Effects of hydrological regime and connectivity on the interannual variation in taxonomic similarity of periphytic algae

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Abstract

The aim of this study was to analyze the effects of flood pulses (intensity) on the richness and composition of periphytic algae in lentic environments of the Upper Paraná River floodplain, over a six-year period. Other factors, such as connectivity of the environments with the main channel of the river and the availability of substrate for the periphyton, were also evaluated. For qualitative analyses, periphyton community was sampled from adult petioles of *Eichhornia azurea* Kunth taken from the littoral regions of the lakes studied. A total of 457 taxa of periphytic algae, distributed within 141 genera and 10 classes, were registered in the four environments. The greatest richness of periphytic algae was observed in connected floodplain lakes, especially in 2007 and during high water periods. In both connected and disconnected lakes, richness correlated positively with water levels of the Paraná River. Richness was also positively correlated with the number of taxa of aquatic macrophytes. The specific composition of periphytic algae differed between high and low water periods, and between connected and disconnected lakes. Therefore, among the considered variables, it is evident that flood pulse constitutes the principal force acting on periphytic algae communities of the floodplain, followed by the degree of connectivity and the presence of aquatic macrophytes.

Keywords: periphyton, species richness, species composition, flood pulse, floodplain, disturbance, degree of connectivity.

Efeito do regime hidrológico e da conectividade na similaridade taxonômica de algas perifíticas: variação interanual

Resumo

Este trabalho visou analisar o efeito do pulso de inundação (intensidade) sobre a riqueza e composição de algas perifíticas, ao longo de seis anos, em ambientes lênticos da planície de inundação do Alto Rio Paraná. A influência da conectividade dos ambientes com a calha principal do rio e disponibilidade de substratos para a comunidade de algas perifíticas também foi avaliada. Para análise, a comunidade perifítica foi amostrada de pecíolos adultos de *Eichhornia azurea* Kunth, retirados da região litorânea das lagoas estudadas. Considerando os quatro ambientes, foram registrados 457 táxons de algas, distribuídos em 141 gêneros e 10 classes. A maior riqueza de algas perifíticas foi observada em lagoas conectadas, com destaque para o ano de 2007 e para o período de águas altas. A riqueza apresentou correlação positiva, nas lagoas conectadas e não conectadas, com nível hidrométrico do Rio Paraná. Também esteve correlacionada positivamente com o número de táxons de macrófitas aquáticas. A composição de algas perifíticas diferiu entre os períodos de águas altas e águas baixas e entre lagoas conectadas e não conectadas. Ficou evidente que, dentre as variáveis consideradas, o pulso de inundação constitui a principal função de força atuando sobre a comunidade de algas perifíticas na planície, seguido pelo grau de conectividade e presença de macrófitas aquáticas.

Palavras-chave: perifíton, riqueza, composição específica, pulso de inundação, planície de inundação, distúrbio, grau de conexão.

1. Introduction

The Upper Paraná River floodplain displays a great heterogeneity of aquatic habitats, which promotes high biological diversity (Thomaz et al., 2007). The changes between hydrological periods and the dynamics created by flood pulse differentiate this floodplain from other systems, while at the same time providing high levels of diversity and productivity (Agostinho and Zalewski, 1996).

The environments composing the Paraná River floodplain display various degrees of connectivity with the main river channel. According to Ward et al. (1999), connectivity is one of the principal structuring factors of aquatic communities, and is fundamental to the maintenance of biodiversity in these ecosystems. Lentic environments from the floodplain (lakes and backwaters) are predominantly shallow and present extensive communities of aquatic macrophytes. These plants increase the heterogeneity of littoral zones, providing space for colonization and supporting specific biota (Junk, 1970; Wetzel, 1983), in particular, the periphyton (Fonseca and Rodrigues, 2005; Leandrini et al., 2008), a complex community either firmly or loosely fixed to submersed substrata (Wetzel, 1983).

