Richness and biomass distribution of the mangrove macroalgal association in a subtropical estuary

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ABSTRACT

The richness and biomass distribution of mangrove macroalgae were evaluated along the main salinity gradient of the Paranaguá Bay subtropical estuarine complex in southern Brazil. We used a spatially hierarchical design to investigate the spatial scales that contributed most to the variation in richness and biomass within the association. A total of eighteen taxa of macroalgae and cyanobacteria were identified with nonlinear patterns of distribution. While richness correlated with the salinity gradient, algal biomass did not follow the predicted pattern. Conversely, most of the mangrove macroalgae distribution patterns were more related to small-scale processes than to salinity variation. These results indicated that even though coastal regions are exposed to large-scale environmental processes, the somewhat disregarded small-scale processes should be also considered to unravel patterns in biological distributions.

Descriptors: *Bostrychia*, Salinity gradient, Hierarchical sampling, Spatial scales.

INTRODUCTION

Mangrove trees support diverse macroalgal associations attached to their branches, roots and pneumatophores in intertidal and subtidal regions (Dawes et al. 1999; Zhang et al. 2014). This unique association of macroalgae was named Bostrychietum by Post (1936), referring to *Bostrychia-Caloglossa* associations. These associations include other genera of red algae, cyanobacteria and Chlorophyta (Pedroche et al. 1995). Although Bostrychietum is commonly identified in mangroves, it can also be found in salt marshes and sheltered habitats in temperate regions (Sluiman, 1978; Reine and Marchand, 1983).

Coastal macroalgae provide essential ecosystem services such as blue carbon sequestration (Hill et al. 2015); along with seagrass, mangrove macroalgae represent more than 50% of the carbon food source for polychaetes, crabs and oligochaetes (Kieckbusch et al. 2004). Bostrychietum itself is the main refuge for invertebrates, such as bivalves, acari, nematodes and terrestrial insects; therefore, it is essential for maintaining mangrove fauna diversity (Heithaus et al. 2011; Vieira et al. 2018).

Studies worldwide have investigated the main scales of spatial and seasonal variations in mangrove macroalgae species in estuarine environments (Fernandes et al. 2005, Melville et al. 2005, Peña-Salamanca 2008, Billah et al. 2016). Salinity gradients play an important role as a source of variability in mangrove macroalgae, causing the species distribution to change within estuaries (Yarish and Edwards 1982, Yokoya et al. 1999; Cunha and Costa

2002, Steinke et al. 2003, Fernandes et al. 2005). In a Brazilian estuary where the horizontal salinity gradient ranges from 0 to 30, species richness increased towards euhaline water (Cunha and Costa 2002). On the other hand, salinity did not affect species distribution in an Australian estuary, where the salinity range is less pronounced (10 to 20) (Melville and Pulkownik 2007).

Macroalgae tolerance to salinity is species-specific based on their physiological responses (Karsten, 2012). For example, under osmotic stress conditions, to maintain constant turgor pressure, species from the genus *Caloglossa* (Delesseriaceae) biosynthesize and accumulate the organic osmolyte mannitol (Karsten et al. 1992). According to species tolerance characteristics, they can be classified as euryhaline, referring to broad halotolerance, or stenohaline species, with a narrow range of salinity tolerance.

Describing the distribution area of algae species along a salinity gradient is facilitated by using a hierarchical sampling design. Hierarchical designs are essential to properly understand organism-environment relationships given the intrinsically scale-dependent patterns in nature (Horne & Schneider 1995). For example, the density of the crab *Ucides cordatus* is not affected by large-scale processes such as horizontal salinity gradients but rather by its patchy distribution at smaller scales (Sandrini-Neto & Lana 2012). In contrast, fauna associated with kelp forests responded to sea surface temperature patterns on a large scale (200 km) as well as to smaller scale processes (1 - 65 km) due to unknown factors (Lamy et al. 2018). Therefore, without properly addressing the involved spatial scales, we can infer incorrect distribution patterns or disregard small-scale interactions between associations, their environment, and biological traits responsible for structuring them (McGarigal et al. 2016).

Our study investigates how Bostrychietum algae distribution changes along an estuarine horizontal salinity gradient and within haline sectors. Changes were measured through macroalgal species richness, biomass, and patterns of association in mangroves from Paranaguá Bay in southern Brazil. We tested the hypothesis that the salinity gradient is a major driver of the Bostrychietum algae spatial distribution by increasing richness, biomass, and overall changes with increasing salinity.

