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Patterns of spatial distribution in macroalgal communities from tropical lotic ecosystems

FÁBIO R. BORGES[1] and ORLANDO NECCHI JÚNIOR[1,2]

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ABSTRACT – (Patterns of spatial distribution in macroalgal communities from tropical lotic ecosystems). Three sampling sites were analysed in each of the following tropical regions: 1) northwestern São Paulo State, representing a disturbed region; 2) Bonito, Mato Grosso do Sul State, representing a hard water region; and 3) Ubatuba, northern costal region of São Paulo State, a well preserved tropical rainforest region. The hard water region had the highest mean values for macroalgal species richness (6.3) and diversity index (*H'* = 0.62). Northwest and rainforest regions had the highest percent cover values (22.5% and 17.0%, respectively). All sites in the northwest region had one or two dominant species (percent cover significantly higher than the remaining species), characterizing the niche pre-emption distribution pattern. The same pattern was found in two sites of the Atlantic rainforest. The hard water region had dominance of one species in two out of the three sites, but differently from the northwest region, niche overlap values were lower, evidencing a patch distribution. Competition for space was one of the main factors to explain spatial distribution. Overall, sites characterized by niche pre-emption had lower species richness, higher values for niche width and overlap, dominance index and percent cover of dominant species. In contrast, sites characterized by patch distribution had higher species richness and lower values for niche overlap and width, dominance index and percent cover.

Key words - distribution, ecological niche, lotic ecosystem, macroalga, tropical region

RESUMO – (Padrões de distribuição espacial de comunidades de macroalgas de ecossistemas lóticos tropicais). Foram analisados três pontos em cada uma das três seguintes regiões tropicais: 1) região Noroeste do Estado de São Paulo, representando região degradada; 2) região de Bonito, Mato Grosso do Sul, representando ambiente de águas duras; e 3) região de Ubatuba, litoral Norte de São Paulo, ambiente de Mata Atlântica bem preservado. A região de águas duras apresentou maiores valores médios de riqueza de espécies de macroalgas e índices de diversidade (6,3 espécies por ponto e *H'* = 0,62). As regiões Noroeste e de Mata Atlântica apresentaram maiores valores médios de cobertura percentual (22,5% e 17,0%, respectivamente). Em todos os pontos da região noroeste ocorreu uma ou duas espécies dominantes (com cobertura percentual significativamente maior que as demais), o que caracteriza o padrão de distribuição do tipo pré-ocupação de nicho. O mesmo padrão foi encontrado para dois pontos da região de mata Atlântica. Na região de águas duras foi verificada dominância de uma espécie em dois dos três pontos amostrados, mas ao contrário da região noroeste, os valores de sobreposição de nicho foram menores, evidenciando o padrão de distribuição em mosaico. A competição por espaço é um dos principais fatores que explica a distribuição espacial. De forma geral, ambientes com o padrão do tipo pré-ocupação de nicho apresentaram baixa riqueza de espécies, altos valores de sobreposição e largura de nicho, alta cobertura percentual para as espécies dominantes e altos valores para o índice de dominância. Em contrapartida, ambientes com o padrão de distribuição em mosaico apresentaram alta riqueza de espécies, baixos valores de largura e sobreposição de nicho, baixa cobertura percentual e baixo índice de dominância.

Palavras-chave - distribuição, ecossistema lótico, macroalga, nicho ecológico, região tropical

Introduction

The partitioning of habitats has been largely investigated in communities of terrestrial plants but sparsely for aquatic plants (French & Chambers 1996). Some descriptive studies focused on the description of spatial and temporal distribution patterns of lotic macroalgal communities; such studies have been conducted in North American (the central-south region of Alaska, U.S.A., by Sheath *et al.* 1986; and eastern region of the boreal forest by Sheath *et al.* 1989, Sheath & Cole 1992) and in Brazilian ecosystems (northwest region of São Paulo State by Necchi Júnior *et al.* 1995a; Atlantic Rainforest by Branco & Necchi Júnior 1996; three drainage basis by Branco & Necchi Júnior 1998; biomes in São Paulo State by Necchi Júnior *et al.* 2000). These studies described mainly the relationships of physical and chemical variables with the characteristics of the community (species richness and abundance), aiming to evidence the spatial distribution patterns for

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[1] Universidade Estadual Paulista, Departamento de Zoologia e Botânica, Rua Cristóvão Colombo, 2265, 15054-000 São José do Rio Preto, SP, Brazil.

[2] Author for correspondence: orlando@ibilce.unesp.br

macroalgal communities from those regions. Such investigations did not approach the ecological relationships among the different species, which are relevant in determining the patterns of distribution of the populations within the communities.

Some general patterns of spatial distribution of lotic macroalgal communities have been evidenced (Sheath *et al.* 1986, 1989, Sheath & Cole 1992, Branco & Necchi Júnior 1996, 1998, Necchi Júnior *et al.* 1995a, 2000) and can be summarized as follows: (1) large quantitative dominance and qualitative predominance of few species; (2) niche pre-emption, in which one or few species occupy most part of the environmental resources (in this case, substratum) and the other species compete for the remaining resources; and (3) patch distribution, which is characterized by the fact that the communities with higher abundance are also the ones that show the higher diversity (in species numbers). It is a general assumption that few species are able to tolerate the fast and wide fluctuations in environmental conditions, typical of lotic ecosystems (Sheath *et al.* 1986, 1989, Sheath & Cole 1992, Branco & Necchi Júnior 1996, 1998, Necchi Júnior *et al.* 1995a, 2000).

Based on the available information the following hypotheses were tested: (1) the competition for space is expected to be one of the main factors that explain the patterns of spatial distribution; (2) the coexistence of a relatively high species number in the same area would be possible by the occupation of different niches in the same stream segment and characterizes the patch distribution; and (3) a high quantitative dominance and qualitative predominance of few species is expected within the study regions. Considering the scarcity of information on the ecological relationships among species within a stream segment, we aimed the evaluation of some aspects of the community structure (species richness and abundance, micro-habitat characteristics and the influence of environmental variables) in lotic ecosystems of three distinct regions from southeastern and mid-western Brazil. We focussed on the occurrence of resource competition or repartition among species of these communities by application of indices of niche overlap and width, as well as to recognize the limiting resources for such relationships.