Some studies (Hoagland et al., 1982; Stevenson, 1996; 1997) show, that for the periphyton, spatial and temporal heterogeneity are the result of complex interactions among multiple causes acting in temporal and spatial scales. However, to understand these alterations, and to predict changes in the community of periphytic algae, it is essential to identify the regulating factors and their hierarchical importance. In the Upper Paraná River floodplain, Rodrigues and Bicudo (2001), Fonseca and Rodrigues (2005) and Algarte et al. (2006) showed that hydrological regime is an important factor affecting periphytic algae, but their analyses encompassed only a short temporal scale.

To better understand possible patterns in the richness and species composition of periphytic algae according to spatial and temporal scales in the Upper Paraná River floodplain, we first analyzed the annual variations in richness and composition of periphytic algae species in lakes connected or disconnected from the main channel of the river. Then, we evaluated the influence of the hydrological regime, the degree of connectivity and the presence of aquatic macrophytes on the richness and composition of periphytic algae. Finally, we evaluated the similarity between periphytic communities each year (from 2002 to 2007) in connected and disconnected lakes. Our hypothesis is that species richness and composition of periphytic algae in the Upper Paraná River floodplain are hierarchically regulated by the flood pulse of each year (temporal scale), in addition to the connectivity with the main channel of the river (spatial scale) and the availability of substrate (presence of macrophytes).

2. Material and Methods

The Upper Paraná River floodplain is located between Porto Primavera and Itaipu reservoirs, and extends for approximately 230 km (Agostinho et al., 2008). Samples were taken between 2002 and 2007, during the high (February) and low (June) water periods. Four lentic environments of the Upper Paraná River floodplain were sampled: two lakes permanently connected to the main channel of the river (Patos and Guaraná Lakes), and two disconnected lakes (Fechada and Ventura Lakes) (Figure 1). These disconnected lakes came into contact with the river only during the high water periods of years 2005 and 2007.

The littoral regions of these lakes are dominated by multispecies stands of aquatic macrophytes, notably *Eichhornia azurea* Kunth. As they were well represented in all the lakes, adult petioles of this macrophyte were chosen as the natural substrate (Schwarzbold, 1990).

Periphyton samples were taken from the littoral regions in all lakes. Then, periphyton was removed from the petioles using steel blades and pressurized distilled water. Periphytic material was conditioned in 150 mL glass flasks and fixed in Transeau solution (Bicudo and Menezes, 2006). For qualitative analyses of the taxa, non-permanent slides were prepared and a binocular microscope was used at 40 and 100×.

Identification of the species was carried out using classic literature (Prescott et al., 1981; Förster, 1982; Prescott, 1982; Croasdale and Flint, 1986; Komárek and Anagnostidis, 1986; 1989; Krammer and Lange-Bertalot, 1986; 1988; 1991; Anagnostidis and Komárek, 1988; Dillard, 1990; 1991), as well as other region-specific literature.

Water level data of the Paraná River was provided by ANA ("Agência Nacional das Águas") (Figure 2).

To compare the average richness of periphyton algae in relation to the factors "years", "hydrological periods" and "environments" (connected or disconnected lakes), an analysis of variance was applied (three way ANOVA). To determine which levels of the factors (years, hydrological periods and environments) differed, we applied, a posteriori, the Fisher test of multiple comparisons. The analysis was accomplished with Log_{10}-transformed data to meet the assumptions of ANOVA (homoscedasticity). For these analyses the software used was StatSoft (version 7.0).

To verify possible relationships among richness of periphytic algae, water level, and the number of taxa of aquatic macrophytes (Thomaz et al., 2009), we applied the Pearson correlation coefficient. The correlations were considered significant when $p < 0.05$.

The similarity of the communities between environments (connected and disconnected), the hydrological periods (high and low waters), and each year studied was measured by group analysis with a Jaccard Index and a Mantel test, using the program NTSYS v1.5 (Rohlf, 1989).