METHODS

STUDY SITE

Paranaguá Bay, Paraná, in southern Brazil (Figure 1), has a subtropical climate, with an average annual precipitation of approximately 2,500 mm. The water temperature in summer and winter ranges from 23-30°C and 18-25°C, respectively, and the tidal cycle is semidiurnal, with a mean tidal range of 2.2 m (Lana et al. 2001). The water salinity ranges from 0 to 35, and the salinity gradient allows for the division of the bay into at least three haline sectors. The sectors are oligohaline (mean salinity of 15), mesohaline (mean salinity of 23) and euhaline (mean salinity of 27) (Lana et al. 2001; Marone et al. 2005). This estuary is also characterized by an energy gradient going from high-energy in the euhaline sector, to low-energy in the oligohaline sector (Lana et al. 2001). Throughout the sectors, the mangrove forests can be mono- or multispecific and composed of *Rhizophora mangle* L. (Rhizophoraceae), *Avicennia schaueriana* Stapf & Leechman ex Moldenke (Acanthaceae) and *Laguncularia racemosa* (L.) C. F. Gaertn (Combretaceae).

SAMPLING DESIGN

To study the spatial variation in the macroalgae association, we used a hierarchical design including two spatial scales of variation: sectors and areas (Figure 1). The minimum distance between sectors was 10 km (S1-Oligohaline, S2-Mesohaline and S3-Euhaline). Nested into sectors there were areas (A1, A2 and A3). The distance between areas within a single sector ranged between 1 and 5 km. Within each area, macroalgae were scraped from three tree stem surfaces, regardless of tree species. Trees were 1 to 5 m distant from each other. Sampling was performed at the mangrove fringe away from tidal river mouths to avoid freshwater discharge (Lana et al., 2001). Two sampling campaigns were carried out, totaling 54 samples. Sampling campaigns were performed at the end of winter (05 October 2011) and at the end of summer (04 April 2012) and were analyzed individually due to lack of seasonal replication.

FIELD AND LABORATORY PROCEDURES

The upper vertical limit of distribution of Bostrychietum algae coincides with mean high tides
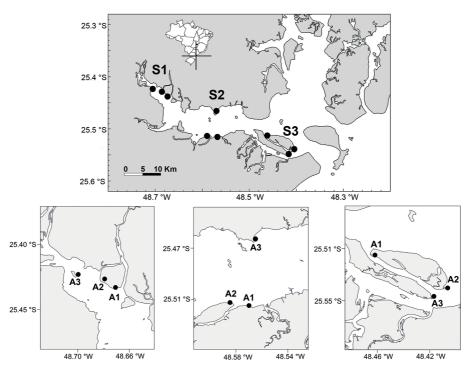
Figure 1. Paranaguá Bay with sectors (S1-Oligohaline, S2-Mesohaline and S3-Euhaline) and areas within sectors (dark circles) where samples were collected. Map source GSHHG database version 2.3.7 from 2017 (Wessel & Smith, 1996).

in Paranaguá Bay. In the euhaline sector, spring tide is approximately 1.7 m, and the upper limit of Bostrychietum algae is approximately 0.5 m, while in the oligohaline sector, spring tide builds up to 2.7 m, and upper limit is approximately 1 m (in relation to mean sea level) (Lana et al. 2001, Spier et al. 2016). Therefore, we used the upper vertical limit as an indicator of mean high tides, and standardized sampling 20-40 cm below this level; we thus reduced the variability in tidal elevation and algal desiccation frequency. The sampled area was calculated by multiplying 20 cm (vertical stem length being sampled) by tree stem diameter. The material was preserved in 4% formaldehyde until further processing.

In the laboratory, the algae were rinsed with freshwater, and the attached sediment was removed with brushes. Taxonomic identification followed Joly (1957, 1965, 1967), Cordeiro-Marino (1978), Hadlich & Bouzon (1985) and updates from Collado-Vides & West (1996), Cunha et al. (1999), West et al. (2001) and Alves et al. (2009), alongside information from the online database AlgaeBase (Guiry & Guiry, 2020). After identification, the material was rinsed one last time with freshwater to remove any residue and dried

in a Thermo Scientific oven at 60ºC until a stable mass was achieved. The dry weight of each species was determined using a balance with a precision of 0.001 g. Biomass values of Chlorophyta were below the scale detection limit, so we pooled all species together to obtain biomass data for the whole group.

