Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Original Article

Cite this article: Longo PADS, Mansur KFR, Leite FPP, Passos FD (2019). The highly diverse gastropod assemblages associated with *Sargassum* spp. (Phaeophyceae: Fucales) habitats. *Journal of the Marine Biological Association of the United Kingdom* **99**, 1295–1307. https://doi.org/10.1017/S0025315419000304

Received: 29 June 2018
Revised: 20 March 2019
Accepted: 2 April 2019
First published online: 3 May 2019

Key words:
Biodiversity; macroalgae; growth series; marine diversity; molluscs; marine snails

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The highly diverse gastropod assemblages associated with *Sargassum* spp. (Phaeophyceae: Fucales) habitats

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Abstract

Macrophytes provide a habitat for many species of marine invertebrates, the gastropods being one of the main components. This study provides new information about *Sargassum*-associated gastropod biodiversity, through characterization of the fauna from a highly impacted area of Brazil, investigating its variation at a small spatial scale and between two main seasons of the year, as well as its relationship with macroalgae parameters. Density of gastropods was higher during the warmest season and varied throughout sampling sites. A significant and positive, however weak, relationship between gastropod density and *Sargassum* dry weight was found in all localities. For all sites, a marked and unusual dominance of *Bittiolum varium* was observed. The high dominance of this species seems to be related to the impacts caused by shipping activities and highway construction in the 1970s and 1980s, which caused a decline in local species diversity that seems to have continued until now. Many species, both typical of these habitats and characteristic of other, nearby habitats, benefit from *Sargassum* sp. These macrophytes allow gastropods to establish and grow during their most vulnerable stages, as shown by the growth series and juvenile forms found for most species of gastropods. The present data highlight the importance of macrophyte habitats for gastropod biodiversity in coastal areas and call attention to the importance of raising knowledge on this fauna, especially in impacted areas, thus contributing to the conservation of these highly diverse and ecologically important macrophyte–gastropod systems.

Introduction

Macrophytes are important ecosystem engineers in the marine environment. They commonly form extensive beds in coastal areas, thereby creating new habitats for a wide variety of organisms, including epiphytic algae as well as invertebrate and vertebrate animals. Living attached to or associated with these macrophytes, these animals benefit from access to food resources, protection from predators and natural environmental impacts, more stable abiotic conditions, or by using them as sites for reproduction and recruitment of larvae (Christie *et al.*, 2009; Thomaz & Cunha, 2010).

The malacofauna is one of the main invertebrate components of this fauna, and the gastropods are the most important, with high numbers of species and trophic diversity (Chemello & Milazzo, 2002; Rueda & Salas, 2003; Urra *et al.*, 2013). Macrophyte-associated gastropods have an important role in aquatic ecosystems as consumers or prey, constituting an important link between different trophic levels (Martin *et al.*, 1992; Heck *et al.*, 2008).

In the Brazilian coast, the brown algae *Sargassum* C. Agardh are among the most representative, especially in south-eastern Brazil (Széchy & Paula, 2000). With many different alien species registered in the region, such as *Sargassum cymosum*, *Sargassum furcatum*, *Sargassum filipendula* and *Sargassum stenophyllum* (Leite *et al.*, 2007; Carvalho *et al.*, 2018), this genus is marked by large fronds, high biomass and extensive branching, thus presenting a complex, highly variable morphology, with structural variations in frond size, number and size of stalks and branches, depending not only on species identity, but also on environmental variables, which generates intraspecific plasticity (Jacobucci & Leite, 2002; Leite *et al.*, 2007). For the present study the sampled algae are collectively referred to hereafter as *Sargassum*.

Macrophyte-invertebrate associations are sensitive to human impacts, since contaminants can accumulate in these systems, resulting in a disequilibrium (Duarte, 2002; Roberts *et al.*, 2008; Waycott *et al.*, 2009) with consequences for their many constituent species (Roberts *et al.*, 2008). Anthropogenic stress can directly affect individuals in molluscan assemblages, causing morphological and physiological alterations that may result in changes in population parameters (Walsh *et al.*, 1994; Feldstein *et al.*, 2003), and also altering the species composition and community diversity (Sánchez-Moyano *et al.*, 2000; Terlizzi *et al.*, 2005; Rumisha *et al.*, 2012).

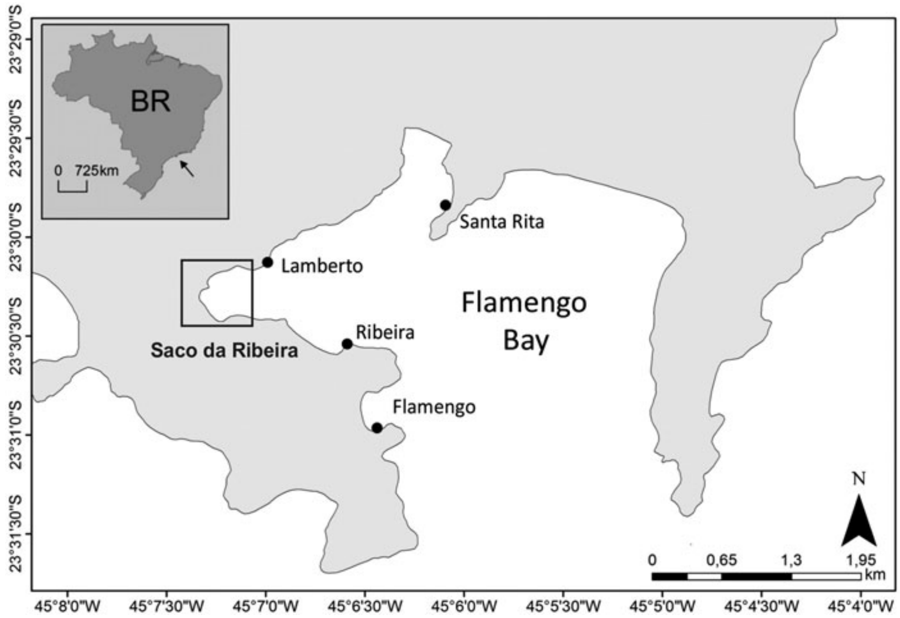

Fig. 1. Flamengo Bay, with the locations of the four rocky shores where the algal fronds were collected. Inset (upper left) shows the position of the bay on the Brazilian coast, indicated by an arrow.

The present study aims to (1) characterize Gastropoda assemblages associated with *Sargassum* spp. beds at a historically impacted area in Brazil, highlighting the importance of these habitats for the establishment of gastropod juveniles, by illustrating the growth stages of the main species and (2) investigate the variation of gastropod densities, as well as macroalgae dry weight, at a small spatio-temporal scale, expecting that higher levels of gastropod densities will occur during the warmest months, and that macroalgae dry weight will positively influence the density of gastropods.

