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Changes in the taxonomic structure of periphytic algae on a free-floating macrophyte (*Utricularia foliosa* L.) in relation to macrophyte richness over seasons

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ABSTRACT

Periphyton has a strong relationship with aquatic macrophytes, which are key components of spatial heterogeneity in the littoral zone. We evaluated the relationship between the community structure of periphytic algae on *Utricularia foliosa* and macrophyte richness and coverage and limnological variables in a shallow reservoir. Water sampling for physical, chemical and biological analyses was performed at sites with contrasting macrophyte coverage and richness in each of the four main seasons of the year. Periphytic algae were evaluated for density and species composition. High densities of diatoms and filamentous cyanobacteria in the periphyton were observed at sites with high macrophyte coverage and richness, while high abundances of flagellates of Chrysophyceae and Chlorophyceae were found at sites with low macrophyte richness. Light and nutrient availability were determining factors of the temporal variability of the periphytic algae community. We concluded that the interaction between seasonality and spatial heterogeneity (macrophyte community structure and limnological variables), explained the variability in species composition and algal density of the periphyton. Therefore, seasonality and spatial heterogeneity acted as determining factors for periphyton structure on a free-floating macrophyte with high structural complexity.

Keywords: epiphytic algae, limnological variables, macrophyte structure, spatial heterogeneity, species composition

Introduction

Periphytic communities play an important role in the functioning of lake and reservoir ecosystems, especially those that are shallow. At the scale of the ecosystem, biotic and abiotic factors can determine algal community structure in periphyton (Stevenson 1997). Among biotic factors, macrophytes are likely to have a strong influence on the development of periphyton. Besides providing areas for colonization, macrophytes can influence light and nutrient availability for the periphyton community (Moeller *et al*. 1988; Souza *et al*. 2015). Most studies recognize that seasonal variation in light and nutrient availability are determining factors of periphyton structure (Larned 2010), including changes between clear and turbid phases of shallow lakes (Cano *et al*. 2012). In addition, biotic and abiotic variables can vary spatially, which can promote the heterogeneous distribution of periphyton in the littoral zone. Spatial heterogeneity of nutrients is a mechanism that maintains periphytic algae species diversity (Pringle 1990). Nonetheless, spatial changes in the taxonomic structure of periphytic algae communities are still poorly understood, especially in tropical lakes and reservoirs.

We investigated the periphyton that occurs upon *Utricularia foliosa*, which is a free-floating, submerged, carnivorous, aquatic macrophyte that is widely distributed among tropical and subtropical aquatic ecosystems (Guisande *et al*. 2007; Walker 2004). Many ecological processes

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depend on submerged macrophytes, such as the retention of nutrients, the minimization of sediment resuspension, and the sedimentation of suspended matter, while they also compete, together with periphyton, with phytoplankton for nutrients and light (Kosten *et al*. 2009). Most research on the periphyton on *Utricularia* has focused on their prey-predator relationship (e.g. Manjarrés-Hernández *et al*. 2006), while few studies have addressed the taxonomic structure of the periphytic algal community (Díaz-Olarte *et al*. 2007; Santos *et al*. 2013). According to Díaz-Olarte *et al*. (2007), the abundance and species richness of periphytic algae on *U. foliosa* depend mostly on environmental conditions, rather than on mechanisms of facilitation by the plant. Santos *et al*. (2013) showed that the architecture (structure, size, and surface area) of *Utricularia foliosa* can be a determining factor of periphytic algae community structure. Thus, the architecture of *Utricularia,* combined with abiotic and biotic variables, influences periphyton biomass accumulation, nutrient status and algal biovolume.