Material and methods

Macroalgal spatial distribution was analized in lotic ecosystems of three regions representing different biomes: (1) the northwest region of São Paulo State, which represents a disturbed region consisting of cerrado (Brazilian savanna) and semideciduous tropical forest, characterized by streams with low or no marginal vegetation cover (high light incidence), moderate levels of nutrients and variable substrata; (2) the region of Bonito, State of Mato Grosso do Sul, representing a hard water environment with variable degrees of shading, high values of pH, conductivity and transparency (due to high concentrations of bicarbonates and carbonates), with a wide variety of substrata; and (3) the region of Ubatuba, northern coastal area of São Paulo State, which represents a well-preserved Atlantic Rainforest environment, characterized by generally shaded streams (low light incidence), low conductivity waters (poor in nutrients), and rocky substrata. Three different sampling sites (stream or river segments) were analyzed in each of the study ecosystems, and the characteristics of each site are summarized in tables 1-3.

In the present study, we adopted the concept of macroalga proposed by Sheath & Cole (1992). For the visualization of the macroalgal communities a sub-aquatic viewing box with a glass bottom was used (Necchi Júnior *et al.* 1994). The samplings of macroalgal communities and the measurements of environmental variables were made from early June to late August, the typical period of higher macroalgal species richness and abundance in lotic ecosystems from tropical regions (Necchi Júnior & Pascoaloto 1993, Branco & Necchi Júnior 1997). This period corresponds to the driest season of the year. Macroalgal sampling was made by the quadrat technique associated to the point interception (Krebs 1989, Necchi Júnior *et al.* 1995b, Necchi Júnior 2004). A 10 meters length stream segment was sub-divided in 1 m-intervals, and at each interval three sampling units were placed (circles with 25 cm in diameter and area = 491 cm^2), equidistantly in relation to the stream width, totalizing 30 unities for the whole segment. The circular shape is suggested to minimize the edge effect (Krebs 1989, Necchi Júnior *et al.* 1995b, Necchi Júnior 2004). The evaluation of the macroalgal species abundance was based on percent cover within the sampling units by visual estimation. The frequency of occurrence of each macroalgal species within the sampling units was further calculated [(number of sampling units with the species presence / the total number of sampling units) × 100]. We consider a species dominant when it had a significantly higher cover than the remaining species. Samples of each species were collected for specific identification in the laboratory (while still alive in most cases). These specimens were later preserved in 4% formaldehyde solution and incorporated to the SJRP Herbarium. Briophytes were also considered in our analyses, since they seem to compete with macroalgae for space (*i.e.* substratum, Necchi Júnior *et al.* 1995b), which is relevant for the purpose of this investigation.

The following environmental variables were measured at the center of each sampling unit: current velocity (measured with a Swoffer current velocity meter model 2100 close to the bottom), depth (with a ruler to the nearest 0.5 cm), irradiance (with a quantameter Li-Cor LI-189 with LI-193SA spherical

Table 1. Characterization of the three sampling sites from the northwest region of São Paulo State. Values represent means (*n* = 30 for substratum, current velocity, irradiance and depth; *n* = 3 for the other variables; BO = boulder; GR = gravel; MF = macrophyte; OT = others; RO = rock; SC = sand-clay).

Location and date	Substratum (%)	Temperature (ºC)	Conductivity (μS cm^{-1})	Turbidity NTU	Current velocity (cm s^{-1})	pH	O_2 (mg L^{-1})	Irradiance (μmol m^{-2} s^{-1})	Depth (cm)
Site 1									
Ipiguá, Córrego Barra Funda 20º38’45” S, 49º24’12” W 5-VII-2003	RO - 88 SC - 10 OT -2	18.2	15	8	35.3	6.8	6.3	1412.0	10.7
Site 2									
Potirendaba, Ribeirão Borá 20º58” S, 49º25’02” W 10-VII-2003	SC - 50 RO - 42 GR - 8	17.3	60	9	23.2	7.1	5.9	1554.0	8.6
Site 3									
S. José Rio Preto, Córrego Boa Esperança 20º52’54” S, 49º22’40” W 10-VII-2003	BO - 63 GR - 15 MF - 10 OT - 12	20.0	27	10	44.4	6.6	5.5	975.5	17.2

Table 2. Characterization of the three sampling sites from the hard water region in Bonito, State of Mato Grosso do Sul. Values represent means (*n* = 30 for substratum, current velocity, irradiance and depth; *n* = 3 for the other variables; GR = gravel; PE = pebble; OT = others; SC = sand-clay).

Location and date	Substratum (%)	Temperature (ºC)	Conductivity (μS cm^{-1})	Turbidity NTU	Current velocity (cm s^{-1})	pH	O_2 (mg L^{-1})	Irradiance (μmol m^{-2} s^{-1})	Depth (cm)
Site 1									
Bonito, Córrego Jenipapo 20°59’07” S, 56°27’08” W 1-VI-2002	SC - 33 GR - 31 PE - 17 OT - 19	21.3	572	4	13.7	7.3	5.2	561	21.0
Site 2									
Bonito, Rio Formoso 21°15’14” S, 56°33’36” W 2-VI-2002	GR - 49 PE - 21 SC - 20 OT - 10	22.5	406	5	24.9	7.7	5.3	1489	26.8
Site 3									
Bonito, Rio Formoso, Balneário Municipal 21°10’08” S, 56°26’40” W 3-VI-2002	SC - 67 GR - 11 OT - 22	21.9	164	2	17.1	7.9	5.7	1296	107.0

Table 3. Characterization of the three sampling sites from the Atlantic Rainforest region in Ubatuba, São Paulo State. Values represent means (n = 30 for substratum, current velocity, irradiance and depth; n = 3 for the other variables; BO = boulder; GR = gravel; OT = others; RO = rock; SA = sand).