Materials and methods

Study area

The collections were performed at four sampling sites on the rocky shores of the Flamengo, Lamberto, Ribeira and Santa Rita beaches in Flamengo Bay (23°29′42″–23°31′30″S 045°05′–045°07′30″W), situated in the Ubatuba municipality, on the northern coast of the state of São Paulo, south-eastern Brazil (Figure 1). This bay is about 2.5 km in diameter and 18 km^2 in surface area, with a maximum depth of 14 m, i.e. quite shallow. The bay is directly connected to the open sea in its southern part; it is a semi-confined system, dominated by coastal waters with moderate hydrodynamics (Lançone *et al.*, 2005). The Flamengo Bay is historically contaminated by differing types of pollutants, such as heavy metals and organic pollution, with a main source of contaminants located at the Saco da Ribeira (Figure 1), a highly impacted area of the bay with large state marinas and intense boating activity (CETESB, 2014, 2015, 2016).

Sampling procedure

Sampling was performed monthly from March 2014 to February 2015 inclusive. In each month, six fronds of the brown alga *Sargassum* sp. were collected through snorkelling at each sampling site. The fronds were taken randomly from 1–4 m depth in order to avoid the effects of the tidal oscillation and placed in individual 0.2 mm mesh bags to prevent loss of the macrofauna. At each sampling site, the water temperature was also obtained at the time of sampling.

In the laboratory, the fronds were washed three times to remove all the associated fauna, which was then fixed in 70% ethanol. The fauna was sorted under a stereomicroscope, and the gastropods were separated to be identified at species levels (or best taxonomic resolution possible) and counted. For each species, all individuals were examined for the occurrence of different sizes, as growth series, which were photographed with a camera coupled to a Zeiss Discovery V8 stereomicroscope. Voucher specimens of these gastropod species are deposited in the Museum of Zoology of State University of Campinas (Unicamp).

During the washing process, other epibionts attached to the frond surfaces, including epiphytic algae, bryozoans and hydrozoans, were also removed. The *Sargassum* sp. fronds and these epibionts were dried separately at 70°C for 48 h and then weighed with a 0.001 g precision balance. The gastropod density was expressed in reference to the dry weight of the algae.

Data analysis

For the analysis in this study, months were divided into two main seasons, in accordance with climatic data from Ubatuba shore (Climate-data.org., 2016): a cool season, from May to October, and a warm season, from November to April.

Therefore, the densities and number of gastropod species, as well as the dry weight of *Sargassum* fronds and its epibionts, were compared among sites and seasons with a linear mixed effects model, considering two fixed factors: season (two levels: warm and cool) and area (four levels, corresponding to the Flamengo, Lamberto, Ribeira and Santa Rita shores), and as a random factor the months of sampling, that were nested in the season factor, in order to avoid temporal correlation of samples in each site and, thus, pseudoreplication (Pinheiro & Bates, 2000). The analysis was performed with the *nlme* package (Pinheiro *et al.*, 2018) and for significant results, a multicomparison *a posteriori* test was performed with the *glht* function of *multcomp* package (Hothorn *et al.*, 2008) in software R v3.2.3 (R Core Team, 2015). Data for gastropod densities, *Sargassum* and epibiont dry weights were transformed to $\log(x + 1)$.

A linear regression analysis was used to determine the relationship between *Sargassum* dry weights and gastropod abundances at each site, with gastropod abundance as the dependent variable. A Pearson linear correlation was used to investigate the relationship between gastropod densities and seawater temperature at each site

Table 1. Linear mixed effects model results (a: *Sargassum* dry weight; b: epibiont dry weight; c: gastropod density; d: number of gastropod species)

Source	numDF	denDF	*F*	*P*
(a) *Sargassum* dry weight				
(Intercept)	1	270	2433.495	<0.0001
Area	3	270	2.95	0.0332
Season	1	10	1.85	0.2035
Area × Season	3	270	0.96	0.4143
Transformation: log(*x* + 1)				
(b) Epibiont dry weight				
(Intercept)	1	270	268.6351	<0.0001
Area	3	270	2.83	0.0388
Season	1	10	1.54	0.2426
Area × Season	3	270	3.19	0.0241
Transformation: log(*x* + 1)				
(c) Gastropod density				
(Intercept)	1	270	599.2951	<0.0001
Area	3	270	100.10	<0.0001
Season	1	10	23.42	<0.0001
Area × Season	3	270	13.67	<0.0001
Transformation: log(*x* + 1)				
(d) Number of species				
(Intercept)	1	270	1615.42	<0.001
Area	3	270	45.8953	<0.001
Season	1	10	7.8826	0.0186
Area × Season	3	270	4.0324	0.0079
No transformation				

during the year. All analyses were performed in software R v3.2.3 (R Core Team, 2015).

The homogeneity of variances and normality of data were checked by visual inspection of residuals.

Results

Macrophytes

Both *Sargassum* spp. and epibiont dry weights did not show any significant variation between warm and cool seasons, whereas *Sargassum* fronds presented a higher dry weight in Ribeira shore and a smaller one in Flamengo, with intermediate values in Lamberto and Santa Rita (Table 1: a, b, Figure 2). The variation of epibiont dry weight, despite being statistically significant for the interaction between season and site, did not show any significant differences in the *a posteriori* test (Table 1: a, b, Figure 2).

Gastropods

A total of 142,996 individual gastropods were obtained, belonging to 68 species. The total gastropod abundance was highest at Ribeira, followed by Flamengo, Lamberto and Santa Rita in that order. The total number of species was higher at Flamengo (58 species), followed by Lamberto, Ribeira and Santa Rita, with 56, 53 and 43 species, respectively. The complete list of species and their total abundances at each site are presented in Table 2.

Gastropod densities varied between seasons and among sampling sites (Table 1: c; Figure 2), with the highest density values during the warm season for all sites except Flamengo, and with higher densities in Ribeira and Flamengo than in Lamberto and Santa Rita. The annual gastropod fluctuation showed the same pattern for all locations, with the highest densities primarily in March and April and between November and February, the periods with the highest seawater temperatures (Figure 3). At Flamengo Beach, the differences among months were less evident (Figure 3). At all sites, a significant and positive correlation was observed between gastropod density and water temperature, with a strong correlation at Lamberto, Ribeira and Santa Rita, and a weaker one at Flamengo (Pearson's correlation, Flamengo: $t = 2.353$, $df = 10$, $P = 0.040$, $r = 0.597$; Lamberto: $t = 4.524$, $df = 10$, $P = 0.001$, $r = 0.820$; Ribeira: $t = 4.219$, $df = 10$, $P = 0.002$, $r = 0.800$; Santa Rita: $t = 3.100$, $df = 10$, $P = 0.011$, $r = 0.700$).