Macrophytes play an important role in structuring communities, especially since they provide physical structure that increases habitat complexity and heterogeneity (Thomaz & Cunha 2010). Studies have also shown that changes in macrophyte richness can influence periphyton biomass (Engelhardt & Ritchie 2002) and taxonomic structure, on artificial substrate and *Nymphaea* (Souza *et al*. 2015; Pellegrini & Ferragut 2018). Thus, our objective was to analyze the relationship between periphyton on *Utricularia foliosa* and macrophyte richness and coverage, and limnological variables, over seasons in a shallow reservoir. Variation in macrophyte richness and limnological variables, mainly light and nutrient availability, were used to analyze spatial heterogeneity and its effects on periphyton. Since limnological conditions vary seasonally and spatially, along with macrophyte community structure, we hypothesized that the taxonomic structure of periphytic algae on *U. foliosa* would be influenced by seasonality and by changes in macrophyte community structure. We aimed to address the following questions: i) Does the taxonomic structure of the periphytic algae community on *U. foliosa* vary seasonally and spatially? ii) Do these changes vary among sites, with their varying levels of macrophyte richness, within the reservoir? By considering these questions, this study contributes to a better understanding of the relationship between periphyton and macrophytes on temporal and spatial scales in a shallow tropical reservoir.

Materials and methods

Study area

The study took place in Ninfeias Lake, an artificial reservoir located in Parque Estadual das Fontes do Ipiranga (PEFI), in the city of São Paulo, São Paulo State, Brazil (23°38'18.95"S 46°37'16.3"W). The reservoir is a shallow mesotrophic system with a surface area of 5,433 m², a volume of 7,170 m³, a mean depth of 1.32 m, a maximum depth of 3.6 m, and a mean theoretical residence time of seven days (Bicudo *et al*. 2002).

Sampling design

Periphyton and water samples were collected at sites with the presence of only *Utricularia foliosa* L. (monospecific sites) and sites with other species of macrophytes. Samplings were performed in autumn (May, 2010), winter (July, 2010), spring (October, 2010) and summer (January, 2011). A total of 30-40 sites of 10 m² were identified along a 1-km stretch of shoreline, each with distinct macrophyte species richness, as described in Souza *et al*. (2015). Sites were categorized as follows: Uf, *U. foliosa* sites; 2M, sites with two species of macrophytes (*Nymphaea* spp. and *U. foliosa*); 3M, sites with three species (*Nymphaea* spp., *U. foliosa* and *Panicum repens* L.); 4M, sites with four species (*Nymphaea* spp., *U. foliosa*, *P. repens*, *Eleocharis acutangular* (Roxb.) Schult., and/or *Eichhornia azurea* Kunth.). We randomly selected three sites from each category for a total of 12 sites to be sampled each season (48 samples).

Sampling occurred within 1 m² areas demarcated by a square made of PVC pipe. Water and periphyton samples were collected and macrophyte coverage measured for each of the areas. The periphyton on *U. foliosa* was obtained from stem internodes. Very young and senescent plants were excluded from sampling to minimize the effects of differences in colonization time. The cut stems were placed in glass flasks, which were then placed in coolers with ice and protected from light, for transport to the laboratory. In the laboratory, the periphyton was carefully removed from stems by scraping with a brush with soft bristles and washing with distilled water. Sub-samples were used for quantitative analysis. We measured the length and width of stems to determine substrate area (cylinder area).

Variables analyzed

Periphyton subsamples were preserved with acetic Lugol's solution for counting algae, which was performed with a Zeiss Axiovert inverted microscope, according to Utermöhl (1958). Counting was performed on transects with the count limit being defined using the species rarefaction curve and until 100 individuals of the most common species was reached (Ferragut *et al*. 2013). Descriptor species were considered those that contributed ≥ 10 % to total density. Species with a relative density equal to or greater than 50 % of the total sample density were considered dominant. Taxonomic samplings were preserved with 4 % formaldehyde solution, and permanent diatom slides were prepared according to Battarbee *et al*. (2001). The algae were classified according to life form type: colonial, flagellate, filamentous and unicellular (Graham & Wilcox 2000).