Location and date	Substratum (%)	Temperature (ºC)	Conductivity (μS cm^{-1})	Turbidity NTU	Current velocity (cm s^{-1})	pH	O$_2$ (mg L^{-1})	Irradiance (μmol m^{-2} s^{-1})	Depth (cm)
Site 1									
Ubatuba, Núcleo Picinguaba, Rio da Fazenda 23º20'32" S, 44º50'18" W 21-VII-2003	RO - 58 BO - 15 GR - 15 AS - 12	17.4	18	2	24.5	6.8	7.0	22	31.7
Site 2									
Ubatuba, Rio Prumirim, Cachoeira 23º22'27" S, 44º57'58" W 21-VII-2003	RO - 82 AS - 18	18.1	39	2	81.2	6.7	6.1	34	11.4
Site 3									
Ubatuba, Rio Grande 23º23'41" S, 45º07'17" W 22-VII-2003	RO - 50 BO - 19 AR - 16 OT - 15	18.3	21	1	13.0	6.5	6.2	192	25.0

quantum sensor) and substratum type (estimated by comparison to the particle size classes, as described by Gordon *et al.* 1992). In addition, we measured temperature, pH, turbidity, conductivity and dissolved oxygen for the whole stream segment. These measurements were obtained with a HORIBA U-10 water quality checker, equipped with a multiple function probe, from water samples taken at three different times along the sampling period within each stream segment.

For each population we calculated niche width using the standardized Kevin index (Krebs 1989), aiming to evaluate the level of specialization of each species, as follows: $B_A = (B - 1)(n - 1)^{-1}$, where $B = 1/\Sigma (p_{xi})^2$, p_{xi} = relative abundance (proportion of percent cover) of species × at sampling unit i (xi/X); $X = \Sigma xi$. Values range within a scale of 0 to 1. Niche overlap was estimated by the Schoener index (Krebs 1989) among the main constituent species for each community: $P_{jk} = [\Sigma (minimum\ p_{ij}, p_{ik})]100$, where P_{jk} = niche overlap (%) beween species j and k for each microhabitat characteristic (irradiance, current velocity, depth and substratum); p_{ij} and p_{ik} = proportional abundance (percent cover) for each species within each microhabitat characteristic "state"; n = total number of microhabitat characteristic "state". This index was applied to evaluate eventual differences in resource uses and interpreted as follows (according to French & Chambers 1996): competition, when the niche overlap value was higher than 50%; and partitioning, when the values were lower than 50%. Niche overlap index was applied only among macroalgal species with frequency higher than 17% (presence in at least 5 of the 30 sampling units), which provided us with a minimal reliability for this index.

Shanon-Wiener diversity index (Krebs 1989) was calculated for each community, aiming a comparison within and among regions, as follows: $H' = \Sigma s\ (pi\ log_n p_i)$, where: p_i = proportion (abundance = % cover) of species i within community; i = 1; s = number of species in the community. Simpson dominance index (Krebs 1989) was also applied, intending to evaluate the dominance of one or few species for the community, as follows: $D = \Sigma pi^2$. Pearson's product-moment correlation coefficient (Zar 1999) was calculated for the evaluation of the associations among the abundance (percent cover) values of the species and the environmental variables. One way analysis of variance (ANOVA) and the Newman-Keuls multiple comparison test (Zar 1999) were applied to verify the occurrence of significative differences among the environment variables and the abundance of the different populations within each sampling site. Statistical tests were performed using the Statsoft Statistica package, version 5.5, whereas graphs were prepared with Microcal Origin, version 5.0 software.

Results

Northwest region of São Paulo State – Two species of macroalgae (*Phormidium retzii* (C. Ag.) Gom. and the 'Chantransia' stage of *Batrachospermum* sp.) and a species of moss (*Fissidens* sp.) were found at site 1; four species of macroalgae occurred at site 2 (*Oedogonium* sp., *P. retzii*, *Stigeoclonium helveticum* Vischer and the 'Chantransia' stage of *Batrachospermum* sp.); and at site 3 four species were observed: *P. retzii*, *Oedogonium* sp., *S. helveticum* and *Batrachospermum delicatulum* (Skuja) Necchi Júnior & Entwisle, plus the 'Chantransia' stage of *B. delicatulum*. The Shannon-Wiener diversity index (*H'*, table 4) ranged from 0.38 (site 3) to 0.76 (site 1), whereas the Dominance index (*D'*) oscillated from 0.49 to 0.83 for sites 1 and 3, respectively.

Two sites of this region have shown one dominant species and at site 1 there were two dominant species (figure 1). Dominance was also revealed by species frequency in each site (figure 1), however in this case, the difference between the first to the second species with higher frequency was not as high as for percent cover for sites 2 and 3. The same algae with higher values of percent cover and frequency were also the ones that had higher values of niche width at sites 1 and 3 (figure 1). The second species with higher percent cover and frequency at site 2 (*S. helveticum*) had the highest niche width, but very close to that of *Oedogonium* sp. (the species with higher cover and frequency).

In general, the values of niche overlap were high for this region (table 4). Niche overlaps were calculated only between *Fissidens* sp. and 'Chantransia' at site 1, which varied from 64.9% (for irradiance) to 83.6% (for dominant substratum). Niche overlaps between *Oedogonium* sp. and *S. helveticum* at site 2 (table 5) varied from 89.6% (for substratrum) to 92.1% (for irradiance), whereas for site 3, the values between *Oedogonium* sp. and 'Chantransia' oscillated from 44% (for substratum) to 67.9% (for irradiance).

