

The structure of gammarid amphipod (Crustacea, Peracarida) assemblages associated with *Sargassum* (Phaeophyta, Fucales) and their link with the structural complexity of algae

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Abstract The structural complexity of algae is an important factor driving the structure of epifaunal assemblages associated with marine macroalgae. We tested how the structural complexity of four *Sargassum* species is related to the structure of gammarid assemblages. We measured different algae traits (frond length, number of branches, and epiphytic hydroid and algae cover) and different ecological descriptors of gammarid assemblages (richness, density, diversity, and evenness). Samples were obtained in southeastern Brazil in early and late summer.

Structural complexity was associated with the occurrence of significantly different gammarid assemblages. *Sargassum cymosum* had more branches and greater hydroid coverage, and a higher gammarid species richness, diversity, and density. The characteristics of the gammarids inhabiting the different *Sargassum* species were similar between sampling periods, indicating that the relationships between the *Sargassum* traits and associated gammarids are strong and persistent. Species richness, diversity, and density were all more dependent on habitat heterogeneity (number of branches and coverage of epiphytic hydroid) than the quantity of habitable space, i.e., frond length. Overall, the variation in structural complexity among *Sargassum* species had a significant effect on gammarid assemblage structure.

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Introduction

Structural complexity can be defined as the three-dimensional arrangement of a habitat (Graham & Nash, 2013). This concept is one of many terms that describe environmental heterogeneity, and is directly related to the spatial complexity, diversity, heterogeneity, and structure of environments (Stein et al., 2014). The structural complexity promoted by algae

has a broad ecological significance in marine environments and is an important factor driving the structure of epifaunal assemblages associated with these plants (Viejo, 1999; Buschbaum et al., 2006).

Macroalgae morphology varies considerably (Christie et al., 2009), and these organisms are thus regarded as ideal models for the evaluation of the effects of structural complexity on ecological assemblages. Variation in the architecture of macroalgae (fronds size and number of branches) and their functional or taxonomic composition (epiphytic hydroid and algae cover) have been found to be important descriptors of the diversity and abundance of their associated epifaunal assemblages (Taylor & Cole, 1994; Davenport et al., 1996; Leite et al., 2007a; Jacobucci & Leite, 2014).

Brown algae are the most common benthic macroalgae found on rocky coasts (Little et al., 2015). In particular, brown algae of the genus *Sargassum* are among the most morphologically complex of the order Fucales (Leite et al., 2007a), exhibiting extensive branching, large fronds, and high biomass (Jacobucci & Leite, 2002). In addition, many hydroids and epiphytic algae are associated with these plants (Russo, 1990; Martin-Smith, 1993). Also, the *Sargassum* species with more branches and leaves, larger holdfasts, and greater epiphytic diversity are more complex (Martin-Smith, 1993; Leite et al., 2007a). Based on the conception of niche theory, more complex habitats provide more microenvironments or niches (Hutchinson, 1957), which can increase the diversity of associated fauna (Dubiasik-Silva & Masunari, 1995; Downes et al., 2000; Jacobucci & Leite, 2014). The benthic fauna associated with *Sargassum* includes different invertebrate groups, with a predominance of gastropods (Montouchet, 1979) and crustaceans (Tararam & Wakabara, 1981; Edgar & Robertson, 1992). Typically, gammarid amphipods are the most abundant taxa (Taylor & Cole, 1994; Jacobucci & Leite, 2002).

Gammarid species have a wide variety of feeding and life habits (Duffy, 1990; Leite et al., 2007a). Furthermore, gammarids are the most important food source for some fish assemblages (Nakamura et al., 2003). Organisms from lower trophic levels suffer intense predation pressure (Nelson, 1979), being particularly susceptible to visually oriented predators (Leite et al., 2007b). Given the important trophic link between consumers and primary producers in seaweed

communities (Taylor & Cole, 1994), a more detailed knowledge of the distribution of these amphipod species is essential for better understanding the role of these organisms in complex systems such as *Sargassum* beds.