Macrophyte species were counted and their coverage estimated at the sampling sites. Percentage coverage was determined using a grid of 100 squares of 10 cm x 10 cm within the 1 m^2 area (Thomaz *et al*. 2004). A single observer conducted the macrophyte quantification for purposes of standardization.

Air temperature, solar radiation and rainfall data were provided by the Meteorological Station of the University of São Paulo (estacao.iag.usp.br). Water temperature, transparency (Secchi disk) and subaquatic radiation (LiCor LI-250A) were measured at each sampling site. Water samples were filtered under low pressure (<0.3 atm) with fiberglass filters (GF/F Whatman, Maidstone, UK) for analysis of dissolved nutrients. The following variables were analyzed on the day of sampling: electrical conductivity (conductivity meter Digimed); dissolved oxygen (DO, Golterman *et al*. 1978); alkalinity (Golterman & Clymo 1971); pH (pH meter Digimed); dissolved inorganic carbon, nitrite and nitrate (Mackereth *et al*. 1978); ammonium (Solorzano 1969); orthophosphate and total dissolved phosphorus (TDP) (Strickland & Parsons 1960); orthosilicate (Golterman *et al*. 1978); total nitrogen; and total phosphorus (Valderrama 1981).

Data analysis

We used permutational multivariate analysis of variance (Two-way PERMANOVA) to analyze changes in the species composition of periphytic algal communities among seasons and sites with different macrophyte richness. This analysis was performed using the Bray-Curtis distance measure and 4999 permutations in Past 3.14 (Hammer *et al*. 2001).

Redundancy analysis (RDA) was used to evaluate the relationships between the periphytic algae (relative density ≥ 1 % of total density) and environmental variables at sites with different macrophyte richness during the four seasons. This analysis was performed because the species ordering by DCA (detrended correspondence analysis) showed that the gradient length was < 2.0, indicating that the relationship between algal density and the environmental gradient was linear (Birks 2010). The main matrix was composed of the periphytic algae species that contributed ≥ 2 % to the total density, while the second matrix was composed of six abiotic variables, which were selected based on PCA (Principal Component Analysis). These analyses were performed using the covariance matrix with abiotic and biotic data transformed by logarithm log (x + 1). A Monte Carlo randomization test was performed, and we considered those axes with $p < 0.05$ as interpretable. Ordinations were performed using the PC-ORD 6.0 program (McCune & Mefford 2006).

Results

Abiotic variables

Table 1 shows the abiotic characterization of the water at the sites sampled in each of the four seasons.

Table 1. Mean values of water depth, temperature and nutrient concentration (n = 3) at sites with different macrophyte richness in the four seasons. Abbreviations: Uf: *Utricularia foliosa* sites, 2-4M sites 2-4 macrophyte species (Data of 2M, 3M e 4M sites obtained in Pellegrini & Ferragut 2018).