Hard water region – Species richness was generally high at sites of this region. Site 1 had six macroalgal species (*Batrachospermum globosporum* Israels., *Thorea hispida* (Thur.) Desv., *Cladophora glomerata* (L.) Kütz., *Nitella furcata* (Bruz.) C. Ag., *Rhizoclonium hieroglyphicum* (C. Ag.) Kutz. and *Vaucheria* sp.), plus the 'Chantransia' stage of *Batrachospermum* sp. We collected specimens of *Compsopogon coeruleus* (C. Ag.) Mont., *N. furcata*, *R. hieroglyphicum*, *Spirogyra* sp., *Phormidium cebennense* Gom. and *P. retzii* at site 2. Six species were also found at site 3: *Chara rusbyana* Howe, *N. furcata*, *Lyngbya ceylanica* Wille, *Phormidium fragile* Gom., *Spirogyra* sp. and *B. globosporum*. Shannon-Wiener index varied from 0.51 to 0.75 for sites 3 and 1, respectively, whereas the dominance index was low for the three sites, ranging from 0.19 to 0.41 for sites 1 and 3, respectively (table 4).

There was dominance of one species upon the others at sites 2 and 3 (figure 2). At site 1 the alga with higher frequency ('Chantransia') was not the one with higher values of percent cover (figure 2), whereas at sites 1 and 2 the species with higher values of niche width ('Chantransia' for site 1 and *P. cebennense* for site 2) were not the ones with the highest values of percent cover. However, these species had high frequencies at both sites (figure 2). In contrast, the species with highest niche width for site 3 (*C. rusbyana*) was also the one with highest values of cover and frequency. Values of niche overlap were relatively low for this region (table 6), ranging from zero, between

Table 4. Biological variables (overal means ± standard-deviations; $n = 3$ except when otherwise specified) for each region studied. Different letters indicate significant differences ($P < 0.05$) by Newman-Keuls test.

Variables	Regions/biomes Northwest	Hard water	Atlantic Rainforest
Species richness	4.0 ± 1.0 (a)	6.33 ± 0.6 (b)	4.7 ± 0.6 (a)
Diversity index (*H'*)	0.52 ± 0.21 (a)	0.62 ± 0.1 (a)	0.48 ± 0.2 (a)
Dominance index (*D*)	0.64 ± 0.17 (a)	0.31 ± 0.1 (a)	0.44 ± 0.3 (a)
Percent cover (%)	6.1 ± 3.5 (a)	1.1 ± 0.6 (a)	4.8 ± 4.0 (a)
Niche width (B_A) - Lewin index	0.26 ± 0.10 (a) ($n = 12$)	0.10 ± 0.02 (a) ($n = 19$)	0.17 ± 0.20 (a) ($n = 15$)
Niche overlap (%) - Schoener index	74.0 ± 17.2 (a) ($n = 12$)	54.6 ± 2.6 (a) ($n = 60$)	64.5 ± 31.1 (a) ($n = 40$)

‘Chantransia’ and *R. hieroglyphicum* and *Vaucheria* sp. for depth and current velocity at site 1, to 100% between *R. hieroglyphicum* and *Vaucheria* sp, for the same variables at the same site (table 6). Niche overlap values (table 6) varied from 42.4% (between *Spirogyra* sp. and *P. retzii*) to 72.2% (between *P. retzii* and *P. cebennense*, both for substratum) at site 2; for site 3 they varied from 31% (among *C. rusbyana* and *P. fragile* for irradiance) to 86% (among *C. rusbyana* and *B. globosporum* for substratum).

Atlantic Rainforest region – Three macroalgal species occurred at site 1 (*Microcoleus subtorulosus* Gom.,