A very similar pattern was observed for the number of species sampled at each site, with a higher mean number of species in Ribeira and Flamengo than in Lamberto and Santa Rita in both seasons. There was no significant variation in species number between seasons at any site (Table 1: d; Figure 2).

About 96% of the gastropods analysed in this study were from only six species, with *Bittiolum varium* as the most dominant at all sampling sites (Figure 3), followed in decreasing order of abundance by *Caecum ryssotitum*, *Eulithidium affine*, *Mitrella dichroa*, *Alvania auberiana* and *Caecum brasilicum*. The remaining 4% of the specimens were from the other 62 species, showing that this gastropod assemblage is composed of a few dominant and many rare species.

Both the common and rarer species showed high proportions of juveniles, as illustrated in the growth series in Figures 4, 5 and 6. For the most common species, *Bittiolum varium*, *Caecum ryssotitum*, *Eulithidium affine* and *Mitrella dichroa*, complete series were found, from the earliest juvenile stages to adults. For other species that are not typically found in these habitats, such as *Stramonita brasiliensis* and *Leucozonia nassa*, which are common on rocky shores, and *Cerithium atratum*, mostly found in soft bottoms, almost exclusively juvenile and sub-adult forms occurred.

Another remarkable feature was the presence of gastropod species that are typically known as parasites, such as the Pyramidellidae (Wise, 1996), with many species well represented in this study, i.e. *Turbonilla multicostata*, *Boonea seminuda* and *Ioleae robertsoni*. Those species could benefit from the other associated species found on these habitats acting as hosts (e.g. other molluscs, sedentary polychaetes, etc.), but that still remains unclear. Adult specimens of all pyramidellid species were rarely found.

Sargassum spp. dry weight and gastropod abundance were significantly and positively related at all sites, except Lamberto (Figure 7).

Discussion

The gastropod fauna exhibited a clear temporal pattern of variation at all sampling sites in Flamengo Bay, with the highest densities during the warmest months of the year. Other studies of the gastropods associated with marine macrophytes have found temporal variations, and most recorded the highest abundances during the summer and/or spring periods (Leite & Turra, 2003; Rueda & Sallas, 2003; Urra *et al.*, 2013).

The peak gastropod abundances during the warm season observed here were not influenced by the biomass of fronds in the *Sargassum* sp. beds, which did not show significant variation between the two seasons. This may be related to biotic factors, such as a higher recruitment rate during this period, as suggested by other studies on macrophyte-associated gastropod assemblages

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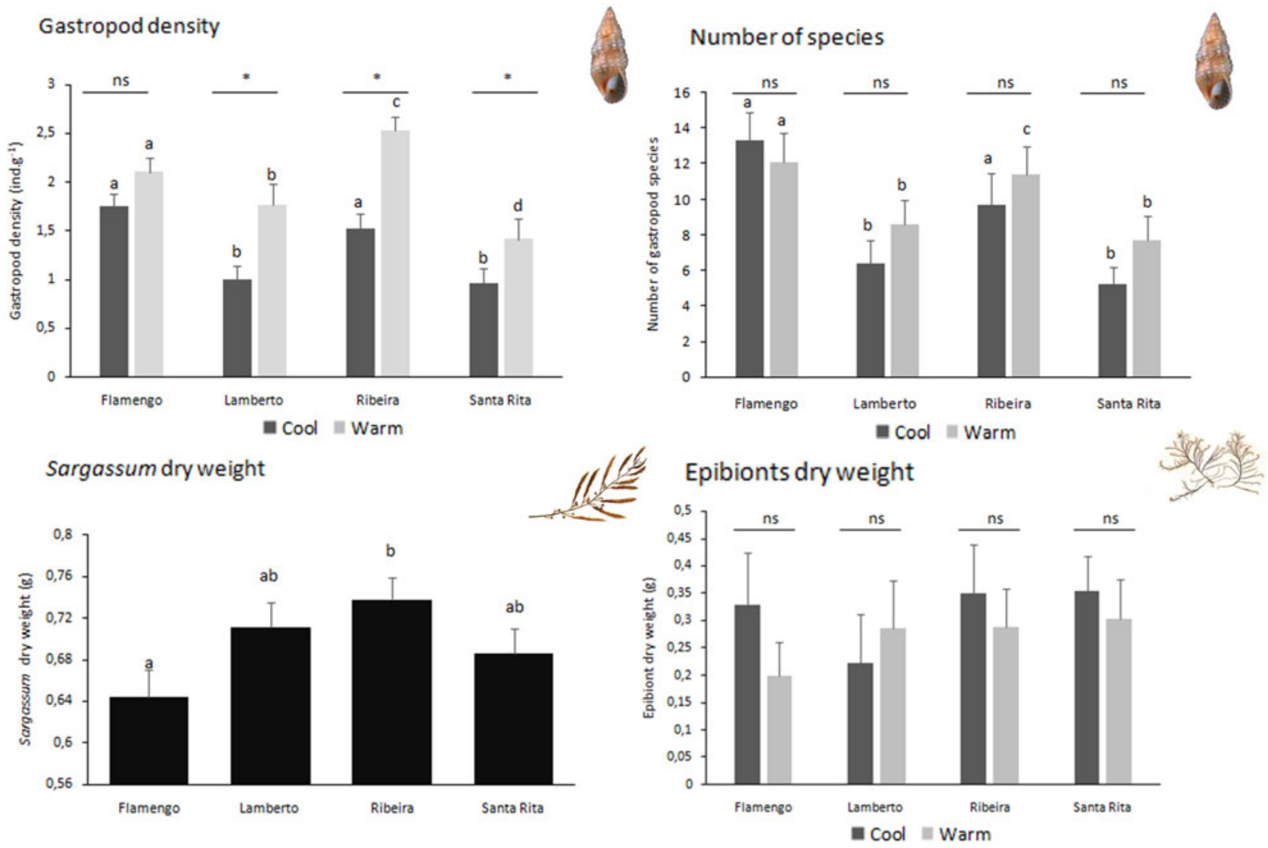

Fig. 2. Differences in gastropod densities (upper left), number of gastropod species (upper right), *Sargassum* spp. dry weight (lower left) and epibionts dry weight (lower right) among seasons and sites. Error bars indicate standard error. Bars of the same colour indicated by the same letter have mean values that are not significantly different among sites ($P \geq 0.05$). Above the lines on top of pairs of bars with differente colours: '*' indicates significant differences between seasons ($P < 0.05$) and 'ns' indicates lack of significant differences between seasons ($P \geq 0.05$). Data transformation for gastropod density, *Sargassum* spp. dry weight and epibiont dry weight: $\log(x + 1)$.