Most studies on the role of *Sargassum* in the structuring of associated benthic assemblages have so far focused on a single species or have been primarily focused on algal physical structure, such as thallus and stem width, algal length, number of branches (Taylor & Cole, 1994; Chemello & Milazzo, 2002), algal biomass (Machado et al., 2015), fractal dimension, and perimeter of the algae (Veiga et al., 2014). Studies using different *Sargassum* species that incorporate algal traits, such as epiphytic hydroid and algae cover, would help to better understand the effects of the structural complexity produced by the algae itself, and by their epibionts, on the small-scale distribution patterns of associated gammarids.

The objective of the present study was to characterize the gammarid amphipod assemblages associated with different *Sargassum* species on a rocky coastline in southeastern Brazil. We tested the hypothesis that the more structurally complex *Sargassum* species (longer fronds, more branches, and greater coverage of epiphytic hydroids and algae) have amphipod assemblages with higher species richness, abundance, diversity, and evenness. We also explored which algal traits (frond length, number of branches, and epiphytic hydroid and algae cover) are more important in explaining the variations in amphipod assemblages associated with different *Sargassum* species.

Methods

Sampling and samples processing

A total of 78 samples were collected in December 2009 and March 2010 along the northern rocky coastline of the state of São Paulo, Brazil (23°20'S/44°54'W to 23°49'S/45°24'W) (Fig. 1). To minimize the influence of environmental characteristics on algae morphology, four similar rocky shores were selected (Lamberto, Lázaro, Fortaleza, and Cigarras). These sites were selected for their similarity regarding morphology (located within bays) (Mahiques et al., 1998; Denadai et al., 2005), level of exposure to wave

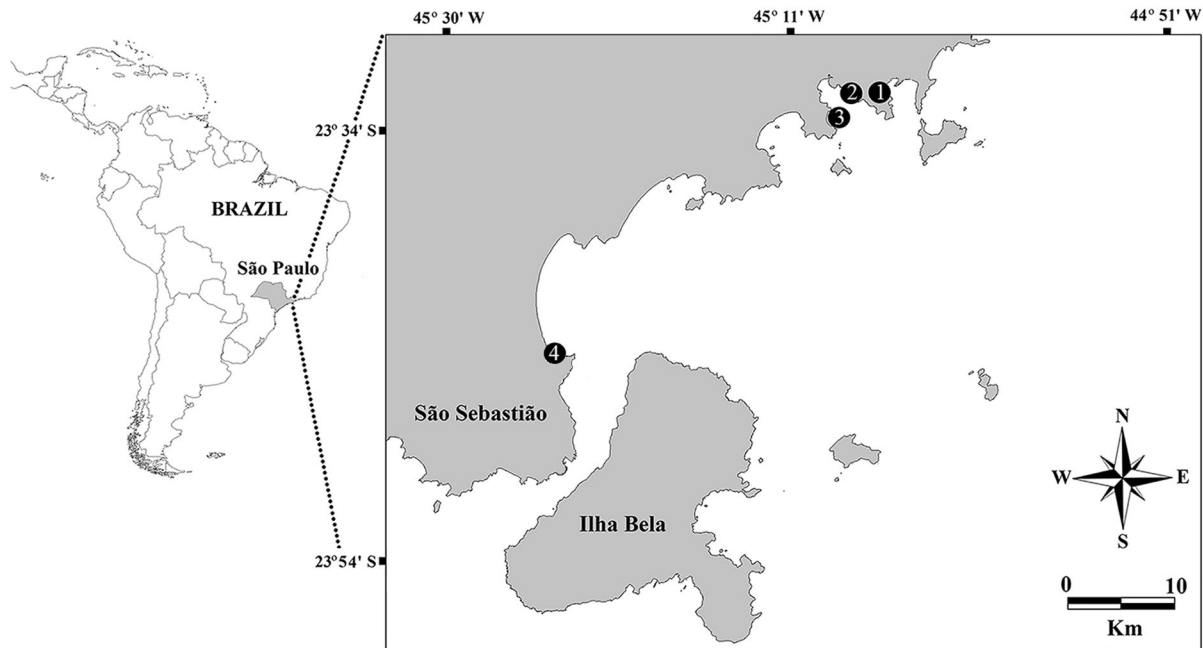


Fig. 1 Map of studies rocky shores (Northern São Paulo coast—Brazil). 1 Lamberto, 2 Lázaro, 3 Fortaleza, 4 Cigarras