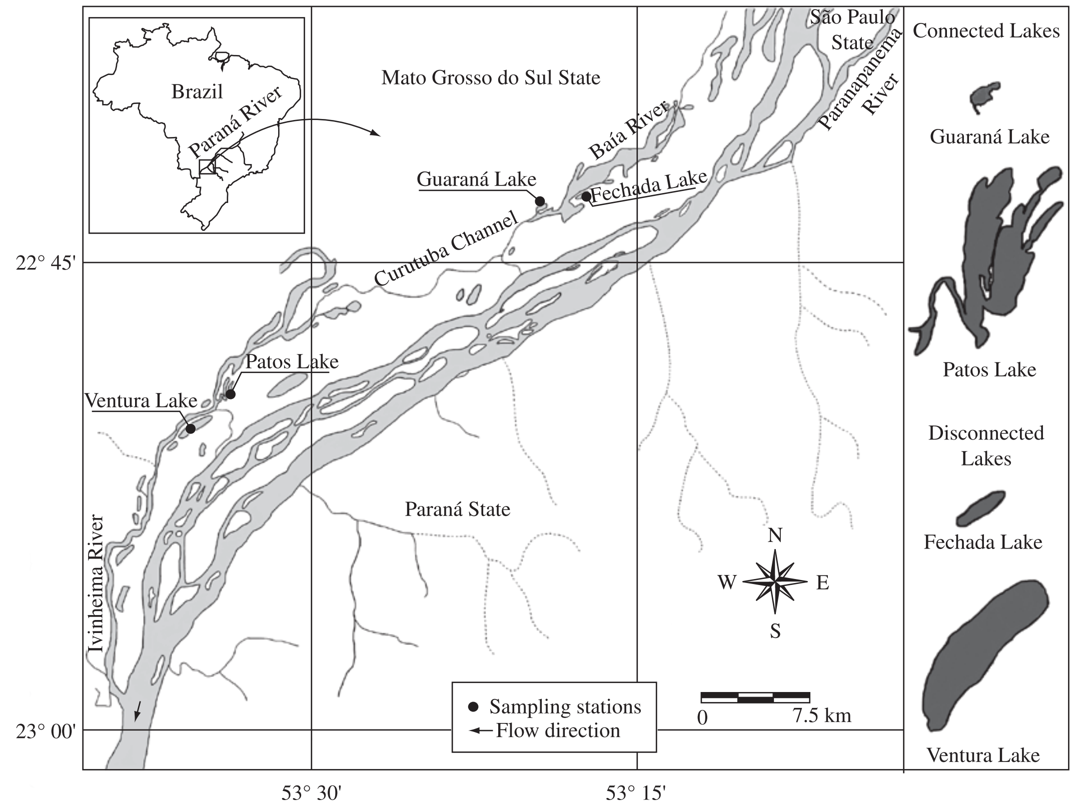

Figure 1. Map of locations of the connected (Guaraná and Patos Lakes) and disconnected lakes (Fechada and Ventura Lakes) in the Upper Paraná River floodplain.

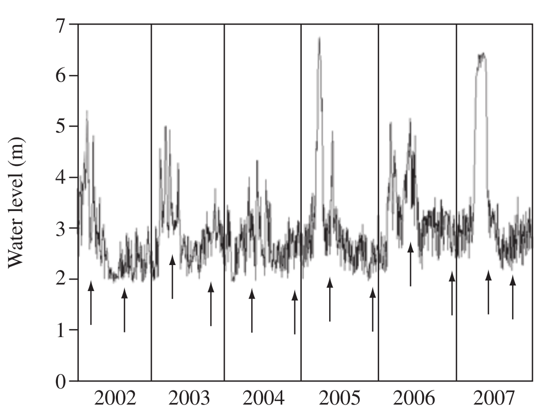

Figure 2. Water levels (m) on the Paraná River from 2002 to 2007 (data: ANA), with sampling dates indicated.

3. Results

During the study period, the water level of the Paraná River oscillated between 1.95 and 6.76 m (high water) and between 1.93 and 3.96 m (low water). The highest water level was observed in 2005 and 2007, reaching over 6.00 m (Figure 2). For the years 2002, 2003 and 2006, mean water levels were similar, reaching 3.21 m in high water and 2.66 m in low water. However, in 2004, the mean water level was 3.00 m during high water, and 2.80 m during low water.