(Leite & Turra, 2003; Arroyo *et al.*, 2006; Rueda *et al.*, 2008), and reinforced here by a high presence of juveniles in this period (Longo, personal observation).

Furthermore, food sources for some species may increase during the warmer months. Organisms that form a biofilm on bottom surfaces grow faster in warmer temperatures (Villanueva *et al.*, 2011), which could benefit many gastropod populations associated with *Sargassum* spp. beds. Many of the gastropod species herein are microherbivores that feed on the biofilm established on the macrophyte fronds, including the most dominant species here, *Bittiolum varium* (Montfrans *et al.*, 1982) and, thus, those epiphytic diatoms and filamentous algal established on macroalgae surface may have an important role on gastropod assemblages (Amsler *et al.*, 2015), that must be further investigated.

Differences were also observed in gastropod density and number of species among the four sampling sites in Flamengo Bay, with the higher values of both variables found in Ribeira and Flamengo. The *Sargassum* spp. populations from each site were morphologically different from each other (Longo, personal observation), possibly indicating different species, which could be influencing the variations on gastropod parameters. Distinct species identities, and thus distinct morphologies among *Sargassum* species, have already been related to differences in community parameters of amphipods (Carvalho *et al.*, 2018) and molluscs (Veiga *et al.*, 2018). Even though the algal structure parameter in this study (algal dry weight) is probably not influencing the faunal differences found, since the two sites with the highest levels of gastropod density and number of species (Ribeira and Flamengo shores) had respectively the highest and lowest values of *Sargassum* dry weight, other unmeasured structural differences (e.g. number and size of branching) should be considered for an understanding of the importance of algal morphology and species identity on gastropod assemblages.

Also, other local differences of environmental parameters (e.g. hydrodynamic forces) could have an important role in the observed differences. Rubal *et al.* (2018), studying molluscan assemblages associated with the macroalga *Asparagopsis armata* in the Iberian Peninsula, raised the hypothesis that local differences found were due to environmental variables, and Tanaka & Leite (2003) have discussed the importance of the association of habitat complexity and physical conditions in the variations of gammarid assemblages living in *Sargassum* habitats at small spatial scales, while Jiménez-Ramos *et al.* (2019) have experimentally demonstrated the importance of habitat structure and abiotic factors such as hydrodynamics, on the structuring of macrophyte ecosystems. Thus, the influence of environmental factors, in association with habitat complexity, may explain the differences found herein and should be further investigated in future studies.

Even though gastropod densities presented some variation throughout the four sampling sites, the dominance of *B. varium* in all sites of Flamengo Bay was remarkable. Although this species often occurs in association with macrophytes, such high dominance levels are unusual, both in studies with other macrophyte species (Leite *et al.*, 2009; Creed & Kinupp, 2011; Barros & Rocha-Barreira, 2013; Zamprogno *et al.*, 2013; Queiroz & Dias, 2014; Duarte *et al.*, 2015; García *et al.*, 2015) and in studies

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Table 2. List of gastropod species associated with *Sargassum* sp. and respective abundances at the four collecting sites

Family/species	Flamengo	Lamberto	Ribeira	Santa Rita
Acteocinidae				
Acteocina bullata (Kiener, 1834)	0	1	0	2
Aglajidae				
Navanax gemmatus (Mörch, 1863)	134	71	51	36
Aplysiidae				
Phyllaplysia engeli Er. Marcus, 1955	50	21	29	24
Aplysia sp.	0	2	0	0
Assimineidae				
Assiminea succinea (Pfeiffer, 1840)	5	0	2	0
Barleeidae				
Amphithalamus glabrus Simone, 1996	5	0	2	1
Buccinidae				
Engina turbinella (Kiener, 1836)	2	1	1	0
Bullidae				
Bulla occidentalis A. Adams, 1850	28	15	13	1
Caecidae				
Caecum brasilicum de Folin, 1874	711	9	218	141
Caecum ryssotitum de Folin, 1867	2032	280	3255	173
Calliostomatidae				
Calliostoma sp. 1	0	1	0	1
Calliostoma sp. 2	1	0	0	0
Calyptraeidae				
Bostrycapullus odites Collin, 2005	0	1	1	0
Crepidula sp.	0	0	1	0
Capulidae				
Capulus sp. 1	29	2	3	1
Capulus sp. 2	15	0	0	0
Cerithiidae				
Bittiolum varium(Pfeiffer, 1840)	24,075	14,058	80,576	5597
Cerithium atratum (Born, 1778)	57	1	16	0
Cerithiopsidae				
Cerithiopsis gemmulosa (C.B. Adams, 1850)	6	5	1	1
Retilaskeya bicolor (C.B. Adams, 1845)	1	1	2	1
Columbellidae				
Anachis fenneli Radwin, 1968	0	0	1	0
Anachis lyrata (G.B. Sowerby I, 1832)	1	4	1	0
Astyris lunata (Say, 1826)	4	0	2	0
Costoanachis sertulariarum (d'Orbigny, 1839)	104	205	139	34
Costoanachis sparsa (Reeve, 1859)	148	78	264	47
Mitrella dichroa (G.B. Sowerby I, 1844)	264	487	364	612
Parvanachis obesa (C.B. Adams, 1845)	66	12	35	19
Eulimidae				
Annulobalcis aurisflamma Simone & Martins, 1995	2	0	0	0
Melanella eburnea (Megerle von Mühlfeld, 1824)	1	0	1	0
Vitreolina bermudezi (Pilsbry & Aguayo, 1933)	0	1	0	0
Eulimostraca sp.	1	0	0	3

(*Continued*)

Table 2. (*Continued.*)

