



Macroalgae ecosystem engineering effects mediated by an invasive reef-builder polychaete in a Southwestern Atlantic coastal lagoon

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ABSTRACT

Macroalgae in Mar Chiquita coastal lagoon (37° 40' S, 57° 23' W, Argentina) settle on small-hard substrates on sediments and complex reef-like structures with tubes and crevices of the invader polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) acting as ecosystem engineers with multiple community structuring effects. In this study, we compared the structural effects of macroalgae generating new habitat for other organisms in two systems with originally different structural complexity. Therefore, we hypothesized that macroalgae relative importance as an ecosystem engineer providing new habitat and refuge for other organisms would be higher in flat soft-sediments than on reefs. Through sampling and experimental studies, results showed that macrofaunal assemblages were different between areas with and without macroalgae in both reefs and sediment. Experimental results on macroalgae and macroalgae-mimics to separate structural effects in both reefs and sediment showed that macroalgae affect macrofauna on both systems but, structural mechanisms did not prevail in the reefs or sediment. The effect varied on species responses and physical gradients (i.e., depth) of each type of area. Therefore, our results did not support our hypothesis and suggest that macroalgae effects are the result of a summary of their multiple effects in interaction with species and habitat type.

1. Introduction

The ecosystem engineering concept (i.e., organisms that modulate the availability of resources to other species by causing physical state changes; Jones et al., 1994) encompass a variety of ecological phenomena not addressed by the historical focus of ecology on trophic relations (Gutiérrez and Jones, 2008), but that had increasingly gained importance in ecological research during the last two decades (Gutiérrez, 2020). In particular, the importance of ecosystem engineering in mudflats is widely known (e.g., Passarelli et al., 2014; Alvarez et al., 2015). Bare sediments are characterized by a lack of habitat structure and therefore when are inhabited by organisms that add habitat such as macroalgae (Wright et al., 2014), bivalves (Gutiérrez et al., 2003), burrowing organisms (Alvarez et al., 2015) or reef-building organisms (Schwindt et al., 2001), they produce enormous ecological effects, particularly on benthic assemblages. These ecosystem engineers convert a low structured environment to a highly structured environment with

an increase in available niches as new habitat or refuge for other organisms (Jones et al., 2010). Moreover, ecosystem engineers can create habitat cascades by generating a biogenic habitat that can be used by another organism that, in turn, creates or modifies the habitat for others (Thomsen et al., 2010, 2018). There had been attempts to make predictions of ecosystem engineering effects (Wright et al., 2006; Grinath et al., 2019), and most of them concluded that the effects would depend on the previous availability of niches (Shea and Chesson, 2002). For example, an ecosystem engineer that increases productivity could have different consequences on the community, depending on the previous productivity of the modified habitat (Wright et al., 2006). Therefore, ecosystem engineering effects would depend on habitat conditions before engineering.

According to the original classification, organisms can be autogenic engineers, when their structure modifies the environment, creating or modifying resources for other organisms, and allogenic engineers, when their activity has substantial and long-lasting effects on the physical

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structure of living and nonliving materials, changing resources for other organisms (see Jones et al., 1994, 2006). In turn, according to mechanisms involved, ecosystem engineers could be classified as structural, bioturbator, light, and chemical engineers, affecting habitat complexity, sediment dynamics, and luminance and biochemical fluxes, respectively (see Berke, 2010). Therefore we can expect that some organisms that generate important structures that modify the environment and resources for other organisms (which are autogenic engineers sensu Jones et al., 1994) will have significant structural effects, but can also generate other important direct and indirect.

The serpulid polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) is an example of an invader ecosystem engineer that has invaded many locations in temperate brackish waters throughout the world (see Hove et al., 1978), including some estuaries of the Southwestern Atlantic (see Brankevich et al., 1988; Obenat and Pezzani, 1994; Borthagaray et al., 2006). In Mar Chiquita coastal lagoon (37° 40'S, 57° 23'W, Argentina), reefs are well-established (Schwindt et al., 2004a), altering native community structure mainly due to the reefs, a “new” hard highly complex substrate in an originally soft-bottom habitat (see Bruschetti, 2019 and references therein). In turn, *F. enigmaticus* drives habitat heterogeneity, generating areas with and without reefs (see Bazterrica et al., 2012), which modifies the relative importance of top-down and bottom-up effects (Bruschetti et al., 2009; Bazterrica et al., 2013) as well as the strength of facilitative interactions (Bazterrica et al., 2014). That leads to different benthic assemblages in terms of macroalgae (Bazterrica et al., 2012) and macrofauna species composition (Martinez et al., 2020) as well as in terms of species population traits (Bazterrica et al., 2020). Polychaete reefs affect the structure and function of the community in the invaded areas through direct and indirect ecosystem engineering mechanisms and top-down control (Schwindt et al., 2001; Bruschetti et al., 2008). For example, reefs increase the density of the crab *Cyrtograpsus angulatus* Dana, 1851 by providing them refuge, and this crab negatively affects macrofauna from nearby sediments by consumption (Schwindt et al., 2001). Likewise, reefs impact macroalgae, which is another potential ecosystem engineer. They increase macroalgae biomass as it grows on reef hard surfaces. In contrast, high sedimentation among reefs covers the hard substrates of the bottom, such as shells (“valves”), avoiding the settlement of macroalgae, and limiting them to the areas without reefs (see Bazterrica et al., 2012).

The different ways reefs affect macroalgae are important since macroalgae play an essential role in structuring natural communities by diverse mechanisms. Macroalgae are primary producers (e.g., Bruno and O'Connor, 2005; Alfaro et al., 2006), drive carbon chemistry changes (e.g., Young and Gobler, 2018; Krause-Jensen and Duarte, 2016) and affect nutrient addition or removal (Savage and Elmgren, 2004; Lomstein et al., 2006) via thallus energy and material uptake, metabolism, waste production and death (i.e., assimilation and dissimilation; see Jones et al., 2006). Macroalgae also compete for available substrate (e.g., Carpenter, 1990; Taplin et al., 2005) and provide new habitat and refuge. Therefore, in some cases, macroalgae can be considered an ecosystem engineer with significant effects increasing or decreasing the relative abundance of other species (e.g., Stewart and Carpenter, 2003; Daleo et al., 2006).

Macroalgae assemblages in Mar Chiquita coastal lagoon are dominated by *Polysiphonia cf. subtilissima* Montagne 1840 growing mainly in reefs surfaces and *Cladophora sp.* Kützing growing mainly in valves from the sediment of reef-free areas. Both macroalgae belong to the filamentous functional group (similar lightly corticated and delicately branched morphology, Littler and Arnold, 1982), and the same Ecological State Group, being filamentous species with high growth rates and short life cycles (Orfanidis et al., 2001). Therefore, both macroalgae can be considered as equivalent in their ecological role as habitat (sensu Steneck and Dethier, 1994).