A total of 457 taxa of periphytic algae distributed within 141 genera and 10 classes were recorded in all lakes and periods. The greatest richness of periphytic algae was found in connected lakes (Table 1). Further, in 2005, 2006 and 2007, years with higher flood pulse intensity (Figure 2), we observed higher periphytic richness, both in connected and disconnected lakes (Table 1).

Richness of periphytic algae differed significantly between years (Figure 3a). The year 2007 was significantly different from 2002, 2003 and 2004, but similar to 2005 and 2006 (Figure 3a). Likewise, richness of the periphyton differed significantly between hydrological periods (Figure 3b) and environments (Figure 3b) ($p < 0.05$; Figure 3). Significant interactions between the considered factors were not observed (Table 2).

The richness of both connected and unconnected lakes was positively correlated with water levels of the Paraná River ($r = 0.51$; $p < 0.05$) (Figure 4a). There was a positive correlation between the richness of periphytic algae and the number of aquatic macrophyte taxa in each lake, whether the lake was connected to or disconnected from the main river ($r = 0.44$; $p < 0.05$; Figure 4b).

Table 1. Number of periphytic algae taxa observed in the lakes of the Upper Paraná River floodplain from 2002 to 2007.

Environment	2002		2003		2004		2005		2006		2007	
	HW	LW	HW	LW	HW	LW	HW	LW	HW	LW	HW	LW
Disconnected	51	69	78	40	66	54	117	50	117	56	122	116
Connected	99	72	117	104	91	82	138	72	142	100	149	121

Table 2. Influence of the variation sources on the richness of periphytic algae (Log) demonstrated through the bifactorial ANOVA values with an asterisk indicating significant differences ($p < 0.05$).

Variation sources	G.L. (effect; error)	F	p
Years	5; 24	4.74	0.0037*
Hydrological Periods	1; 24	17.64	0.0003*
Environments	1; 24	14.01	0.0010*
Years × Hydrological Periods	5; 24	1.90	0.1320
Year × Environments	5; 24	0.71	0.6248
Hydrological Periods × Environments	1; 24	0.002	0.9684
Years x Hydrological Periods × Environments	5; 24	0.51	0.7690

