Acta Limnologica Brasiliensia, 2014, vol. 26, no. 3, p. 296-305 http://dx.doi.org/10.1590/S2179-975X2014000300009

Composition and species richness phytoplankton in a subtropical floodplain lake: a long-term study

Composição e riqueza de espécies fitoplanctônicas em um lago de inundação subtropical: um estudo de longa duração

Jascieli Carla Bortolini[1], Vânia Mara Bovo-Scomparin[1], Aline Caroline Magro de Paula[1], Geovani Arnhold Moresco[1], Larissa Mozini Reis[2], Susicley Jati[3] and Luzia Cleide Rodrigues[1,3]

[1]Programa de Pós-graduação em Ecologia de Ambientes Continentais, Centro de Ciências Biológicas, Departamento de Biologia, Universidade Estadual de Maringá, Avenida Colombo, 5790, CEP 87020-900, Maringá, PR, Brazil
e-mail: jasci_biologa@hotmail.com; vaniascomp@gmail.com; alinecmagro@gmail.com; geovanimoresco@gmail.com
[2]Graduação em Ciências Biológicas, Centro de Ciências Biológicas, Departamento de Biologia, Universidade Estadual de Maringá, Avenida Colombo, 5790, CEP 87020-900, Maringá, PR, Brazil
e-mail: larissareis1@hotmail.com
[3]Núcleo de Pesquisas em Limnologia, Ictiologia e Aquicultura, Universidade Estadual de Maringá, Avenida Colombo, 5790, Bloco H-90, Sala 23, CEP 87020-900, Maringá, PR, Brazil
e-mail: susi@nupelia.uem.br; luziac.rodrigues@gmail.com

Abstract: Aim: Phytoplankton species diversity in floodplain lakes is influenced by different conditions imposed by the hydrosedimentological regime of the main channel. This study evaluated the predictors of composition and species richness phytoplankton in the long-term scale, in a floodplain lake directly connected to the Paraná River. We hypothesized that species richness of the floodplain lake is directly related to the degree of connectivity with the main channel. **Methods:** Quarterly samplings were conducted between February 2000 and March 2013 (except in 2001 and 2003), under the water surface of the pelagic zone of the lake. Data were analyzed with Spearman correlation, PCA, DCA, ANOVA and regression analysis. **Results:** We identified 397 taxa with high contribution of rare species (72%). Chlorophyceans and diatoms were the most frequent groups. There was a trend of increasing of diatoms and decrease of cyanobacteria. The DCA showed differences in phytoplankton composition. The highest mean richness values were found in years with high number of days under potamophase. Significant differences between years were detected for total species richness and first axis of DCA. Regression analysis indicated that the predictors of species richness were Z_{eu} and Z_{max}. **Conclusion:** The species richness phytoplankton of the floodplain lake is directly related to the level of connectivity with the main channel.

Keywords: phytoplankton community, diversity, interannual variation, shallow lake, upper Paraná river floodplain.

Resumo: Objetivo: A diversidade de espécies fitoplanctônicas em lagos de inundação é influenciada pelas diferentes condições impostas pelo regime hidrossedimentológico do canal principal. Foram avaliados quais os fatores preditores da composição e riqueza de espécies fitoplanctônicas, em escala de longa duração, em um lago de inundação diretamente conectado ao rio Paraná. Nós hipotetizamos que a riqueza de espécies do lago de inundação está diretamente relacionada ao índice de conectividade com o canal principal. **Métodos:** Amostragens trimestrais foram realizadas entre fevereiro de 2000 e março de 2013 (exceto em 2001 e 2003), à sub-superfície, na região limnética do lago. Dados foram analisados através de correlação de Spearman, PCA, DCA, ANOVA e análise de regressão. **Resultados:** Foram inventariados 397 táxons com alta contribuição de espécies raras (72%). Clorofíceas e diatomáceas foram os grupos mais frequentes. Observou-se uma tendência de aumento de diatomáceas e decréscimo de cianobactérias. A DCA mostrou diferenças na composição fitoplanctônica. Os maiores valores médios de riqueza foram registrados em anos com alto número de dias de potamofase. Diferenças significativas para a riqueza total de espécies e primeiro eixo da DCA foram observadas entre os anos. A análise de regressão evidenciou que os fatores preditores da riqueza de espécies foram Z_{eu} e $Z_{max.}$ **Conclusão:** A riqueza de espécies fitoplanctônicas do lago de inundação está diretamente relacionada ao índice de conectividade com o canal principal.

Palavras-chave: comunidade fitoplanctônica, diversidade, variação interanual, lago raso, planície de inundação do alto rio Paraná.

