Combined engineering effects of clams and crabs on infaunal assemblages and food availability in intertidal systems

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ABSTRACT: In soft sediments, ecosystem engineers (EEs) may play key roles in modifying habitats and therefore affecting bottom-assemblage species. In the southwestern Atlantic mud flats, 2 EEs coexist: the stout razor clam *Tagelus plebeius* and the burrowing crab *Neohelice* (*Chasmagnathus*) *granulata*. Clams create small depressions (i.e. millimeters), while crabs build large burrows (i.e. centimeters) generating crab beds covering many hectares. We hypothesized that these differences in the bioturbation scale may have different consequences for infaunal assemblages. We found that (1) microscale sediment-surface heterogeneities created by clams (e.g. holes and surrounding depressions) were related to higher organic-matter content and microphytobenthic biomass (measured as chlorophyll *a*), (2) abundances of meiofaunal groups (copepods, ostracods, and nematodes) were higher in clam holes than outside at all tidal levels, and (3) habitats with a more heterogeneous structure — such as clam holes inside a crab bed — had a higher food availability and an abundance of several meiofaunal groups (e.g. ostracods, and principally nematodes). Large-scale bioturbation (crab-bed formation) also affected primary producers, infaunal assemblages, and clam distribution, because at the highest intertidal levels clams were absent outside the crab beds. Our results thus demonstrate the differential effects of 2 contrasting EEs on the organization of soft-bottom communities and the key role of microheterogeneities in adding specific structures to already modified systems on a larger scale.

KEY WORDS: Ecosystem engineers · Habitat structure · Infaunal assemblages · Clams · Crabs

INTRODUCTION

Habitat structure — which may affect species abundances, assemblages, and diversities in many systems (Connell 1961, Downes et al. 2000) — includes the degree of complexity (McCoy & Bell 1991, Beck 1998), defined as the abundance of structural components (e.g. pits and burrows; McCoy & Bell 1991, Beck 2000), and the heterogeneity, referring to the variation in the relative abundance of different structural ele-

ments (Downes et al. 1998). In general, habitats with a more complex and/or heterogeneous structure increase the diversity and density of organisms (Downes et al. 1998, Beck 2000) through the provision of a large variety of niches, thus enabling resource partitioning (Schoener 1974, Bell et al. 1991). Consequently, a positive relationship obtains between habitat complexity and biotic diversity (Crooks 2002), with the former often assumed to be an essential determinant of species assemblages (Bishop et al. 2007).

Organisms that act as ecosystem engineers (EEs) become particularly relevant because EEs generate habitat heterogeneity, creating spatial and temporal variation in the biotic and abiotic resources for other species (Jones et al. 1994, Pickett et al. 2000). Particularly in soft-bottom systems — where 3-dimensional abiotic features are limited — structures such as tubes, burrows, shells, or reefs lead to increased food availability (reefs: Connell 1978, Bruschetti et al. 2009), refuge from predators (shells: Gutiérrez et al. 2003; tubes: Rabaut et al. 2007; reefs: Connell 1978), and substrates for new organisms (shells: Sousa et al. 2009; reefs: Huston 1985, Bazterrica et al. 2012) in addition to altering the characteristics of the hydraulic flow (burrows: Botto & Iribarne 2000; shells: Coen et al. 2007; stalks and tubes: Eckman 1983). Consequently, in such soft-bottom systems, EEs generally support high densities of associated fauna (Rabaut et al. 2007, Bruschetti et al. 2009) and play key roles in modulating species dynamics or altering ecosystem processes and structures (Jones et al. 1997, Sousa et al. 2009).

Furthermore, in soft-bottom systems, burrowing crustaceans — those being among the most abundant EEs (Bertness 1985, Pillay et al. 2007) — reach high densities (Bertics & Ziebis 2009) and remove large quantities of sediment (Griffis & Suchanek 1991). In parallel with crustaceans, bivalves co-dominate the macrobenthic community (Dame 1996, Gosling 2003) and may also act as EEs (Ólafsson et al. 2005, Sousa et al. 2009); for example, through fecal excretion, those molluscs increase the available organic material in the sediment (Newell et al. 2002, Newell 2004) that can be used as substrate by microalgae and other microorganisms (Reise 1983, Vaughn & Hakenkamp 2001) and in so doing also attract meiofauna (Pinckney & Sandulli 1990, Braeckman et al. 2011). The activity of clams and crabs, however, is performed on different spatial scales; therefore, although both groups are widely distributed in coastal areas, when those taxa do coexist, their combined EE effect is still unknown.

In southwest Atlantic estuaries, the intertidal crab *Neohelice* (*Chasmagnathus*) *granulata* (from 32°S to 43°S) (Boschi 1964) coexists with the stout razor clam *Tagelus plebeius* (from 42°N [Leal 2002] to 41°S [Scarabino 1977]). Crabs strongly affect species assemblages (Botto et al. 2000, Martinetto et al. 2011) and primary resources (Botto et al. 2006, Alvarez et al. 2013a), and increase the landscape's environmental complexity (with burrowing assemblages covering many hectares; Iribarne et al. 1997). Clams, however, create a spatial heterogeneity on a smaller scale

through shallow depressions around siphon openings (Gutiérrez & Iribarne 2004) where feces are deposited and thus increase the organic-matter content (OMC) of sediment (Gutiérrez & Iribarne 2004), as well as modify the distribution of other organisms (e.g. *N. granulata* juveniles; Gutiérrez & Iribarne 1998).

These mud flats, where both species coexist, thus allow an evaluation of the combined effect of 2 EEs acting on different scales. The aim of this investigation was therefore to evaluate the effect of the micro-heterogeneities produced by clams on the abundance of the infauna and the microphytobenthos (measured as chlorophyll content) present, and to measure the OMC and the water content (WC) after consideration of the possible differences resulting from modifications by *N. granulata* crabs. We hypothesized that (1) the abundances of the microphytobenthos and meiofaunal organisms, as well as the OMC and WC, would be higher inside the holes generated by clams — and, specifically, inside the exhalant hole because of the fecal deposition there — and (2) that this interaction would be modified by the effects of the bioturbation created by crabs, with different outcomes from the 2 situations that would depend on the intertidal level.

MATERIALS AND METHODS

Study site

The study was performed in the Mar Chiquita coastal lagoon, Argentina (37°40'S, 57°23'W), a United Nations Educational, Scientific and Cultural Organization Man and Biosphere Reserve, during summer (January to March) 2011. This lagoon is a body of brackish water (46 km^2) with a low tidal amplitude (≤1 m) and permanently connected to the sea (Reta et al. 2001). The southern part of the lagoon is dominated by small creeks and channels with surrounding flats covered by *Spartina densiflora*. A narrow tidal flat devoid of macrophytes is present at the lower end of the halophyte zone, where the sediments are composed of fine sand, silt, and clay (Spivak et al. 1994). Clams and crabs coexist in this study area with different abundances over the various intertidal levels (Gutiérrez & Iribarne 1998). The burrowing crab *Neohelice* (*Chasmagnathus*) *granulata* reaches high densities in mud flats and salt marshes (up to 60 crabs m^{-2}) (Iribarne et al. 1997), but with wide variations (6.55 burrows m^{-2}: Alvarez et al. 2013b; 20.3 burrows m^{-2}: Botto & Iribarne 2000; 32.2
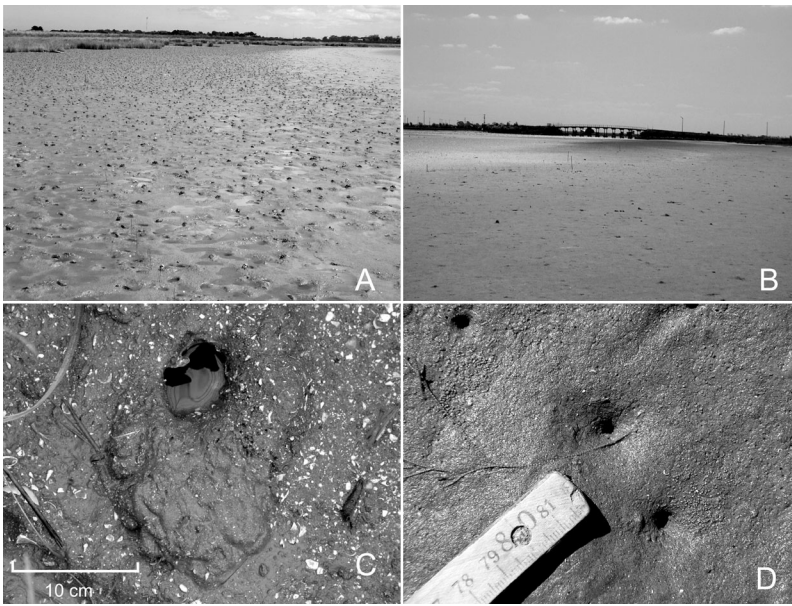
Fig. 1. Heterogeneity at different spatial scales. (A) Crab-bed site, (B) outside crab bed, (C) crab burrow, and (D) clam holes. Photo credits: (A) Paulina Martinetto, (B,D) M. Fernanda Alvarez, and (C) Diana Montemayor