Data analysis

To identify the overall patterns in Bostrychietum algae along the salinity gradient, we explored algae richness, total biomass, and the most abundant species. Total biomass data were based on the algal biomass (mg cm^{-2}) of each tree, regardless of algae species. Next, we identified the most abundant species of algae (>10 mg cm^{-2}) in the entire estuary (5 species in total). Richness and biomass means are reported with standard errors.

Spatial variability of richness, total biomass and most abundant species data were tested using nested ANOVA with fixed (sectors) and random factors (areas and replicates) in a balanced design. Prior to statistical tests, normality and homoscedasticity assumptions were verified using Shapiro-Wilk and Cochran's C tests, respectively, accepted for P >

0.05. When ANOVA results indicated significant differences, Student-Newman-Keuls post hoc analysis (SNK) was performed testing paired means. Cochran's test, nested ANOVA and SNK post hoc analysis were performed using the GAD package (Sandrini-Neto & Camargo, 2020). The percentage of contribution (PC%) was calculated using the function VarCorr from the lme4 package (Bates et al. 2015) and added to ANOVA tables. All statistics in this study were performed in R version 4.0.2 (R Core Team, 2020).

The Bostrychietum algae were evaluated as associations using multivariate analyses of association biomass and association composition. Association biomass takes into consideration the biomass data from each individual algae species identified (10 species in summer, 9 species in winter and the pooled Chlorophyta). Due to the high abundance of null values, the association biomass data were transformed to log $(x + 1)$, followed by PERMANOVA analysis based on the Bray-Curtis dissimilarity matrix (9999 permutations). The association biomass data were then transformed into presence/absence data for association composition analysis using PERMANOVA based on the Jaccard dissimilarity matrix (9999 permutations). Homoscedasticity of association biomass and composition data was checked with function betadisper, and PERMANOVAs were executed using adonis (model: matrices ~ sector + area:sector), both from vegan package (Oksanen, 2020). In case of significant differences, post hoc tests were performed using the pairwise.adonis function from the pairwiseAdonis package (Arbizu, 2017).

We applied non-Metric Multidimensional Scaling (nMDS) to the abovementioned distance matrices (Bray-Curtis and Jaccard) to visualize the spatial distance among samples. The nMDSs were generated using the metaMDS function from the vegan package (try=150) (Oksanen, 2020). The stress value is reported as an indicator of how well the data distribution represents the real distance among samples (< 0.1 good, > 0.2 random ordination (Clarke, 1993)).

RESULTS

SPATIAL VARIATION - TAXA

A total of sixteen species of macroalgae and two genera of cyanobacteria were identified (Table 1).

The mean richness per sample was 7.7 ± 0.30 and 6.6 ± 0.33 in summer and winter, respectively (Figure 2). In the summer campaign, the mean richness values were different among sectors (Table 2). Richness was higher at S3 (9 ± 0.7) than at S1 and S2 (6 ± 1 and 7 ± 1, respectively) (SNK, P < 0.05). Among areas, richness means were different within S1 and S3 (SNK, P < 0.05). In the winter campaign, richness was similar between sectors (S1: 6, S2: 6, S3: 7) and varied within S1 and S3, with mean richness ranging from 5 to 11 taxa per sample (SNK, P < 0.05).

The association composition based on presence/absence data varied at all spatial scales in both sampling campaigns (Table 2). The post hoc test was unable to detect the source of variation among areas. However, it showed differences among sectors (PERMANOVA, P < 0.001), and these differences can be visualized through the absence overlap of S3 with other sectors on the nMDS ordination plot (Figure 3A).

SPATIAL VARIATION - BIOMASS

The biomass data analyzed here belong to 10 species of Rhodophyta in the summer and 9 in the winter, plus the pooled Chlorophyta biomass, without distinction of species or genera. Individual Chlorophyta species and *Canistrocarpus cervicornis* biomass were below the scale detection limit. The outcome of the association biomass PERMANOVA analysis showed significant variation along the estuarine gradient in both sampling campaigns (Table 3). The nMDS ordination indicated S3 as being the most clearly separated from the others. The areas within S3 were not clearly separated in the nMDS plot; however, within S1 and S2, areas were grouped (PERMANOVA, P < 0.001) (Figure 3B, Table 3).

