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Periphytic algal community in lentic environments of the Upper Paraná River floodplain: seasonal and spatial variation

Comunidade de algas perifíticas em ambientes lênticos da planície de inundação do Alto Rio Paraná: variação sazonal e espacial

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Abstract: Aim: This study aimed to evaluate the influence of seasonal variation in the hydrological regime and of limnological variables on species richness of periphytic algae in lakes of the Upper Paraná River floodplain. **Methods:** The study area is located in the last undammed stretch of the Paraná River in this floodplain, in which three lakes were sampled quarterly (May, August and November 2014, and February and May 2015) for one year. The periphytic material was obtained from petioles of the aquatic macrophyte *Eichhornia azurea* (Sw.) Kunth. **Results:** We registered 149 taxa of periphytic algae, distributed in 9 classes. Algal richness changed as a function of the seasonal dynamics of the Paraná River's hydrological regime. Water level fluctuations directly influenced periphytic algae species. During periods of high water level, species richness increased. Limnological variables showed a close relationship with the hydrological regime, and the dissolved nutrients and turbidity were the abiotic factors that most influenced the algal community. The following species were present in all lakes: *Fragilaria capucina* Desmazières, *Gomphonema gracile* Ehrenberg and *Navicula cryptotenella* Lange-Bertalot (Bacillariophyceae) and two species of the genus *Oedogonium* (Oedogoniophyceae). **Conclusions:** The hydrological regime of the Paraná River played an important role in structuring communities of periphytic algae. Seasonal variation in hydrological regime and in limnological variables together influenced the species richness of these organisms in these floodplain lakes.

Keywords: periphyton; hydrological regime; species richness; limnological variables.

Resumo: Objetivo: Este trabalho objetivou avaliar a influência da variação sazonal do regime hidrológico e das variáveis limnológicas sobre a riqueza de espécies de algas perifíticas em lagos na planície de inundação do alto rio Paraná. **Métodos:** A área de estudo está inserida no último trecho livre de barramentos nesta planície, e incluiu três lagos amostrados trimestralmente (maio, agosto e novembro de 2014, e fevereiro e maio de 2015), durante um ano. O material perifítico foi obtido de pecíolos da macrófita aquática *Eichhornia azurea* (Sw.) Kunth. **Resultados:** Foram registrados 149 táxons, distribuídos em 9 classes. A riqueza de algas modificou-se em relação com a dinâmica sazonal do regime hídrico do rio Paraná. As mudanças do nível influenciaram diretamente as espécies de algas perifíticas. Nos períodos com alto nível d'água a riqueza de espécies aumentou. As variáveis limnológicas apresentaram uma estreita relação com a variação do regime hidrológico. As formas assimiláveis dos nutrientes e a turbidez foram os fatores abióticos que mais influenciaram a comunidade de algas. As espécies presentes em todos os ambientes foram *Fragilaria capucina* Desmazières, *Gomphonema gracile* Ehrenberg e *Navicula cryptotenella* Lange-Bertalot (Bacillariophyceae) e duas espécies do gênero *Oedogonium* (Oedogoniophyceae). **Conclusões:** O regime hidrológico do rio Paraná constitui papel importante na estruturação das algas perifíticas. Variações sazonais do regime hidrológico e nas caraterísticas limnológicas influenciaram a riqueza desses organismos nos lagos desta planície.

Palavras-chave: perifíton; regime hidrológico; riqueza de espécies; variáveis limnológicas.

1. Introduction

Floodplains are fluvial systems with high structural and functional complexity and elevated biological diversity; they are also considered highly productive (Neiff, 1990; Ward et al., 2002; Agostinho et al., 2008). The Upper Paraná River floodplains show seasonal variation of physical and chemical characteristics, that in association with alterations of the hydrological regime (flood pulses), influence the development of aquatic communities and the functional dynamics of these ecosystems (Junk et al., 1989; Thomaz et al., 2007; Wantzen et al., 2008). Seasonal changes in hydrology and the dynamics created by the flood pulse distinguish this floodplain from other systems, while at the same time providing high levels of diversity and productivity (Agostinho et al., 2008; Algarte et al., 2009).

