002. Influence of *Corophium volutator* and *Hydrobia ulvae* on intertidal benthic diatom assemblages under different nutrient and temperature regimes. Mar. Ecol. Prog. Ser. 245, 47–59.
Hicks, G.R.F., Coull, B.C., 1983. The ecology of marine meiobenthic harpacticoid copepods. Oceanogr. Mar. Biol. Annu. Rev. 21, 67–175.
Hindák, F., 1990. Studies on the chlorococcal algae (Chlorophyceae). V. Biol. Pracé. Veda, Bratislava.
Holme, N.A., McIntyre, A.D., 1971. Methods for the study of marine benthos. IBP Handbook no. 16Blackwell Scientific Publications, Oxford.
Iribarne, O., Bortolus, A., Botto, F., 1997. Between-habitat differences in burrow characteristics and trophic modes in the southwestern Atlantic burrowing crab *Chasmagnathus granulata*. Mar. Ecol. Prog. Ser. 155, 137–145.
Iribarne, O., Bruschetti, M., Escapa, M., Bava, J., Botto, F., Gutiérrez, J., Palomo, G., Delhey, K., Petracci, P., Gagliardini, A., 2005. Small-and large-scale effect of the SW Atlantic burrowing crab *Chasmagnathus granulatus* on habitat use by migratory shorebirds. J. Exp. Mar. Biol. Ecol. 315, 87–101.
Isacch, J., Costa, C., Rodríguez, L., Conde, D., Escapa, M., Gagliardini, D., Iribarne, O.O., 2006. Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the southwest Atlantic coast. J. Biogeogr. 33, 888–900.
James-Pirri, M.J., Raposa, K.B., Catena, J.G., 2001. Diet composition of mummichogs, *Fundulus heteroclitus*, from restoring and unrestricted regions of a New England (U.S.A.) salt marsh. Estuar. Coast. Shelf Sci. 53, 205–213.
Jeffrey, S.W., Humphrey, G.F., 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. Biochem. Physiol. Pflanzen. 167, 191–194.
Jones, C.G., Lawton, J.H., Shachak, M., 1994. Organisms as ecosystem engineers. Oikos 69, 373–386.
Kelaher, B., Levinton, J., Hoch, J.M., 2003. Foraging by the mud snail, *Ilyanassa obsoleta* (Say), modulates spatial variation in benthic community structure. J. Exp. Mar. Biol. Ecol. 292, 139–157.
Kneib, R.T., 1997. The role of tidal marshes in the ecology of estuarine nekton. Oceanogr. Mar. Biol. 35, 163–220.
Komárek, J., Anagnostidis, K., 2005. Süßwasserflora von Mitteleuropa. Cyanoprokaryota. Teil: Oscillatoriales, 2. Elsevier GmbH, München.
Lee, S., Silliman, B., 2006. Competitive displacement of a detritivorous salt marsh snail. J. Exp. Mar. Biol. Ecol. 339, 75–85.
Lei, Y., Stumm, K., Volkenborn, N., Wickham, S.A., Berninger, U.-G., 2010. Impact of *Arenicola marina* (Polychaeta) on the microbial assemblages and meiobenthos in a marine intertidal flat. Mar. Biol. 157, 1271–1282.
Lever, M., Valiela, I., 2005. Response of microphytobenthic biomass to experimental nutrient enrichment and grazer exclusion at different land-derived nitrogen loads. Mar. Ecol. Prog. Ser. 294, 117–129.
Lillebo, A.I., Pardal, M.A., Marques, J.C., 1999. Population structure, dynamics and production of *Hydrobia ulvae* (Pennant) (Mollusca: Prosobranchia) along an eutrophication gradient in the Mondego estuary (Portugal). Acta Oecol. 20, 289–304.
Mak, Y.M., Williams, G.A., 1999. Littorinids control high intertidal biofilm abundance on tropical, Hong Kong rocky shores. J. Exp. Mar. Biol. Ecol. 233, 81–94.
McAlice, B.J., 1971. Phytoplankton sampling with the Sedgwick–Rafter cell. Limnol. Oceanogr. 16, 19–28.
Méndez Casariego, A., Alberti, J., Luppi, T., Daleo, P., Iribarne, O., 2011. Habitat shifts and spatial distribution of the intertidal crab *Neohelice (Chasmagnathus) granulata* Dana. J. Sea Res. 66, 87–94.
Miller, D.C., Geider, R.J., MacIntyre, H.L., 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. II. Role in sediment stability and shallow-water food webs. Estuaries 19, 202–212.
Moksnes, P.-O., 2004. Interference competition for space in nursery habitats: density-dependent effects on growth and dispersal in juvenile shore crabs *Carcinus maenas*. Mar. Ecol. Prog. Ser. 281, 181–191.