Family/species	Flamengo	Lamberto	Ribeira	Santa Rita
Vitreolina sp.	0	1	0	0
Fasciolariidae				
Leucozonia nassa (Gmelin, 1791)	48	0	2	1
Fissurellidae				
Fissurella rosea (Gmelin, 1791)	40	16	24	36
Fissurellidae sp. 1	0	0	1	1
Haminoeidae				
Haminoea antillarum (d'Orbigny, 1841)	15	10	34	0
Litiopidae				
Alaba incerta (d'Orbigny, 1841)	1	1	0	0
Littorinidae				
Echinolittorina lineolata (d'Orbigny, 1840)	0	3	1	0
Littoraria flava (King, 1832)	2	0	0	0
Mangeliidae				
Tenaturris fulgens (E.A. Smith, 1888)	2	0	1	0
Muricidae				
Morula nodulosa (C.B. Adams, 1845)	3	1	1	0
Stramonita brasiliensis Claremont & D.G. Reid, 2011	8	5	6	3
Olivellidae				
Olivella minuta (Link, 1807)	0	0	0	1
Phasianellidae				
Eulithidium affine (C.B. Adams, 1850)	891	298	1412	2013
Eulithidium bellum (M. Smith, 1937)	2	0	0	0
Planaxidae				
Fossarus ambiguus (Linnaeus, 1758)	0	1	0	0
Pseudomelatomidae				
Pilsbryspira leucocyma (Dall, 1884)	0	4	0	0
Pilsbryspira zebroides (Weinkauff & Kobelt, 1876)	0	1	1	0
Pyramidellidae				
Boonea jadisi (Olsson & McGinty, 1958)	63	7	11	10
Boonea seminuda (C.B. Adams, 1839)	190	39	153	13
Eulimastoma canaliculatum (C.B. Adams, 1850)	2	1	3	0
Eulimastoma didymum (Verrill & Bush, 1900)	15	1	8	1
Fargoa bushiana (Bartsch, 1909)	35	14	29	5
Iolaea robertsoni (van Regteren Altena, 1975)	115	33	119	20
Odostomia laevigata (d'Orbigny, 1841)	0	1	1	1
Oscilla somersi (Verrill & Bush, 1900)	1	0	0	1
Trabecula krumpermani (De Jong & Coomans, 1988)	0	0	2	0
Turbonilla multicostata (C.B. Adams, 1850)	172	112	384	37
Turbonilla penistoni Bush, 1899	11	3	12	3
Turbonilla sp.	1	1	0	0
Rissoellidae				
Rissoella ornata Simone, 1995	14	0	0	3
Rissoidae				
Alvania auberiana (d'Orbigny, 1842)	719	26	446	31

(*Continued*)

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Table 2. (*Continued.*)

Family/species	Flamengo	Lamberto	Ribeira	Santa Rita
Rissoinidae				
Schwartziella bryerea (Montagu, 1803)	77	60	322	15
Scaliolidae				
Finella dubia (d'Orbigny, 1840)	6	0	3	4
Tegulidae				
Tegula viridula (Gmelin, 1791)	1	1	3	7
Tornidae				
Parviturboides interruptus (C.B. Adams, 1850)	3	2	0	0
Triphoridae				
Marshallora nigrocincta (C.B. Adams, 1839)	18	12	29	2
Nototriphora decorata (C.B. Adams, 1850)	3	1	0	1
Total	30,220	15,922	87,947	8907

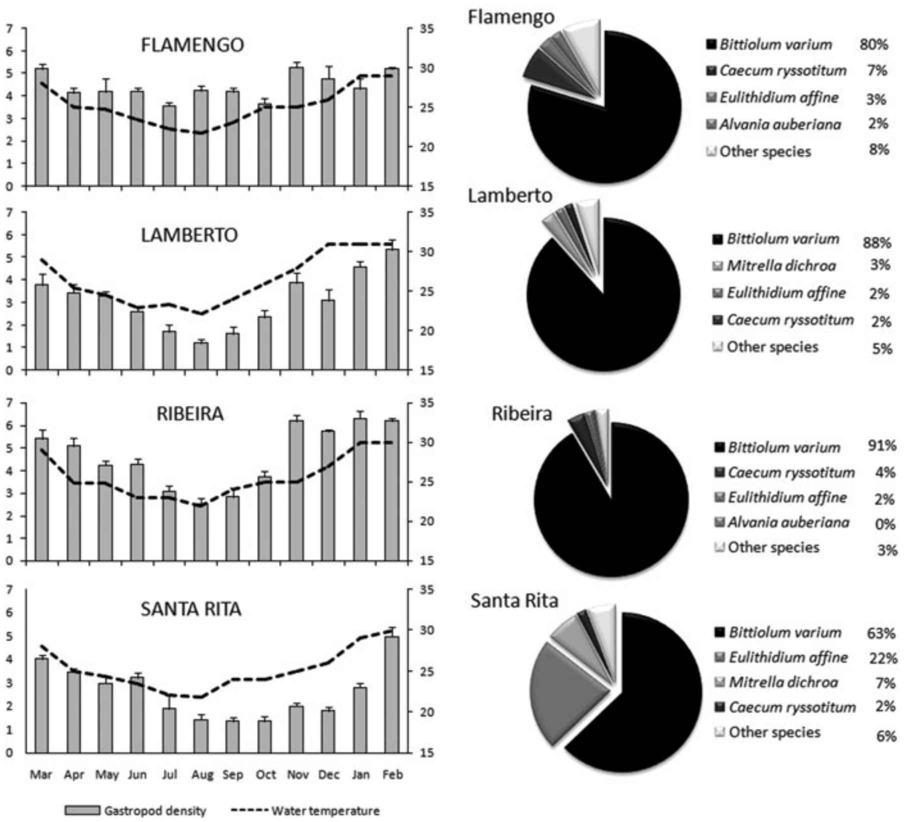

Fig. 3. Left: annual fluctuations of seawater temperature and gastropod density (mean ± standard error). Right: total relative abundances of the four most abundant species at each collecting site.

with *Sargassum* sp. beds elsewhere on the Brazilian coast (Almeida, 2007; Jacobucci *et al.*, 2006; Longo *et al.*, 2014).

A historical analysis of Flamengo Bay reveals that such high dominance levels of *B. varium* were not always observed. In an inventory of the gastropod species associated with *Sargassum* sp. beds in this area, Montouchet (1979) observed that other species such as *Eulithidium affine* and *Astyris lunata* showed the highest abundance levels, whereas *B. varium* comprised only 1.57% of the total 'prosobranch' gastropods. Later, Leite & Martins (1991), working in the same area, found a striking increase in *B. varium* dominance, with a 98% relative abundance. The time interval between these two studies was marked by anthropogenic modifications in this area, including a highway construction near the bay, the development of state marinas in the bay, and a regional increase in the human population (Buzato, 2012). The impact of these activities on Flamengo Bay may be affecting the local fauna, favouring the establishment and dominance of opportunistic species, such as the micrograzer *B. varium*.