1. Introduction

Phytoplankton is an important tool for understanding the maintenance of species diversity (Stomp et al., 2011) and species richness can be a simple measure to quantify and express the complexity of an area (Nabout et al., 2007). According to McCann (2000), the influence of species richness has been increasingly recognized over the dynamics and functioning of the community, especially in relation to stability and productivity, essential for to understand the factors that drive the phytoplankton richness.

The remarkable environmental heterogeneity produced by complex interactions between surface water, groundwater and riparian vegetation in floodplain systems results in high biodiversity (Ward and Tockner, 2001). In these systems, the occurrence of limnophase (low water) and potamophase periods (high water) strongly influence the organization of aquatic communities (Neiff, 1990).

Besides, the relative importance of local and regional environmental factors in controlling species richness depends on, among other factors, the dispersal ability of the species in question (Ptacnik et al., 2010), directly influenced by the connectivity between habitats. Significant variations of the phytoplankton community in floodplain lakes in response to the hydrosedimentological regime has been evidenced by several authors (Train and Rodrigues, 2004; Nabout et al., 2007; Bovo-Scomparin and Train, 2008; Borges and Train, 2009; Bovo-Scomparin et al., 2013; Passarinho et al., 2013).

In floodplain lakes, natural fluctuations in the water level have been modified by the regulation of flow of channels associated. Due to the construction of dams, many floodplain lakes have been isolated from the main water bodies (Wantzen et al., 2008). However, the influence of climate changes has caused significant impacts on the magnitude, speed and frequency of extreme events of drought or flood (Abrahams, 2008).

In the Upper Paraná River, the presence of upstream dams and their operational processes (Agostinho et al., 2008; Souza Filho, 2009; Bovo-Scomparin et al., 2013), and climatic events (Borges and Train, 2009; Train and Rodrigues, 2004; Bovo-Scomparin and Train, 2008; Rodrigues et al., 2009) are identified as important causes of changes in the hydrosedimentological regime and connectivity between the main channel and floodplain lakes, and consequently, changes in the phytoplankton community.

Thus, this study evaluated what are the predictors factors of phytoplankton composition and richness, in a long-term scale, in a floodplain lake directly connected to the Paraná River. We hypothesized that the species richness in the floodplain lake is directly related to the index of connectivity with the main channel. Therefore, it is expected a higher phytoplankton richness in years with high number of days under potamophase.

2. Material and Methods

2.1. Study area

The Paraná River has variable width and is associated with a very large floodplain. This floodplain, especially on the western margin of the Paraná, may be up to 20 km wide and is composed of numerous secondary channels, lakes and rivers. Due to its importance as a river–floodplain system, this floodplain was given status as an Environmental Protection Area (APA) to preserve the islands and 'várzeas' of the Paraná River (Souza Filho, 2009). This APA comprises all stretches of the upper Paraná River that have not yet been dammed, from the mouth of the Paranapanema River to the beginning of the Itaipu Reservoir.

The study was conducted in a lake permanently connected to the Paraná River (Garças Lake) through a narrow channel (Figure 1), in the middle section of the Upper Paraná River, downstream of the Porto Primavera Reservoir. The Garças Lake (22°43'S 53°13'W) is 2.128 m in length and 14.1 ha in area, with a perimeter of 4.328 m and an average depth of 2 m, and has a large coverage of macrophytes, including *Eicchornia*, *Salvinia* and *Polygonum*.

2.2. Methods

This study was carried out for twelve years (February 2000–March 2013) as a part of a long-term ecological research (Brazilian Long Term Ecological Program/CNPq), with samples taken quarterly (except in 2001 and 2003, when only two samplings were conducted), totaling 49 samples in this study.

Phytoplankton samples were taken under the water surface (20 cm deep), at the pelagic zone of the lake. Samples were collected directly with bottles and preserved in 1% Lugol's solution. The counting was performed in random fields, in an inverted microscope, according to Utermöhl (1958) and Lund et al. (1958). Phytoplankton richness was considered the number of taxa present in each