The mean total biomass was 6.3 ± 0.59 mg cm^{-2} and 7 ± 0.66 mg cm^{-2} for winter and summer, respectively. There was a tendency of increase in total biomass towards higher salinities in winter and more evidently so in summer when biomass values were 2.2 times higher in S3 than in S1 (S1: 4, S2: 7, S3: 9 mg cm^{-2}). This tendency was driven by high biomass of *B. montagnei* and *B. binderi* in S3 and their null values in S1 (Figure 4). However, a statistical test did not identify biomass mean value differences, probably due to differences in biomass among areas in S3 in both campaigns (SNK, P < 0.05).

Table 1. Presence and absence of the 18 species identified in Paranaguá Bay. Values are the relative biomass percentage of each species along the estuary in each sampling campaign. The asterisk (*) indicates the presence of the species in the sampling area when biomass was below the detection limit.

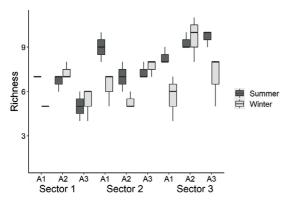|	Winter									Summer								
	S1-Oligohaline			S2-Mesohaline			S3-Euhaline			S1-Oligohaline			S2-Mesohaline			S3-Euhaline		
	A1	A2	A3	A1	A2	A3	A1	A2	A3	A1	A2	A3	A1	A2	A3	A1	A2	A3
Rhodophyta																		
Bostrychia radicans (Montagne) Montagne	24	20	3	24	16	7	>1	4	1	20	17	36	3	6	>1	1	14	3
Bostrychia calliptera (Montagne) Montagne	26	18	>1	2	31	8	2	10	2	>1	1	>1	19	20	40	2	16	1
Bostrychia pinnata J. Tanaka and Chihara	10	6	35	2	10	27	2	5	3	>1	6	25	20	15	29	2	2	>1
Bostrychia montagnei Harvey						3	16	54	27				4	7	>1	32	17	39
Bostrychia moritziana (Sonder ex Kützing) J. Agardh																	90	10
Bostrychia tenella (J.V. Lamouroux) J. Agardh	27						2	62	7								63	37
Bostrychia binderi Harvey	1							45	54							>1	53	46
Catenella caespitosa (Withering) L.M. Irvine	10	4	55	31						67	32	>1						
Caloglossa leprieurii (Montagne) G. Martens	7	7	14	12	22	31		2	5	56	3		2	2	>1	31	3	2
Caloglossa beccarii (Zanardini) De Toni				33		*		67		100						*	*	
Chlorophyta																		
Rhizoclonium riparium (Roth) Harvey	*	*	*	*		*	*	*	*	*	*	*	*	*	*	*	*	*
Pseudorhizoclonium africanum (Kützing) Boedeker					*	*	*	*				*		*	*			
Cladophoropsis membranacea (Hofman--Bang ex C. Agardh) Børgesen					*				*				*					
Cladophora rupestris (Linnaeus) Kützing								*					*					
Boodleopsis pusilla (Collins) W.R. Taylor, A.B. Joly and Bernatowicz		*						*					*	*			*	
Ochrophyta																		
Canistrocarpus cervicornis (Kützing) De Paula and De Clerck																		*
Cyanobacteria																		
Microcoleus sp. Desmazières ex Gomont	*	*	*			*	*	*	*	*	*	*	*	*	*	*	*	*
Lyngbya sp. C. Agardh ex Gomont																	*	

Figure 2. Boxplot of the richness of taxa identified along the estuarine gradient. Winter (gray) and summer sampling campaign (black).

The overall most abundant species were *B. radicans*, *B. pinnata*, *B. montagnei*, *B. calliptera* and *B. binderi*, all of which had a total biomass above 10 mg cm^{-2} (Figure 4). The testing of the ANOVA assumptions for these species resulted in heteroscedasticity in *B. montagnei*, *B. pinnata*, and *B. radicans* biomass data, requiring fourth root transformation to reduce the heterogeneity of the variances in both sampling campaigns. Furthermore, *B. calliptera* data were square root transformed in winter and fourth root transformed in summer. *B. calliptera* data (winter) and *B. montagnei* data (summer) were not normally distributed even after data transformation. None of the requirements could be reached for *B. binderi* (both sampling campaigns) and *B. montagnei* (winter campaign). Given the general robustness of ANOVA

against non-normality and heterogeneity of variance under balanced designs (Underwood 1997), we opted for doing the analyses but lowered the significance level from 0.05 to 0.01 (Underwood 1997).