Among the habitats of the Upper Paraná River floodplain, lentic environments are predominant. They are home to a great variety of communities of aquatic algae, characterized by greater species richness than other types of habitats in this floodplain (Thomaz et al., 1997; Agostinho et al., 2000). These environments show favourable conditions for the development and establishment of diverse algal communities (Agostinho et al., 2000; Thomaz et al., 2004) because they have different degrees of connectivity to the Paraná River's main channel and especially because they support a great variety of aquatic macrophytes, which provide surfaces supporting biota such as periphyton (Rodrigues & Bicudo, 2001a; Thomaz et al., 2007; Algarte et al., 2009; Biolo et al., 2015).

Organisms of the periphyton are important primary producers in lakes, rivers and river-floodplain systems, playing a key role in the metabolism and functioning of aquatic ecosystems (Rodrigues & Bicudo, 2001b; Rodrigues et al., 2003; Algarte et al., 2009; Felisberto & Murakami, 2013; Camargo & Ferragut, 2014). Periphytic algae, the most studied component of this community, participate in mineralization and nutrient cycling, and assume a key position in energy flow in food webs of aquatic ecosystems (Fonseca et al., 2009; Felisberto & Murakami, 2013; Rodrigues et al., 2013).

This algal community is directly or indirectly influenced by environmental characteristics such as temperature, nutrient availability, light intensity and water flow velocity, and by hydrological cycles of the Paraná River. This river experiences constant variation and oscillation, altering the structural attributes of the algal community, which responds rapidly to changes in environmental conditions (Agostinho et al., 2000; Lobo et al., 2004; Ferragut & Bicudo, 2010; Rodrigues et al., 2013; Algarte & Rodrigues, 2013; Dunck et al., 2015; Wetzel et al., 2012). Therefore, due to their short life cycle, sessile lifestyle and usually high species richness, periphytic algae constitute a rich source of information about the ecological status of habitats they inhabit (Rodrigues et al., 2003; Fonseca et al., 2009; Ferragut & Bicudo, 2009).

Thus, monitoring the lentic environments of the Upper Paraná River floodplain is essential for understanding of how periphytic algal communities respond to changes in the water level of the Paraná River. In this way, we aimed to analyze the structure of periphytic communities in different hydrological periods in lakes of the Upper Paraná River floodplain not previously studied, and evaluate the influence of local factors on the structure of periphytic algal communities in different lentic environments of this floodplain.

The high water period has led to a greater species richness of periphytic algae in many tropical (Rodrigues & Bicudo, 2004; Marazzi, 2004; Fonseca & Rodrigues, 2005; Taniguchi et al., 2005; Algarte et al., 2009; França et al., 2011; Carapunarla et al., 2014; Biolo et al., 2015; Bichoff et al., 2016) and temperate floodplain (Pfeiffer et al., 2013). One prediction for this is owing to the increased number of propagules carried in high waters (Rodrigues & Bicudo, 2001b; Dunck et al., 2016). We hypothesized that periphyton species richness in the Upper Paraná River floodplain would change as a function of the seasonal variation in the hydrological regime (temporal scale), and additionally, that it would be influenced by variation in the limnological characteristics of different lentic environments (spatial scale). So, it can be expected that, during high water periods, periphyton species richness will be higher than during low water periods.

2. Material and Methods

2.1. Study area

This study was performed in the Upper Paraná River floodplain, which encompasses the last undammed stretch of the Paraná River in Brazilian territory, located between the Porto Primavera-São Paulo and Itaipu-Paraná reservoirs (Agostinho et al., 2008). This stretch includes several natural conservation units, such as the Ilha Grande National Park, an important area for the preservation and conservation of the great diversity of aquatic species present in this ecosystem.

We sampled three lentic environments (São João, Pavão and Saraiva Lakes) in this floodplain from May 2014 to May 2015 (May/2014, Aug/2014, Nov/2014, Feb/2015 and May/2015). These lakes, which show different morphologies, are permanently connected to the main channel of the Paraná River. All have large macrophyte stands dominated by *Eichhornia azurea* (Sw.) Kunth, whose petioles were used as a substrate to sample periphytic algal communities (Figure 1).