Considering that reefs have higher three-dimensional complexity than sediments (see Bazterrica et al., 2012), macroalgae on the sediment will proportionally increase the availability of crevices and surface more

significantly than on reef surfaces (see McKindsey and Bourget, 2001). In this context, the objective here is to evaluate the role of macroalgae as an ecosystem engineer in the association or not of the invasive ecosystem engineer *F. enigmaticus*. We hypothesize that macroalgae structural effects on the density of macrofauna will be proportionally less important on reefs (high complexity substrate) than in sediments (less complexity substrate).

2. Methods

2.1. Study site

We worked at the Mar Chiquita coastal lagoon (a Man and the Biosphere UNESCO Reserve; Fig. 1). It is a body of brackish water (46 km²) connected to the sea, with a wide salinity range (2 to 35 ppt; in Schwindt et al., 2004a, 2004b) and low amplitude tides (≤ 1 m; Isla, 1997). Sampling, and experiments, were performed at the low intertidal. There, we identified two areas (separated 100 m away, within an area of 10 ha) similar in tidal height and current flow, but one with reefs and the other without reefs (hereafter sediment). For this study, we compared the role of filamentous macroalgae as ecosystem engineer adding structure in the habitat, between the reef surface (mainly *Polysiphonia cf. subtilissima*) and sediment (mainly *Cladophora* spp., which grows on small substrates, mainly valves Bazterrica et al., 2012). In both cases, macroalgae are patchily distributed (Bazterrica et al., 2013). *P. subtilissima* is a cosmopolitan perennial or pseudo perennial algae restricted to brackish water embayments (Hehre and Mathieson, 1970). The thallus reaches a maximum length of 10 to 12 cm in the summer (Knight and Parke, 1931; Fralick and Mathieson, 1975) and, in this area, reaches dry biomass of 300 g.m⁻² (Bazterrica et al., 2012). *Cladophora* arises from a consistent branching pattern with a flexible thallus allowing water flowing (Dodds, 1991; Dodds and Gudder, 1992), reaching in this area mats of 20 cm (Bazterrica, unpublished data). Macrofaunal assemblages in Mar Chiquita show relatively low

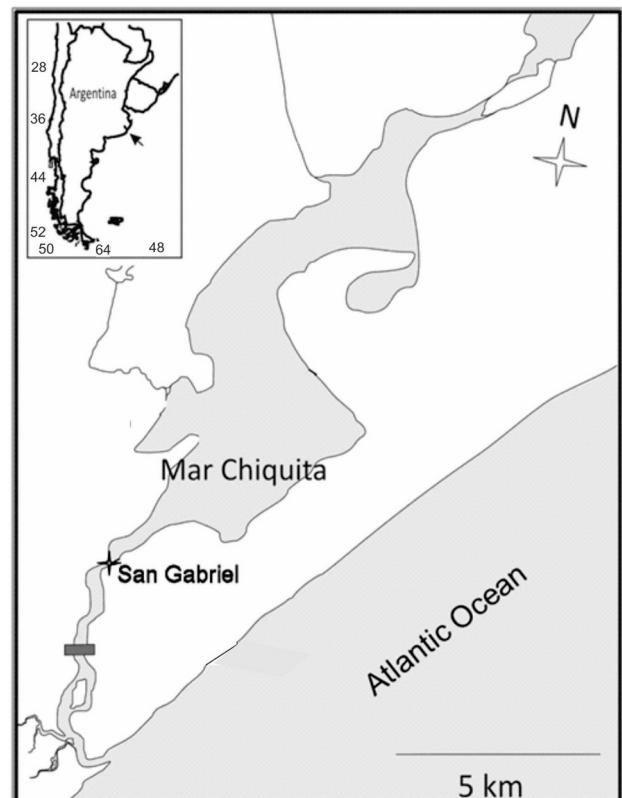


Fig. 1. Map of Mar Chiquita coastal lagoon with San Gabriel fishing site.

biodiversity in comparison with other similar systems (are up to 12 macrofaunal species). The macrofaunal assemblage includes polychaetes (*Laeonereis acuta* (Treadwell, 1923), *Nephtys fluviatilis* Monro 1937, *Heteromastus similis* Southern, 1921, *Boccardiella ligerica* (Feronnière, 1898)), bivalves (*Brachidontes rodriguezii* (d'Orbigny 1842)), gastropods (*Heleobia* spp. (Stimpson 1865), amphipods (*Melita palmata* (Montagu 1804), *Monocorophium insidiosum* (Crawford 1937)), crabs (*Neohelice granulata* (Dana 1851), *Cyrtograpsus angulatus* Dana 1851), ostracods (Cyprididae Baird, 1845), barnacles (*Balanus improvisus* Darwin 1854) and bryozoans. Sessile species and *B. ligerica* are exclusive from reefs, while *N. fluviatilis* are in sediments. In general, species from reefs and sediment are the same, and the density of macrofauna is higher in reefs with a trend for intermediate values in reef-free sediment (in [Martinez et al., 2020](#)).

2.2. Macrofauna in macroalgae from reefs and sediment

As an indicator of the macrofaunal use of macroalgae as habitat, we compared the total density of macrofauna (individuals per g of macroalgae) living in filamentous macroalgae mats between reef and sediment (see [Table 1](#) A). Macroalgae were collected in the intertidal on each habitat with a core (PVC cylinder, diameter = 10 cm) on random transects ($n = 20$ for each) in January 2008. Samples were cleaned, sieved (500 mm), weighed (dry weight in g; oven-dried 3 days at 70 °C to reach a constant weight). Macrofauna was identified as the lowest species-level possible. Organisms per species were counted under a binocular microscope (3×, 20×, and 40×). Hydrobiid snails were classified into genus since it was not possible to separate species based on external morphometric characteristics and there are at least two species in the region (*H. australis* (d'Orbigny, 1835) and *H. conexa* (M. C. Gaillard, 1974); [De Francesco and Isla, 2003, 2004](#)).