action (moderately exposed) (Széchy & Paula, 2000; Széchy et al., 2001; Jacobucci & Leite, 2002; Cunha et al., 2009), slope of rock substrate (intermediate) (Széchy et al., 2001), tidal processes, and current regimes (Harari & Mesquita, 2007). To avoid differences in algal chemical composition, common in algae from different phylum and families (Amsler, 2008), the studied algal species belonged to the same genus (*Sargassum*). All species of this genus have similar basic morphology, which comprises a holdfast, main cylindrical stem, primary and secondary lateral branches (Paula, 1988). These choices allowed us to focus on the relationship between algal complexity (length, number of branches, epiphytic and hydroid cover) and gammarid assemblage structure.

At each rocky shore, a 100-m transect divided in 2-m sections was established at 2.5–3 m depth from the surface. Ten sections were sampled at each site during sampling months. One frond from the dominant *Sargassum* species (*S. filipendula*, *S. stenophyllum*, *S. cymosum*, and *S. furcatum*) (Online Supplementary material 1) was randomly collected while snorkeling in each section. Prior to the collection of the samples, bags with 0.2 mm mesh size were fastened around the algae to prevent the escape of motile fauna. The algae were then extracted from the

substrate using a spatula to dislodge the holdfast, and subsequently preserved in 4% saline formalin. The algae were transported to the laboratory, where they were immersed in freshwater and vigorously shaken several times. The water was then filtered through a 0.2-mm mesh to collect the amphipods. The gammarids were identified to the lowest taxonomic level possible based on Conlan (1982) and Serejo (2004). After identification, the number of gammarids of each taxa was counted per sample. Gammarid density (N: number of individuals), richness (S: total number of taxa), diversity (λ : Simpson's index), and evenness (J: Pielou's index) were calculated for each sample and were expressed per gram of dry mass of *Sargassum*.

The following traits were determined for each algal sample: (i) length (distance between the holdfast and the distal portion); (ii) number of branches between the holdfast and primary branches; (iii) epiphytic algae and hydroids cover (Berchez et al., 1993; Cunha & Jacobucci, 2010), with the amount of cover placed into one of the following classes: 0 = no epibionts, 1 = 0–25% coverage, 2 = 25–50% coverage, 3 = 50–75% coverage, and 4 = 75–100% coverage (Jacobucci & Leite, 2002); and (iv) biomass, which was obtained after drying the algal sample (*Sargassum*) in an oven at 80°C for 48 h. Since most

assemblage descriptors and algae traits were significantly correlated with *Sargassum* biomass, all variables were expressed as per gram of dry algae.