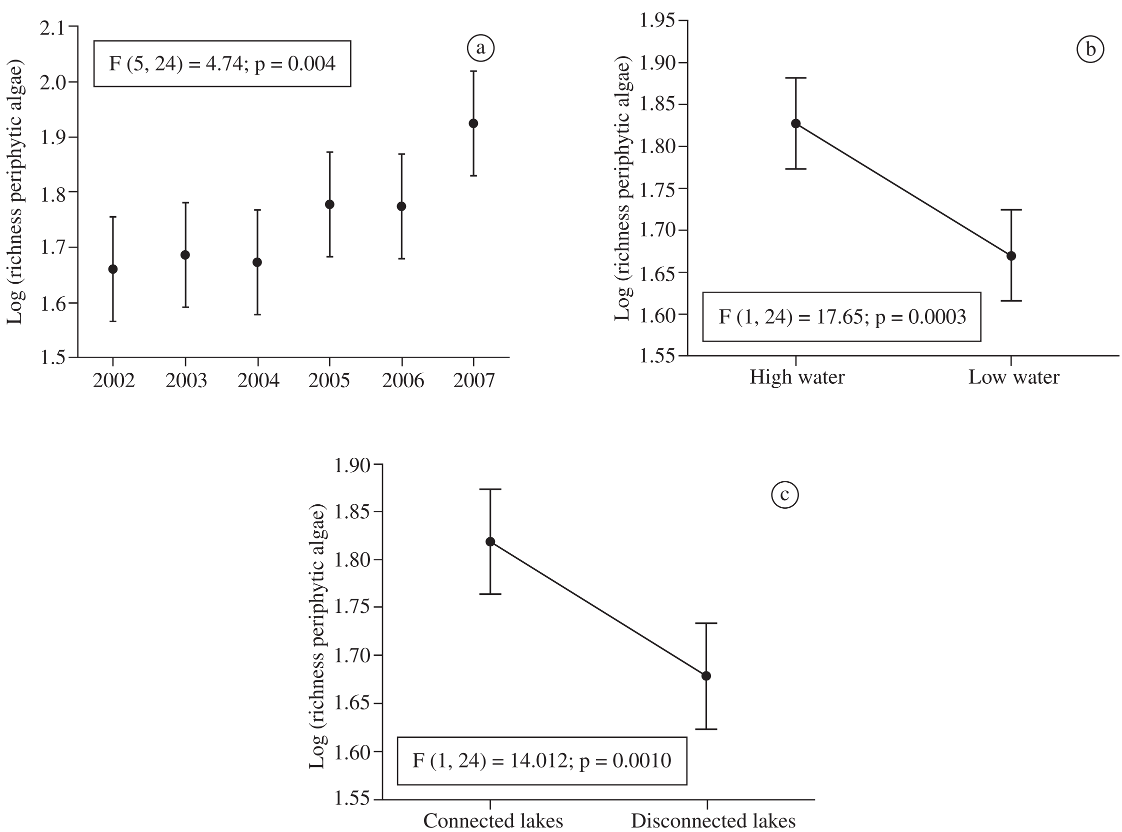

Figure 3. a) Effect of the year, b) hydrological period and c) environment in the periphytic algae communities in the Upper Paraná River floodplain. Within rectangle indicate significant differences by the Fisher test ($p < 0.05$). Means ± Standard deviation.

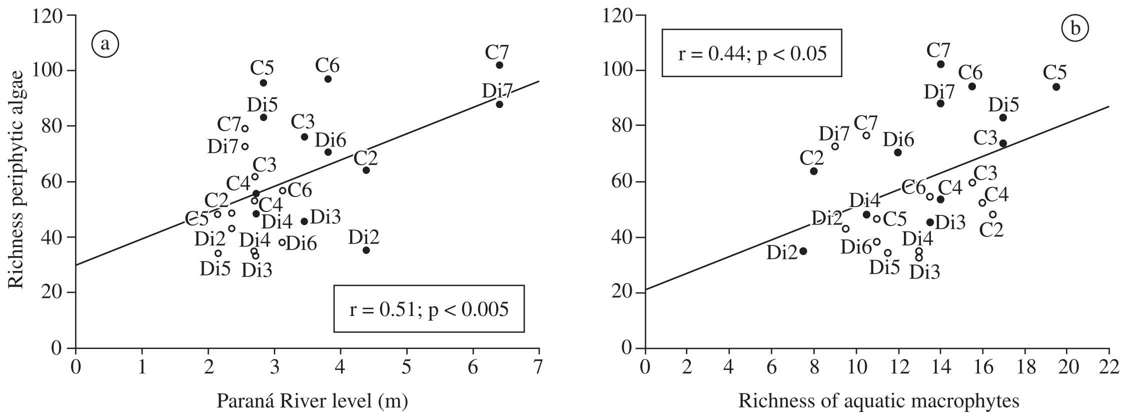

Figure 4. Pearson correlation between periphytic algae richness taxa and the water level of the a) Paraná River and b) aquatic aquatic macrophytes richness for connected (C) and disconnected (Di) lakes of the Upper Paraná River floodplain during high water (●) and low water (○) periods of 2002 to 2007.

Table 3. Number of periphytic algae taxa per class observed in high water and low water in the Upper Paraná River floodplain from 2002 to 2007.

Algae class	High water	Low water
Zygnemaphyceae	123	82
Chlorophyceae	74	65
Bacillariophyceae	66	92
Cyanophyceae	60	33
Euglenophyceae	30	20
Xanthophyceae	13	10
Other	16	13
Total	382	315

Classes with the greatest number of taxa were, in order of dominance, Zygnemaphyceae, Bacillariophyceae, Chlorophyceae, and Cyanophyceae; together totalling 86.21%. During high water periods, in general, the number of periphytic taxa recorded was greater than during the low water periods (Table 3). In high water, the dominant class, according to the number of taxa, was Zygnemaphyceae followed by Chlorophyceae, Bacillariophyceae and Cyanophyceae. In low water, we registered a reduction in species richness for all groups, with the exception of Bacillariophyceae (diatoms) (Table 3).