Bostrychia radicans was present throughout the estuarine gradient, however, it had higher biomass in S1 (SNK, $P < 0.05$). *Bostrychia pinnata* was also present at all sampling sites, and its biomass varied within sectors rather than among sectors. In contrast, *B. montagnei* and *B. binderi* biomasses were higher in S3 than in the other sectors. Although the *B. binderi* and *B. montagnei* distribution patterns were similar, *B. montagnei* biomass was higher in S3 in both campaigns, while *B. binderi* had higher biomass only in the summer campaign (Table 3). The statistical analysis of *B. calliptera* biomass data had inconclusive outcomes. Significantly different mean values were identified among areas in winter and among sectors in summer.

DISCUSSION

Our working hypothesis was partially refuted. Although the richness and composition of Bostrychietum algae correlated positively with the salinity gradient, algal biomass did not follow this pattern and did not vary significantly on a larger spatial scale. The richness associated with hard substrate provided by regional mangroves was in fact influenced by the estuarine salinity gradient, with a greater richness in S3, a tendency even more evident in the summer campaign. The association composition

Table 2. Summary of statistical analyses applied to taxon data. Richness was analyzed with nested ANOVA. Association composition (presence/absence) was analyzed with a PERMANOVA, for which R² values are shown. (df: degrees of freedom; MS: Mean of Squares; F: (random nested factor corrected by residuals), R2: Correlation, PC%: Percentage of Contribution). P. value < alpha level in bold.

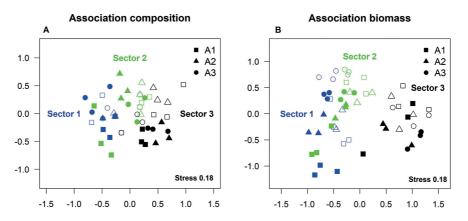|	**Winter**					**Summer**				
ANOVA	df	MS	F	PC%	P	df	MS	F	PC%	P
Richness										
Sector	2	5.60	0.79	0	0.497	2	18.81	6.77	46	0.028
Area	6	7.11	5.65	55	**0.001**	6	2.78	5.36	30	0.002
Residuals	18	1.26		45		18	0.51		25	
PERMANOVA	df	MS	F	R²	P	df	MS	F	R²	P
Association composition										
Sector	2	0.52	8.35	31	**< 0.001**	2	0.88	28.12	60	**< 0.001**
Area	6	0.20	3.25	36	**< 0.001**	6	0.10	3.28	21	**< 0.001**
Residuals	18	0.06		33		18	0.31		19	

Figure 3. Non-Metric Multidimensional Scaling ordination (nMDS) from association composition (A) and association biomass (B). Markers symbolize each sampling site in each sampling campaign, winter (empty symbols) and summer (filled symbols). Sectors are differentiated by color, blue - Oligohaline sector (Sector 1); green: Mesohaline sector (Sector 2) and black: Euhaline sector (Sector 3). Areas within each sector are differentiated by symbols (A1 - square, A2 - triangle, A3 - circle). The value stress is reported as an indicator of quality of the scaling.

also changed along the estuarine gradient due to the limited distribution of *C. caespitosa* and the absence of *B. montagnei, B. moritziana, B. tenella, B. binderi, C. membranacea* and *C. rupestris* in the low salinity sector. Other species were present along the entire estuarine gradient, such as *B. radicans, B. calliptera, B. pinnata, C. leprieurii, R. riparium* and *Microcoleus* sp.

At the large spatial scale, there was a tendency of total biomass increase in S3, detected mainly in the summer sampling campaign. This tendency was induced by the biomass of *B. montagnei* and *B. binderi*, which were restricted to higher salinity environments and are the largest algae among Bostrychietum. Morphologically, *B. binderi* has denser cortication than other species, and *B. montagnei* has up to seven pericentral cells. Therefore, they are able to produce more biomass by area of fixation when at optimum growth conditions compared to the dominant species in other sectors. However, *B. binderi* distribution was patchy and had high variability among replicates within areas. Association biomass was significantly different among all scales. This indicates that the association biomass may have had the same amount of biomass throughout the estuary, but this biomass is not equally distributed among species at any of the spatial scales. The most abundant species corroborated the uneven biomass pattern of distribution, showing greater variability at small scales. In summary, our hypothesis of biomass increase with higher salinity

was not corroborated, reinforcing the need to better understand the small-scale processes inducing the Bostrychietum algae biomass distribution.