Data analysis

To summarize multivariate patterns in gammarid amphipods across the different *Sargassum* species, a canonical analysis of principal coordinates (CAP; Anderson & Willis, 2003) was performed for each sampling date. The resemblance matrices were calculated using Bray–Curtis similarity based on fourth-root transformed amphipod abundance. For linking amphipod assemblages structure and algae traits (length, number of branches, epiphytic hydroid and algae cover), a distance-based linear model (DistLM; Anderson, 2000) was performed. This technique analyzes and models the relationship between a multivariate data cloud, as described by a resemblance matrix and predictor variables. Resemblance matrices were calculated using Euclidean distance ($\log(x + 1)$ transformed data) and Bray–Curtis similarity (fourth-root transformed data), respectively. Multiple linear regressions (MLR) were fitted for amphipod assemblage descriptors (N, S, λ , and J—dependent variables) against algae traits (length, number of main branches, and epiphytes algae and hydroids coverage—dependent variables). Assemblage descriptors and algae traits were $\log(x + 1)$ transformed prior analyses. Significance levels of the test statistics (F test, R square, and t tests of regression coefficients) were evaluated using permutation through the ‘loringin’ function in the ‘R’ package ‘ape’ (Paradis et al., 2004). The relative importance of each variable in the model (% variability explained) was assessed a posteriori through the ‘lmg’ function in the ‘R’ package ‘relaimpo’ (Groemping, 2006). The best models in DistLM and MLR were chosen using a forward routine with 9999 permutations based on AIC selection criterion. This criterion is more appropriate to use with a small ($N/v < 40$) ratio of number of samples (N) to number of predictor variables (v) (Anderson et al., 2008). The DistLM and MLR were performed separately for samples from December and March. Analyses and tests were performed using the ‘R’ language and environment (RStudio, 2018, version 1.1.442) and PRIMER 6 + PERMANOVA (Anderson et al., 2008) at $\alpha = 0.05$.

Results

Algae structural complexity and gammarid assemblage

Algal traits and gammarid assemblage descriptors are shown in Table 1. A total of 14,435 gammarids belonging to 10 species were recorded (Online Supplementary material 2). Gammarid assemblage structure clearly differed among *Sargassum* species (Fig. 2). This is reinforced by the high degree of success in the classification of the samples (92.1% of the samples classified correctly in December, and 90.0% in March) (Fig. 2).

Association between the structural complexity of *Sargassum* species and amphipod assemblages

The best distance-based linear models (DistLM) explained 18% of the total variation in gammarid assemblages in December, and 22% in March. The number of branches and hydroid coverage were significantly correlated with gammarid assemblage structure and were always included in the models. In December, the number of branches contributed most (11%) to the variation, followed by hydroid coverage (7%) (Table 2). In March, hydroid coverage contributed more (13%) than the number of branches (9%) (Table 2).

When considering the individual descriptors of gammarid assemblages, the best models (MLR) were fitted for species richness and evenness, which explained more than 60% of the variation. The worst models were obtained for gammarid density (44% in December and 38% in March). In most models, the number of branches and hydroid coverage were positive and significantly correlated with the descriptors and contributed most to explaining the variation in assemblage descriptors (Table 3), while algae length was negative and significantly correlated with the ecological descriptors of gammarid assemblages (Table 3).

Discussion

The different *Sargassum* species found along the rocky coastline of northern São Paulo exhibited distinct patterns of complexity. *Sargassum* species

Table 1 Algae traits and descriptors (mean \pm standard error, $n = 78$) of gammarid assemblages in São Paulo coast in December 2009 and March 2010