2.3. Effects of macroalgae on macrofaunal density in reefs

The effects of macroalgae, on macrofauna, in reefs were experimentally evaluated with artificial macroalgae in January 2009. The experiment had three treatments ($n = 10$ each): areas without macroalgae ("bare-reef"), with macroalgae ("macroalgae"), and with artificial macroalgae ("mimic") ([Fig. 2](#)). Comparisons between bare-reef and macroalgae treatments were used to identify macroalgae effects. Then, comparisons between mimic and macroalgae treatments allow discriminating the occurrence of macroalgae structural effects (i.e., habitat provision) from not structural effects (i.e., no structural and trophic effects). Experimental units were placed in the external ring of randomly reef surfaces. Macroalgae, and bare-reef plots (30 × 30 cm), were randomly selected in the field according to macroalgae cover (> 70% and < 5% cover, respectively). Mimics were created on initially bare plots using cotton fabric hair of brown-dark color, cut into squares (1 × 1 cm). The diameter (≤ 1 mm), length (≤ 3 cm), and grouping, of cotton hair, mimicking filamentous macroalgae thalli size, shape and density. Cotton hair squares, cut in strips to mimic thallus movement, were nailed with wooden sticks (2 mm in diameter and 20 cm long) on reef surfaces to cover the experimental unit surface. The experiment ran 15 days to minimize usually fast epibionts development on mimics that could be potential food supply and additional foraging grounds ([Schoener, 1974](#); [Wootton, 1998](#)), and to minimize possible deflections due to environmental variability (for example, the rain that can significantly change population densities; see [Obenat et al., 2006](#)). Experimentation was run during a peak of macroalgae abundance in the sediment, which is variable and unpredictable (see [Bazterrica et al., 2012](#)). At the end of the experiment, macrofauna was sampled using a core (PVC cylinder of 10 cm in diameter) buried 10 cm in the center of the experimental units. To consider possible macroalgae effects on macrofauna vertical distribution samples were divided into two layers: "surface" (5 cm depth) and "bottom" (next 5 cm; [Fig. 2](#)). Samples were in cold until to be processing. The whole treatment combinations were bare-reef-surface, bare-reef-

Table 1
Summary of comparative analyses.

Research Question	Parameter	Hypothesis	Null hypothesis	Analysis
A) Are the total abundance of macrofauna held by macroalgae from reefs or sediments equivalent?	Total species abundance	Macroalgae from reefs and sediment are equivalent as habitat.	There are no differences in total macrofauna abundance between macroalgae from reefs and sediment.	Welch Two Sample <i>t</i> -test for heterogeneous variances (1)
B) Does the macrofauna assemblage composition in reefs vary among macroalgae, bare space, or mimics?	Species density	Macroalgae structural effect affects the density of macrofaunal species in reefs.	There are no differences in the density of the species of reef's macrofauna assemblage among samples from macroalgae, bare space, or mimic.	PERMANOVA, nMDS, and SIMPER. ANOVAs
C) Does macrofauna assemblage composition in sediment vary among macroalgae, valves, bare space, or mimic?	Species density	Macroalgae structural effect affects the density of species in sediment macrofauna assemblages.	There are no differences in the density of the species of sediment's macrofauna assemblage among samples from macroalgae, valve, bare space, or mimic.	PERMANOVA, nMDS, and SIMPER. ANOVAs
D) What is the frequency of positive and negative effects, and structural or not structural effects in both reefs and sediment?	Species density	Macroalgae effects in reefs include structural and not structural ones that could be positive or negative.	Not applicable.	Comprehensive classification
E) Does the frequency of macroalgae positive and negative effects and structural or not structural ecosystem engineering effects vary between reefs and sediment?	Frequency of effects	Macroalgae positive structural effects are less frequent in reefs than in sediment since sediment is less structured habitat	Frequencies of structural and not structural effects, positive or negative, are independent of the substrate	Fisher exact Test (2)

(1) Hereafter *t* test; [Zar, 1999](#); (2) [Conover, 1998](#).

bottom, macroalgae-surface, macroalgae-bottom, and mimic-surface and mimic-bottom. Macrofauna was processed as in the previous section. Sessile species (*Brachidontes rodriguezii*, *Balanus improvisus*, and bryozoans) were not quantified because the experiment duration was not enough for these species' recruitment and growth. For each sample, species density (ind/sample) were calculated and nonmetric-multidimensional-scaling ordinations (nMDS) were used to provide visual representations of dissimilarities between the samples ([Clarke and](#)

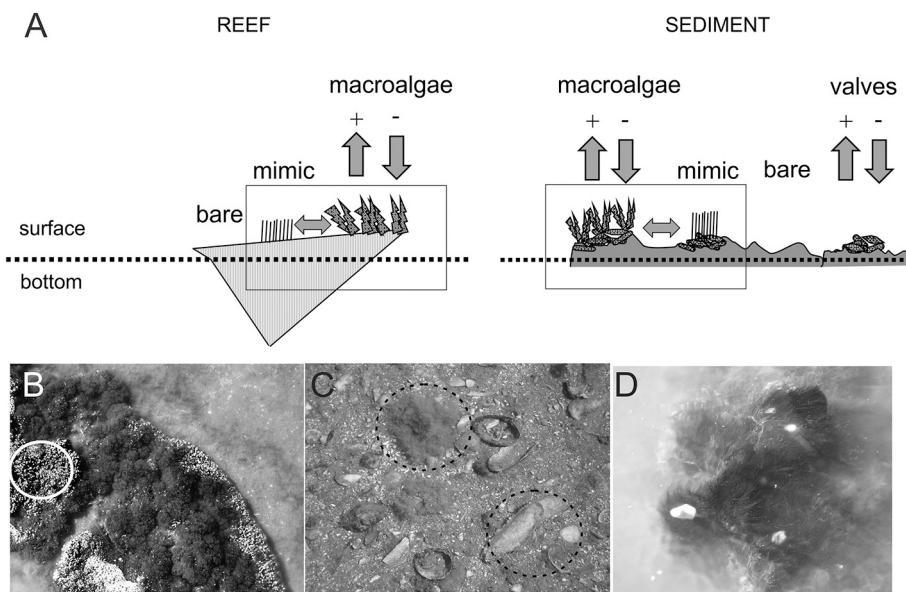


Fig. 2. A) Schematization of macroalgae effects comprehensive classification for each species in layers. Arrows indicate an increase (upward) or decrease (downward) in macrofauna density, and therefore, positive (+) or negative (-) effect, respectively. Comparisons between mimic and macroalgae (two-point horizontal arrows) allow classifying effects as structural (not differences in macrofauna density) or not structural effects (differences in macrofauna density). The dotted line shows the division into layers. Graphical differences between macroalgae and mimics are illustrative. B) Macroalgae in a reef and sympatric reef-bare areas (white circle). C) Macroalgae-valve and bare-valve nearby areas (dotted black circles). D) Mimic on the reef's surface.

Warwick, 2001). Possible differences in macrofaunal assemblages among treatments (bare-reef, macroalgae, and mimic), with layers as nested factor, were compared with PERMANOVA followed by SIMPER analysis, then ANOVAs were performed for the species contributing up to 90% of the dissimilarity found (see Table 1 B).