Although both areas can harbor certain unknown intrinsic differences, the two are nevertheless similar in terms of hydrodynamic conditions; furthermore, many studies have shown that most differences in sedimentary characteristics result from active crab bioturbation (Iribarne et al. 1997, Botto & Iribarne 2000).

Density of structural heterogeneities

One aim of this study was to evaluate whether the densities of crab burrows and clam holes, as structural heterogeneities, changed between sites with and without crab bioturbation (see previous section). As the clam and crab densities change in relation to the intertidal levels (clams: Iribarne et al. 1998; crabs: Escapa et al. 2004), the tidal flat was divided into 7 levels parallel to the shore (separated by 12 cm in tidal elevation, from the lowest at 1 to the uppermost at 7). For each intertidal level, at both sites, the density of crabs and clams was estimated by counting the active burrows of the crabs (following Iribarne et al. 2005) and the number of pairs of clam-siphon holes (following Gutiérrez & Iribarne 1998) inside square areas (0.5 × 0.5 m, n = 20) randomly allocated in transects perpendicular to the coast and covering the entire intertidal zone. The holes of clams are identified in the sediment by 2 small and adjacent holes corresponding to the inhalant and exhalant siphons that persist over several tidal cycles (Gutiérrez & Iribarne 2004) (see Fig. 1).

The null hypotheses of no differences in the clam or in the crab density between intertidal levels and sites were evaluated independently by 2-way ANOVA (Zar 1999), while Tukey's honestly significant difference (HSD) tests were used for post hoc contrasts. Normality and homoscedasticity were evaluated through the Shapiro-Wilks and Cochran's C-tests, respectively. In this and all subsequent analyses, monotonic transformations were used when data failed to fulfill the assumptions. In cases where the assumptions could not be met, we considered the difference in the data to be marginally significant if $0.05 > p \geq 0.005$ and significant if $p < 0.005$, thus reducing the likelihood of committing a Type I error (Zar 1999).

burrows m^{-2}: Iribarne et al. 2005). These crabs build burrows with entrance-opening diameters as large as 52.8 mm, with the amount of sediment removed reaching up to 2234.6 g m^{-2} d^{-1} (Botto & Iribarne 2000). Previous studies have shown that crab burrowing, and consequently the bioturbation, stimulates and increases the soil-oxygen availability in the sediments (Daleo et al. 2007, Fanjul et al. 2007). Moreover, inside the crab bed the OMC, WC, and penetrability of the sediment increases, whereas the sediment hardness and resistence to torsion decreases relative to areas without crab bioturbation (Botto & Iribarne 2000, Escapa et al. 2004). Likewise, the razor clam *Tagelus plebeius* inhabits the mud flat at a mean density of around 39.5 clams m^{-2} (M. F. Alvarez unpubl. data); the clam's density becomes minimal at the upper distribution boundary of the species (at around 10 clams m^{-2}) (Gutiérrez & Iribarne 1998), though it is able to attain a maximum of up to 200 clams m^{-2} in the intermediate intertidal regions (Iribarne et al. 1998). In contrast to the crab burrows, the clam holes are between 4.46 and 5.81 mm in diameter (Gutiérrez & Iribarne 1998).

Most samples were taken to compare a site inhabited by high densities of crab burrows and thus strongly bioturbated (CB+) (Iribarne et al. 1997) (Fig. 1) with a second site not bioturbated by crabs, but with some occasional isolated crab burrows during the warm season (CB−) (Alvarez et al. 2013b).

Infaunal assemblages and food supply in the holes of *T. plebeius*

To evaluate whether depressions around the holes created by *T. plebeius* increased the sediment OMC and WC, samples consisting of a sediment surface layer (1 cm in diameter and 2 cm in depth, n = 15) were collected from (1) sediment associated with holes (either inhalant or exhalant) (Ho+) and (2) sediment without any clam holes (i.e. at least 30 cm away from clam holes) (Ho−) in both sites (i.e. inside a crab bed, CB+, and outside crab beds, CB−) and at 3 intertidal levels: the lowest, intermediate, and uppermost intertidal zones corresponding to the second, fourth, and sixth levels cited in the previous section. These zones were selected both through their being representative of different densities of structural heterogeneity (see 'Results: Density of structural heterogeneities') and for the purpose of future discussion and comparison with other investigations at this study site. The OMC was estimated as the percentage of ash-free dry weight, where the ashes were obtained after incinerating samples (approximately 10 g at 550°C for 6 h); the WC was determined on the basis of the difference between wet and dry weights (after drying at 70°C to a constant weight). Moreover, to evaluate whether this heterogeneity was related to the chlorophyll content, sediment samples (n = 15, 1.5 cm in diameter and 2 cm in depth) were obtained to measure epipelic-algal biomass as chlorophyll *a* (chl *a*). The samples were kept in the dark, taken to the laboratory, and frozen (−8°C) until analysis. Chl *a* was determined by the extraction of pigments from the sediment (with 90% [v/v] aqueous acetone) and measured spectrophotometrically (Jeffrey & Humphrey 1975, Lorenzen 1967). The null hypotheses of no differences in OMC, WC, and chl *a* concentration between sites CB+ versus CB− and between Ho+ and Ho− were evaluated by a 2-way ANOVA (Zar 1999) for each intertidal level.

To determine whether holes — as structures produced by clams — were correlated with the abundance and distribution of meiofaunal organisms, sediment samples (n = 10) were obtained with cores (1.5 cm in diameter and 2 cm in depth) at all the sites and intertidal levels (as previously defined) and then filtered through a 63 μm mesh sieve. The organisms obtained were preserved in 5% (v/v) aqueous formaldehyde, stained with rose bengal to facilitate visualization, and then counted under a binocular microscope (at 40× magnification). The taxa were identified down to the larger taxonomic groups, since only scanty information on the taxonomy of the meiofauna in this area was available.

A non-metric multidimensional scaling of the abundance data was used to provide 2-dimensional ordinations (Clarke & Warwick 2001) on the basis of a Bray-Curtis dissimilarity matrix with square-root-transformed data by means of the PRIMER 6 software (Anderson 2001). Permutational multivariate analyses of variance (PERMANOVAs) of 999 unrestricted random permutations were run on matrices of Bray-Curtis dissimilarity among the samples after transformation of data to the fourth root. The variables Ho+/Ho− and CB+/CB− were then used as fixed factors in a cross design of PERMANOVA. When treatments differed significantly, *a posteriori* pair-wise comparisons were run. After the PERMANOVA, analyses of multivariate dispersion (PERMDISP) were also done to test for the homogeneity of dispersions within each group, based on the sample distance to the group centroid (Anderson 2004). The percent contribution of each taxon to patterns of dissimilarity between the sites (CB+/CB−) and between the features (Ho+/Ho−) was calculated by the analysis of similarity of percentages (SIMPER) (Clarke 1993). Taxa contributing at least 10% of the dissimilarity were considered significant differentiators (Bulleri 2005). The abundances of these taxa were analysed separately by 2-way ANOVAs to evaluate whether that parameter was different between Ho+/Ho− and CB+/CB− (considering both as fixed factors), for each intertidal level, followed by Tukey's post hoc tests (Zar 1999).