	Algae traits				Descriptors of gammarid assemblages			
	Length (cm)	Number of branches	Epiphytic hydroids coverage	Epiphytic algae coverage	Species richness	Density (ind. g ⁻¹ algae)	Diversity (λ)	Evenness (J)
December								
<i>Sargassum cymosum</i>	18.61 \pm 3.07	0.78 \pm 0.60	0.23 \pm 0.11	0.02 \pm 0.08	1.77 \pm 0.42	18.62 \pm 7.74	0.12 \pm 0.09	0.28 \pm 0.18
<i>Sargassum filipendula</i>	30.00 \pm 12.34	0.18 \pm 0.11	0.10 \pm 0.12	0.25 \pm 0.31	0.45 \pm 0.20	3.94 \pm 1.67	0.04 \pm 0.02	0.07 \pm 0.04
<i>Sargassum furcatum</i>	31.88 \pm 17.79	0.18 \pm 0.16	0.13 \pm 0.13	0	0.41 \pm 0.20	18.17 \pm 20.83	0.03 \pm 0.01	0.04 \pm 0.02
<i>Sargassum stenophyllum</i>	34.55 \pm 16.39	0.30 \pm 0.21	0.21 \pm 0.31	0.25 \pm 0.26	0.80 \pm 0.52	8.75 \pm 7.67	0.06 \pm 0.03	0.10 \pm 0.06
March								
<i>Sargassum cymosum</i>	16.50 \pm 3.59	0.76 \pm 0.40	0.82 \pm 0.26	0.22 \pm 0.21	2.14 \pm 1.03	95.96 \pm 40.60	0.13 \pm 0.11	0.20 \pm 0.09
<i>Sargassum filipendula</i>	21.70 \pm 3.71	0.36 \pm 0.12	0.57 \pm 0.37	0.40 \pm 0.12	1.02 \pm 0.31	15.83 \pm 7.35	0.03 \pm 0.01	0.11 \pm 0.02
<i>Sargassum furcatum</i>	30.70 \pm 11.49	0.55 \pm 0.19	0.27 \pm 0.29	0.42 \pm 0.28	1.07 \pm 0.62	37.94 \pm 22.91	0.11 \pm 0.05	0.10 \pm 0.07
<i>Sargassum stenophyllum</i>	24.70 \pm 4.87	0.33 \pm 0.13	0.65 \pm 0.31	0.22 \pm 0.24	0.85 \pm 0.28	33.79 \pm 39.30	0.08 \pm 0.03	0.08 \pm 0.04

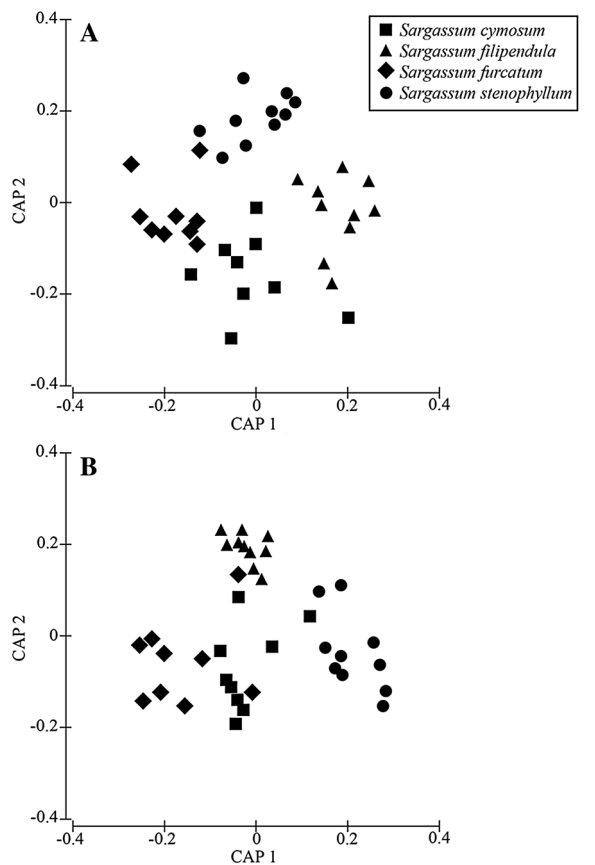


Fig. 2 Canonical analysis of principal coordinates (CAP) plots based on the abundance of gammarids. **A** December 2009; **B** March 2010. Samples from São Paulo coast (Brazil)

(e.g., *S. cymosum*) with greater structural complexity, such as more main branches and highest coverage of epiphytic hydroids, harbored gammarid assemblages with higher richness, density, diversity, and evenness, supporting the first hypothesis of the present study. The second hypothesis that algal traits also played an

important role in the structuring of gammarid assemblages was also supported. The number of branches and hydroid cover were the most important traits explaining the variation in gammarid assemblage structure. The characteristics of the gammarid assemblages associated with different *Sargassum* species were maintained in both sampling occasions (early and late summer), indicating that the relationship between the complexity and the gammarids is strong and persistent.