The number of exclusive periphytic algae taxa was highest during high water periods (140) than low water periods (75). In high water periods, these species belonged to Zygnemaphyceae (51 taxa), Cyanophyceae (36 taxa), and Chlorophyceae (24 taxa). In low water periods, most of the species belonged to Bacillariophyceae (36 taxa). The number of exclusive algae taxa was higher in connected lakes (123) than in disconnected lakes (64).

The floristic distinctions among the periphytic communities of the hydrological periods and the connectivity of the environments are demonstrated in the similarity dendrogram (Mantel test; r = 0.73; Figure 5). Only during the high water period of 2002 the disconnected lake showed very low similarity with the other years or environments. Two groups were formed when considering showed 28% similarity in species richness, essentially dividing the hydrological periods (Figure 4). In both group A (low water) and group B (high water), distinct subgroups were found based on the degree of connectivity, indicating differences between connected and disconnected lakes, regardless of the hydrological period. During low water, all disconnected lakes showed similar characteristics, except during 2007. A similar pattern was observed for connected lakes, except in 2006. During high water, the grouping of environments according to years – for connected and disconnected lakes – was also remarkable. Connected lakes in 2002, 2003 and 2004 were grouped together, while in the years 2005, 2006 and 2007, connected and disconnected lakes, formed distinct group from each other.

4. Discussion

In the Upper Paraná River floodplain, most groups of aquatic organisms show great species diversity and remarkably dynamic ecological patterns in response to the heterogeneity of the environment and fluctuations in the water level (Agostinho et al., 2004), the latter of which is the strongest functional characteristic force of this floodplain.

Periphyton response to disturbances, such as flood pulse, depends on the intensity of the event (Biggs and Thomsen, 1995; Rodrigues and Bicudo, 2004). In this study, the flood pulse influenced both the richness