Infaunal assemblages and food supply inside inhalant and exhalant holes of *T. plebeius*

Given that the abundance of the meiofauna and the chl *a* concentration were both higher in the sediment associated with holes (Ho+) (see 'Results: Infaunal assemblages and food supply in the holes of *T. plebeius*'), we evaluated whether or not differences existed between the exhalant and inhalant siphons with respect to the abundance of the meiofauna, the microphytobenthos biomass (as estimated by the chl *a* content), and the OMC and WC. We hypothesized that the abundance of the meiofauna, the microphytobenthos, and the OMC would be higher in the exhalant hole, where feces are deposited. Therefore, samples of sediment (n = 10) were collected from inhalant and exhalant clam-siphon holes as described in the previous section at only the low intertidal level, where we found the highest clam density (see

Table 1. Results of 2-way ANOVAs for clam and crab density inside crab beds (CB+) and outside crab beds (CB−) in 7 different intertidal levels. Data transformed to square root + 1 for clam density and to fourth root for crab density. **p < 0.005

Variable	Source of variation	df	MS	F
Clam density	CB+/CB−	1	3.37	14.61**
	Level	6	28.75	124.46**
	Interaction	6	5.68	24.59**
	Error	266	0.23	
Crab density	CB+/CB−	1	21.9	153**
	Level	6	0.79	5.56**
	Interaction	6	0.87	6.09**
	Error	266	0.14	

'Results'). The null hypotheses of no differences in OMC, WC, meiofaunal abundance, and chl *a* concentration between sites CB+ and CB−, and between inhalant/exhalant holes, were evaluated by 2-way ANOVAs (Zar 1999).

RESULTS

Density of structural heterogeneities

An interaction between sites and intertidal levels was found for the clam and crab densities (Table 1, Fig. 2). Tukey's analysis showed that the minimum value was obtained in the highest intertidal level (the 7th) at CB−, where no clams were registered, while the maximum density was found also at CB− but in the next-to-lowest intertidal level (the 2nd) (Fig. 2). The crab-burrow density was higher at CB+ as expected, and specifically at the sites in the highest intertidal levels (the 6th and 7th).

Infaunal assemblages and food supply in the holes of *Tagelus plebeius*

With the OMC and WC, no interaction was found between factors (i.e. the sites and Ho+/Ho−). The OMC differed between the features Ho+/Ho− as well as between CB+/CB− in the upper and intermediate intertidal levels, and there the OMC was always higher at Ho+ and CB+ than at the CB− and Ho−, respectively. In the lower intertidal level, the OMC differed only between those sites with a high percentage of CB+ (Table 2). A pattern similar to that of the OMC was found for the WC, where the values were higher at Ho+ in the upper and intermediate
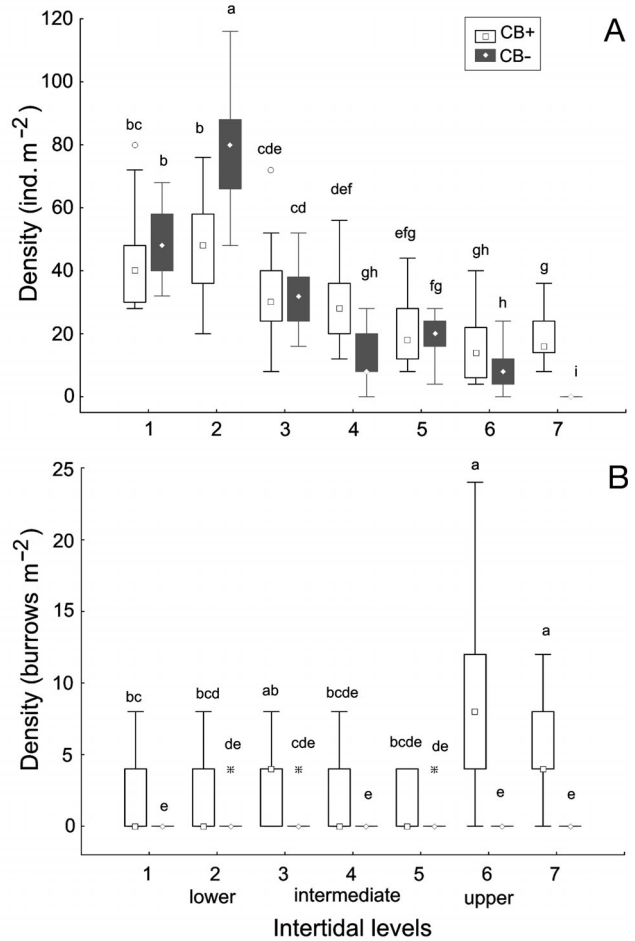

Fig. 2. Densities of (A) the clam *Tagelus plebeius* or (B) burrows of the crab *Neohelice granulata* inside crab beds (CB+) and outside crab beds (CB−) in no. m^{-2} in the 7 different tidal levels. 'lower', 'intermediate' and 'upper': 2nd, 4th and 6th intertidal levels, respectively. Symbols within the boxes denote the median, boxes denote the 25th and 75th percentiles (50% of the data), whiskers denote non-outlier range, and circles and asterisks outside the boxes denote outliers and extremes, respectively. All data are shown before transformations. Different lower-case letters indicate interactions between factors
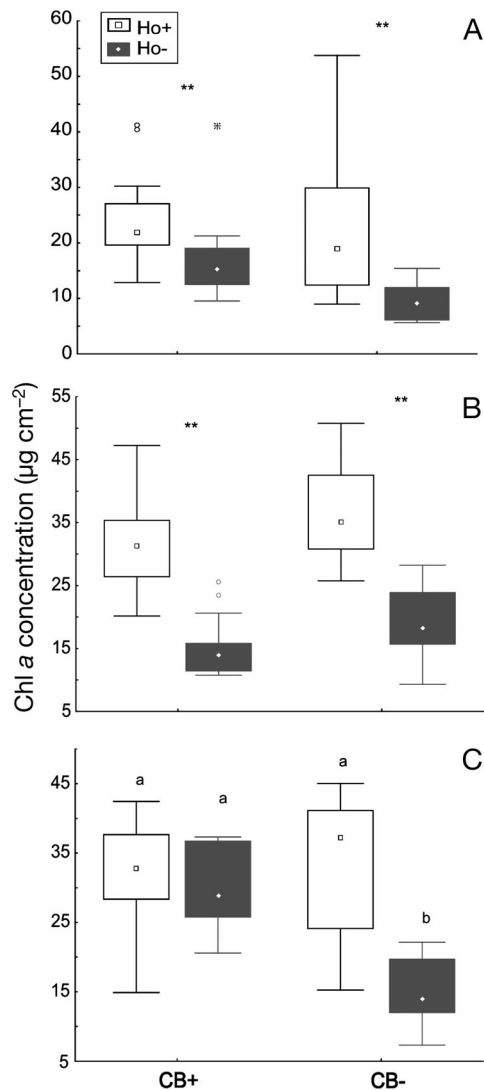
intertidal levels as well as at CB+ in the intermediate and lower intertidal levels (Table 2).

In the upper and intermediate intertidal levels, the chl *a* concentration was almost 80% higher at Ho+ than at Ho− (see Table 2, Fig. 3); in the lower intertidal level, the chl *a* exhibited interactions between the factors (Table 2, Fig. 3), with the concentration being almost 50% lower at Ho− and CB− than at the other sites and features.