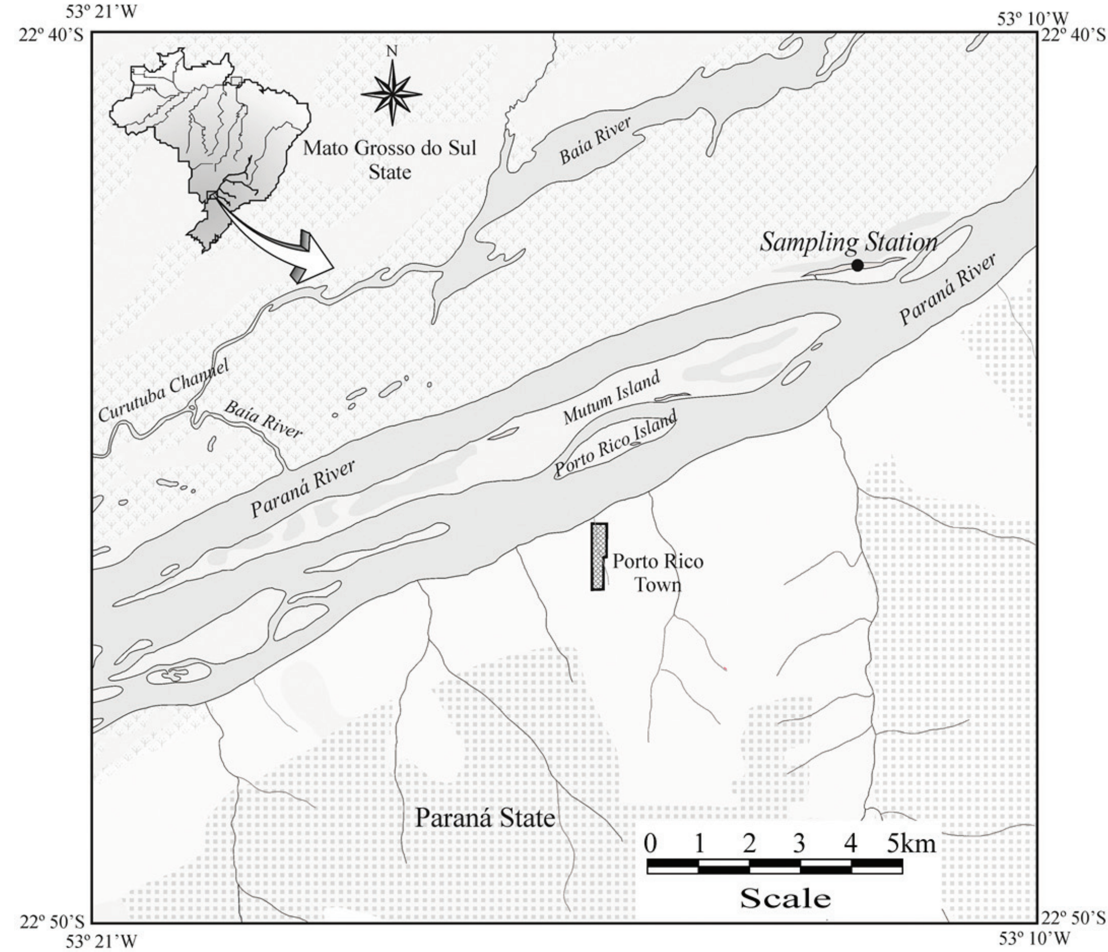

Figure 1. Map showing the location of the sampling station in the floodplain lake, in the Upper Paraná River floodplain.

quantitative sample. The frequency of occurrence of the species was calculated according to Dajoz (2005).

Water temperature, pH, electrical conductivity (EC) and dissolved oxygen (DO) were measured with portable digital potentiometers. The transparency was determined with a Secchi disk and the turbidity with a turbidimeter. The euphotic zone (Z_{eu}) was calculated as being 2.7-fold the depth of the Secchi disk. Variations in water level of the floodplain lake were evaluated by the values of maximum depth (Z_{max}). The Z_{eu}/Z_{max} ratio was used to evaluate the light availability.

Concentrations of total phosphorus - TP, soluble reactive phosphorus - SRP, nitrate - $N\text{-}NH_3$ and ammonium - $N\text{-}NH_4$ were also determined. Concentrations of dissolved inorganic nitrogen - DIN were estimated by the sum of concentrations of nitrate and ammonium. Details of the methods employed for obtaining limnological variables are found in a specific study in this floodplain (Roberto et al., 2009). The daily water levels of the Paraná River (HL) were provided by Itaipu Binational, the Brazilian National Water Agency (ANA) and Nupelia.

Periods of potamophase were considered when the hydrometric level of the Paraná River was greater than 3.5 m, which signals the beginning of the flooding process of the lentic environments associated with the Upper Paraná River (Souza Filho, 2009). Low and high water levels and connectivity index were calculated by the Pulse Program (Neiff and Neiff, 2003). Periods of low water levels have been associated with low connectivity of the Paraná River to other environments in this floodplain, because the inflow of water from this river to connected environments begins when water levels exceed 3.5 m (Thomaz et al., 2007).

Spearman correlation was used to determine the relationship between the water level of the Paraná River and Z_{max} of the lake. Principal Components Analysis (PCA) was employed to summarize the environmental variability contained in abiotic variables and to reduce the number of predictor variables in the multiple regression model (see below). Detrended Correspondence Analysis (DCA) was applied to evaluate the similarity in species composition of the lake in different years. ANOVA (*one-way*) tested the differences in values of the total phytoplankton richness and scores of the first two DCA axes over the years sampled. Tukey's Test compared the means when significant differences were detected. Multiple regression analyses were run to identify abiotic variables influencing phytoplankton community in the floodplain lake, using the following response variables: total phytoplankton richness and the first two DCA axes. Residuals were analyzed to check for the validity of multiple regression assumptions (normal distribution and homogeneity of variances). PCA and DCA were performed using PCORD 6.0 (McCune and Mefford, 1999), whereas Spearman correlation, ANOVA, Tukey's Test and multiple regression were performed using Statistica TM 7.1 (StatSoft, 2005).