2.4. Effects of macroalgae on macrofauna density in sediment

An experiment for reefs was done to evaluate the effects of macroalgae on macrofaunal density in sediment, where valves are the primary substrate for macroalgae growth (Bazterrica et al., 2012). Therefore, 40 experimental plots similar in size (30 × 30 cm) were denuded and randomly assigned to four treatments ($n = 10$ each). Treatments were: plots without valves and macroalgae ("bare-sediment"), plots with valves without macroalgae ("bare-valves"), plots with valves holding macroalgae ("macroalgae-valves"), and plots with valves with mimic ("mimic-valves"; Fig. 2A). The comparison between bare-sediment and bare-valves allows identifying if there are structural valve effects. The comparison between bare-valves and macroalgae-valves allows identifying if there are macroalgae effects. The comparison between macroalgae-valves and mimic-valves allows discriminating structural from not structural macroalgae effects. Valves for the experiment were collected in the area, brushed and dried, and then located in experimental units simulating natural densities (348 valves.m⁻², SE = 22; in Bazterrica et al., 2012). Cotton hair squares were glued in the center of the bare valves with a small sphere of putty epoxy. Experimentation was made in February 2009 for 15 days. Data collection and statistical analysis were made as previously described (see Table 1 C).

2.5. Macroalgae effects on macrofauna density on reefs and sediment

First, on the results of each experiment (subsections 3.2 and 3.3), a comprehensive classification of macroalgae effects for species was done for reef and sediment, describing the potential direction (positive, negative) and mechanisms (structural or not structural effects) of the macroalgae effects (see Table 1 D). For this work, in reef or sediment, we considered that there was "no effect" when there were no differences in species densities between bare (reef or valve) and macroalgae (reef or valve) (see Fig. 2). Then, if there was an effect, the direction was positive when a species was only present, or with higher density, in macroalgae (Fig. 2); or negative when a species was absent, or with lower density in macroalgae (Fig. 2). Following the objectives of this work, mechanisms

were sorted as structural effects if densities were equal between macroalgae (in reefs or valves) and mimic (in reefs or valves) (see Fig. 2); and not structural effects if densities were different. In sediment, the valve's effects were sorted contrasting bare-sediment with bare-valves on the same criteria used to compare bare-reef and macroalgae (see Fig. 2). Higher, or lower, species densities in mimics, were interpreted in the light that mimics may have some different qualities than macroalgae thallus (e.g., breaking strength, Bazterrica pers. obs.) and assuming mimic effect as habitat input. Second, frequencies of the species affected were ordered by direction and mechanisms for each substrate (reefs and sediment) along with layers. Based on these frequencies, the following null hypotheses were answered: (1) there are no differences in the frequency of species affected and not affected by macroalgae and between layers and substrates; (2) there are no differences in the frequency of positive and negative macroalgae effects between substrates; (3) there are no differences in the frequency of structural or not structural macroalgae effects between substrates and, (4) direction and mechanisms of macroalgae effects are independent of the vertical layers (see Table 1 E). Third, the frequency in which valves have positive, negative, or no effects on macrofaunal density was also estimated.

2.6. Data analysis

Statistical analyses were done using PRIMER 6 and PERMANOVA+ statistical package (PRIMER-E Ltd., Plymouth Marine Laboratory, Plymouth, United Kingdom; Anderson et al., 2008) and R i386 3.3.3 Version. A non-metric multidimensional scaling (nMDS) of the abundance data was used to provide 2-dimensional ordinations (Clarke and Warwick, 2001) based on a Bray-Curtis dissimilarity matrix with square-root transformed to reduce the influence of most abundant species (density). Repeated measure permutational analyzes of variance (PERMANOVA) were done on a dissimilarity matrix built using Bray-Curtis distances among each sample and 9999 permutations (Anderson, 2001; Anderson et al., 2008) with layer nested in treatments. When treatments differed significantly, differences among factors were compared with pairwise comparisons, with an additional PERMANOVA among the levels with differences (Anderson et al., 2008). Also, analyses of multivariate dispersion (PERMDISP) were done to test for the homogeneity of dispersions within each group based on the sample distance to the group centroid (Anderson et al., 2008). The identification of the species driving the differences and the percent contribution of each taxon to patterns of dissimilarity (expected minimum of contribution; Bulleri, 2005) was

calculated by the analysis of similarity of percentages (SIMPER) on the Bray-Curtis dissimilarity matrix (Clarke and Warwick, 1994). For parametric analysis, normality was tested with the Shapiro-Wilks test, and the null hypothesis of equal variances with Bartlett tests (Zar, 1999); when variances were heterogeneous, data were log and rank transformed (see Quinn and Keough, 2002). Specific mean comparisons were made with the Tukey HSD test on corresponding factors ($p < 0.05$). Holm correction of p -values for multiple comparisons (Bretz et al., 2016) was made for the 2-factor nested ANOVAs (layers in treatments).

3. Results

3.1. Macrofauna in macroalgae from reefs and sediment

Macrofauna total abundance in macroalgae of both reefs (mean = 54.39, SE = 13.10) and sediment (mean = 208.32, SE = 84.93) were not different ($t = -0.36$, $df = 25.24$, $p > 0.05$). Species found in both macroalgae were the amphipods *Melita palmata*, *Monocorophium insidiosum*, *Heleobia* spp., the polychaete *Laeonereis acuta*, and ostracods Cypridae. The crab *Cyrtograpsus angulatus* and the capitellid polychaete *Heteromastus similis*, were found in the macroalgae of reefs.

3.2. Effects of macroalgae on macrofauna density in reef surfaces

The total of species found in reefs during the experiment is in Fig. 3.

Our results show that the macrofaunal assemblage varied with experimental treatments and layers (PERMANOVA; treatment: $df = 2$, pseudo- $F = 6.97$; $p < 0.0001$; layer (in treatment): $df = 3$, pseudo- $F = 4.43$; $p < 0.001$; Fig. 4 A and B); assemblage are different among macroalgae, mimic and bare-reef and between surface and bottom (pair-wise tests; $p < 0.05$). PERMDISP analysis was not significant among treatments ($F = 0.95$, $df_1 = 2$, $df_2 = 55$, $p > 0.05$) or layers ($F = 2.05E-3$, $df_1 = 1$, $df_2 = 56$, $p > 0.05$). All species contributed to differences in macrofauna assemblage among layers and treatments. In the reef, *Melita palmata* and *Heleobia* spp., contributed to than 60% of the dissimilarity observed for all pairwise comparisons, except for the bare - mimic pair where both amphipods (*M. palmata* and *Monocorophium insidiosum*) were the most representative (Supplementary material, Table A). Overall, the mean density of the amphipod *M. palmata*, the hydrobiid snail *Heleobia* spp., and the polychaete *Laeonereis acuta* were different among treatments (bare-reef, macroalgae, and mimic) and layers (surface and bottom) within the treatments (Table 2 A, B, and C). In particular, the density of *M. palmata* was highest in mimic, and within macroalgae in the bottom (Tukey HSD; Fig. 3 A). The mean density of *Heleobia* spp. was lowest in mimic and within macroalgae in the surface (Tukey HSD; Fig. 3 B). *L. acuta* density was highest in macroalgae and within mimic, in the bottom (Tukey HSD; Fig. 3 C). Then, the mean density of the amphipod *M. insidiosum*, *Cyrtograpsus angulatus*, and the ostracods Cypridae did not vary among treatments or any factor level (Table 2 D, E, and F). In turn, *C. angulatus* variances were highest in bare from the bottom, and lowest