The effects of anthropogenic impacts can frequently be observed in the diversity parameters of marine assemblages, resulting in lower evenness values and a higher dominance of one or a few species (Hillebrand *et al.*, 2008; Johnston & Roberts, 2009). This pattern, associated with impacted areas, has been described for coastal molluscan assemblages (Terlizzi *et al.*, 2005; Mendes *et al.*, 2006; Amin *et al.*, 2009) and could be observed in Flamengo Bay in recent decades, which indicates the effects of anthropogenic impacts in the area. The high

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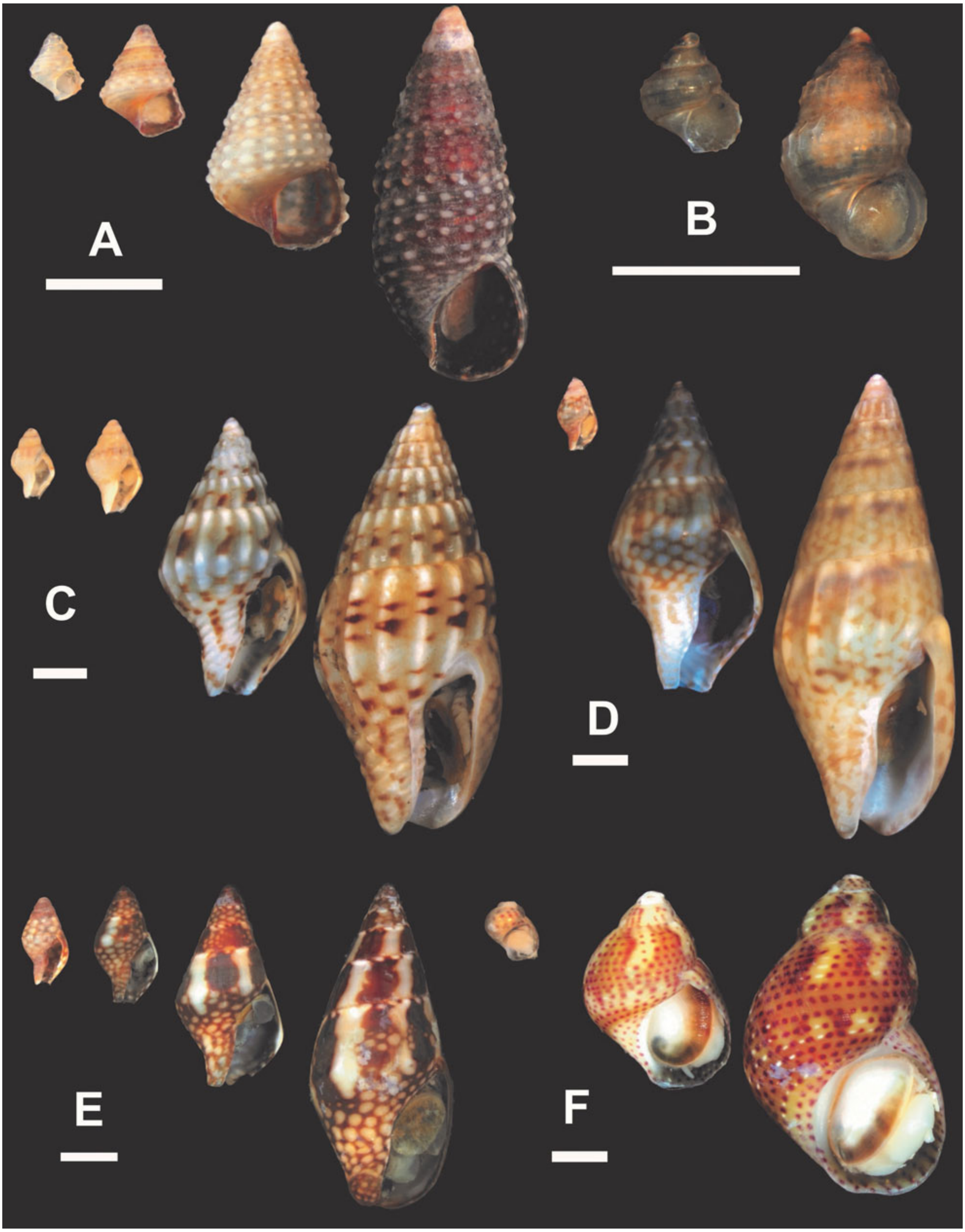

Fig. 4. Species growth series. (A) *Bittiolum varium*; (B) *Alvania uberiana*; (C) *Costoanachis sparsa*; (D) *Costoanachis sertulariarum*; (E) *Mitrella dichroa*; (F) *Eulithidium affine*. Scale bar: 1 mm.

dominance values of *B. varium* in this study suggest that these effects may have continued until the present time, an issue that is being further investigated (Longo *et al.*, in prep.). Therefore, this result is in accordance with other studies that documented the vulnerability of gastropod–macrophyte systems under human-induced stress (Conti & Cecchetti, 2003; Terlizzi *et al.*, 2005; Roberts *et al.*, 2008).

In Flamengo Bay, although a positive and significant relationship between the dry weight of *Sargassum* sp. fronds and gastropod abundance was observed in most periods, this relationship was weak. The importance of the macrophyte beds for the establishment and growth of their epifauna in general (e.g. Veiga *et al.*, 2014; Torres *et al.*, 2015) and for gastropods specifically (e.g. Norton & Benson, 1983; Vincent *et al.*, 1991; Wang *et al.*,