São João lake (23°49' 20.9"S, 53°59'16.6"W), is oval in shape, approximately 3 km long and approximately 1.8 m deep, connecting to the Paraná river through a 2 km long channel. Pavão lake (23°58'31.1"S, 54°09'49.1"W), is irregular-elongate in shape, approximately 0.35 km long with an average width of 20 m and approximately deep 2.6 m. Its connection channel is narrow and short. Saraiva lake (24°00'41.2"S, 54°08'23.3"W), considerably larger than the two other lakes studied, is elongate in shape, approximately 9.5 km long with an average width of 180 m. Its approximately deep is 2.6 m.

2.2. Limnological variables

The following abiotic parameters were measured in each sampling site: water temperature (°C; measured using a digital thermistor); dissolved

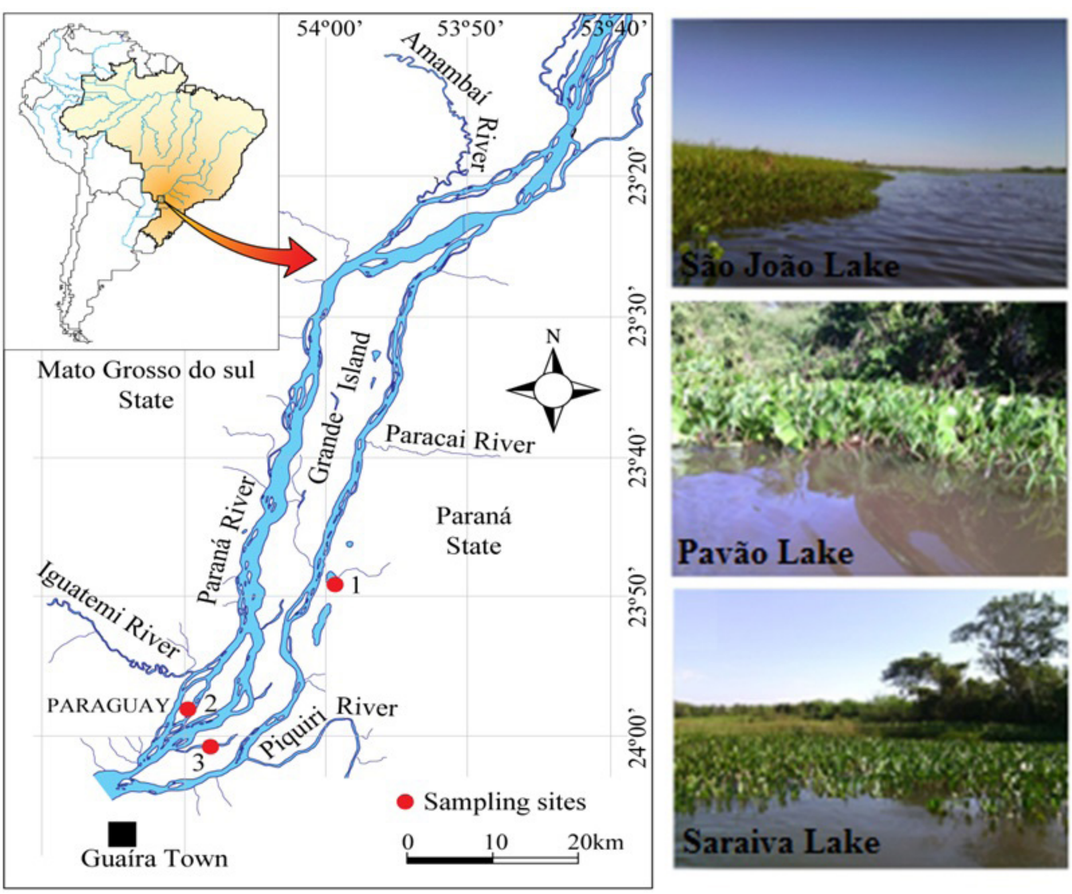

Figure 1. Upper Paraná River floodplain and location of the sampling Lakes.

oxygen (% saturation and mg L^{-1}; digital oximeter); pH (pH meter); conductivity (μS cm^{-1}; conductivity meter); transparency (m; Secchi disk); turbidity (NTU; turbidity meter) alkalinity (μEq L^{-1}; measured following Wetzel & Likens (2000); ammoniacal nitrogen, orthophosphate, total nitrogen and total phosphorus (μg L^{-1}; measured following Mackereth et al. (1978). To analyze the dissolved nutrients and estimate the amount of suspended material, samples were filtered using Whatman GF/F filters under low pressure (< 0.5 atm) and kept cool for further determination in the laboratory.