3. Results

The hydrosedimentological regime of the Paraná River pointed out annual irregular cycles with high water level variation (CV = 28.7%). The years 2000, 2001 (355 and 362 days under limnophase, respectively) were under the influence of the *La Niña* phenomenon, with negative rainfall in the region, showing the lower connectivity indices. While the years 2005, 2007 and 2010 (305, 311 and 263 days under limnophase, respectively) were under the influence of the *El Niño* phenomenon, with positive values of rainfall and high connectivity indices (Table 1). The Z_{max} of the lake varied according to the water level of the Paraná River ($r_{=}$ 0.49; $p < 0.05$; n = 49) and fluctuated between the highest annual values registered in 2006, 2007, 2010 and 2011 and the lowest, in 2000, 2001 and 2004 (Figure 2).

A Principal Component Analysis identified two axes that explained 45% of inertia of the whole data set (Figure 3) and discriminated in the first axis the years of 2000, 2001 and 2008, at the right of the diagram. This axis was positively correlated to the turbidity (0.75) and negatively to Z_{eu} (-0.93). The second axis showed a positive correlation with Z_{eu}/Z_{max} (0.64) and negative with Z_{max} (-0.58), HL (-0.57) and SRP (-0.55) and discriminated the years 2004, 2005 and 2006.

Were registered 397 species, and distributed into Chlorophyceae (30%), Bacillariophyceae or diatoms (17%), Cyanobacteria (16%), Euglenophyceae (15%), Zygnemaphyceae (11%), Xanthophyceae (4%), Chrysophyceae (3%), Cryptophyceae (2%), Dinophyceae (1%) and Raphidophyceae (0.2%). There was a high contribution of rare species (72%). *Cryptomonas marssonii* Skuja (94%), *Chroomonas* sp. (82%) and *Mallomonas* sp. (71%) were the constant species. Chlorophyceans and diatoms were the most frequent groups (Figure 4).

High mean values of richness, above 30, were registered in most of the study period, mainly in 2002 and 2012 (Figure 5). Lower mean values of this attribute were recorded in 2000 and 2001. There was an upward trend for the richness mean values of diatoms and a downward trend for cyanobacteria. The DCA (axis 1 = 0.39 and axis 2 = 0.32) showed a separation of years (Figure 6)

Table 1. Attributes Pulse of the daily hydrometric levels in the Upper Paraná River (ΣAA = days of potamophase, ΣAB = days of limnophase, IC = connectivity index) for every year. The values for 2013 corresponds only to the month of March.

	ΣAA	ΣAB	IC
2000	11	355	0,03
2001	3	362	0,01
2002	36	329	0,11
2003	27	338	0,08
2004	10	356	0,03
2005	54	311	0,17
2006	56	309	0,18
2007	60	305	0,20
2008	39	327	0,16
2009	93	272	0,34
2010	102	263	0,39
2011	81	284	0,29
2012	32	333	0,09
2013	2	88	0,02

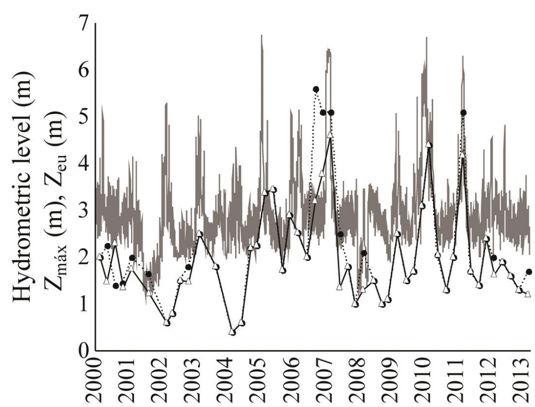

Figure 2. Hydrometric levels of the Paraná River (lines), $Z_{máx}$ (points) and Z_{eu} (triangle) of the lake from February 2000 to March 2013. The sampling days are indicated by points.