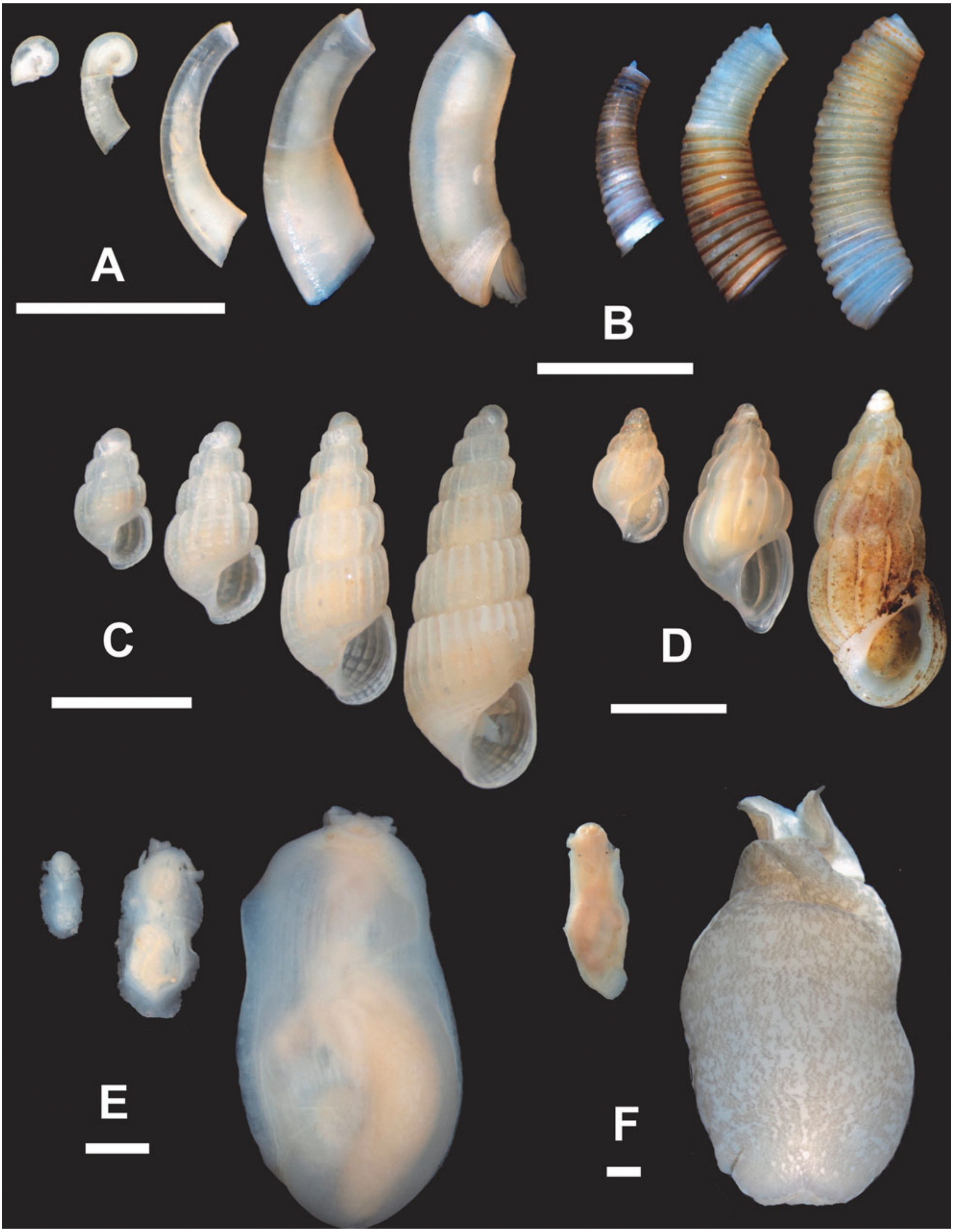

Fig. 5. Species growth series. (A) *Caecum ryssotitum*; (B) *Caecum brasilicum*; (C) *Turbonilla multicostata*; (D) *Schwartziella bryerea*; (E) *Phyllaplysia engeli*; (F) *Navanax gemmatus*. Scale bar: 1 mm.

2006) was demonstrated by the significant and highly positive relationship between the macrophyte biomass and the abundance of associated individuals. Veiga *et al.* (2018) demonstrated that, besides biomass, molluscan assemblages were also highly influenced by algal architecture, measured as the fractal area of each frond, a variable that could be included in future studies. Nevertheless, possibly other factors such as the anthropogenic impacts on Flamengo Bay (CETESB, 2014, 2015, 2016) may be limiting the occurrence of this fauna there, thus affecting the linear relationship between macrophytes and associated species. This

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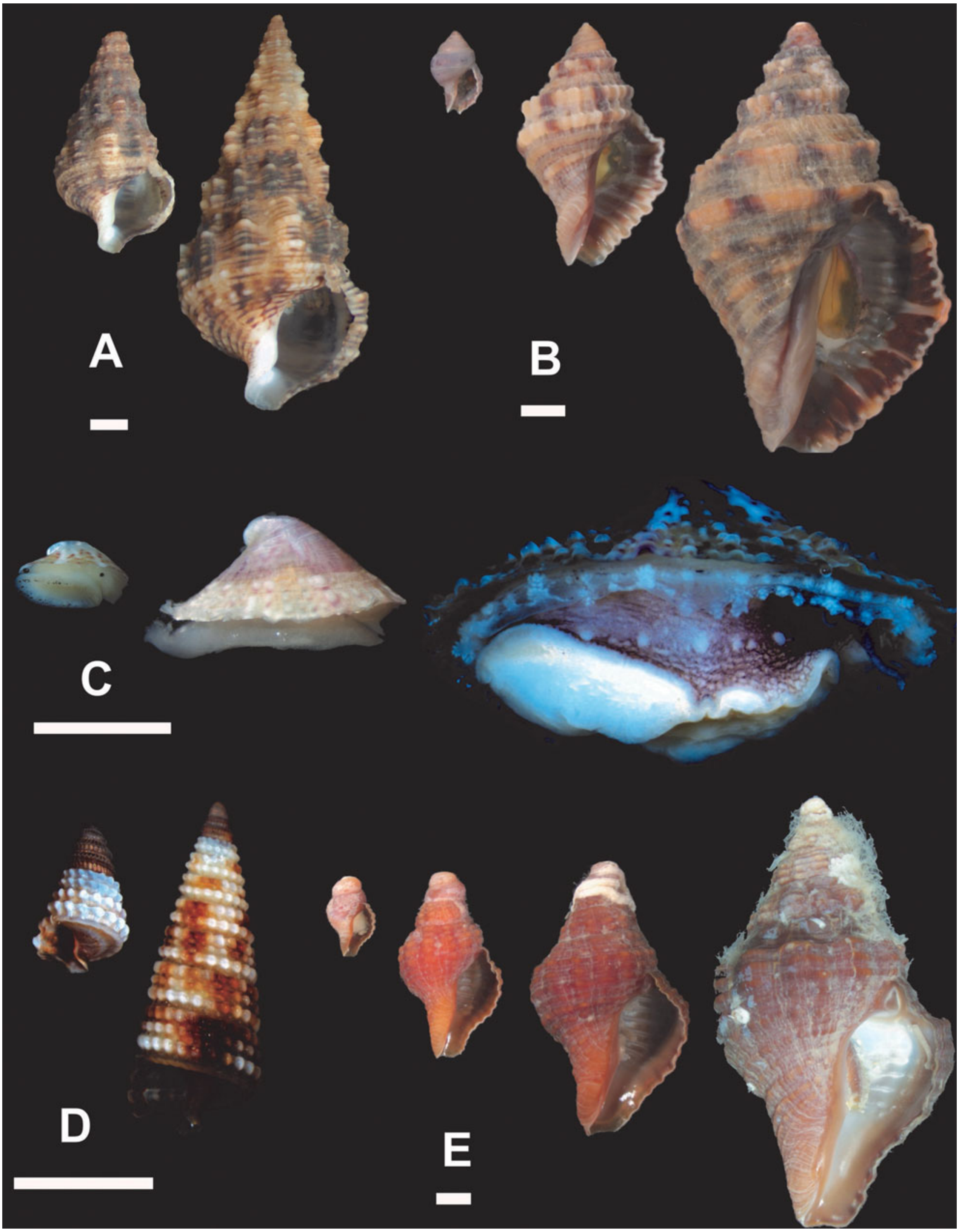

Fig. 6. Species growth series. (A) *Cerithium atratum*; (B) *Stramonita brasiliensis*; (C) *Fissurella rosea*; (D) *Nototriphora decorata*; (E) *Leucozonia nassa*. Scale bar: 1 mm.

hypothesis becomes stronger when we observe that in Lamberto Beach, the site closest to the polluted Saco da Ribeira, the *Sargassum* dry weight–gastropod abundance relationship was not significant.