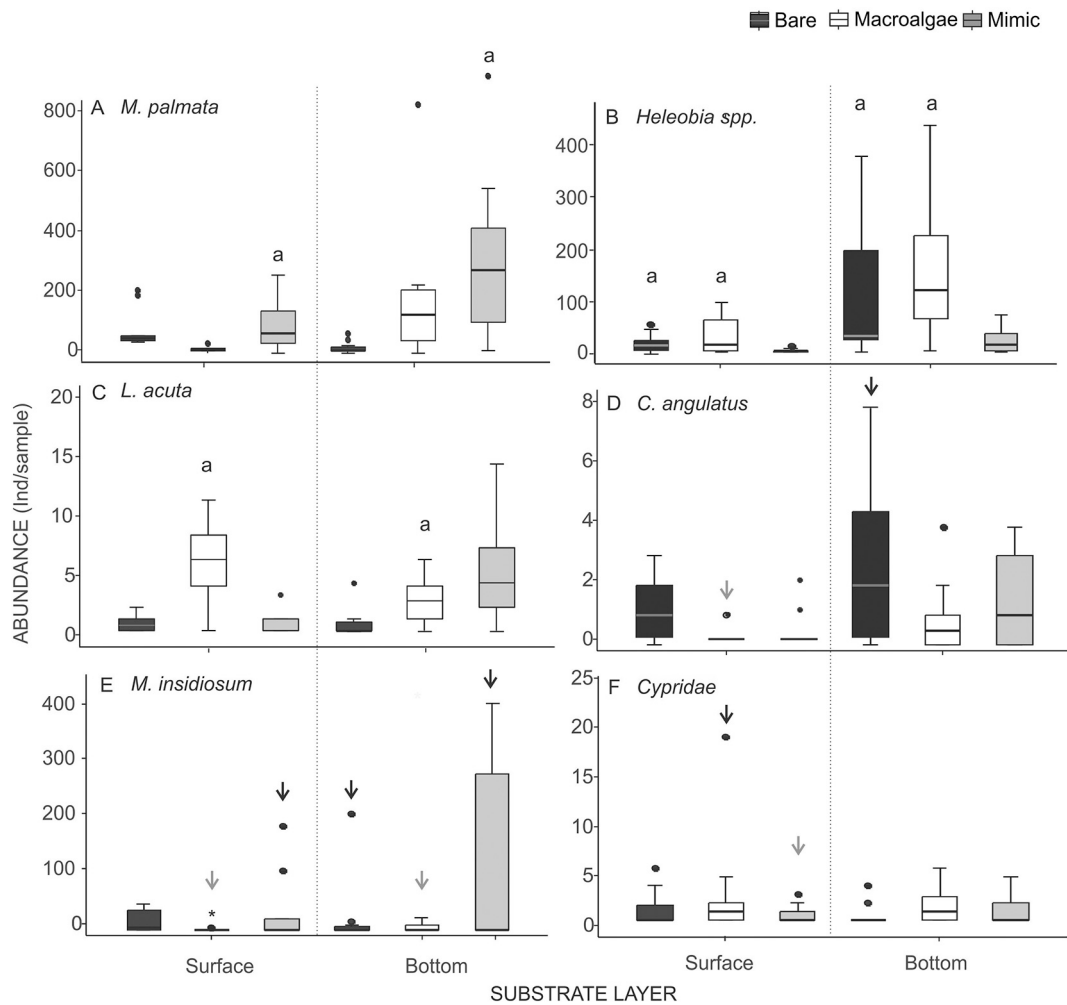


Fig. 3. Densities of (A) *Melita palmata*, (B) *Heleobia* spp., (C) *Laeonereis acuta*, (D) *Cyrtograpsus angulatus*, (E) *Monocorophium insidiosum*, and (F) Cypridae on bare, macroalgae and mimic areas on reefs, discriminated by layers. The bar in the boxes shows the median. Letters indicate the highest abundance among treatments (Tukey HSD test, $p > 0.05$). Black arrows show the highest variances, and grey arrows the lower ones.

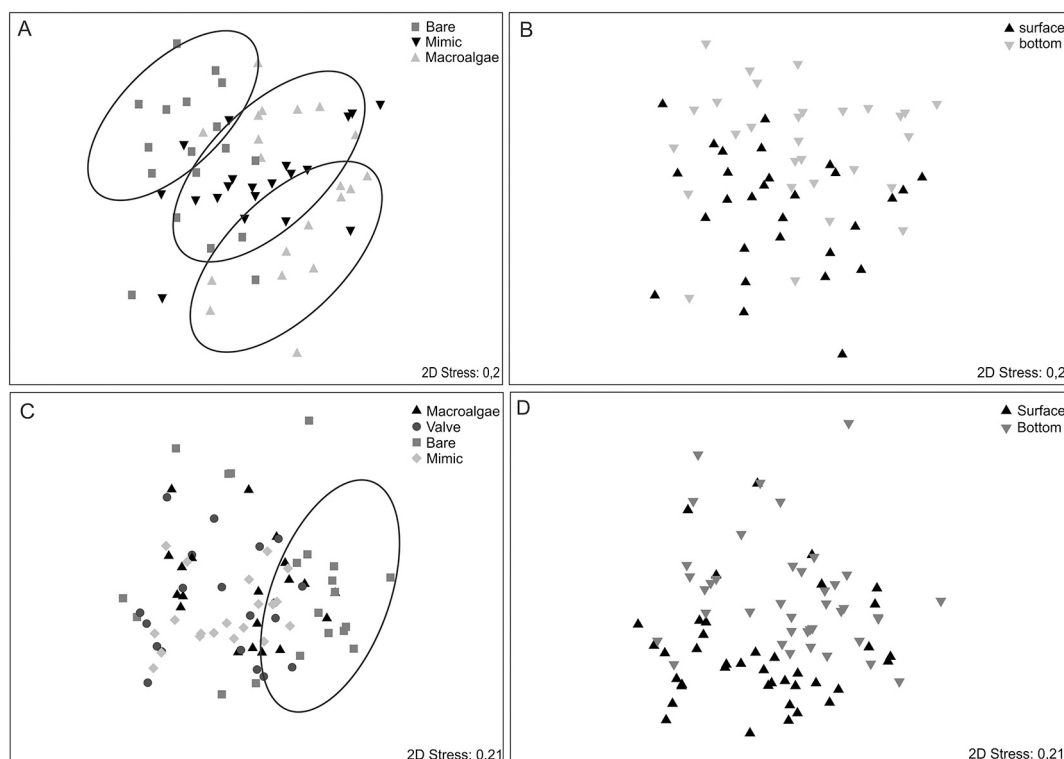


Fig. 4. Results of nMDS comparing the macrofaunal assemblages in reefs (A) among macroalgae, bare-reef (bare) and mimic, and (B) between surface and bottom, and in sediment (C) among macroalgae-valves (macroalgae), bare-valves (valves), bare-sediment (sediment), and mimic-valves (mimic) and (D) between surface and bottom. Circles in A show samples clustering by treatments (mimic, bare-reef, and macroalgae from top to bottom), in B show bare samples clustering.