Data on water levels of the Paraná River were obtained at the Fluviometric Station of Porto Rico Base and limnological variables were provided by the Laboratory of Basic Limnology of the Research Center in Limnology, Ichthyology and Aquaculture of the State University of Maringá.

2.3. Sampling of periphytic algal communities

Two stands of the aquatic macrophyte *Eichhornia azurea* (Sw.) Kunth were sampled in each lake. In each stand, at each of the five sampling periods, one petiole in adult stage was sampled (Schwarzbold, 1990; Algarte et al. 2016; Bichoff et al., 2016; Algarte et al., 2017). We thus collected two petioles (n = 2) *per site*, totalling 30 samples. Sampling days of the periphytic algal communities were 08-09-11/05/2014, 06-07-08/08/2014, 04-05-08/11/2014, 03-04-08/02/2015 and 06-07-10/05/2015.

The periphytic material was collected by scraping part of the *E. azurea* petioles using a stainless-steel blade wrapped in aluminium foil and washed by jets of distilled water (Bicudo, 1990). The material removed was preserved with acidified (0.5%) Lugol's solution for later counting, and the material for the qualitative analysis was preserved in Transeau's solution (1:1) as recommended by Bicudo & Menezes (2006).

Qualitative analyses were carried out. Quantitative analyses were based on the method of Utermöhl (1958). Samples of periphytic algae were quantified using sedimentation chambers in an inverted microscope. Counts were carried out in random fields until reaching at least 100 individuals of the most common species in each sample and depending on the species accumulation curve (Bicudo, 1990).

Algal species were identified by mounting temporary slides and observing them in a binocular optical microscope with ocular micrometer and coupled bright chamber at 400× and 1000× magnification (Bicudo & Menezes, 2006). Identification was performed to the lowest taxonomic level possible, using taxonomic keys and specialized bibliography. We used the classification system proposed by Komárek & Anagnostidis (1989) and Anagnostidis & Komárek (1988) for Cyanophyceae, and that by Round et al. (1990) for the other classes (Bicudo & Menezes, 2006).

2.4. Data analysis

Algal richness was estimated from algal density, using the species accumulation curve obtained through quantitative analysis. A Redundancy Analysis (RDA) was performed to evaluate the relationship between abiotic and biotic data over time and interpret which factors most influenced the periphytic algae. In this analysis, the abiotic data were previously log-transformed (except pH) and we considered the variables with $p<0.05$ significance. All analyses were performed using R software (R Development Core Team, 2014). Graphs were constructed using Statistica 7.1 (STATSOFT Inc., 2005).

3. Results

3.1. Hydrological regime

During the studied period, variation in the hydrological regime of the Paraná River was moderate, with relatively small flood pulses (< 3.5 m). Water level never reached the overflow level (4.5 m). Highest water levels were registered from November 2014 to April 2015, with values ranging from 2.5 m to 3.0 m, which were considered as high-water periods (Figure 2). During the sampling period, May 2014 (1.8 m) and August 2014 (1.7 m) showed the lowest levels, followed by May 2015, with approximately 1.8 m. August was considered to be a low-water period, and both May 2014 and May 2015 were considered to be transition periods.

3.2. Limnological variables

In general, abiotic variables showed remarkable variation over time (Table 1). Pavão Lake was the most distinct one, showing the lowest values of dissolved oxygen, the highest values of conductivity and alkalinity, and also the highest concentration of assimilable forms of nutrients over time. Briefly, temperature varied with season, with higher values (greater than 26.6 °C) between November 2014 and February 2015, when water level was highest. Values of pH varied from 6 to 7.7, conductivity from 30.6 to 72.4, dissolved oxygen concentrations from 1.6 to 8.5, alkalinity from 208.9 to 978.8 and turbidity from 2.88 to 36.93. (Table 1).

Regarding nutrient concentrations, the highest values of assimilable forms of nitrogen (NO_3) were registered in August 2014 (lowest water level), and the highest values of assimilable forms of phosphorus (PO_4) in November 2014 (highest water level). Saraiva Lake showed the highest total nutrient concentrations.