	Autumn				Winter				Spring				Summer			
	Uf	2M	3M	4M	Uf	2M	3M	4M	Uf	2M	3M	4M	Uf	2M	3M	4M
Conductivity ($\mu S\ cm^{-2}$)	57.4	57.5	56.8	57.3	56.7	56.7	54.1	57.0	53.6	56.8	57.1	58.0	47.6	46.8	46.2	49.6
Dissolved Oxygen ($mg\ L^{-1}$)	3.9	3.0	3.9	4.4	4.4	4.8	5.6	6.0	4.4	4.6	4.1	4.5	2.2	6.5	1.8	3.2
Free CO_2 ($mg\ L^{-1}$)	16.4	16.7	14.0	13.4	16.4	16.7	14.0	13.4	32.4	15.0	23.3	21.7	9.5	7.0	11.6	11.3
HCO_3 ($mg\ L^{-1}$)	12.0	13.7	12.4	11.4	16.0	13.9	15.9	9.4	17.6	17.6	17.4	16.5	16.3	15.9	18.1	15.2
pH	6.1	6.1	6.2	6.2	6.0	6.2	6.1	5.9	6.5	6.6	6.4	6.4	6.1	6.1	6.1	6.1
Nitrogen Inorganic Dissolved ($\mu g\ L^{-1}$)	1316	1172	1264	1550	670	1322	520	1072	178	194	143	320	611	585	317	922
Orthosilicate ($mg\ L^{-1}$)	2.4	2.1	2.3	2.3	3.16	2.95	3.09	3.38	2.26	2.52	2.44	2.03	2.99	3.08	3.00	3.23
Subaquatic radiation ($\mu mol\ m^{2}\ s^{2}$)	268.5	173.3	160.1	153.0	353.9	155.9	222.7	163.8	698.8	1197.5	927.5	1031.8	76.6	250.4	415.4	503.6
Total Dissolved Phosphorus ($\mu g\ L^{-1}$)	4.0	4.0	4.0	4.0	4.0	4.0	4.0	4.0	5.7	5.2	6.3	6.1	5.9	7.2	5.7	8.9
Total Phosphorus ($\mu g\ L^{-1}$)	20.9	14.4	23.3	28.4	9.8	7.2	10.6	9.9	10.5	8.5	12.8	13.3	14.3	13.1	15.9	17.9
Total Nitrogen ($\mu g\ L^{-1}$)	2558	1495	2175	2606	774	1504	943	1146	375	331	305	490	563	582	364	926
Temperature (°C)	22.0	22.5	22.0	22.0	18.1	19.7	18.7	19.1	21.6	22.8	21.9	21.5	24.9	24.9	25.0	24.1
Water Depth (m)	0.6	0.7	0.7	0.4	0.4	0.4	0.4	0.4	0.6	1.1	0.4	0.4	0.8	1.1	0.7	0.7

Utricularia foliosa

Regarding total macrophyte coverage, *U. foliosa* coverage was higher in spring and summer than in autumn and winter (Fig. 1).

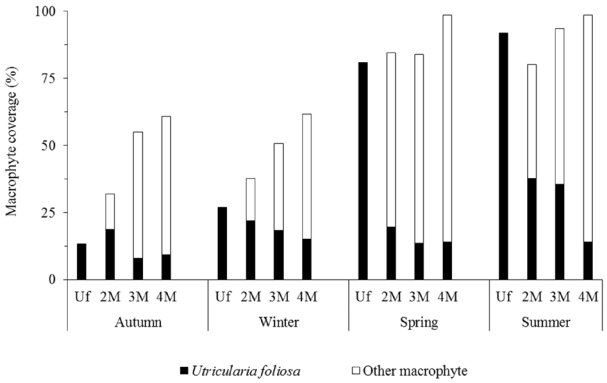

Figure 1. Seasonal variation of *Utricularia foliosa* coverage and other macrophyte species at sites with different macrophyte richness in the four seasons (n = 3; Uf - *U. foliosa*; 2-4M = 2-4 macrophytes species).

Periphyton

In total, 188 algal and cyanobacterial taxa were identified in the periphyton on *U. foliosa:* 65 Chlorophyceae; 49 Zygnematophyceae; 26 Bacillariophyceae; 15 Cyanobacteria; 14 Euglenophyceae; nine Chrysophyceae; four Xanthophyceae; three Cryptophyceae; two Oedogoniophyceae; and one Dinophyceae.

Based on algal class density, Bacillariophyceae, Chlorophyceae and Chrysophyceae were the most representative classes during the study period (Fig. 2A). Flagellate was the predominant life form of the periphyton at all sites (41-84 %), except in summer when the density of unicellular forms increased at Uf, 2M and 3M sites (Fig. 2B).