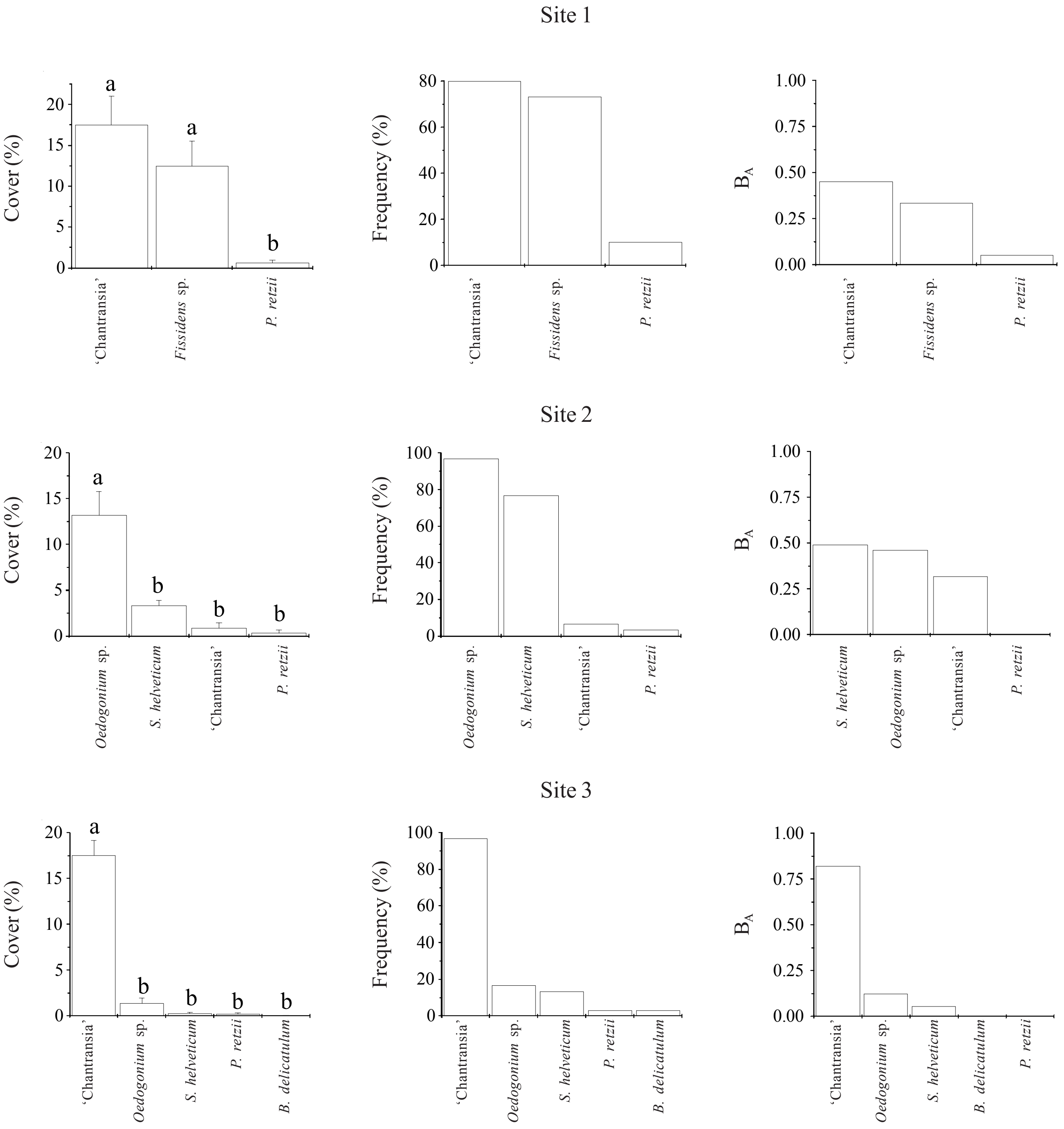

Figure 1. Percent cover, frequency and niche width (Lewin index, B_A) of macroalgal species at sampling sites from the northwest region of São Paulo State. Bars represent “ standard-deviations ($n = 30$), whereas different letters (for values of cover) indicate significant differences ($P < 0.05$) by Newman-Keuls test.

Table 5. Niche overlap (Schoener index, %) among macroalgal species for microhabitat characteristics at sampling sites from the northwest region of São Paulo State.

	Irradiance	Depth	Current velocity	Dominant substratum
Site 1				
Fissidens sp. × 'Chantransia'	64.9	65.6	81.4	83.6
Site 2				
Oedogonium sp. × *Stigeoclonium helveticum*	92.1	91.4	91.9	89.6
Site 3				
'Chantransia' × *Oedogonium* sp.	67.9	59.2	56.2	44.0

Hydrosera whampoensis (Schw.) Deby and the 'Chantransia' stage of *Batrachospermum* sp.) plus an undetermined species of moss. We found three macroalgal species at site 2 (*M. subtorulosus*, *Phormidium aerugineo-caeruleum* (Gom.) Anag. & Kom. and *H. whampoensis*), and two undetermined species of bryophytes (one moss and one liverwort). Four species were collected at site 3: *P. aerugineo-coeruleum*, *Fragilaria ulna* Nitzsch) Lange-Bertalot, *H. whampoensis* and *Vaucheria* sp., plus the 'Chantransia' stage of *Batrachospermum* sp. and an undetermined species of moss. Values of diversity index varied from 0.26 to 0.64 (for sites 1 and 3, respectively - table 4), whereas dominance index varied between 0.28 and 0.72 (for sites 3 and 1, respectively - table 4).

Site 1 was the only with a dominant macroalga ('Chantransia') (figure 3). Frequency values for site 1 were high (*ca.* 90%) for the two most frequent macroalgae (figure 3). The other two sites had lower frequency values (maximum of 50%) with a relatively small narrow and gradual difference among the species. Niche width values were considerably low (≤ 0.15) and relatively similar for the sites of this region (figure 3), except for site 1, where high values were found for the two most frequent macroalgae. Site 1 had high values for niche overlap (≥ 99%, table 7) in comparison to the others (0-75%).

Table 6. Niche overlap (Schoener index, %) among macroalgal species for microhabitat characteristics at sampling sites from the hard water region.

	Irradiance	Depth	Current velocity	Dominant substratum
Site 1				
'Chantransia' × *Rhizoclonium hieroglyphicum*	40.4	0	0	36.6
'Chantransia' × *Vaucheria* sp.	40.4	0	0	36.6
'Chantransia' × *Cladophora glomerata*	41.2	0.8	0.7	36.6
Rhizoclonium hieroglyphicum × *Vaucheria* sp.	85.5	100.0	100.0	81.5
Rhizoclonium hieroglyphicum × *Cladophora glomerata*	96.4	99.2	99.2	86.0
Vaucheria sp. × *Cladophora glomerata*	82.0	99.2	99.2	67.5
Site 2				
Spirogyra sp. × *Phormidium retzii*	54.9	54.6	44.7	42.4
Spirogyra sp. × *Phormidium cebennense*	71.6	57.8	69	70.1
Phormidium retzii × *Phormidium cebennense*	61.3	45.6	47.4	72.2
Site 3				
Chara rusbyana × *Batrachospermum globosporum*	63.0	53.2	78.9	86.0
Chara rusbyana × *Phormidium fragile*	31.0	57.1	41.7	41.5
Chara rusbyana × *Spirogyra* sp.	37.9	71.6	35.2	50.9
Batrachospermum globosporum × *Phormidium fragile*	55.0	39.0	50.0	35.0
Batrachospermum globosporum × *Spirogyra* sp.	79.2	35.2	44.8	50.2
Phormidium fragile × *Spirogyra* sp.	69.2	64.6	60.9	37.0

Environmental variables for the three regions – The hard water region had the widest variety of substrata (seven different substrata per site), followed by the Atlantic Rainforest region (five) and the northwestern region of São Paulo (four, tables 1-3). A predominant type of substratum was observed at hard water and rainforest regions (sand-clay or gravel and rock, respectively), whereas the substrata were different at each site in northwest region (tables 1-3). Mean values of temperature and conductivity for the hard water region (21.9 ± 0.6 °C and 381 ± 205 µS cm^{-1}) were significantly higher (F = 16.7 and 8.6, $P < 0.05$) than those for the other regions (17.9-18.5 °C and 26-34 µS cm^{-1}, tables 1-3). Turbidity values were significantly higher (F = 35.3,