3.3. Periphytic algal community

A total of 149 taxa of periphytic algae were found is samples from the three lakes. These belonged to nine classes Bacillariophyceae (44 spp), Zygnemaphyceae (34 spp.), Chlorophyceae (31 spp.), Cyanophyceae (16 spp.), Euglenophyceae (11 spp.), Xanthophyceae (5 spp.), Oedogoniophyceae (6 spp.), Chrysophyceae (1 sp.) and Chlamydophyceae (1 sp.). Bacillariophyceae (diatoms) thus showed the highest species richness, followed by Zygnemaphyceae and Chlorophyceae (Figure 3).

The diatoms (Bacillariophyceae) predominated in most lakes during the studied periods, mainly between August and November 2014. February 2015 and May 2015 showed an increase in species belonging to classes Zygnemaphyceae, Chlorophyceae and Cyanophyceae (Figure 3). Regarding variation among sites, during most sampling periods Saraiva Lake showed higher species richness than the other environments (Figure 4), with a predominance of diatoms, followed by Zygnemaphyceae and Chlorophyceae.

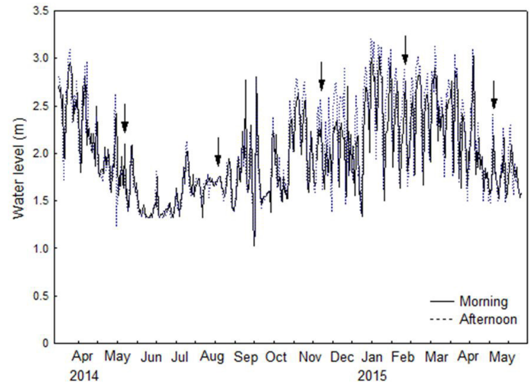

Figure 2. Daily variation in the water level of the Paraná River during the studied period (May/2014 to May/2015). Arrows indicate sampling days of the periphytic algal community.

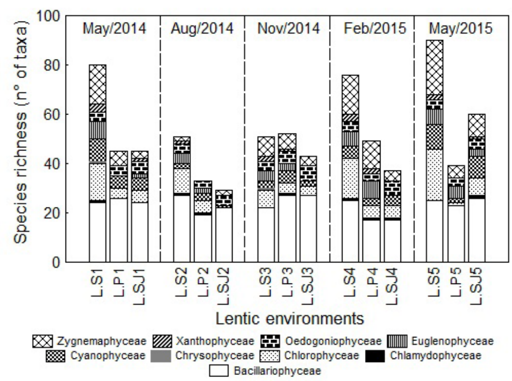

Figure 3. Spatial and temporal variation in species richness of periphytic algae by classes in the sampling sites of the Upper Paraná River floodplain. Saraiva Lake (L.S), Pavão Lake (L.P) and São João Lake (L.SJ). August (Aug/2014), November (Nov/2014), February (Feb/2015).

Table 1. Means (n = 2) of limnological variables analyzed in lentic environments of the Upper Paraná River floodplain in different sampling periods. Water temperature (TEMP), Dissolved oxygen (DO), pH, Conductivity (COND), Alkalinity (ALK), Turbidity (TURB), Total Nitrogen (TN), Nitrate (NO_3), Total Phosphorus (TP), Orthophosphate (PO_4).

Variables	São João Lake					Pavão Lake					Saraiva Lake				
	May/2014	Aug/2014	Nov/2014	Feb/2015	May/2015	May/2014	Aug/2014	Nov/2014	Feb/2015	May/2015	May/2014	Aug/2014	Nov/2014	Feb/2015	May/2015
TEMP (°C)	23	21.5	28	27.5	22.1	23.6	19.7	26.6	28.5	22	23.9	20.25	27.8	29	23
DO (mg L^{-1})	5.37	8.03	6.81	6.38	6.89	2.45	2.76	3.16	2.14	3.40	6.20	6.07	5.47	5.69	6.83
pH	6.15	6.86	6.74	7.37	6.62	6.20	6.57	6.03	7.18	6.56	6.37	6.33	6.04	7.71	7.57
COND (µS cm^{-1})	30.6	31.3	31.9	36.4	38.1	55.6	72.4	67.7	68.9	59.4	40.2	31.7	41.5	55.1	53.4
ALK (µEq L^{-1})	369.2	297.5	208.9	225.6	215.4	795.4	978.8	499	516.8	402.9	427.5	290.5	320.7	421.5	354.8
TURB (NTU)	33.56	30.67	36.93	18.52	7.98	5.42	12.85	9.17	2.88	7.40	3.25	7.82	5.23	5.33	9.15
TN (µg L^{-1})	693.6	688.6	817.2	589.9	775.3	624.3	1153.9	804.5	718.9	662.9	729.2	1392.9	1127.2	984	1143.3
NO_3 (µg L^{-1})	0	112.1	17.8	20.5	5.79	153.4	249.8	119	24.4	94.24	0	17.1	17.1	16.3	1.22
TP (µg L^{-1})	29.3	21.7	30.7	29.03	18.2	21.1	26.6	32.4	42.1	23.5	29.7	34.05	36.9	60.6	38.5
PO_4 (µg L^{-1})	5.5	9.2	9.8	3.1	3.5	4.8	7.2	13.2	4.5	5.9	3.03	7.1	8.6	4.1	4.7