The greater variability of Bostrychietum algae at the smaller scale (areas) than large scale (sectors) seemed to be in responce to environmental conditions other than salinity. Even though we tried to standardize the environmental conditions where samples were collected (e.g. same day, same tide, at mangrove fringe, same substrate and sampling height), the areas are subject to other variables not easily correlated to the Bostrychietum algae distribution. First, Bostrychietum algae compete for hard substrates inside mangroves. High canopy density and high shade levels tend to decrease thermal exposure and humidity loss, therefore reducing emersion stress and leading to an increase in algal diversity and biomass (Yokoya et al. 1999, Zhang et al. 2014). Environmental disturbances such as waves, sediment in suspension, availability of nutrients, and other habitat conditions are known to cause variations on small scale (Seangkaew et al. 2016). Finally, we collected algae within a 20 cm vertical distribution, *Bostrychia scorpioides* and *Catenella caespitosa* may show different phenotypes and physiological responses already within a vertical range of 30 cm (Sánchez de Pedro et al. 2016). In this context, our small-scale sampling analyses (within areas) were limited by a low replicate number (3) and we did not account for all

Table 3. Summary of statistical analyses applied to biomass data. Association biomass was analyzed with PERMANOVA for which R^2 values are shown. The total biomass and the biomass of the five most abundant species were analyzed with nested ANOVA. (df: degrees of freedom; MS: mean of squares; F: F-ratio (random nested factor corrected by residuals), R2: correlation, PC%: percentage of contribution). P. value < alpha level in bold.

	Winter					Summer				
PERMANOVA	df	MS	F	R^2	P	df	MS	F	R^2	P
Association biomass										
Sector	2	1.31	14.92	44	**< 0.001**	2	1.82	27.60	55	**< 0.001**
Area	6	0.28	3.23	29	**0.034**	6	0.28	4.34	26	**< 0.001**
Residuals	18	0.26		27		18	0.66		18	
ANOVA	df	MS	F	PC%	P	df	MS	F	PC%	P
Total biomass										
Sector	2	0.31	0.32	0	0.731	2	125.45	4.41	37	0.066
Area	6	0.96	5.46	55	**0.002**	6	85.30	2.66	27	**0.050**
Residuals	18	0.17		45		18	96.19		36	
B. radicans										
Sector	2	0.80	5.06	29	0.051	2	0.45	6.18	45	**0.034**
Area	6	0.15	3.09	25	**0.029**	6	0.07	4.10	25	**0.009**
Residuals	18	0.05		46		18	0.01		30	
B. pinnata										
Sector	2	0.40	0.99	8	0.422	2	1.60	4.66	37	0.060
Area	6	0.40	2.42	42	0.068	6	0.34	4.76	34	**0.004**
Residuals	18	0.16		50		18	0.07		29	
B. calliptera										
Sector	2	0.15	0.23	0.0	0.797	2	1.97	10.32	43	**0.011**
Area	6	0.66	6.35	43	**< 0.001**	6	0.19	2.59	18	0.054
Residuals	18	0.10		57		18	0.07		39	
B. montagnei										
Sector	2	5.72	33.43	51	**< 0.001**	2	3.79	22.35	54	**0.001**
Area	6	0.17	4.90	31	**0.003**	6	0.16	2.23	0	0.087
Residuals	18	0.03		18		18	0.07		46	
B. binderi										
Sector	2	0.33	2.73	30	0.143	2	7.41	7.58	39	0.023
Area	6	0.12	1.10	0	0.395	6	2.93	27.96	36	**< 0.001**
Residuals	18	0.10		70		18	0.01		25	

environmental variables. Therefore, studies including smaller spatial scales appropriately correlated with environmental forces will be necessary for a better understanding of the variation within areas.