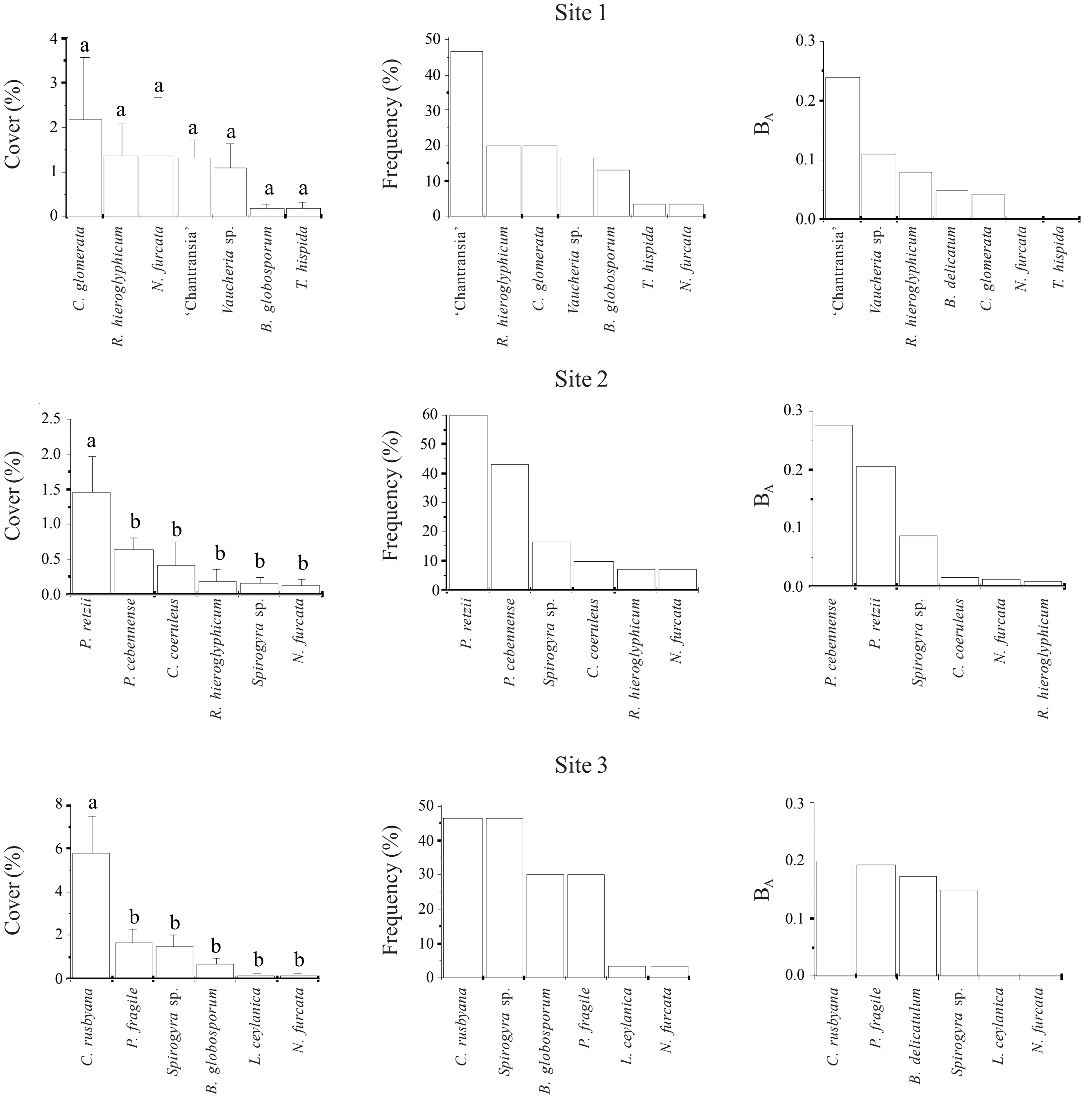

Figure 2. Percent cover, frequency and niche width (Lewin index, B_A) of macroalgal species at sampling sites from the hard water region. Bars represent standard-deviations (n = 30), whereas different letters (for values of cover) indicate significant differences ($P < 0.05$) by Newman-Keuls test.

$P < 0.05$) in the northwest region (9 ± 1 NTU) than in the other regions (2-4 NTU, tables 1-3). Mean values of current velocity were not significantly different ($F = 6.7$, $P > 0.05$) among the regions, probably due to a wide variation in sampling sites within each region, *e.g.* from 13 cm s^{-1} (site 3) to 81.2 cm s^{-1} (site 2) in the rainforest region (tables 1-3). pH values were significantly higher ($F = 13.3$, $P < 0.05$) for the hard water region (7.6 ± 0.3 × 6.7-6.8, tables 1-3). Dissolved oxygen concentrations were not significantly different ($F = 5.0$, $P > 0.05$) among the three regions, with a slightly higher mean for the rainforest region (6.4 × 5.4-5.9 mg L^{-1}, tables 1-3). Irradiance values were significantly lower ($F = 11.6$, $P < 0.05$; 83 ×