The highest total density of periphytic algae was found at Uf sites in all seasons. The density of the descriptor species of the periphytic algae community on *U. foliosa* varied among seasons and sites with different macrophyte richness (Fig. 3A). The chrysophyte *Chromulina elegans* was the most abundant species in all seasons and at all sites, but its relative density varied among sites with different macrophyte richness (26-70 %). This species was dominant at Uf sites in autumn, winter and spring, 4M sites in autumn and spring and 2M sites in spring. The chlorophytes *Chlamydomonas sagittula* and *Chlamydomonas epibiotica* were more abundant at 3M and 4M sites in spring and summer (11-18 %). Other species also showed high relative density in summer, such as the cyanobacteria *Pseudanabaena galeata* and *Synechoccocus nidulans* at Uf sites (<11 %) and the diatoms *Navicula cryptotenella* and *Frustulia crassinervia* at 2M and 3M sites (13-17 %). A higher density of the cyanobacterium *Anagnostidinema amphibium* was found at Uf and 4M sites (26 % and 57 %, respectively) in spring (Fig. 3B).

Two-way PERMANOVA indicated that the species composition of the periphytic algal community on *U. foliosa* was significantly influenced by both season (F= 2.61; p = 0.0002) and the macrophyte richness of the site (F= 4.34; p = 0.0002); the interaction between space and time was significant (F= 0.58; p = 0.0002).

RDA was performed with six abiotic variables and 46 periphytic algal species on *U. foliosa* (Fig. 4, Tab. 2). The eigenvalues for axes 1 (λ= 8.83) and 2 (λ = 4.15) explained 28.2 % of the total variability. The high species-environment correlation for axes 1 (r = 0.98) and 2 (r = 0.89) indicated a strong relationship between species distribution and environmental variables. A Monte Carlo randomization

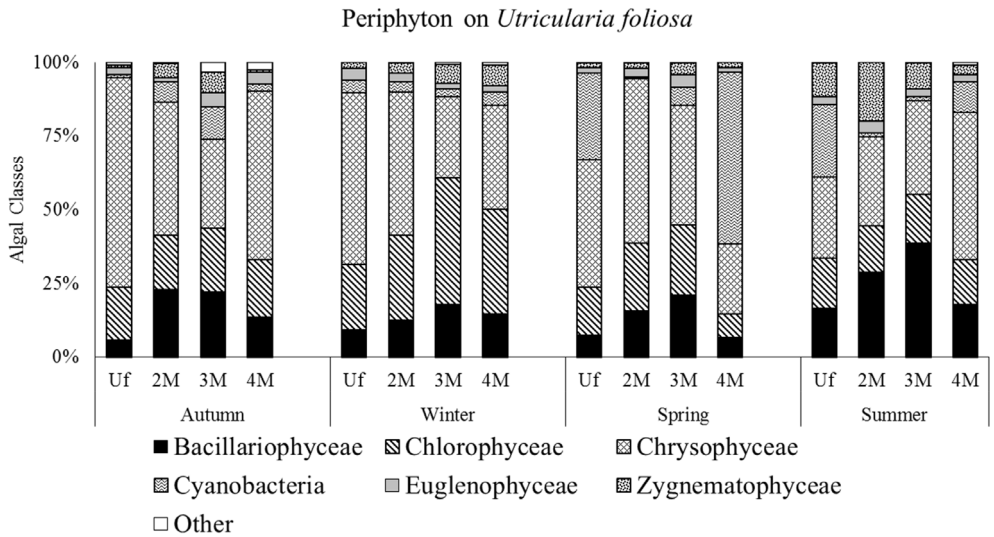

Figure 2. Relative density of algae classes (**A**) and life forms (**B**) in periphyton on *Utricularia foliosa* at sites with different macrophyte richness in four seasons (Uf = *U. foliosa*; 2-4M = 2 - 4 macrophyte species).