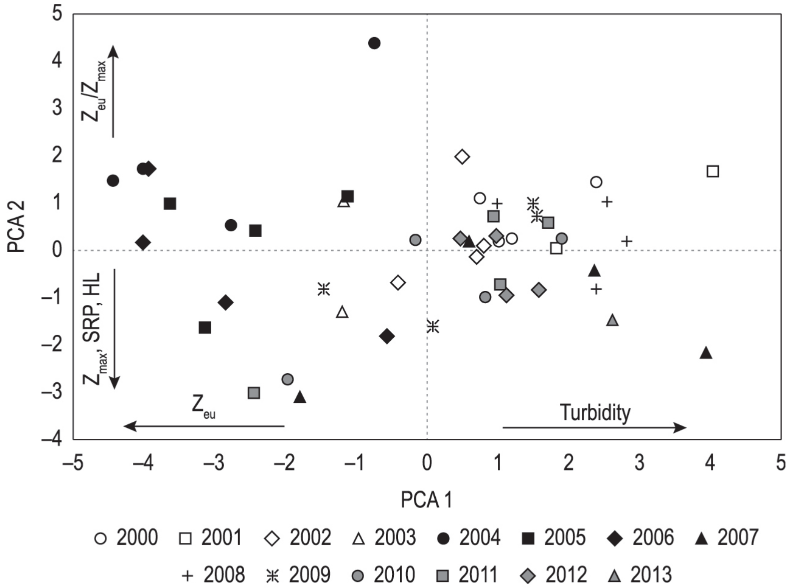

Figure 3. Ordination showing the variables most correlated to the first two axes of a Principal Components Analysis for floodplain Lake. (See legends in Methods).

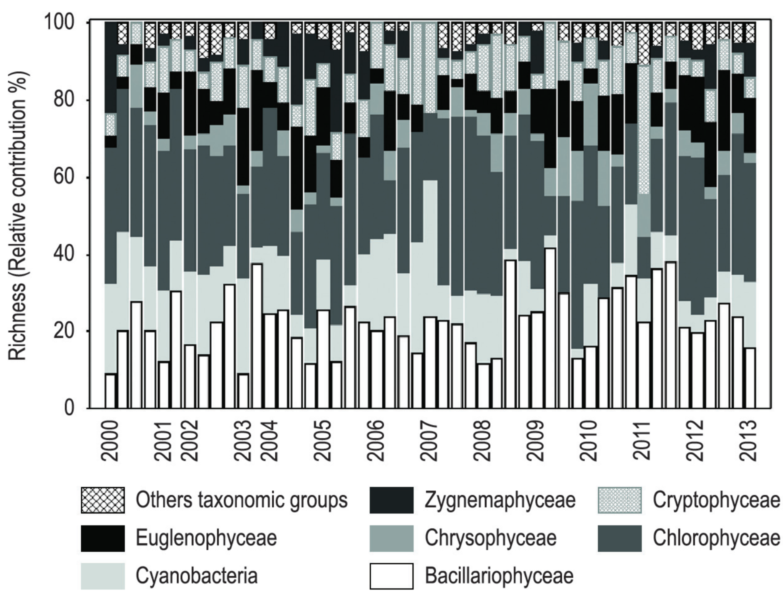

Figure 4. Interannual variation in the relative contribution of phytoplankton groups for richness in the floodplain lake.

and changes in the phytoplankton composition (Figure 7). Significant differences were observed between years for total species richness (F=3,32; p=0.002) and DCA 1 (F=11,1; p=0.000). Tukey's test evidenced significant differences for total species richness between the first two years (2000 and 2001) and 2002, and between 2002 and the years of 2006, 2008, 2009, 2010 and 2011. Considering DCA 1, it has been found that the years 2000 and 2001 differed from the years 2007 to 2013.

A multiple regression analysis (Table 2) showed a significant relationship between total species richness and Z_{eu} and Z_{max} (89% explanation). A relationship between DCA 1 and PCA 1 and PCA 2 was also found (32% explanation). For all models tested, residuals were analyzed, and there were no outliers, or trends, or serial correlation, thus meeting the assumptions of the analysis.

4. Discussion

The high phytoplankton richness registered in the floodplain lake studied can be considered a recurrent pattern for shallow lakes of the Upper Paraná River floodplain (Train et al., 2004; Bovo-

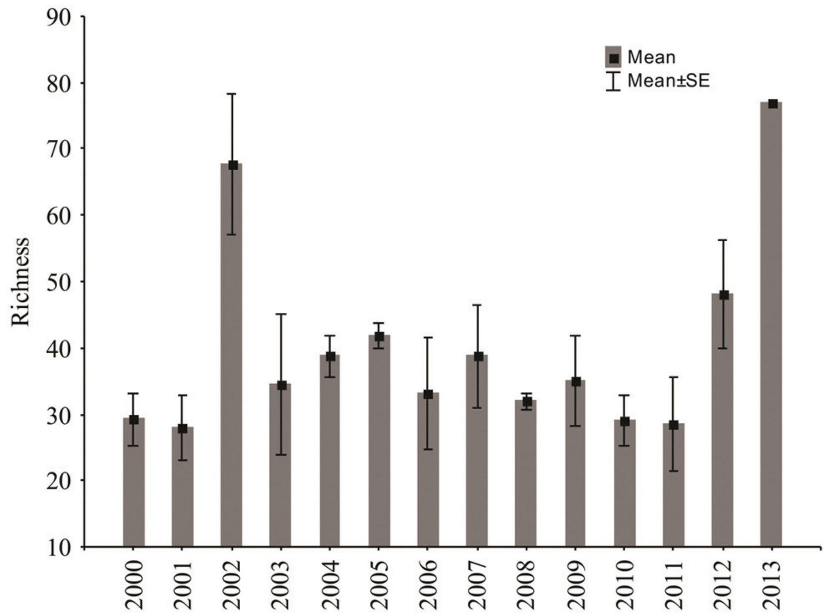

Figure 5. Interannual variability of mean values of phytoplankton richness in the floodplain lake.