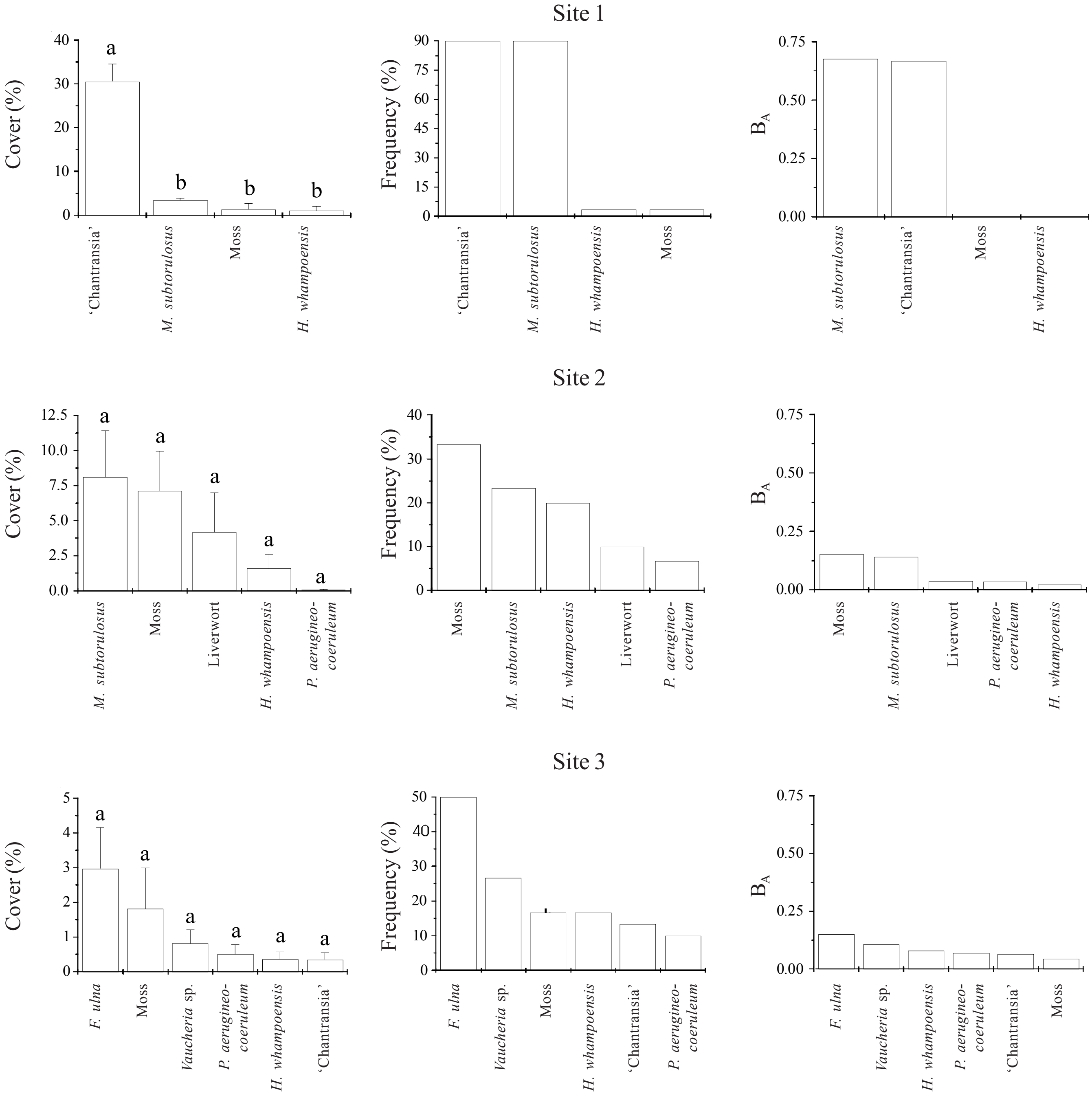

Figure 3. Percent cover, frequency and niche width (Lewin index, B_A) of macroalgal species at sampling sites from the Atlantic Rainforest region. Bars represent ± standard-deviations ($n = 30$), whereas different letters (for values of cover) indicate significant differences ($P < 0.05$) by Newman-Keuls test.

Table 7. Niche overlap (Schoener index, %) among macroalgal species for microhabitat characteristics at sampling sites from the Atlantic Rainforest region.

	Irradiance	Depth	Current velocity	Dominant substratum
Site 1				
‘Chantransia’ × *Microcoleus subtorulosus*	99.0	99.0	99.2	99.2
Site 2				
Microcoleus subtorulosus × *Hydrosera whampoensis*	16.5	0	4.3	83.5
Microcoleus subtorulosus × Moss	11.7	0	2.3	83.5
Hydrosera whampoensis × Moss	50.2	50.4	64.7	100.0
Site 3				
Fragilaria ulna × *Vaucheria* sp.	23.3	60.6	67.3	41.4
Fragilaria ulna × Moss	27.3	70.6	63.3	32.0
Fragilaria ulna × *Hydrosera whampoensis*	37.3	25.8	28.2	47.4
Vaucheria sp. × Moss	63.3	48.4	74.8	65.1
Vaucheria sp. × *Hydrosera whampoensis*	44.9	41.7	26.5	40.6
Moss × *Hydrosera whampoensis*	44.9	44.9	44.9	48.5

115-1315 μmol m^{-2} s^{-1}) at the rainforest region, whereas depths were not significantly different ($F = 1.5$, $P > 0.05$) among the regions (12.2, 22.7 and 51.6 cm, tables 1-3). Biological variables for the three regions – No significant differences were revealed by ANOVA and Newman-Keuls test for the biological variables among the three regions (table 4). However, some relevant trends were evident by comparison of mean values. The hard water region had the highest means of species richness, as well as the highest mean values for the Shanon-Wiener diversity index, whereas the lowest values were observed for the Simpson dominance index (table 4). In contrast, the rainforest region had the lowest mean values of diversity (table 4). However, species richness for this region was slightly higher and dominance was lower than for the northwest region. The highest mean values of percent cover were found at rainforest and northwest regions (table 4). One or two dominant species occurred at all sites from the northwest region and the same trend was found at sites 2 and 3 from hard water and at site 1 from rainforest region. As a rule, species with highest percent covers at each sampling site had not the highest frequencies, except at the northwest region. The highest niche width values were observed for the northwest region, whereas the lowest for the hard water region (table 4). Considering the nine sampling sites of the three regions, we found the following significant correlations: positive of niche width with percent cover ($r = 0.81$, $P < 0.05$), niche overlap ($r = 0.92$, $P < 0.05$) and dominance index ($r = 0.78$, $P < 0.05$); negative of percent cover with species richness ($r = -0.86$, $P < 0.05$).