Algal traits are important drivers of the composition and abundance of gammarid assemblages associated with marine macroalgae (Viejo, 1999; Chemello & Milazzo, 2002; Veiga et al., 2014). In the present study, the number of branches (habitat availability and heterogeneity) and hydroid cover (which may indicate the supply of nutrients and refuges) were the algal traits with the greatest effects on gammarid assemblages. Structural complexity can be linked directly to niche theory (Hutchinson, 1959; Rosenzweig, 1995). More complex vegetation offers a greater amount of resources and a larger number of microhabitats for settlement and colonization (Ronowicz et al., 2008), reducing competition for biological substrates among amphipods (Leite et al., 2007a). Structural complexity also provides refuge from predators and shelter from hydrodynamic flow, as well as favoring the deposit of detritus (Fenwick, 1976; Heck & Wetstone, 1977; Russo, 1990; Hacker & Steneck, 1990; James & Heck, 1994).

Most of our models applied to account for the variation in gammarid assemblages included hydroid cover, which appears to be related to the direct or indirect exploitation of nutrients by amphipods. The presence of hydroids may favor the accumulation of detritus through the secretion of mucus to which the

Table 2 Best distance-based linear models (DistLM) fitted for gammarid assemblages against algae traits measured in different *Sargassum* species in São Paulo (Brazil) coast in December 2009 and March 2010

Variable	AIC	Pseudo- <i>F</i>	<i>P</i>	Prop	res.df
December—Sequential tests for stepwise model (Adjusted $R^2 = 0.18$)					
Number of branches	247.44	4.62	< 0.01	0.11	36
Epiphytic hydroids coverage	246.78	3.14	< 0.01	0.07	35
March—Sequential tests for stepwise model (Adjusted $R^2 = 0.22$)					
Epiphytic hydroids coverage	274.08	5.55	< 0.01	0.13	38
Number of branches	271.86	3.74	< 0.01	0.09	37

Prop. proportion of variability explained, res.df residuals degrees of freedom

Table 3 Best multiple linear regression models (MLR) fitted for gammarid assemblages against algae traits measured in different *Sargassum* species in São Paulo (Brazil) coast in December 2009 and March 2010

Variable	Beta	t	Pr(> t)	Prop. (%)
Richness				
December— $F_{(3,34)} 27.37, P < 0.01, R^2 0.70$				
Number of branches	0.62	6.15	< 0.01	43.29
Epiphytic hydroids coverage	0.33	3.38	< 0.01	16.39
Length	− 0.15	− 1.52	< 0.01	11.03
March— $F_{(2,38)} 28.45, P < 0.01, R^2 0.61$				
Epiphytic hydroids coverage	0.49	3.85	< 0.01	33.85
Number of branches	0.37	2.85	< 0.01	26.74
Density				
December— $F_{(4,33)} 6.52, P < 0.01, R^2 0.44$				
Epiphytic hydroids coverage	0.39	2.64	0.01	13.21
Length	− 0.38	0.26	0.02	13.44
Epiphytic algae coverage	0.34	2.18	0.06	4.53
Number of branches	0.23	0.53	0.03	12.95
March— $F_{(3,36)} 7.38, P < 0.01, R^2 0.38$				
Epiphytic hydroids coverage	0.53	3.02	< 0.01	22.49
Number of branches	0.28	1.66	0.11	12.53
Length	− 0.27	1.63	0.11	3.06
Diversity				
December— $F_{(2,35)} 29.78, P < 0.01, R^2 0.62$				
Number of branches	0.74	6.98	< 0.01	55.77
Epiphytic hydroids coverage	0.18	1.68	0.1	7.21
March— $F_{(3,36)} 11.26, P < 0.01, R^2 0.48$				
Epiphytic hydroids coverage	0.52	3.25	< 0.01	25
Number of branches	0.38	2.46	0.02	19
Length	− 0.24	1.62	0.11	4
Evenness				
December— $F_{(2,35)} 42.38, P < 0.01, R^2 0.71$				
Number of branches	0.72	7.33	< 0.01	56.13
Epiphytic hydroids coverage	0.29	3.18	< 0.01	14.63
March— $F_{(4,35)} 23.79, P < 0.01, R^2 0.73$				
Length	− 0.38	− 3.38	0.62	22.75
Epiphytic hydroids coverage	0.32	2.69	< 0.01	22.66
Number of branches	0.24	1.92	< 0.01	20.31
Epiphytic algae coverage	0.22	2.26	0.17	7.39