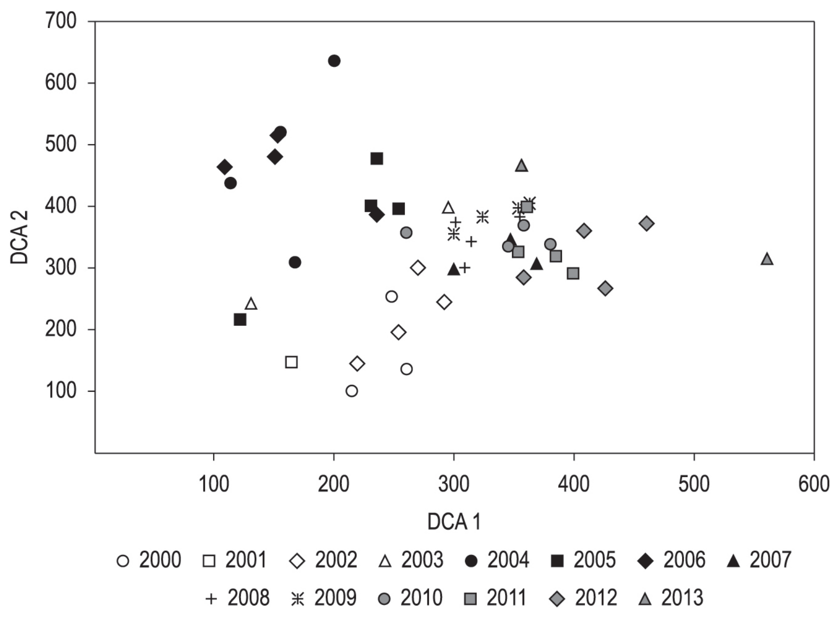

Figure 6. Dispersion of scores (years) in the first two axes of DCA performed for the phytoplankton composition in the floodplain lake.

Scomparin and Train, 2008; Borges and Train, 2009) as well as for other floodplains (Melo and Huszar, 2000; Nabout et al., 2006; Nabout et al., 2007; Nogueira et al., 2010). The constant changes in physical and chemical conditions in floodplain lakes enables the coexistence of a high number of nanoplanktonic species, opportunistic and with high growth rate (Bovo-Scomparin and Train, 2008), even in limnophase periods, which may explain the high contribution of rare species in this study. The low contribution of common species is because most species in ecological communities are rare (Magurran and Henderson, 2003).

Great contribution of chlorophyceans and diatoms to phytoplankton richness was also found in other lentic environments of this floodplain (Train and Rodrigues, 2004; Train et al., 2004; Bovo-Scomparin and Train, 2008; Borges and Train, 2009), and in environments associated with the middle Paraná River (Garcia de Emiliani, 1997),

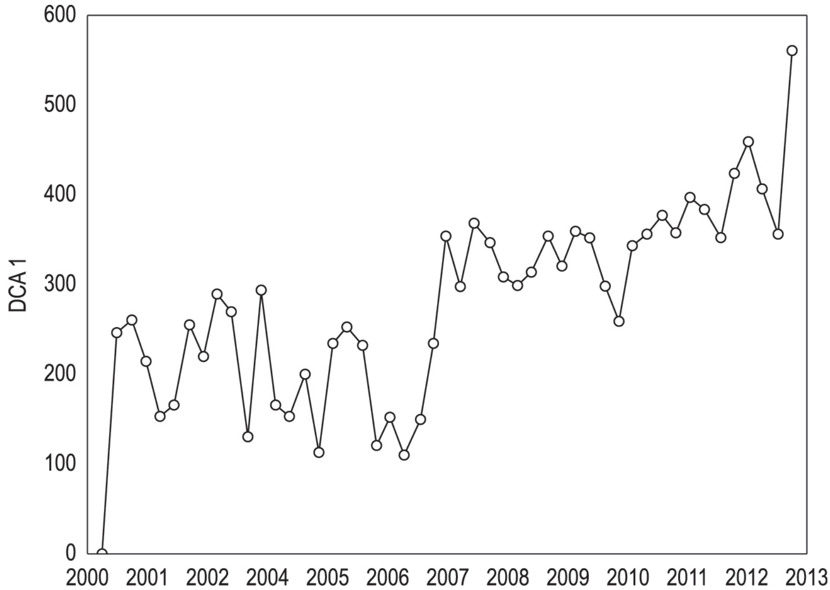

Figure 7. Temporal sequence of the scores of the first axis of the DCA for the floodplain lake demonstrating the changes in the phytoplankton composition.