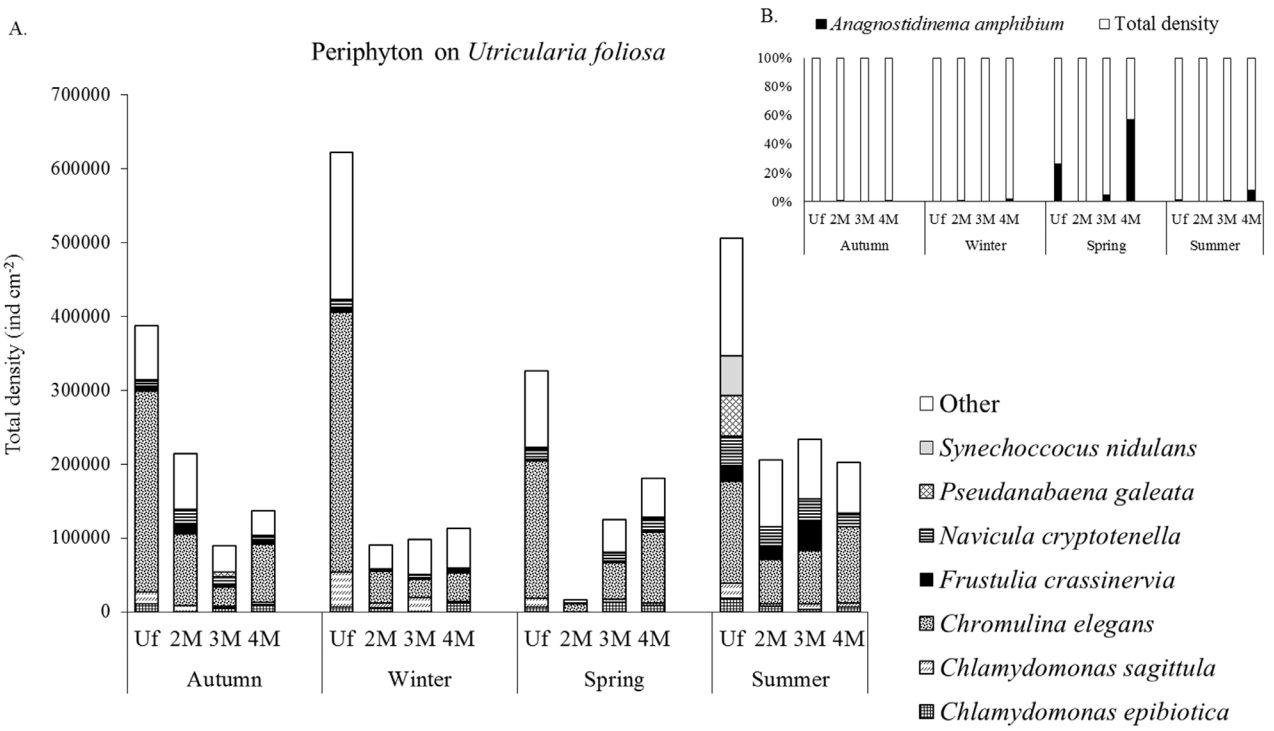

Figure 3. Density of periphytic descriptor species (**A**) and *Anagnostidinema amphibium* (**B**) on *U. foliosa* at sites with different macrophyte richness in the four seasons (Uf = U. foliosa; 2 - 4M = 2-4 macrophyte species).