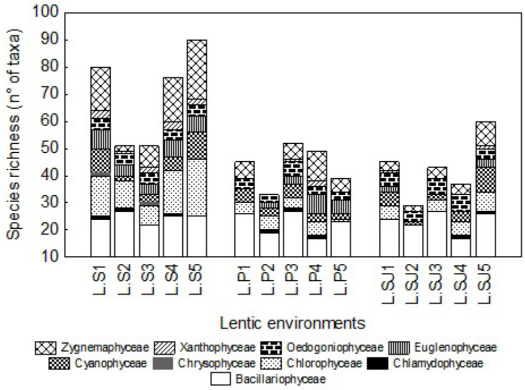

Figure 4. Spatial variation in species richness by classes in the sampling sites of the Upper Paraná River floodplain. Saraiva Lake (L.S), Pavão Lake (L.P) and São João Lake (L.SJ). Numbers represent the sampling periods between 2014 and 2015. 1) May/2014, 2) Aug/2014, 3) Nov/2014, 4) Feb/2015 and 5) May/2015.

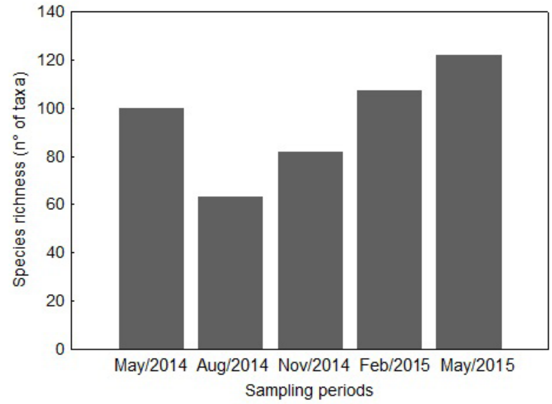

Figure 5. Temporal variation in total species richness during the sampling periods. May (May/2014) August (Aug/2014), November (Nov/2014), February (Feb/2015) and May (May/2015).

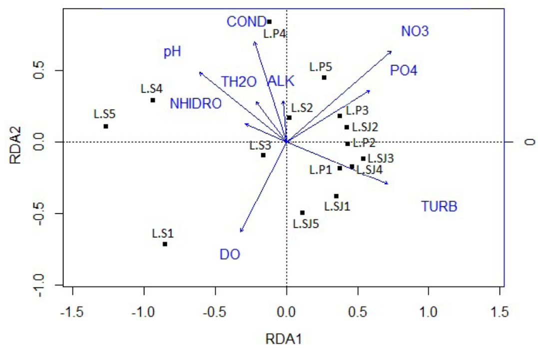

Figure 6. Ordination diagram of Redundancy Analysis (RDA), illustrating the relationships between environmental variables and lentic environments over time, based on species composition data. Saraiva Lake (L.S), Pavão Lake (L.P) and São João Lake (L.SJ). Numbers represent sampling periods between 2014 and 2015. 1) May/2014, 2) August/2014, 3) November/2014, 4) February/2015 and 5) May/2015.

Considering all lakes taken together, total species richness was highest in May 2015 (122 spp.), followed by February 2015 with 107 species (Figure 5). August 2014 showed the lowest number of taxa registered (63 spp.). Species richness of periphytic algae was associated with the water level of the Paraná River, with a larger number of taxa registered during periods of higher water levels than in the other months studied (Figure 5). Singly, in each lake the lowest species richness values also occurred in August 2014. The highest values occurred in May 2015 for Saraiva and São João Lakes and in November 2014 for Pavão Lake (Figure 4).