Morrison, R.I.G., Ross, R.K., 1989. Atlas of Neartic shorebirds on the coast of South America. Can. Wildl. Serv. Spec. Publ., 2, pp. 131–323.
Ólafsson, E., Ndaro, S.G.M., 1997. Impact of the mangrove crabs *Uca annulipes* and *Dotilla fenestrata* on meiobenthos. Mar. Ecol. Prog. Ser. 158, 225–231.
Palmer, M.A., 1988. Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. Mar. Ecol. Prog. Ser. 48, 81–91.
Paterson, D.M., Hagerthey, S.E., 2001. Microphytobenthos in contrasting coastal ecosystems: biology and dynamics. In: Reise, K. (Ed.), Ecological Comparisons of Sedimentary Shores. : Ecological Studies, 151. Springer-Verlag, Berlin, pp. 105–126.
Pillay, D., Branch, G., Forbes, A., 2007. Effects of *Callianassa kraussi* on microbial biofilms and recruitment of macrofauna: a novel hypothesis for adult–juvenile interactions. Mar. Ecol. Progr. Ser. 347, 1–14.
Pillay, D., Branch, G.M., Steyn, A., 2009. Complex effects of the gastropod *Assiminea globulus* on benthic community structure in a marine-dominated lagoon. J. Exp. Mar. Biol. Ecol. 380, 47–52.
Pinckney, J.L., Carman, K., Lumsden, S., Hymel, S., 2003. Microalgal–meiofaunal trophic relationships in muddy intertidal estuarine sediments. Aquat. Microb. Ecol. 31, 99–108.
Prescott, G.W., 1962. Algae of the Western Great Lakes Region. W. C. Brown Co., Dubuque, Iowa.
Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press.
Reta, R., Martos, P., Perillo, G.M.E., Piccolo, M.C., Ferrante, A., 2001. Características hidrográficas del estuario de la laguna de Mar Chiquita. In: Iribarne, O. (Ed.), Reserva de biosfera Mar Chiquita: características físicas, biológicas y ecológicas. Editorial Martín, Mar del Plata, pp. 31–52.
Ribeiro, P.D., Iribarne, O.O., 2011. Coupling between microphytobenthic biomass and fiddler crab feeding. J. Exp. Mar. Biol. Ecol. 407, 147–154.
Riera, P., 2010. Trophic plasticity of the gastropod *Hydrobia ulvae* within an intertidal bay (Roscoff, France): a stable isotope evidence. J. Sea Res. 63, 78–83.
Schmitz, O.J., 2006. Predators have large effects on ecosystem properties by changing plant diversity, not plant biomass. Ecology 87, 1432–1437.
Schoener, T.W., 1983. Field experiments on interspecific competition. Am. Nat. 122, 240–285.
Schratzberger, M., Warwick, R.M., 1999. Impact of predation and sediment disturbance by *Carcinus maenas* (L.) on free-living nematode community structure. J. Exp. Mar. Biol. Mar. 235, 255–271.
Silliman, B.R., Bertness, M.D., 2002. A trophic cascade regulates salt marsh primary production. Proc. Natl. Acad. Sci. U. S. A. 99, 10500–10505.
Stachowicz, J.J., Fried, H., Osman, R.W., Whitlatch, R.B., 2002. Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. Ecology 83, 2575–2590.
Sullivan, M.J., Currin, C.A., 2000. Community structure and functional dynamics of benthic microalgae in salt marshes. In: Weinstein, M.P., Kreeger, D.A. (Eds.), Concepts and Controversies in Tidal Marsh Ecology. Kluwer Academic Publishers, Dordrecht, pp. 81–106.
Tell, G., Conforti, V., 1986. Euglenophyta pigmentadas de la Argentina. J. Cramer, Berlin.
Underwood, A.J., 1997. Experiments in Ecology: Their Logical Design and Interpretation Using Analysis of Variance. Cambridge University Press, Cambridge.
Valiela, I., Cole, M.L., McClelland, J., Hauxwell, J., Cebrian, J., 2000. Role of salt marshes as part of coastal landscapes. In: Weinstein, M.P., Kreeger, D.A. (Eds.), Concepts and Controversies of Tidal Marsh Ecology. Kluwer Academic Publishers, Dordrecht, pp. 23–38.
Wilson, W., 1991. Competition and predation in marine soft-sediment communities. Annu. Rev. Ecol. Syst. 21, 221–241.
Worm, B., Lotze, H.K., Hillebrand, H., Sommer, U., 2002. Consumer versus resource control of species diversity and ecosystem functioning. Nature 417, 848–851.
Young, K.A., 2004. Asymmetric competition, habitat selection, and niche overlap in juvenile salmonids. Ecology 85, 134–149.
Zar, J.H., 1999. Biostatistical Analysis, 4th edn. Prentice Hall, Englewood Cliffs, New Jersey.