Discussion

The dominance of one or two species for six out of the nine sampling sites of the three regions has clearly evidenced the pattern of niche pre-emption (Sheath *et al.* 1986), which confirms results found in macroalgal communities of distinct regions of North America (Sheath & Burkholder 1985, Sheath *et al.* 1986, 1989) and Brazil (Necchi Júnior *et al.* 1994, 1995a; Branco & Necchi Júnior 1996, 1998). The generally high values of niche overlap among the dominant species suggests the occurrence of competition for the stream segments analyzed at the northwest region of São Paulo State. However, the impossibility to calculate niche overlap for species with low abundance did not allow us to state that such species compete for the non-used resources with the dominant species, as implied by this theory. The mean values of niche width for species of this region was the highest among the three regions, which indicates that such species were generalists. If one considers that few species are able to survive in lotic ecosystems due to the wide and fast variations of environmental conditions (Necchi Júnior *et al.* 2000, Sheath *et al.* 1986), then one can suppose that species richness would tend to be low. This trend is clearly applicable to the data for the northwest region in comparison to the other two, whose species would be more generalists.

According to Ricklefs (2001), the addition of species to a community would occur according to three general modes: 1) with no changes in niche parameters, with the global community niche size expanded following a direct proportion of the number of species; 2) with no changes in niche width, an increase in the diversity would occur by an increase in niche overlap (in this case the productivity of each species decreases due to the higher resources partition); and 3) with no increases for niche overlap, an specialization increment would account for the increase in the space of the communitary niche. Considering that the niche size in this study can be assumed as fixed, since we delimited the size of the sampling area, the niche overlap values were high, as well as those of niche width for species of each stream segment. Thus, it is suggested that species richness for the northwest region are theoretically close to the maximum. Site 3 can be an exception, since low niche overlap occurred for substratum, which would allow the establishment of new species to colonize available space or even compete with the dominant species.

The pattern of dominance of one species was observed in two of the three sampling sites of the hard water region. However, a distinct trend was found in comparison to the northwest region, because the values of niche partitioning for this region were considerably lower (the lowest among the three study regions), which is more closely related to the pattern of patch distribution. Such values demonstrate the partitioning of the environment in several micro-habitats that were occupied by species with low niche widths (the lowest values among the three regions), which suggest more specialized species. Our results are in accordance with the hypothesis raised by Tilman (1994), that the diversity of plant communities can be partially explained by the competition into a heterogeneous environment. Pringle *et al.* (1988) have complemented this rationale by stating that when individual plant species plants tend to maximize the competitive abilities into a specific and limited variation of resources, the spatial variation in the resource supplies can lead to the coexistence of several species. French & Chambers (1996) observed that the coexistence of aquatic macrophytes species in a given area can be viewed in two ways: with and without the evidence of habitat partitioning. Considering the four environmental variables analyzed in this study, we realized that few species in the hard water region had high values of niche overlap (*e.g. R. hieroglyphicum*, *Vaucheria* sp., and *C. glomerata* at the site 1). Therefore, they might share resources allowing to suggest that such species coexist in this region without habitat partitioning. However, the majority of the species had low values of niche overlap, evidencing habitat partitioning. Thus, the high species richness associated to the low niche overlap for this region clearly suggests the pattern as patch distribution.

For the rainforest region, we found that in only one site the dominance by one species can be applied, with similar characteristics to those from the northwest region: high values of niche width and overlap (the highest values for the the entire study). Such factors together allow us to conclude that this site fits better within the niche pre-emption pattern. For the other two sites of this region we found no dominance of few species, associated to low values of niche width and overlap, thus indicating the pattern of patch distribution. The significantly lower values of irradiance for this region suggest a strong light limitation. The relatively low values of niche width and species richness in this region can be ascribed to such limitation, since only specialized species can tolerate these conditions in light-limited streams.

The set of species was similar for streams of a same region but different among distinct regions. Thus, we presume that species predominance are probably influenced mainly by regional factors. Only the ‘Chantransia’ stage of *Batrachospermum* spp. was found in all regions, showing its generalist character. The key role of the ‘Chantransia’ stage for the dispersion and maintenance of *Batrachospermum* species was previously reported (Hambrook & Sheath 1991, Necchi Júnior 1993), as well as its tolerance to wide environmental conditions (either in temporal and spatial scales). On the other hand, stream segments of the same region sometimes had different patterns of distribution, indicating a major influence of local factors (current velocity, irradiance and substrata) and to a lesser extent of regional characteristics (geomorphology, rainfal regime and temperature).

Our results clearly indicate that the competition for space was one of the main factors that explains the spatial distribution. We found a trend of higher species number associated to higher substratum variety. This factor can influence the values of niche width and overlap since a higher variety of substratum types can favour the colonization of a higher number of species on those niches (leading to lower values of niche width). Competition among more specialized species tends to be reduced, leading to lower values of niche overlap. This trend was confirmed when were found that the stream segments with the highest diversity of substratum have shown the lowest values of niche width and overlap. However, the analysis of niche overlap alone has proven to be weak to confirm that competition for space is one of the main factor to explain the spatial distribution patterns, but in combination with the other variables discussed here it was more useful.

The study of the nine stream segments demonstrated that patterns for spatial distribution of macroalgae for the three regions/biomes basically agreed with those previously described (Sheath *et al.* 1986, 1989, Sheath & Cole 1992, Branco & Necchi Júnior 1996, 1998, Necchi Júnior *et al.* 1995a, 2000): high dominance and predominance of few species; niche pre-emption, in which one or few species occupy most part of the environmental resources (in this case substratum), whereas the other species compete for the remaining resources; patch distribution, characterized by communities with the highest abundance being also the ones with the highest diversity (in terms of species richness). Two different patterns of spatial distribution can occur in a same region (*e.g.* hard water and rainforest). The global analysis of the community characteristics evidenced some general trends: environments characterized by the niche pre-emption pattern had lower species richness, higher values of niche width and overlap, dominance index and percent cover for dominant species. In contrast, environments with pattern of patch distribution had higher species richness, lower values of niche width and overlap, dominance index and percent cover for dominant species.

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