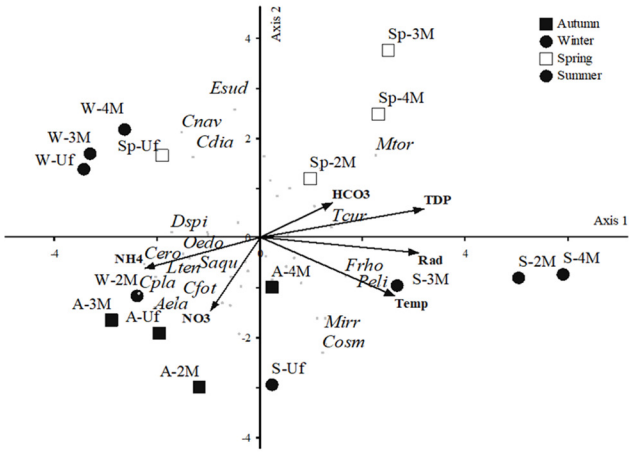

Figure 4. RDA diagram of periphytic algae species on *Utricularia foliosa* and six environmental variables. Score abbreviations: first letters refers to season (A-autumn, W-winter, Sp-spring, S-summer) and second letters indicates site categories (Uf – U. foliosa sites; 2-4M = 2-4 macrophytes species). Vector: NH_4=N-NH_4, Temp=water temperature, NO_3=N-NO_3, PO_4=P-PO_4, Rad=subaquatic radiation, HCO_3=Bicarbonate. Species correlation with axes 1 and 2, and the respective codes are given in Table 2.

Table 2. Pearson correlation of periphytic algae density on *Utricularia foliosa* with RDA axes 1 and 2, and their respective codes.

Taxa	Code	Axis 1	Axis 2
Aphanocapsa elachista West & G.S.West	Aela	-0.771	-0.358
Chlamydomonas planctogloea Skuja	Cpla	-0.884	-0.286
Closterium dianae Ehrenberg ex Ralfs	Cdia	-0.309	0.504
Coenochloris fottii (Hindák) Komárek	Cfot	-0.606	-0.328
Cosmarium sp.	Cosm	0.454	-0.593
Cryptomonas erosa Ehrenberg	Cero	-0.846	-0.139
Cymbopleura naviculiformis (Auerswald ex Heiberg) Krammer	Cnav	-0.576	0.541
Desmodesmus spinosus (Chodat) E.Hegewald	Dspi	-0.647	0.027
Eunotia sudetica Otto Müller	Esud	-0.184	0.655
Frustulia rhomboides (Ehrenberg) De Toni	Frho	0.619	-0.199
Leptolyngbya tenuis (Gomont) Anagnostidis & Komárek	Lten	-0.764	-0.205
Monoraphidium irregulare (G.M.Smith) Komárková-Legnerová	Mirr	0.478	-0.548
Monoraphidium tortile (West & G.S.West) Komárková-Legnerová	Mtor	0.840	0.422
Oedogonium sp.	Oedo	-0.564	-0.084
Protocryptomonas ellipsoidea Skv. ex Castro, C. Bicudo & D. Bicudo	Peli	0.756	-0.205
Synechocystis aquatilis Sauvageau	Saqu	-0.518	-0.106
Trachelomonas curta A.M.Cunha	Tcur	0.515	0.054

test showed that both axes are interpretable ($p < 0.05$). The interest correlations showed that TDP, subaquatic radiation and temperature were the most important variables in the ordination axis 1 ($r > 0.8$). The first ordination axis represented seasonality, showing that spring and summer samplings were associated with higher values of subaquatic radiation, temperature and TDP ($r > -0.9$). On the positive side of axis 1, the winter and autumn samplings were correlated with high ammonium concentration ($r = 0.6$). In relation to axis 1, *Chlamydomonas planctogloea*, *Cryptomonas erosa*, *Aphanocapsa elachista*, *Leptolyngbya tenuis*, *Desmodesmus spinosus*, and *Coenochloris fotti* were correlated with autumn and winter ($r > 0.6$), while *Trachelomonas curta*, *Frustulia rhomboides*, *Protocryptomonas ellipsoidea*, and *Monoraphidium tortile* were correlated with spring and summer ($r > 0.5$).