Table 2. Sumary of multiple linear regressions (only significant relationships are shown).

Dependent variables	Explanatory variables	Beta	t	p	R^2
Total richness	Z_{eu}	–1.31	–3.2	0.003	0,89
	Z_{max}	1.04	2.40	0.025	
DCA 1	PCA 1	22,96	3,87	0,000	0,32
	PCA 2	–24,4	–2,66	0,010	

Paraguay (Oliveira and Calheiros, 2000), Amazon (Melo and Huszar, 2000) and in the lakes of the Paranapanema River (Granado and Henry, 2014). The high frequency of chlorophyceans and diatoms is probably due to their cosmopolitan distribution.

The constancy of *Cryptomonas marssonii* (Skuja), *Chroomonas acuta* (Utermöhl) and *Mallomonas* sp. may be related to their broad physiological plasticity, enabling their occurrence in a wide array of environmental conditions, and because they are benefited by mixotrophy. Moreover, these taxa have characteristics such as small size, high surface/volume ratio and high metabolic activity, which favor their permanence in these dynamic environments (Reynolds et al., 2002; Padisák et al., 2009).

The significant difference observed for the species richness and composition of phytoplankton between the years 2000 and 2001 from the others reflected the influence of connectivity on this community in floodplain lakes. The lower connectivity index registered in those years resulted in lower mean values of richness. On the other hand, in 2002, when occurred significant increase in connectivity, it was registered the highest mean richness.

The low connectivity index of the lake with the main channel in 2000 and 2001 is possibly due to energetic crisis occurring in this period, a significant amount of water was retained for electricity production by the reservoirs. Additionally, this period coincided with the impoundment of the Porto Primavera Reservoir, which had completed its filling at the beginning of 2001. Low rainfall in this period was related to the influence of *La Niña* phenomenon (McPhaden et al., 2006), which caused negative anomalies in rainfall in the Paraná River basin (Borges and Train, 2009).

Water fluctuations, in the long term, cause changes in vertical mixing of shallow lakes, occurring conditions of total mixture of the water column, by the wind, when occurs marked decrease in the water level (Hofmann et al., 2008). In this sense, low values of Z_{max} and high nutrient concentrations recorded in the Garças lake, during the period under the influence of *La Niña* phenomenon, may have contributed to the decline in phytoplankton richness. These results emphasized the importance of functional connectivity, which takes into account the organism-landscape interaction, being considered an essential element for biodiversity maintenance (Matisziw and Murray, 2009).

The highest connectivity index recorded from 2007 promoted a complete turnover of phytoplankton as evidenced by DCA. Furthermore, the ANOVA and Tukey's test indicated significant differences between the years with higher and lower values of this index. These changes may be associated with increased dispersion of species from other environments of floodplain or even the reservoirs upstream of the Paraná River, which may have occurred mainly during periods of increased connectivity from this year. The relationship between hydrological connectivity and biodiversity depends on the exchange of organisms and gene flow through processes of colonization and extinction (Cloern, 2007).

Regarding the intrinsic knowledge that the functioning of lake systems is partially controlled by the amount and frequency of water resource, which is directly related to the level fluctuation (Coops et al., 2003), the positive correlation between the Z_{max} of Garças lake and the water level of the Paraná river points out that the level of this lake is directly influenced by the river. Thus, fluctuations in total richness and composition phytoplankton were determined by the depth of the lake and light availability, which in turn are influenced by variations in the hydrosedimentological regime of the Paraná River, as evidenced by direct relationships between these variables and total richness obtained and the first DCA axis.

Intensity, frequency and amplitude of the potamophase and limnophase events play a key role in structuring, functioning and integrity of the adjacent floodplain environments (Neiff, 2001). The variation of Z_{max} of the Garças lake, which is affected by daily fluctuations in water level of the Paraná River, due to the influence of upstream reservoirs (Souza Filho, 2009) has provided the conditions for mixing the water column and increased circulation of nutrients during most periods, conditions that may have favored meroplanktonic diatom species, resulting in the trend of increase of diatom richness, and inversely, leading to a decline in cyanobacteria richness in the floodplain lake.

Although cyanobacteria are adapted to a range of environmental conditions, they require certain stability in environment for its development. Thus, the magnitude, duration and frequency of pulses and daily variations of the discharge and the water level of the river (Souza Filho, 2009; Stevaux et al., 2009) directly influence the decline in cyanobacteria richness in this floodplain lake.