The meiofaunal groups found were ostracods, nematodes, foraminiferans, copepods, small polychaetes (members of the family Ctenodrillidae plus *Laeonereis acuta*), flagellates, and nauplii larvae. In

Table 2. Results of 2-way ANOVAs for organic-matter content (OMC), water content (WC), and chl *a* concentrations in 3 intertidal levels with the parameters inside clam holes (Ho+) and outside clam holes (Ho−), and sites inside crab beds (CB+) and outside crab beds (CB−) as factors. Data transformed to square root for OMC and chl *a*, and to fourth root for WC in the intermediate level. *p < 0.05, **p < 0.005

Level	Source of variation	df	OMC		WC		Chl *a*	
			MS	*F*	MS	*F*	MS	*F*
Upper	CB+/CB−	1	2.017	13.71**	3.31	1.32	75.92	2.12
	Ho+/Ho−	1	1.564	10.63**	37.52	14.98**	588.82	16.44**
	Interaction	1	0.002	0.015	2.64	1.05	45.36	1.26
	Error	56	0.147		2.51		35.8	
Intermediate	CB+/CB−	1	2.046	123.79**	0.016	8.5*	1.6	1.82
	Ho+/Ho−	1	0.090	5.47*	0.011	5.7*	16.34	18.62**
	Interaction	1	0.003	0.22	0.002	1.2	0.26	0.29
	Error	52	0.016		0.001		0.87	
Lower	CB+/CB−	1	13.702	42.8**	200	11.96**	234.4	7.12*
	Ho+/Ho−	1	0.232	0.72	24.34	1.45	368.7	11.21**
	Interaction	1	0.086	0.27	40.05	2.39	463.21	14.08**
	Error	56	0.32		16.72		32.89	

Fig. 3. Concentration of chlorophyll *a* (in µg cm^{-2}) in the (A) upper, (B) intermediate, and (C) lower intertidal level inside clam holes (Ho+) and outside clam holes (Ho−), and at sites inside crab beds (CB+) and outside crab beds (CB−). Symbols within the boxes denote the median, the boxes denote the 25th and 75th percentiles (50% of the data), whiskers denote non-outlier range, and circles and asterisks outside the boxes denote outliers and extremes, respectively. All data are shown before transformations. Different lower-case letters indicate interactions between factors and double asterisks show differences between features (Ho+/Ho−)

the upper intertidal level, the PERMANOVA test comparing meiofaunal assemblages indicated interactions (pseudo-$F_{1,36}$ = 6.31, p < 0.01; Fig. 4, Table 3) between the features Ho+/Ho− and the sites CB+/CB−. The multivariate variability was significantly different between the assemblages (PERMDISP, pseudo-$F_{3,36}$ = 10.01, p < 0.01), while the post hoc comparisons demonstrated a greater assemblage heterogeneity at Ho− and CB− (mean = 33.39, SE = 1.98) and Ho− CB+ (mean = 28.03, SE = 5.26). The data from 5 groups could explain these dissimilarities (i.e. nematodes, flagellates, ostracods, foraminiferans, and copepods). ANOVA for the nematodes indicated an interaction, with the abundance in Ho+ and at CB+ being higher than at the other features and sites. Differences between the CB+/CB− and Ho+/Ho− were found for the flagellates and the copepods, with higher abundances being registered in Ho+ and at CB−. Furthermore, the abundances of foraminiferans and ostracods were higher in Ho+ (Fig. 5, Table 4) than in Ho−.

In the intermediate intertidal level, the analysis comparing meiofaunal assemblages also revealed
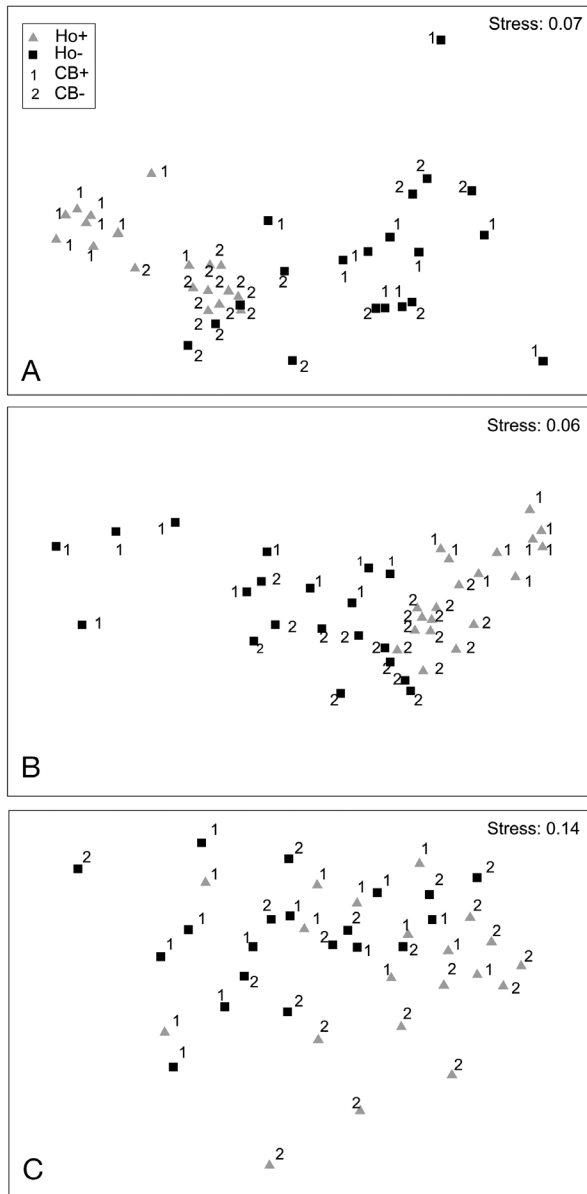
Fig. 4. Non-metric multidimensional scaling (NMDS) plots on transformed data comparing meiofauna assemblages inside clam holes (Ho+) with those outside clam holes (Ho−), and at sites inside crab beds (CB+) and outside crab beds (CB−) in (A) the upper, (B) the intermediate, and (C) the lower intertidal level

Table 3. Results of PERMANOVAs for different meiofaunal assemblages in the upper, intermediate, and lower intertidal level with respect to inside clam holes (Ho+) and outside clam holes (Ho−), and sites inside crab beds (CB+) and outside crab beds (CB−) as factors. **p < 0.005

Level and source of variation	df	MS	Pseudo-F	Unique perm
Upper				
CB+/CB−	1	5789.2	7.88**	999
Ho+/Ho−	1	24470	33.31**	998
Interaction	1	4637.8	6.31**	999
Error	36	734.45		
Intermediate				
CB+/CB−	1	5444.2	12.3**	999
Ho+/Ho−	1	14678	33.1**	999
Interaction	1	3693.3	8.34**	998
Error	36	442.4		
Lower				
CB+/CB−	1	1858.5	4.16**	998
Ho+/Ho−	1	3227.9	7.23**	999
Interaction	1	1007.9	2.25	998
Error	36	446.36		

CB− (mean = 19.6, SE = 1.41). ANOVA detected interactions with respect to copepods, ostracods, foraminiferans, and nematodes, with the abundance of copepods being higher in Ho+ CB− than at other sites, and the density of the ostracods lower in Ho− CB+ than at the others (Fig. 6, Table 5). The nematode abundance was higher at Ho+ CB+ than at the other sites (Fig. 6). The density of the foraminiferans was higher at the Ho+ CB+ than at the Ho− CB+ site, while the flagellate abundance was higher in Ho+ and CB− than elsewhere (Fig. 6, Table 5).