Discussion

Our results showed that the taxonomic structure of the periphytic algae community on *Utricularia foliosa* changed among seasons and sites with different macrophyte richness, evidencing the heterogeneous distribution of the periphyton in the littoral zone. However, periphyton structure was determined by the interaction of factors, specifically seasonality and macrophyte richness in the reservoir. The influence of seasonality on the periphyton on macrophytes has been commonly reported for temperate lakes (e.g. Messyasz & Kuczyńska-Kippen 2006; Cano *et al*. 2012) and in Brazilian lakes and reservoirs (e.g. Felisberto & Rodrigues 2005; Pellegrini & Ferragut 2012). In the current reservoir, previous studies reported a negative relationship between periphytic algal density on *Nymphaea* and artificial substrate and total macrophyte coverage, since high coverage caused strong shading of the periphyton (Souza *et al*. 2015). Therefore, as observed on artificial substrate, periphyton on *U. foliosa* also differed among sites with different macrophyte richness in the four main seasons, evidencing temporally and spatially different habitat structures in the reservoir. Variation in macrophyte richness and coverage played significant roles in the taxonomic structure of the periphytic algae community on free-floating macrophytes.

Light and nutrient availability were determining factors for the temporal variability of the periphytic algae community on *U. foliosa*. Therefore, our results showed the strong influence of seasonal changes in limnological conditions on structural changes in periphytic algae community for all site categories. Although seasonality presented the greatest weight in the organization of algal assemblages of the periphyton, we found significant differences in species composition among the site categories. According to Souza *et al*. (2015) found that high macrophyte coverage influenced light availability for the periphyton in the studied reservoir. Although macrophyte architecture may favor periphyton development (Santos *et al*. 2013), algal density on *U. foliosa* was higher at monospecific sites. At the multispecies sites (2-4M), the most abundant macrophyte was *Nymphaea* spp., which can shade periphyton due to its large floating leaves. In comparison to *Nymphaea* spp., *U. foliosa* does not drastically reduce light availability to the periphyton via shading (Laugaste & Reunanen 2005). Studies have reported an inverse relationship between macrophyte coverage and algal density in periphyton on artificial substrate and *Nymphaea* (e.g. Souza *et al*. 2015). Thus, increased macrophyte richness and coverage did not favor the growth of periphytic algae on *U. foliosa* in all seasons.

We found a high predominance of flagellated forms, which indicates the high participation of algae loosely adhered to the periphyton on *U. foliosa*. In relation to the flagellate forms, the chrysophyte *Chromulina elegans* was the most representative species in the periphyton structure at all sites and in all seasons (except 4M sites / summer). This species is a nanoplanktonic algae, and has a high surface area:volume ratio, which allows greater uptake of nutrients (Happey-Wood 1988). Moreover, the cyanobacterium *Anagnostidinema amphibium* was found to be associated with the periphyton at Uf and 4M sites in spring, when metaphyton is generally abundant in the shallowest parts of the littoral zone. In the studied reservoir, this species forms dense masses (metaphyton) in the macrophyte stands or occurs floating freely (T Rodrigues *et al*. unpubl. res.). In addition, the depths of the Uf and 4M sites were lowest in the spring, which certainly favored a greater association between metaphyton and periphyton on *Utricularia foliosa*. A strong association between metaphyton and the epiphyton on *Utricularia purpurea* was observed in the Florida Everglades, where the green algae *Spirogyra* was more representative in the metaphyton and epiphyton during the wet season (McCormick *et al*. 1998). The growth form of *Anagnostidinema amphibium* is filamentous, which is an efficient adaptive strategy for periphyton that develops on macrophytes that move freely through the reservoir, as is the case with *U. foliosa*.

Conclusions

We conclude that variability in the species composition and algal density of the periphyton on *U. foliosa* were related to seasonality and the spatial heterogeneity of the environmental conditions. Spatial differences in limnological conditions and macrophyte community structure were determinant for the periphytic algae community structure, as evidenced by the heterogeneous distribution of the periphyton in the littoral zone. As hypothesized, the community structure of periphytic algal was influenced by seasonality and differences in macrophyte community structure. Therefore, despite the recognized host macrophyte influence (e.g. Burkholder 1996), the periphyton on *U. foliosa* was influenced by environmental conditions on temporal

and spatial scales. Our findings increase understanding of the factors driving periphyton structure on *Utricularia foliosa*, a macrophyte that is widely distributed among Brazilian reservoirs.

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