The sampling design adopted does not allow for the evaluation of temporal variations due to the lack of seasonal replication. However, seasonal variations in the composition and total biomass of Bostrychietum have already been reported in several studies (Bouzon & Ouriques 1999; Melville et al. 2005; Zhang et al. 2014; Billah et al. 2016). In this sense, seasonal variability may explain the differences or inconsistencies in Bostrychietum algae responses among sampling campaigns, such as for the biomass of *B. calliptera*. The Paranaguá Bay climate has a typical rainy season (late spring to most of the summer) and a dry season (late autumn to late winter) (Lana et al., 2001), which could affect the vertical distribution
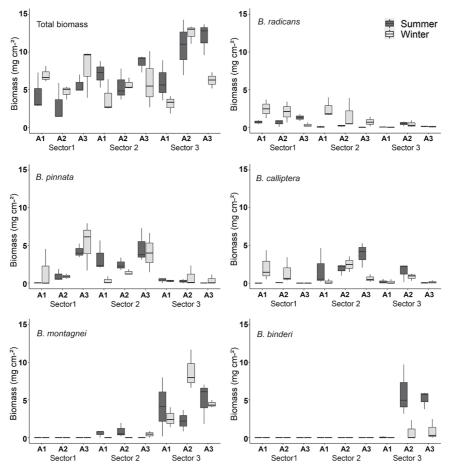
Figure 4. Box plots of total biomass and biomass data of the five most abundant species along the estuarine gradient. Dry weight values given in mg cm^{-2}.

and photosynthesis rate and thus the growth and biomass accumulation of *Bostrychia* and *Caloglossa* (Fernandes and Alves 2011. Peňa et al., 1999).

Macroalgae are well adapted to salinity variation (Bisson & Kirst 1995, Karsten 2012). For example, *Bostrychia* species are known to maintain photosynthetic rates at salinities ranging from 5 to 45, and they can tolerate exposure to freshwater for up to two days without experiencing permanent damage (Mann and Steinke 1988). In addition, *B. radicans*, *B. calliptera* and *B. pinnata* have adaptations to adjust the intracellular osmotic response to variations in salinity (Karsten et al. 1996)one of the citric acid cycle (malate dehydrogenase, MDH. Contrary to expectations, *Catenella caespitosa* was restricted to the oligohaline sector. *Catenella* has physiological adaptations to cope with salinity variation (Karsten et al. 1996) one of the citric acid cycle (malate dehydrogenase,

MDH and *Catenella caespitosa* was found in the Adriatic Sea (salinity 38) (Battelli 2004) and close to river mouths (salinity ~20) (Pedroche et al. 1995, Sánchez de Pedro et al. 2016). Other factors must have affected its distribution limited to the low salinity sector of Paranaguá Bay, such as competition with *Bostrychia montagnei* and *B. binderi*. The variability of Bostrychietum algae among areas emphasizes the need for additional studies regarding environmental forces acting on smaller scales, including biological interactions among species, for a better understanding of the dynamics of Bostrychietum algae.

Differences in the salinity tolerance of the Bostrychietum algae and their cosmopolitan distribution could provide applications regarding their use as mangrove environmental biomonitors (Melville and Pulkownik 2006, 2007). AlgaeBase (Guiry and Guiry, 2016) data show that *B. calliptera*, *B. montagnei*,

B. moritziana and *B. radicans* are present along the entire Brazilian coast and have a broad global distribution, generally accompanying the geographical limits of mangroves. Among those species, *B. radicans* and *B. pinnata* were present along the entire salinity gradient in both campaigns in Paranaguá Bay. This makes both species suitable for use as environmental biomonitors.

CONCLUSION

The estuarine horizontal salinity gradient will affect the distribution of a few species of Bostrychietum, such as *B. montagnei*, *B. binderi* and *B. tenella*, which were commonly identified in the higher salinity sector. Therefore, higher richness was observed in higher salinity regions, partially corroborating our hypothesis. However, the salinity gradient has no apparent or linear effect on the total biomass along the estuary. Overall, we identified that salinity is not the main driver of the distribution of Bostrychietum algae; conversely, the main variations were found on the small scale (areas). Understanding the small scale, heterogeneous variability in the distribution of mangrove algae will demand a finer hierarchical sampling design and monitoring of environmental variables.

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AUTHOR CONTRIBUTIONS

I.R.W.M.: Conceptualization; Formal analysis; Investigation; Writing - original draft; Writing - review & editing.

P.C.L.: Conceptualization; Resources; Supervision; Writing - review & editing.

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