At the lower intertidal level, PERMANOVA revealed that meiofaunal assemblages were different with respect both to the different sites (pseudo-$F_{1,36}$ = 4.16, p < 0.01) and to Ho+/Ho− ($F_{1,36}$ = 7.23, p <0.01; Fig. 3, Table 3). The data from the ctenodrillids, nematodes, foraminiferans, ostracods, copepods, and flagellates could explain the dissimilarities found here. No heterogeneity occurred in the multivariate dispersion between the crab sites (pseudo-$F_{1,38}$ = 0.26, p = 0.63) and Ho+/Ho−($F_{1,38}$ = 0.31, p = 0.61). ANOVA for the copepods and ctenodrillids demonstrated an interaction between the factors, resulting in a higher abundance of both groups at Ho+ CB− than at other features and sites. Differences between sites were found for the foraminiferans, ostracods, and flagellates with higher abundances in CB− relative to their densities elsewhere. ANOVA showed differences between Ho+/Ho− for nematodes and ostracods with a higher abundance at Ho+ (Fig. 7, Table 6).
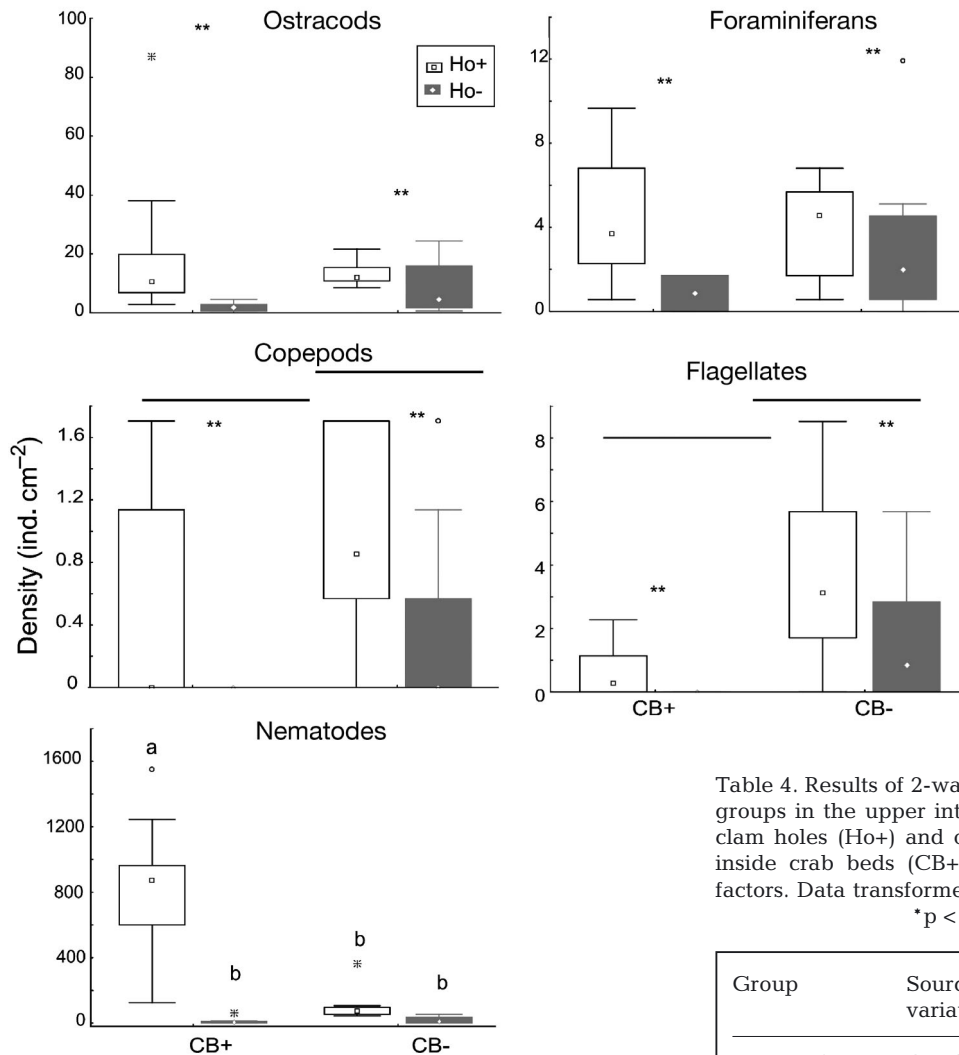
interaction between the crab sites and Ho+/Ho− (pseudo-$F_{1,36}$ = 8.34, p < 0.01; Fig. 4, Table 3). The data from the same 5 groups that were present at the upper level could explain the dissimilarities found. The PERMDISP analysis was significantly different among the assemblages (pseudo-$F_{3,36}$ = 23.55, p < 0.01), and the post hoc comparisons indicated a greater heterogeneity principally between Ho− and CB+ (mean = 28.7, SE = 2.6) and between Ho− and

Fig. 5. Density (in ind. cm^{-2}) of ostracods, foraminiferans, copepods, flagellates, and nematodes inside clam holes (Ho+) and outside clam holes (Ho−), and at sites inside crab beds (CB+) and outside crab beds (CB−) in the upper intertidal level. Symbols within the boxes denote the median, the boxes denote the 25th and 75th percentile (50% of the data), whiskers denote non-outlier range, and circles and asterisks outside the boxes denote outliers and extremes, respectively. All data are shown before transformations. Different lower-case letters indicate interactions between factors, double asterisks show differences between features (Ho+/Ho−), and solid straight lines above the boxes indicate statistically different values between sites (CB+/CB−)

Table 4. Results of 2-way ANOVAs for different meiofaunal groups in the upper intertidal level, with respect to inside clam holes (Ho+) and outside clam holes (Ho−), and sites inside crab beds (CB+) and outside crab beds (CB−) as factors. Data transformed to square root for foraminiferans. *p < 0.05, **p < 0.005

Group	Source of variation	df	MS	F
Nematodes	CB+/CB−	1	3 888 770	27.59**
	Ho+/Ho−	1	6 101 172	43.29**
	Interaction	1	4 046 232	28.71**
	Error	36	140 906	
Copepods	CB+/CB−	1	7.22	7.62*
	Ho+/Ho−	1	9.02	9.52**
	Interaction	1	0.62	0.65
	Error	36	0.94	
Flagellates	CB+/CB−	1	160	18.99**
	Ho+/Ho−	1	48.4	5.74*
	Interaction	1	14.4	1.7
	Error	36	8.42	
Ostracods	CB+/CB−	1	10	0.01
	Ho+/Ho−	1	4284.9	7.58[a]
	Interaction	1	1638.4	2.89
	Error	36	565	
Foraminiferans	CB+/CB−	1	1.64	1.5
	Ho+/Ho−	1	13.77	12.67**
	Interaction	1	3.75	3.45
	Error	36	1.08	

[a]Marginally significant at 0.05 > p ≥ 0.005 (because of non-compliance with the assumptions of normality and homoscedasticity, see 'Materials and methods')

Infaunal assemblages and food supply inside inhalant and exhalant holes of *T. plebeius*

Among the samples, an interaction was found for the OMC, with higher content in the inhalant holes at the CB+ sites than elsewhere. WC was likewise high at the CB+ sites, whereas the chl *a* concentrations were higher in the exhalant than in the inhalant clam holes (Table 7).