Table 2

Results of the two way nested ANOVAs comparing macrofaunal densities on the mimic experiment in reefs (A–F) and sediment (G–K). Fixed factors were layers nested in treatments. In reefs, treatments were: bare, macroalgae, and mimic. In sediment, treatments were: bare, valves, macroalgae, and mimic. Layers are surface and bottom. Data transformations are in parentheses before the corresponding species. Differences (adjusted *p*-value < 0.05) are shown in bold.

Reefs	Treatments	Treatments		Layers nested in treatments			
		df	F	df	F	p	
A	(ln) <i>Melita palmata</i>	2	9.08	0.008	3	10.05	0.00052
B	(ranks) <i>Heleobia</i> spp.	2	8.35	0.013	3	6	0.02309
C	(ln) <i>Laonereis acuta</i>	2	11.51	0.001	3	5.4	0.03618
D	(ln) <i>Monocorophium insidiosum</i>	2	2.09	1	3	0.7	1
E	(ln) <i>Cyrtograpsus angulatus</i>	2	4.42	0.202	3	2.39	0.790
F	(ln) Cypridae	2	2.51	0.09	3	0.6	1
Reef-free sediment							
G	(ln) <i>Heteromastus similis</i>	3	5.57	0.026	4	1.75	1
H	(ln) <i>Heleobia</i> spp.	3	5.74	0.023	4	4.08	0.063
I	(ln) <i>Melita palmata</i> (1)	2	4.11	0.240	3	16.99	1.5E-06
J	(ln) Cypridae	3	0.41	1	4	0.24	1
K	(ln) <i>Laonereis acuta</i>	3	0.46	1	4	0.360	1

(1) Areas were valve, macroalgae, and mimic since there were no amphipods in bare-sediment from the surface and bottom.

in macroalgae from the surface (Bartlett test; Fig. 3 D). *M. insidiosum* variances were highest in mimics and lowest in macroalgae of both surface and bottom (Bartlett test; Fig. 3 E). Cypridae variance was higher in macroalgae than in mimic form surface (Bartlett test; Fig. 3 F).

3.3. Effects of macroalgae on macrofauna density in sediment

Our results show that the species density composition varied with experimental treatments or layers (PERMANOVA; treatment: $df = 3$, pseudo- $F = 3.57$, $p < 0.001$; layers (in treatments): $df = 4$, pseudo- $F = 3.10$; $p < 0.001$; Fig. 4 C and D). Macrofauna assemblage from bare was different from macroalgae, valves, and mimic, and between surface and bottom for valves and mimic. In turn, assemblage in macroalgae was marginally different from assemblage in valves and mimic. (pair-wise tests; $t = 1.63$; $p = 0.05$). PERMDISP analysis was significant among treatments ($F = 4.16$, $df_1 = 3$, $df_2 = 76$, $p < 0.05$) not between layers ($F = 0.44$, $df_1 = 1$, $df_2 = 78$, $p > 0.05$). The post hoc comparison indicated a greater heterogeneity between bare and mimic (bare average = 49.5, SE = 2.2; mimic average = 36.6, SE = 2.3). Other pairs compared were not different ($p > 0.05$). Species found in sediment explaining differences are shown in Fig. 5. Cypridae contributed to the differences (always close to 40%) between all the layers and treatments, reaching more than 60% dissimilarity together with *Melita palmata* (Supplementary material, Table B). *Monocorophium insidiosum*, *Cyrtograpsus angulatus*, and the polychaete *Nephtys fluviatilis* were also present but did not explain the differences among samples. *M. insidiosum* was only in the bottom of valves (mean density = 0.8 ind.core-1, SE = 0.8). *N. fluviatilis* was in low densities in the bottom, except bare-sediment (mean density: macroalgae-valves = 0.3 ind.core-1, SE = 0.15; bare-valve and mimic-valves = 0.1 ind.core-1, SE = 0.1). *C. angulatus* was absent from bare-sediment and present in macroalgae-valves in the surface layer and bare-valves in the surface and bottom layers. Overall, the mean density of *Heteromastus similis* and *Heleobia* spp. were different among treatments (bare-sediment, bare-valves, macroalgae-valves, and mimic-valves; Table 2 G, and H). *M. palmata* mean densities did not vary among treatments, but with layers within treatments (Table 2 I). Cypridae and *Laonereis acuta* mean densities did not vary among treatments or layers (Table 2 J and K). In