The following species were present in all lakes and all sampling periods: *Fragilaria capucina* Desmazières, *Gomphonema gracile* Ehrenberg, and *Navicula cryptotenella* Lange-Bertalot (Bacillariophyceae) and *Oedogonium* sp.1 and *Oedogonium* sp.3 (Oedogoniophyceae). However, *Achinanthidium minutissimum* (Kützing) Czarnecki, *Eunotia incisa* Smith ex Gregory and *Gomphonema lagenula* Kützing were common in two of the lakes, and were absent only in one environment over time.

Results of Redundancy Analysis (RDA) are shown in figure 6. The first two axes explained 47% of total variability in the data (RDA1 = 33% and RDA2 = 14%). However, only the first axis was significant ($F = 4.399$; $p = 0.02$). This ordination separated the sampled lakes according to limnological variables and species composition of periphytic algae.

Saraiva Lake appeared on the left side of axis 1 during all but one of sampling periods (except August 2014), along with Pavão Lake in February 2015. These samples showed relatively high values of pH, dissolved oxygen, water level, conductivity, water temperature and alkalinity, associated with most species, including *Achnanthidium minutissimum*, *Aphanocapsa annulata* McGregor, *Bulbochaete* sp.1, *Calothrix fusca* Bornet & Flahault, *Characium ornithocephalum* Braun, *Coleochaete orbicularis* Pringsheim, *Cosmarium laeve* var. *rotundatum* Messikommer, *Cyclotella meneghiniana* Kützing, *Encyonema neogracile* Krammer, *Encyonema silesiacum* (Bleisch) Mann, *Euglena* sp.2, *Eunotia flexuosa* (Brébisson ex

Kützing) Kützing, *Gomphonema subtile* Ehrenberg, *Oedogonium* sp.7, *Pseudanabaena* cf. *mínima* (An) Anagnostidis, *Spirogyra* sp.1, *Trachelomonas volvocina* (Ehrenberg) Ehrenberg.

Samples from São João Lake and Pavão Lake (except for February 2015) appeared on the right side of the first axis, which showed higher values of nitrate, turbidity and orthophosphate, associated with a smaller number of species of periphytic algae, for example, *Encyonema minutum* (Hilse) Mann, *Eunotia incisa*, *Eunotia pectinalis* (Kützing) Rabenhorst, *Fragilaria capucina, Gomphonema affine* Kützing, *Gomphonema gracile*, *Gomphonema lagenula*, *Navicula cryptotenella*. Among the abiotic variables analyzed, only nitrate ($p = 0.02$) and turbidity ($p = 0.03$) significantly influenced the species composition of periphytic algae.

4. Discussion

Our results demonstrate that species richness of periphytic algae changed over time in response to variation in the hydrological regime of the Paraná River, showing the influence of hydrological dynamics and environmental changes on periphytic algae of these floodplain lakes. Previous studies have also found this influence on attributes of periphytic algal communities other than richness, such as biomass and abundance, in lakes of this floodplain (Fonseca & Rodrigues, 2005; Algarte et al., 2009; Biolo et al., 2015).

High values of species richness were registered in May and February 2015, coinciding with high water level, and the lowest number of algal species was found in August 2014, which presented the lowest water levels of the Paraná River. Other studies performed in lentic and semi-lotic environments of the Upper Paraná River floodplain also registered higher species richness of periphytic algae during high-water periods (Rodrigues & Bicudo, 2004; Fonseca & Rodrigues, 2005; Algarte et al., 2009, 2017; Carapunarla et al., 2014; Biolo et al., 2015; Bichoff et al., 2016), in agreement with our results.

However, May 2015, which was characterized by low water levels, had surprisingly high species richness values. The higher water levels in previous months probably favoured the dispersal of propagules and the arrival and establishment of new species in these environments (Rodrigues & Bicudo, 2001b; Rodrigues et al., 2013), in addition to increasing the input of allochthonous material, leading to increased nutrient availability (Esteves, 2011; Thomaz et al., 2004). These factors could favoured high algal species richness despite the low water levels.