The meiofaunal organisms found in these samples were the same taxa as had been previously found (see previous section), but the PERMANOVA test indicated that the infaunal assemblages were different among the sites (pseudo-$F_{1,36}$ = 3.95, p < 0.05). PERMDISP did not, however, show differences among the assemblages (pseudo-$F_{1,38}$ = 0.86, p = 0.37). ANOVA indicated an interaction with the nematodes, whose abundance in the exhalant holes at CB+ was 1.5 times higher than at other sites. The
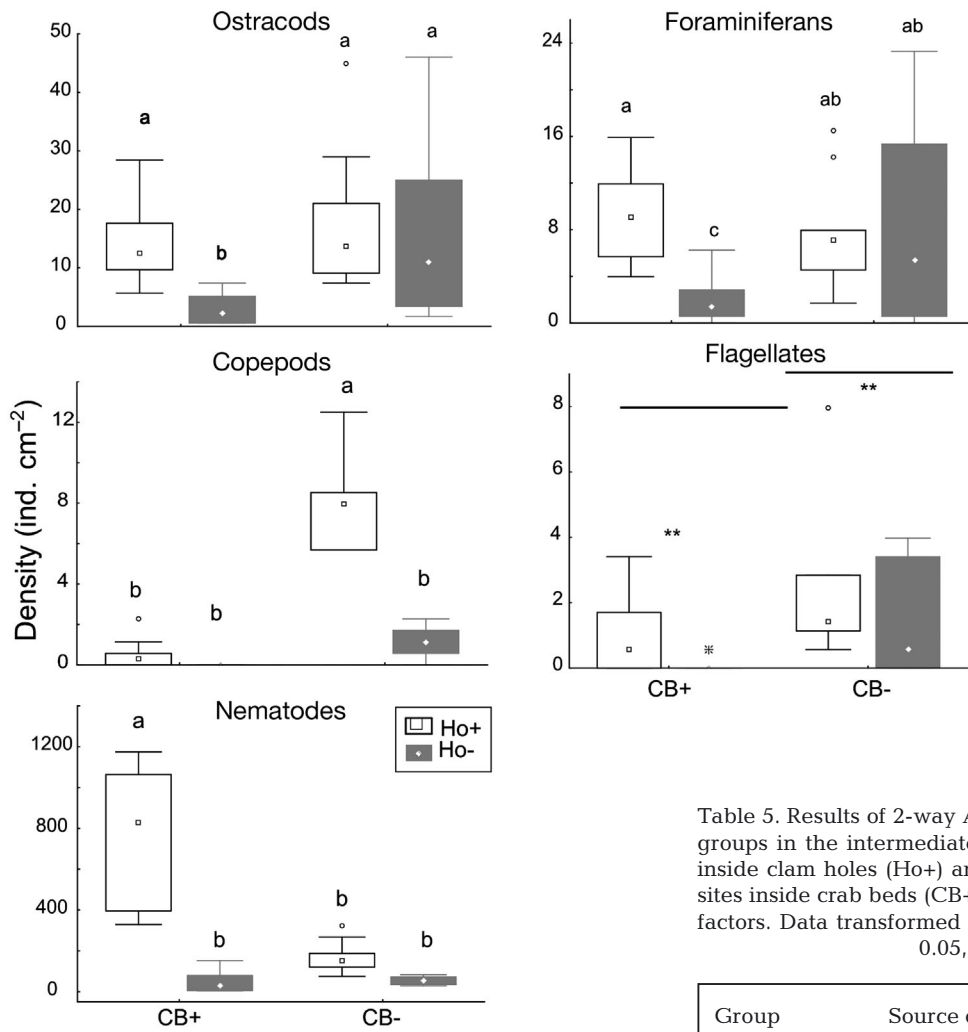
Fig. 6. Density (in ind. cm^{-2}) of ostracods, foraminiferans, copepods, flagellates, and nematodes inside clam holes (Ho+) and outside clam holes (Ho−), and at sites inside crab bed (CB+) and outside crab beds (CB−) in the intermediate intertidal level. Symbols within the boxes denote the median, the boxes denote the 25th and 75th percentiles (50% of the data), whiskers denote non-outlier range, and circles and asterisks outside the boxes denote outliers and extremes, respectively. All data are shown before transformations. Different lower-case letters indicate interactions between factors, double asterisks show differences between features (Ho+/Ho−), and solid straight lines above the boxes indicate statistically different values between sites (CB+/CB−)

ostracods and flagellates (Fig. 8, Table 7) were more abundant in CB−. In addition, the flagellates also evidenced a higher abundance in the inhalant holes, but the ANOVA analyses revealed no such differences for the copepods, foraminiferans, and ctenodrillids.

DISCUSSION

Our results show that meiofaunal organisms such as copepods, ostracods, and nematodes were more abundant in the sediment associated with holes generated by clams than in sediment without holes in all the intertidal levels at both CB+ and CB− sites. The OMC and microphytobenthos biomass (estimated as the chl *a* content) were also higher inside the clam holes at both crab sites, though principally in the intermediate and upper intertidal levels. Moreover, the assemblage of meiofauna associated with clam
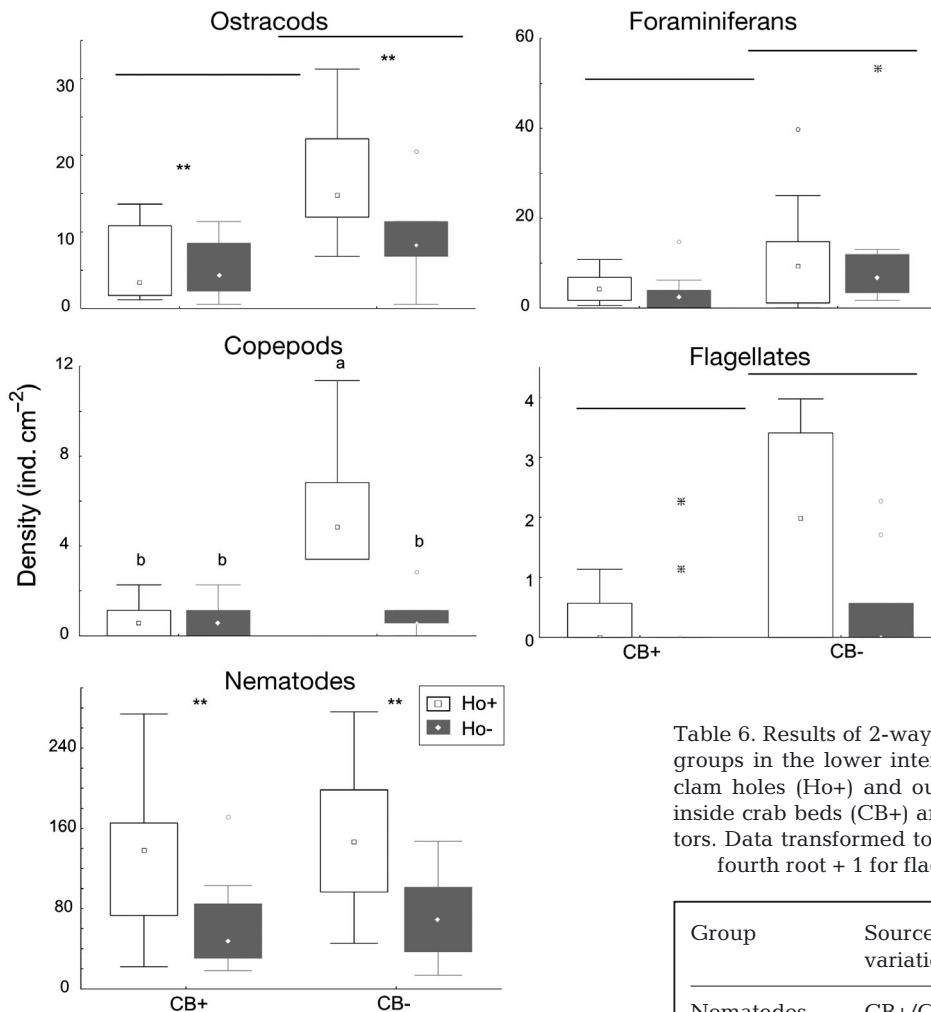
Table 5. Results of 2-way ANOVAs for different meiofaunal groups in the intermediate intertidal level, with respect to inside clam holes (Ho+) and outside clam holes (Ho−), and sites inside crab beds (CB+) and outside crab beds (CB−) as factors. Data transformed to fourth root for ostracods. *p < 0.05, **p < 0.005