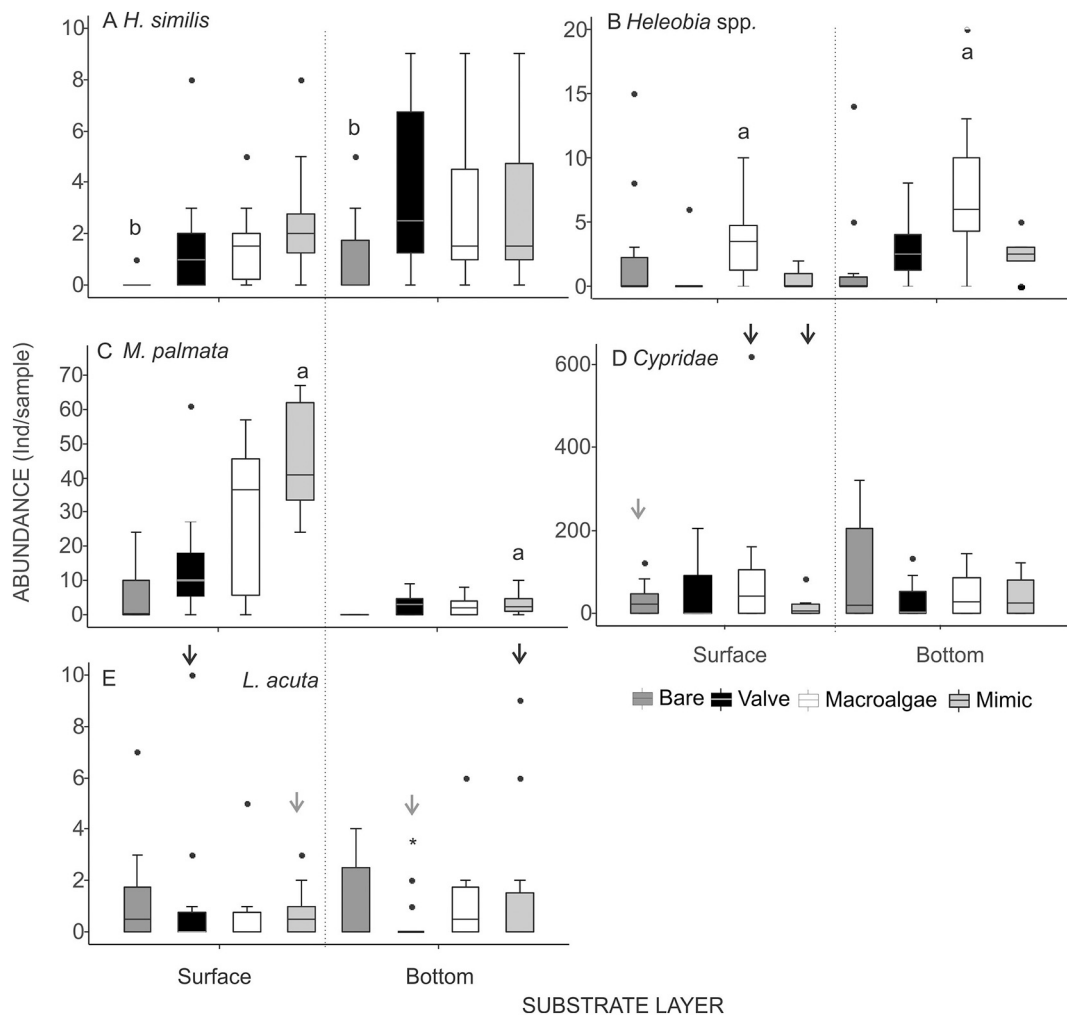


Fig. 5. Densities of (A) *Heteromastus similis*, (B) *Heleobia* spp., (C) *Melita palmata* (D) Cypridae and (E) *Laeonereis acuta* in sediment among bare-sediment (Bare), bare-valves (Valves), macroalgae-valves (Macroalgae), and mimic-valves (Mimic), discriminated by layers. Bars in the boxes show the median. Letters show the highest abundance among treatments (Tukey HSD, $p > 0.05$). Black arrows show higher variances and grey arrows show lower ones.

particular, the mean density of *H. similis* was lower in bare-sediment than other treatments (Tukey HSD; Fig. 5 A). *Heleobia* spp. mean density was highest in macroalgae (Tukey HSD; Fig. 5 B). *M. palmata* was absent from bare-sediment, and in remaining treatments, the mean density showed the highest values in bare-valves and mimic-valves from the surface (Tukey HSD; Fig. 5 C). Cypridae variance was highest in macroalgae-valve and mimic-valve and lowest in bare-sediment of the surface (Bartlett test; Fig. 5 D). Variability in the density of *L. acuta* was highest in surfaces 'valve and bottoms' mimic and lowest in surfaces 'mimic and bottoms' valves (Bartlett test; Fig. 5 E).

3.4. Macroalgae effects on macrofauna density on substrates with different structural complexity

Macroalgae and valves' effects, comprehensive classification on the variation in species abundances among treatments of mimic experiments from reefs and sediment, are shown in Table 3. Macroalgae only have positive, not structural effects on *L. acuta* in reefs and *Heleobia* spp. in sediment. Valves' only had positive effects on *H. similis*.

4. Discussion

Our results show that species assemblages are different in areas with macroalgae from areas without macroalgae, in reefs, and reef-free sediment. Besides, in areas with macroalgae, species assemblages

differed according to depth. These differences are reflected in changes in the abundance of some species (i.e., *Melita palmata*, *Heleobia* spp., and *Laeonereis acuta*) and could explain abundance variability in the remaining ones. In reef-free sediment, the most important differences are between bare areas and areas with valves and valves with macroalgae. In turn, differences between valves and valves with macroalgae are less marked. Our results highlight that macroalgae's role as a structuring factor is the result of the summary of their multiple effects in interaction with species responses and habitat type.

In reefs, macrofauna assemblages change between areas with and without macroalgae. Macroalgae effects were positive by not structural mechanisms for the polychaete *Laeonereis acuta*. In turn, there were positive and negative mimic effects for *Melita palmata* and *Heleobia* spp., respectively. Macroalgae effects could be direct or indirect and could be by not structural ecosystem engineering and trophic effects. For example, direct trophic interactions might positively affect the polychaete *L. acuta* that consumes macroalgae thallus or its epibionts (see Hay et al., 1989). Equally, our results suggest that macroalgae positively affect *Heleobia* spp. and *M. palmata*, given that are more abundant in deeper layers than surfaces from macroalgae areas: these organisms can be benefited by sediment enriched in nutrients due to a higher macroalgae detritus deposition (*Heleobia* spp.: see Eckman and Duggins, 1991; *M. palmata*: see Guerra-García et al., 2014). In turn, the abundance of the individuals of smaller sizes of *M. palmata* can be positively correlated with macroalgae in reef's surfaces (Bazterrica et al., 2020). The presence

Table 3

Macroalgae effects comprehensive classification for each species according to density variations among treatments discriminated by effects' direction, mechanism, and layer (A) in the reefs and (B) in sediment. (C) Classification for valves effects.

(A) Effects on reefs		Surface	Bottom
Positive	Structural		
	Not structural	<i>L. acuta</i>	<i>L. acuta</i>
Negative	Structural		
	Not structural		
No effect		<i>M. palmata</i>	<i>M. palmata</i>
		<i>Heleobia</i> spp.	<i>Heleobia</i> spp.
		<i>C. angulatus</i>	<i>C. angulatus</i>
		<i>M. insidiosum</i>	<i>M. insidiosum</i>
		Cypridae	Cypridae
(B) Effects on reef-free sediment			
Positive	Structural		
	Not structural	<i>Heleobia</i> spp.	<i>Heleobia</i> spp.
Negative	Structural		
	Not structural		
No effect		<i>H. similis</i>	<i>H. similis</i>
		<i>M. palmata</i>	<i>M. palmata</i>
		Cypridae	Cypridae
		<i>L. acuta</i>	<i>L. acuta</i>
(C) Effects of valves			
Positive		<i>H. similis</i>	<i>H. similis</i>
Negative			
No effect		<i>M. palmata</i>	<i>M. palmata</i>
		Cypridae	Cypridae
		<i>L. acuta</i>	<i>L. acuta</i>
		<i>Heleobia</i> spp.	<i>Heleobia</i> spp.