The remarkable diversity of gastropods living in association with *Sargassum* spp. beds illustrated here, with a large occurrence of juvenile stages of the most common resident species as well as the less abundant species typical of other, nearby habitats, calls attention to the need to extend our knowledge of the biology and dynamics of these species, as well as to better understand the role performed by this macroalga in the establishment and development of the gastropod species, especially in impacted

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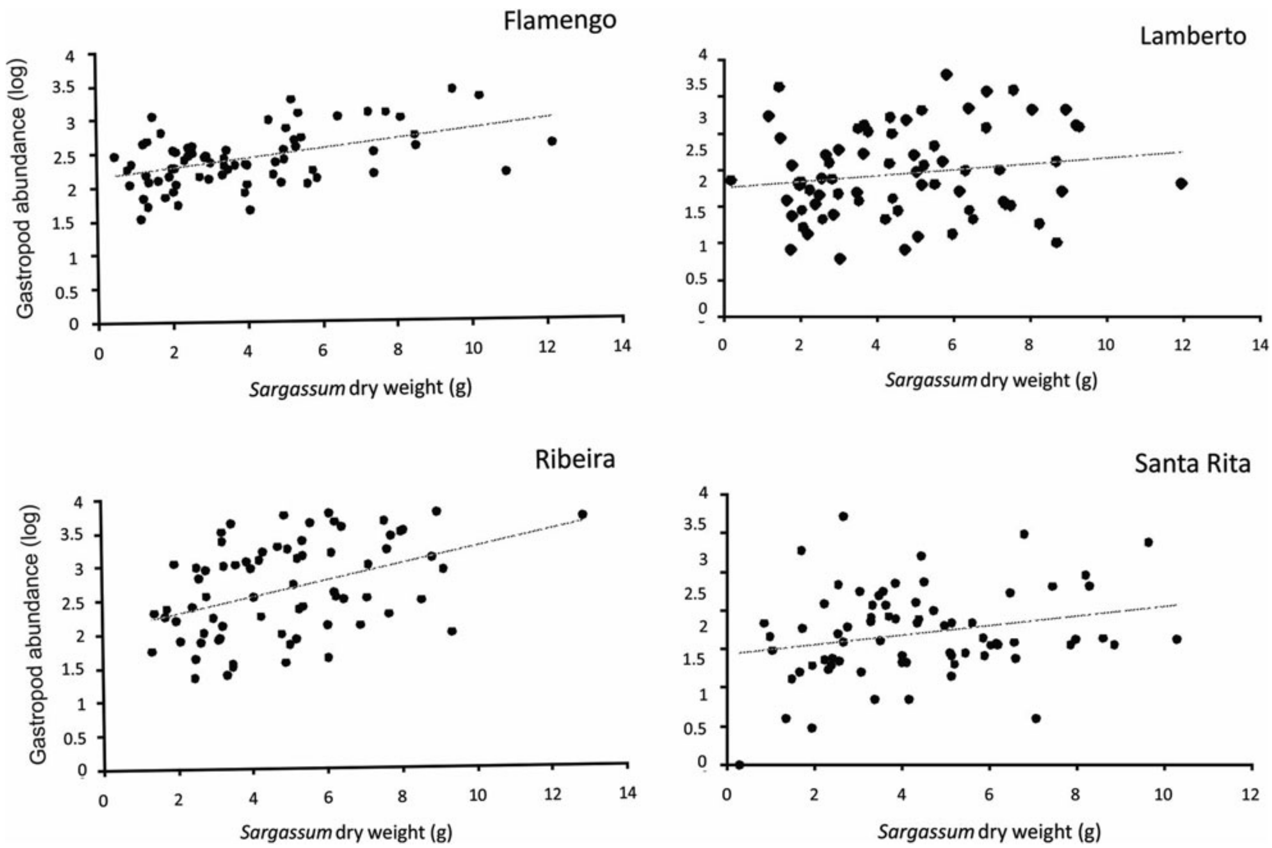

Fig. 7. Linear regressions between gastropod abundances and algal dry weight. Flamengo: $y = 0.07x + 2.145$, N = 72, $F = 18.61$, adjusted $R^2 = 0.1987$, $P < 0.0001$. Lamberto: $y = 0.040x + 1.75$, N = 72, $F = 1.992$, adjusted $R^2 = 0.0138$, $P = 0.1626$. Ribeira: $y = 0.119x + 2.067$, N = 72, $F = 13.62$, adjusted $R^2 = 0.1509$, $P < 0.0001$. Santa Rita: $y = 0.060x + 1.434$, N = 72, $F = 4.283$, adjusted $R^2 = 0.0442$, $P = 0.0422$.

areas. Similar observations have already been made for molluscan assemblages associated to *Cystoseira* spp., another canopy-forming brown alga, from other localities (Pitacco *et al.*, 2014; Lolas *et al.*, 2018). Those numerous juvenile forms found could indicate that macroalgae such as *Sargassum* sp. provide a favourable environment for the development of gastropods, acting as a nursery, as has been well established for other invertebrate and vertebrate groups (Haywood *et al.*, 1995; Perkins-Visser *et al.*, 1996; Cocheret de la Morinière *et al.*, 2002; Heck *et al.*, 2003; Bulleri *et al.*, 2006). Further investigations are needed for gastropod assemblages, since most studies have focused on a few species, such as *Strombus gigas* (Stoner, 2003).

The generation of further information on the highly diverse gastropod assemblages associated with macrophyte habitats, their structure patterns in impacted areas such as Flamengo Bay, and the interactions between gastropods and macroalgae will enable the development and implementation of effective conservation measures for these ecologically important habitats formed by macrophyte beds in coastal regions.

Acknowledgements. We wish to thank the northern Clarimundo de Jesus Research Base (Oceanographic Institute, University of São Paulo), as well as all the technicians, for their help and support during the collecting process; A. Mouro, A.P. Ferreira and M.B. Fernandes, for help with material processing and/or data analysis; A.L. Lorenço, V. Vicente and I. Capistrano for valuable help with material processing; members of the LICOMAR – Unicamp, for their help during collection, processing and discussions; D. Zaya, for helping with the photographs; P.V.F. Corrêa for designing the map; and C.M. Cunha and L. Souza for their help during the identification process.

Financial support. This work was supported by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES).

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