Group	Source of variation	df	MS	F
Nematodes	CB+/CB−	1	2 777 817	28.31**
	Ho+/Ho−	1	5 356 044	54.59**
	Interaction	1	2 840 357	28.95**
	Error	36	98 098	
Copepods	CB+/CB−	1	555.02	138.27**
	Ho+/Ho−	1	403.22	100.45**
	Interaction	1	297.02	73.99**
	Error	36	4.01	
Flagellates	CB+/CB−	1	70.22	7.17[a]
	Ho+/Ho−	1	42.02	4.29[a]
	Interaction	1	1.22	0.12
	Error	36	9.79	
Ostracods	CB+/CB−	1	1.57	9.71**
	Ho+/Ho−	1	2.29	14.1**
	Interaction	1	1.01	6.27*
	Error	36	0.16	
Foraminiferans	CB+/CB−	1	160	1.72
	Ho+/Ho−	1	280.9	3.03
	Interaction	1	504.1	5.44[a]
	Error	36	92.57	

[a]Marginally significant at 0.05 > p ≥ 0.005

Fig. 7. Density (in ind. cm^{-2}) of ostracods, foraminiferans, copepods, flagellates, and nematodes inside clam holes (Ho+) and outside clam holes (Ho−) and at sites inside crab beds (CB+) and outside crab beds (CB−) in the lower intertidal level. Symbols within the boxes denote the median, the boxes denote the 25th and 75th percentile (50% of the data), whiskers denote non-outlier range, and circles and asterisks outside the boxes denote outliers and extremes, respectively. All data are shown before transformations. Different lower-case letters indicate interactions between factors, double asterisks show differences between features (Ho+/Ho−), and solid straight lines above the boxes indicate statistically different values between sites (CB+/CB−)

holes was different from the assemblage outside those holes in the lower intertidal level. In the exhalant holes, the microphytobenthos biomass and nematode density were 1.5 times higher than in the inhalant holes, although some other groups were not characterized by such differences, while others exhibited the opposite pattern (e.g. the flagellates). In addition, the CB+ areas at all the intertidal levels displayed high structural heterogeneities as both clams and crabs were present. In contrast, outside the crab beds the structural heterogeneities were generated by the clams alone, because the crabs were either absent altogether or present at much lower densities. In fact, principally in the upper and intermediate intertidal levels, several meiofaunal groups — such as the nematodes, ostracods, foraminiferans, and copepods — were more abundant in the holes generated by clams that were located inside crab beds.

Through their feeding behavior and feces or pseudofeces excretion, the benthic organisms modify the

Table 6. Results of 2-way ANOVAs for different meiofaunal groups in the lower intertidal level, with respect to inside clam holes (Ho+) and outside clam holes (Ho−), and sites inside crab beds (CB+) and outside crab beds (CB−) as factors. Data transformed to square root + 1 for copepods and fourth root + 1 for flagellates. *p < 0.05, **p < 0.005

Group	Source of variation	df	MS	F
Nematodes	CB+/CB−	1	6554	0.52
	Ho+/Ho−	1	156750	12.65**
	Interaction	1	1232	0.09
	Error	36	12391	
Copepods	CB+/CB−	1	9.08	37.3**
	Ho+/Ho−	1	7.15	29.3**
	Interaction	1	6.19	25.4**
	Error	36	0.24	
Flagellates	CB+/CB−	1	0.25	6.061*
	Ho+/Ho−	1	0.13	3.36
	Interaction	1	0.16	4.06
	Error	36	0.04	
Ostracods	CB+/CB−	1	1904.4	17.57**
	Ho+/Ho−	1	448.9	4.14*
	Interaction	1	422.5	3.89
	Error	36	108.3	
Foraminiferans	CB+/CB−	1	1690	5.1*
	Ho+/Ho−	1	14.4	0.04
	Interaction	1	8.1	0.02
	Error	36	331.1	
Ctenodrilids	CB+/CB−	1	156.02	6.28[a]
	Ho+/Ho−	1	455.6	18.36**
	Interaction	1	164.02	6.61[a]
	Error	36	24.8	

[a]Marginally significant at 0.05 > p ≥ 0.005

Table 7. Results of 2-way ANOVAs in the lower intertidal level for different meiofaunal groups, organic-matter content (OMC), water content (WC), and chl a concentrations with respect to inside crab beds (CB+), outside crab beds (CB−), and inside inhalant (inha) and exhalant (exha) holes as factors. Data transformed to fourth root for flagellates, ostracods and foraminiferans. *p < 0.05, **p < 0.005

Group	Source of variation	df	MS	F
OMC	CB+/CB−	1	3.23	18.21**
	Inha/Exha	1	1.35	7.06[a]
	Interaction	1	13.76	77.35**
	Error	36	0.17	
WC	CB+/CB−	1	76.38	6.06*
	Inha/Exha	1	0.05	0.00
	Interaction	1	2.98	0.23
	Error	36	12.6	
Chl a	CB+/CB−	1	15.55	0.18
	Inha/Exha	1	399.67	4.84*
	Interaction	1	9.11	0.11
	Error	36	82.49	
Nematodes	CB+/CB−	1	30 969	1.18
	Inha/Exha	1	20 205	0.77
	Interaction	1	161 929	6.2*
	Error	36	26 084	
Flagellates	CB+/CB−	1	2.5	22.57**
	Inha/Exha	1	0.55	4.99*
	Interaction	1	0.02	0.24
	Error	36	0.11	
Ostracods	CB+/CB−	1	1.21	11.44**
	Inha/Exha	1	0.06	0.59
	Interaction	1	0.35	3.32
	Error	36	0.1	
Copepods	CB+/CB−	1	32.4	1.29
	Inha/Exha	1	12.1	0.48
	Interaction	1	14.4	0.57
	Error	36	24.97	
Foraminiferans	CB+/CB−	1	1.95	3.71
	Inha/Exha	1	0.29	0.55
	Interaction	1	0.89	1.69
	Error	36	0.52	
Ctenodrilids	CB+/CB−	1	11.02	0.12
	Inha/Exha	1	18.25	0.2
	Interaction	1	3.02	0.03
	Error	36	90.04	

[a]Marginally significant at 0.05 > p ≥ 0.005

Fig. 8. Density (in ind. cm^{-2}) of nematodes, ostracods, and flagellates inside inhalant and exhalant clam holes, inside crab beds (CB+), and outside crab beds (CB−) in the lower intertidal level. Symbols within the boxes denote the median, the boxes denote the 25th and 75th percentile (50% of the data), whiskers denote non-outlier range, and circles and asterisks outside the boxes denote outliers and extremes, respectively. All data are shown before transformations. Different lower-case letters indicate interactions between factors, double asterisks show differences between features (Ho+/Ho−), and solid straight lines above the boxes indicate statistically different values between sites (CB+/CB−)