of more refuge inside macroalgae may also explain these results (see Morales-Núñez and Chigbu, 2019) and could also be significant for *L. acuta* since its abundance also increases under areas covered by mimics of macroalgae. In turn, on the surface, macroalgae might act as a barrier to grazing as the lowest density of *Heleobia* spp. in mimic areas suggests (see Magalhães et al., 2014). *Cyrtograpsus angulatus* abundance was less variable (and relatively small) in macroalgae and more variable below bare areas. Crab and refuge's size range might hold this variability since larger crabs could avoid macroalgae on the surface but heterogeneously select deeper layers with different refuge size availability (see Méndez Casariego et al., 2004). Besides, crabs can disturb macroalgae mats by feeding on macroalgae thallus (probably eating epibionts; see Bazterrica et al., 2013) and therefore increment the variability of the abundance of species in macroalgae such as Cypridae. Finally, considering that *Monocorophium insidiosum* is tube-building (Ulrich et al., 1995), the lack of direct delivery of macroalgae detritus in and under artificial macroalgae might explain their variability in abundance, which can be higher with macroalgae (Martinez et al., 2020). Here, we did not investigate all the potential direct and indirect macroalgae effects but, our results suggest that in accordance to previous studies (see Mckindsey and Bourget, 2001), effects might depend on requirements of species involved, the interactions, and responses, along the vertical distribution gradient.

On sediment, macrofaunal assemblages change with valves and macroalgae. Valves (with or without macroalgae) positively affect the polychaete *Heteromastus similis*, and valves with macroalgae positively affect *Heleobia* spp. by not structuring mechanisms. Other representative species, as *M. palmata* and others less abundant (*M. insidiosum*, *Nephtys fluviatilis* and *C. angulatus*), were directly absent of bare area. In turn, as in reefs, there were positive and negative mimic effects for *M. palmata* and *Heleobia* spp., respectively. The positive effects of ecosystem engineers (i.e., valves and macroalgae) in sediments offering refuge can simultaneously modify habitat properties (e.g., increasing anoxia; see Kraufvelin et al., 2006, Bolam et al., 2000). Therefore, they can affect species abundance according to their anoxia tolerance, incrementing

resistant species abundances as *H. similis* (see Van Colen et al., 2010) or variability in less tolerant species abundance as *L. acuta* (da Rosa et al., 2005). In turn, macroalgae as food could counteract anoxic negatives effects, as in the case of *Heleobia* spp. Another consequence of ecosystem engineer modifications could be an active migration of mobile species among different patches to optimize their habitat use (see Everett, 1991; Ellis et al., 2000). In the case of *M. palmata*, it almost was exclusively from the valves (see Bazterrica et al., 2020). Cypridae abundance was more variable in macroalgae than in bare areas as in reefs (except for mimics). Furthermore, the abundance of Cypridae and *M. insidiosum* can be correlated with the presence of macroalgae (Martinez et al., 2020). This pattern might be reflecting that macroalgae is a heterogeneous habitat probably due to disturbance. Different factors could determine disturbance, for example, as was suggested for sediment areas, the mechanical effects of predators feeding on macroalgae (see Bazterrica et al., 2013). Even when generalizations on macroalgae effects on soft sediments are hard to perform (see Everett, 1991), our results suggest that in reef-free areas, valves and macroalgae affect macrofaunal density but, macroalgae had positive effects in sediment via no structural engineering or trophic effects.

Our results suggest that macroalgae exerted community-structuring forces on reef surfaces and sediments. Effects of macroalgae as ecosystem engineers are widely studied (i.e., kelp forest: Teagle et al., 2017; *Cladophora*: Zulkifly et al., 2013; Bellgrove et al., 2017 for review). Overall, filamentous macroalgae in estuaries promote macrofauna taxonomic and functional diversity by increasing benthic habitat complexity, by modifying the physical environment, and by modulating the biogeochemical cycling, even in interactions with another foundational species (e.g., Kraufvelin and Salovius, 2004; Ward and Ricciardi, 2010; Zulkifly et al., 2013). Here, contrary to the expected, macroalgae effects not varied between substrates with higher and lower complexity, and the effects observed were primary as primary producers, but for some species, macroalgae effects vary in intensity with substrate depth. Therefore, the importance (i.e., magnitude) of the macroalgae effect as an ecosystem engineer in the studied system remains unclear but should not be discarded.

The multiple mechanisms by which macroalgae affect macrofaunal species, species interactions, and macroalgae interactions with valves and reefs (e.g., additive effects, Thomsen et al., 2010, 2018) may explain the high variability found (see also Martinez et al., 2020). Nevertheless, macroalgae ecosystem engineering effects could also depend on thalli constitutive characteristics as stability and perdurability (see ecosystem engineers' key factors, Jones et al., 1997), therefore macroalgae effects could be seasonal and depend on the growth conditions of macroalgae (i.e., thallus structure). For example, some species unaffected by macroalgae were in some cases more abundant (i.e., *M. palmata*), or less abundant (*Heleobia* spp.) in the artificial thallus, often having more or less heterogeneous effects than macroalgae (more: *M. insidiosum* in reefs; Cypridae in sediment; less: Cypridae in reefs; *L. acuta* in sediment). These results could be the consequence of artificial thallus being less fragile than natural ones, which may amplify the effects of thallus as habitat (e.g., Godoy and Coutinho, 2002; Bouma et al., 2009) or physical barrier.

Other species interactions should also be taken into account in considering the observed pattern. For example, differences in vertical distribution could be driven by competition (e.g., amphipods: Nicolaidou and Karakiri, 1989). However, *Heleobia* spp. might positively select the bottom probably for refuge (see Magalhães et al., 2014) or detritus accumulation. Our results suggest that macroalgae affect the macrofaunal assemblage and can be considered an autogenic ecosystem engineer following Jones et al. (1994) classification. When trying to differentiate the mechanisms of engineering (Berke, 2010), our results showed that macroalgae structural effects are highly variable according to substrates and species responses, and those trophic and other engineer mechanisms are also important. Moreover, other population factors such as seasonality or macroalgae peaks (see Bazterrica et al., 2012), should be considered in the evaluation of the importance of the macroalgae

community structuring forces.

5. Conclusion

Contrary to our hypothesis, the effect of macroalgae as an ecosystem engineer (i.e., thallus as habitat provision) on the bare sediments was not proportional more important than in the reef, which poses a more complex structure. It could be a consequence of the numerous interactions observed and differences between primary substrates (reef and valves) and macroalgae thallus.

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Declaration of Competing Interest

The authors declare no conflicts of interest.

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