Prop. (%) proportion of variability explained by each variable

suspended particulate organic matter adheres, or through the accumulation of sediment and organic matter in their branches, supporting a large detritus-feeding assemblage (Bavestrello et al., 1996; Bradshaw et al., 2003). Hydroids are consumed, accidentally or intentionally, by marine turbellarians, molluscs, polychaetes, picnogonids, crustaceans, and echinoderms (Ebbs, 1966; MacLeod & Valiela, 1975; Breitbart, 1985; Staples & Watson, 1987; Russell &

Hedgpeth, 1990; Alarcón-Ortega et al., 2012). Guerra-García et al. (2014) found more detritus than hydroids in the gut contents of some gammarid families, indicating that while they may feed on the hydroids, they are in fact targeting the detritus they accumulate. Bavestrello et al. (1996) and Di Camillo et al. (2008) have proposed that complex trophic chains exist, including hydroids and their associated vagile fauna,

where the hydroids are used as substrate and represent a food source for amphipods.

Epiphytic algae cover contributed little to explain variation in gammarid assemblage descriptors. These findings contradict those of previous studies, which indicated that epiphytic algae cover is as important as that of hydroids in the structuring of epifaunal assemblages, given that they also provide nutrients and add structural complexity to the habitat (Martin-Smith, 1993; Attrill et al., 2000; Schreider et al., 2003; Wikstrom & Kautsky, 2004; Jacobucci & Leite, 2014). It is likely that the epiphytes are linked to an increase in the structural complexity of the habitat, supporting a higher density and number of species. However, high densities of grazers, such as gammarids, may decrease epiphytic cover, losing its function as a predictive variable in habitat structural complexity. According to an experiment carried out by Poore et al. (2012) on the abundance of epiphytic algae, the removal of grazers did increase epiphytes. Epiphytes may affect the growth and survival of macroalgae (Buschmann & Gómez, 1993; Reis et al., 2003), so grazers are often hypothesized to benefit macroalgae by removing epiphytes (Poore et al., 2012). Therefore, as the coverage of epiphytic algae recorded in our samples was low (less than 25% in most cases), this may have limited its effects on the gammarid assemblages.

The negative correlation between the length of the *Sargassum* and gammarid assemblage descriptors (richness and density in December, diversity and evenness in March) also contradicts the findings of previous studies, which found a positive correlation between these variables (Attrill et al., 2000; Veiga et al., 2014; Torres et al., 2015). Space does not appear to be a limiting factor in macrophyte beds (Heck & Wetstone, 1977), in particular for gammarids that are able to move between patches (Tanaka & Leite, 2004). The structure of the gammarid assemblages associated with studied *Sargassum* spp. appears to be more dependent on structural complexity, hence the large number of positive and significant correlations between assemblage descriptors and number of branches and epiphyte cover, than on quantity of habitable area, given the low or negative correlations found with algae length. However, as with all models that attempt to explain the composition of epifaunal assemblages, a significant proportion of the variation was not accounted for, indicating the potential

influence of other environmental factors not evaluated in the present study.

Here, we show that an increase in algae structural complexity, which are associated with greater habitat heterogeneity (especially the number of branches and hydroid coverage), contributes to an increase in gammarid species richness, abundance, and diversity. We also highlighted the effects of macroalgae complexity on the structuring of gammarid assemblages. Both results contribute to the understanding of vagile epifauna distribution in macroalgal beds at a small spatial scale. However, there is the possibility that some difference among sites may have occurred, resulting in some variations in the structural algal and/or gammarid assemblages. Therefore, we suggest that further research should be conducted at sites where all species occur together.

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