sediment's characteristics — in particular, the OM and microphytobenthic biomass (Graf & Rosenberg 1997). For example, burrows and pits may concentrate food by accumulating particles (Retraubun et al. 1996, Reise 2002) and stimulate microbial gardening (Reise 2002, Mermillod-Blondin et al. 2004) through increased irrigation of the surrounding sediment with oxygen-rich water (*Callianassa* and *Lanice*: Forster & Graf 1995; *Arenicola* and *Nereis*: Kristen-
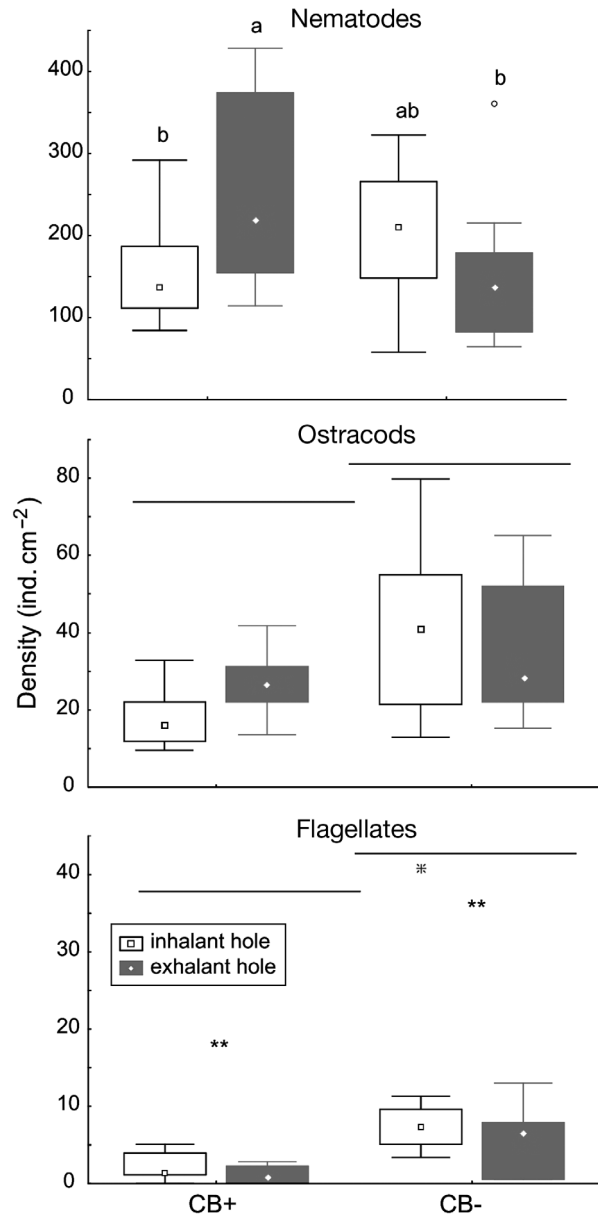
sen 2001; *Mya arenaria*: Michaud et al. 2006), thus creating a mosaic of organic-rich microenvironments with different properties that favor the development of micro- and meiobenthic communities (Fenchel

1996). Accordingly, *Tagelus plebeius* directly affects the tridimensional configuration of sediments by creating small depressions (Gutiérrez & Iribarne 2004). Our results show that, during low tide, the water content in the sediment in these depressions was higher, probably because surface water was retained (M. F. Alvarez pers. obs.). Moreover, an enrichment of OM was also found in Ho+ and, along with this retained water, may be the reason why the microphytobenthos biomass was twice as high in those holes than in the adjacent areas without such depressions. In addition, in the sediment associated with the holes the higher abundances of flagellates, copepods, foraminiferans, nematodes, and ostracods may result from an increased food supply. Earlier studies in other areas observed that nematode assemblages develop differently depending on the clam density (Ullberg & Ólafsson 2003) and also indicated that the attraction of nematodes and copepods to microalgal patches may explain the patchiness and distribution of those fauna (Santos et al. 1995, Ullberg & Ólafsson 2003). Therefore, in agreement with our initial hypothesis, *T. plebeius* holes exert a positive effect on the abundance, distribution, and assemblages of benthic species.

As explained above, because the holes created by *T. plebeius* modify the availability of resources for other organisms, that species may be considered an EE as a result of its ability to shape habitats and create microenvironments (Aller & Aller 1998, Kristensen 2000) with specific properties where different communities develop (Widdicombe & Austen 1999, Papaspyrou et al. 2006). As habitats are species-specific (Beck 2000), large and small organisms may perceive the environment on different scales and respond in divergent ways (Holland et al. 2004). For example, habitat complexity can offer refuge to small organisms but exclude the larger ones (Bishop et al. 2007). Our study contains evidence of different effects on the microphytobenthos biomass and meiofaunal assemblages depending on the bioturbation generated by crabs or on the microheterogeneities created by clams. Our results in the low intertidal level, in particular, indicate that outside the crab beds the structures built by clams became relevant, with groups such as ctenodrillids and copepods being more abundant there; no comparable differences were found inside the crab beds. By contrast, in the upper and intermediate intertidal levels the opposite pattern occurred: inside the crab beds, groups such as ostracods, foraminiferans, and mainly nematodes were more abundant in the clam holes. Furthermore, because dispersion analysis demon-

strated that meiofaunal assemblages were less dispersed in the structural heterogeneities created by clams within those intertidal levels at both the CB+ and the CB– sites, these structures would appear to be more stable and similar to each other, thus probably providing the organisms with a more constant or secure habitat than areas outside (i.e. Ho–).

In intertidal systems, abiotic conditions are more stressful to organisms in the upper intertidal levels: for example, temperature and desiccation increase as immersion decreases. Thus, positive interactions tend to be influential in determining species distribution (Bertness 1989) because infaunal taxa that create enhanced subsurface conditions are favorable to other infauna (Volkenborn & Reise 2006, Braeckman et al. 2011). Therefore, bioturbation becomes highly relevant because that effect can ameliorate negative conditions (Bertness & Callaway 1994, Crain & Bertness 2006). Consistent with these principles, our results demonstrate that in the upper and intermediate intertidal levels, where harsh physical conditions prevail, the bioturbation effected by crabs may increase clam abundances (compared to the environment outside the crab beds, as indicated in 'Results'); hence, the bioturbation generated by both organisms results in sediments that are even more heterogeneous (i.e. containing burrows of crabs plus holes of clams) with a higher food concentration (i.e. having a greater microphytobenthos biomass and OM content), thus increasing the abundance of meiofaunal groups. In the low intertidal level, however, the abundance of meiofaunal groups was higher in the clam holes, but only in those outside the crab beds. This pattern could be explained by the active and continuous bioturbation generated by crabs, including their habit of wandering, which may be a negative influence that increases the mortality of infaunal organisms. Other reports have indicated that large macrofaunal species affect meiofaunal assemblages by direct predation or non-selective feeding, or by competition for food sources (Nascimento et al. 2011; Ingels et al. 2014) so as to reduce, for example, nematode abundance with consequent effects on community structure and evenness (Ingels et al. 2014). Nevertheless, different groups of organisms that intervene could respond in diverse ways (i.e. nematodes, ostracods: Nascimento et al. 2011; macrofaunal species: Ingels et al. 2014), while the overall effects would reflect a combination of the interactions between the macro- and meiofauna as well as the structural and biogeochemical changes produced by their presence and behavior (Braeckman et al. 2010, 2011). These complex interrelationships exist along

with other specific and influential features that were not considered here and would explain this variability — such as food supply, chemical requirements, vertical distribution, the presence of predators, or other interactions.

In soft-bottom environments, large-scale bioturbation is recognized as one significant influence that can change the physico-chemical (Reise 2002, Chapman & Tolhurst 2007) and biological (Papaspyrou et al. 2006) characteristics of sediments and, as a consequence, modify infaunal abundances and their interactions (Pillay et al. 2007, Alvarez et al. 2013b). Small-scale EE effects, however, also affect those abiotic and biotic sediment characteristics (Ólafsson et al. 2005, Sousa et al. 2009). As mentioned above, in our study area, the mud flats are dominated by the bioturbator crab *Neohelice* (*Chasmagnathus*) *granulata* (Iribarne et al. 1997), but the clam *T. plebeius* probably dominates the macrobenthic community. In accordance with our hypothesis, we observed in the present study that this interaction between 2 EE species was relevant in the upper and intermediate intertidal levels, where harsh physical conditions prevail. Thus, inside a sizeable matrix of crab burrows, where conditions would be more favorable to different organisms, smaller biota such as clams that add habitat heterogeneity over a lesser spatial scale could have significant consequences, through acting as foci where infaunal species would be attracted and could benefit from an enhanced survival.

Through the changes they effect in habitat heterogeneity, EEs have a major influence on the organization of soft-bottom communities by their ability to increase the diversification of spatial resources (Reise 2002, Bouma et al. 2009). Thus, our study, in conjunction with others (e.g. Crooks 2002, Gutiérrez et al. 2011), demonstrates the relationships between the environment and the necessities of species-specific habitats. Moreover, these results highlight the significance of habitats created by different organisms, along with the way in which the interaction between 2 EEs — that, between them, produce architectural changes on different scales in the environment — can affect, in a complex way, the primary production and structure of, as well as the interactions among, infaunal assemblages.

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