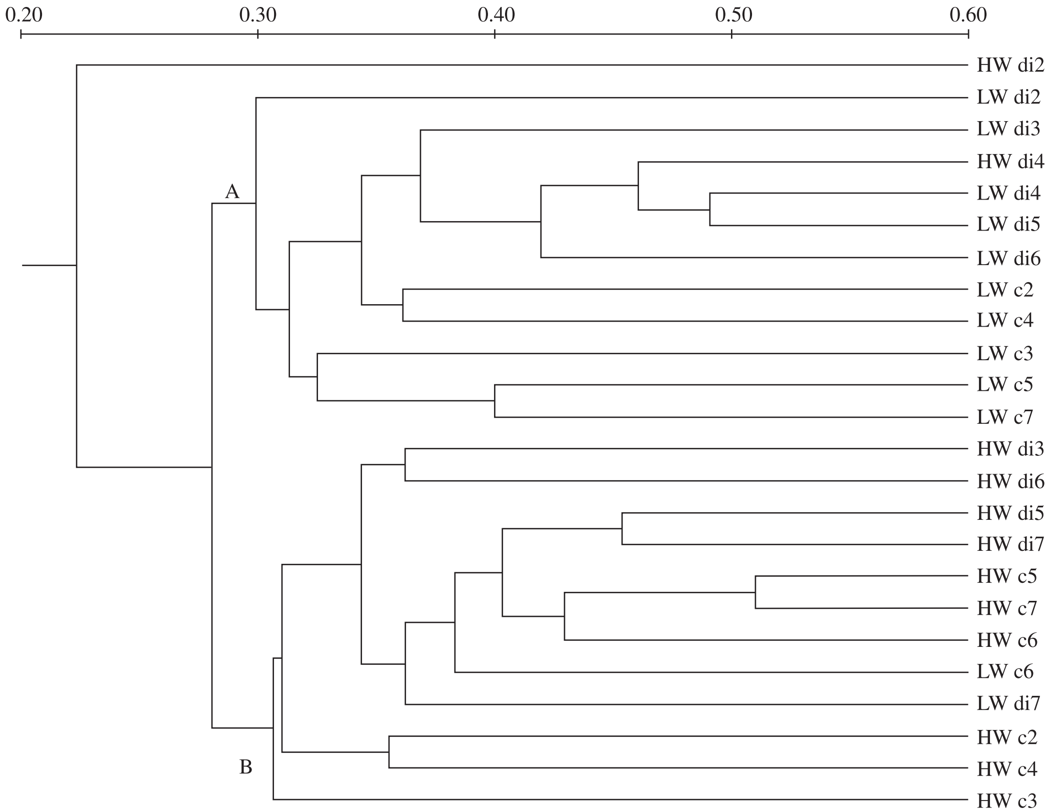

Figure 5. Similarity dendrogram of periphytic algae communities for connected (c) and disconnected (di) lakes of the Upper Paraná River floodplain for the periods of high water (HW) and low water (LW) of the years 2002 to 2007.

and composition of periphyton. In general, richness of periphytic algae in the lakes studied was greater during high water periods than low water periods, as shown by the positive significant correlation between periphytic algae richness and the level of the Paraná River, and by the analyses of variance. Rodrigues and Bicudo (2004) and Leandrini et al. (2008) observed that the periphytic biomass in the Upper Paraná River floodplain was more influenced by hydrological periods, especially in high water. Fonseca and Rodrigues (2005) and Algarte et al. (2006) observed that both periphyton density and richness in the Upper Paraná River floodplain were more influenced by hydrological periods than any other factor. In the Amazon floodplain, Putz and Junk (1997) also found changes in periphytic community structure when comparing hydrological periods.

Decrease in periphytic algae richness was observed in 2002, 2003 and 2004, both in connected and disconnected lakes. The year 2002, specifically, was a period that closely followed an extended dry period and drought associated with 2001 (La Niña). The greatest richness was recorded during the water period of 2007, which also marked the highest water level recorded in the floodplain during this study. The analysis of variance separated 2007 and 2002, as well as 2003 and 2004; however, no differences were found between 2005 and 2006, probably due to the high water level of 2005 and the high water amplitude and duration in 2006.

Two additional aspects that were associated with hydrological regimes and fundamental in determining structural differences in the periphytic community were also studied: a) the degree of connectivity of the environment with the river, and b) the availability of substrate via the increase in richness of aquatic macrophytes. In this study, connected lakes presented higher richness than disconnected lakes, mainly in high water periods, when intense flooding promoted high connectivity between environments and promoted the exchange of propagules, nutrients and organisms between environments (Thomaz et al., 2007).

Total richness of periphytic algae was positively correlated with the richness of aquatic macrophytes, especially in high water. These plants promote greater diversity and habitat heterogeneity by providing an abundant substrate for colonization and development of periphyton (Wetzel, 1990; Stevenson, 1997; Rodrigues and Bicudo, 2004). Felisberto and Rodrigues (2005) assert that reservoirs also demonstrate this positive relationship between periphytic algae richness and aquatic macrophytes.

The presence of aquatic macrophytes led to an elevated number of species of Zygnemaphyceae and Chlorophyceae, as observed by Algarte et al. (2006) and Murakami et al. (2009). Furthermore, during low water, all algae groups decreased in richness, excepting Bacillariophyceae, confirming Algarte et al. (2006). The predominance of diatoms possibly occurs in low water because several diatom species are capable of occupying substrata in a short time period (Hoagland et al., 1982; Morin, 1986; Azim and Asaeda, 2005) and developing in variable environmental conditions. Furthermore, a variety of morphological adaptations of the algae in this group could confer adaptive advantages in stressed conditions, as well as low water.

The data from six years (2002 to 2007) included in this study show that the community of periphytic algae reflected the hydrological cycle of each year on the Upper Paraná River floodplain, separating connected and disconnected lakes. In addition, the richness of periphytic algae was associated with a greater availability of substrate due to high species richness of aquatic macrophytes. According to the results, we accept the hypothesis that species richness and composition of periphytic algae in the floodplain are hierarchically regulated by the intensity of the flood pulse, by the connectivity with the main channel of the river and by the presence of aquatic macrophytes.

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