Similarly, the seasonal dynamics of limnological variables were closely related to the pattern of variation in the hydrological regime of the Paraná River, in large part because the periods of high water levels coincided with the warmest months of the year. Therefore, these periods showed higher values of temperature, total nutrients concentrations, pH, dissolved oxygen and nutrient availability. Algae are sensitive to changes in water quality, and these environmental conditions contributed to high species richness of periphytic algae (Rodrigues & Bicudo, 2001a, 2001b). Increased nutrient concentrations were due to the increase in the water level, which allowed a greater input of water, organic matter and allochthonous material from nearby areas such as seasonal wetlands (Agostinho et al., 2000; Rocha & Thomaz, 2004).

Regarding May and August 2014, limnological variables showed a transition phase from autumn to winter, with decreases in temperature, alkalinity, conductivity and light penetration, and increases in turbidity and concentrations of dissolved oxygen and nutrients. Those environmental conditions, associated with low water levels reduced the species richness of periphytic algae. These physical-chemical characteristics reduce the possibility of algal dispersal, restricting their distribution in water bodies (Esteves, 2011).

This study demonstrated that diatoms (class Bacillariophyceae) predominated in all environments over time. Compared to other periphytic algae, diatoms show higher tolerance to seasonal changes in the hydrological regime, and adapt more easily to different environmental conditions (Round, 1991; Rodrigues & Bicudo, 2001b; Algarte et al., 2009). Besides colonizing all types of environments and being r-strategists (Biggs, 1996), diatoms have morphological adaptations to produce mucilage (such as in peduncles), which favour adhesion to the substrate (Biggs, 1996; Azim & Asaeda, 2005; Schneck et al., 2008; Bichoff et al., 2016).

In addition to diatoms, classes Zygnemaphyceae and Chlorophyceae were also represented by many species. Richness of those classes varied according to the water level and limnological characteristics, and increased over time. Chlorophyceans and desmids (which accounted for most species of Zygnemaphyceae) develop best at high temperatures (Coesel & Wardenaar, 1990; Vercellino & Bicudo, 2006; Murakami et al., 2009). Moreover, they are easily carried and distributed by water currents and establish in environments with abundant stands of macrophytes, which contribute to an increase in species number (Algarte et al., 2009, 2017; Biolo et al., 2015).

Saraiva Lake yielded the highest number of taxa in all sampling periods, followed by Pavão and São João Lakes. Saraiva Lake presented higher concentrations of total nitrogen and total phosphorus than the other lakes, and the higher availability of nutrients generated favorable conditions for increased algae richness (Bourassa & Cattaneo, 2000; Hillebrand & Sommer, 2000; Ferragut & Bicudo, 2009). This lake is relatively large and the connection channel is greater, favoring the reception and dispersal of propagules, and thereby the arrival and establishment of new species.

São João Lake presented higher values of turbidity than the two other lakes. Its greater turbidity restricted the distribution of periphytic algae (Hill et al., 2000; Dunck et al., 2015) leading to lower richness. In general, the differences in the species richness among these lakes can be attributed to the differences in their physical and chemical characteristics, in association with the hydrological regime of the Paraná River.

Our study also showed that some species were associated with high nutrient availability and turbidity (RDA). Those variables were more important in the structuring, organization and presence of diatom species, *Gomphonema augur* var *sphaerophorum* (Ehrenberg) Grunow, and *Cymbella tropica* Krammer. These species were associated with high nitrate concentrations, a relationship previously indicated in other studies (Moro & Fürstenberger, 1997; Lobo et al., 2004). *Gomphonema turris* (Bacillariophyceae), *Uronema gigas* Vischer (Chlorophyceae), and *Phormidium* sp.1 (Cyanophyceae) were associated with high values of turbidity, a relationship also formerly observed by Moro & Fürstenberger (1997) and Ferragut et al. (2005). Species belonging to genus *Phormidium* may occur in various types of habitats, and are common in lentic environments (Bicudo & Menezes, 2006).

We conclude that seasonal variation in the hydrological regime of the Paraná River, associated with variation in the limnological characteristics of different lentic environments of the Upper Paraná River floodplain, directly influenced the species richness of periphytic algae. We showed that hydrological dynamics have an important role and constitute a key factor affecting the species richness of the periphyton community in floodplains.

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