The interannual variation of flood pulses and the connectivity between the main channel and floodplain lakes interfere with adaptations of species and consequently promote the occurrence of different species between years (Wantzen et al., 2008). Thus, the frequency and intensity with which hydrosedimentological regime influenced the hydrodynamics of this environment, our results corroborate our hypothesis that species richness in floodplain lakes is directly related to the index of connectivity with the main channel. Therefore, phytoplankton richness is an important criterion in assessing the preservation and conservation of this stretch of the Upper Paraná River, as well as an important element to be considered when proposing strategies for maintenance of biodiversity.

Acknowledgments

We would like to thank to researches of the Nupélia´s Limnology laboratory by assistance with physical and chemical variables of water. Research has been supported by PELD/CNPq and by the Núcleo de Pesquisas em Limnologia, Ictiologia and Aquicultura (Nupelia).

References

AGOSTINHO, AA., PELICICE, FM. and GOMES, LC. 2008. Dams and the fish fauna of the Neotropical region: impacts and management related to diversity and fisheries. *Brazilian Journal of Biology*, vol. 68, no. 4, p. 1119-1132. Supplement. PMid:19197482. http://dx.doi.org/10.1590/S1519-69842008000500019

ABRAHAMS, C. 2008. Climate change and lakeshore conservation: a model and review of management techniques. *Hydrobiologia*, vol. 613, no. 1, p. 33-43. http://dx.doi.org/10.1007/s10750-008-9470-5

BORGES, PAF. and TRAIN, S. 2009. Phytoplankton diversity in the Upper Paraná River floodplain during two years of drought (2000 and 2001). *Brazilian Journal of Biology*, vol. 69, no. 2, p. 637-647. Supplement. PMid:19738970. http://dx.doi.org/10.1590/S1519-69842009000300018

BOVO-SCOMPARIN, VM. and TRAIN, S. 2008. Long-Term variability of the phytoplankton community in an isolated floodplain lake of the Ivinhema River State Park, Brazil. *Hydrobiologia*, vol. 610, no. 1, p. 331-344. http://dx.doi.org/10.1007/s10750-008-9448-3

BOVO-SCOMPARIN, VM., TRAIN, S. and RODRIGUES, LC. 2013. Influence of reservoirs on phytoplankton dispersion and functional traits:

a case study in the Upper Paraná River, Brazil. *Hydrobiologia*, vol. 702, no. 1, p. 115-127. http://dx.doi.org/10.1007/s10750-012-1313-8

COOPS, H., BEKLIOGLU, M. and CRISMAN, TL. 2003. The role of water-level fluctuations in shallow lake ecosystems-workshop conclusions. *Hydrobiologia*, vol. 506-509, no. 1-3, p. 23-27. http://dx.doi.org/10.1023/B:HYDR.0000008595.14393.77

CLOERN, JE. 2007. Habitat connectivity and ecosystem productivity: implications from a simple model. *American Naturalist*, vol. 169, no. 1, p. 21-33. PMid:17206578. http://dx.doi.org/10.1086/510258

DAJOZ, R. 2005. *Princípios de ecologia*. Porto Alegre: Artmed.

GARCIA DE EMILIANI, MO. 1997. Effects of water level flutuations on phytoplankton in a river-floodplain lake system (Paraná River, Argentina). *Hydrobiologia*, vol. 357, no. 1-3, p. 1-15.

GRANADO, DC. and HENRY, R. 2014. Phytoplankton community response to hydrological variations in oxbow lakes with different levels of connection to a tropical river. *Hydrobiologia*, vol. 721, no. 1, p. 223-238. http://dx.doi.org/10.1007/s10750-013-1664-9

HOFMANN, H., LORKE, A. and PEETERS, F. 2008. Temporal scales of water-level fluctuations in lakes and their ecological implications. *Hydrobiologia*, vol. 613, no. 1, p. 85-96. http://dx.doi.org/10.1007/s10750-008-9474-1

LUND, JWG., KIPLING, C. and LECREN, ED. 1958. The inverted microscope method of estimating algal number and the statistical basis of estimating by counting. *Hydrobiologia*, vol. 11, p. 980-985.

MAGURRAN, AN. and HENDERSON, PA. 2003. Explaining the excess of rare species in natural species abundance distributions. *Nature*, vol. 422, p. 714-716. PMid:12700760. http://dx.doi.org/10.1038/nature01547

MATISZIW, TC. and MURRAY, AT. 2009. Connectivity change in habitat networks. *Landscape Ecology*, vol. 24, no. 1, p. 89-100. http://dx.doi.org/10.1007/s10980-008-9282-z

MCCANN, KS. 2000. The diversity-stability debate. *Nature*, vol. 405, no. 6783, p. 228-233. PMid:10821283. http://dx.doi.org/10.1038/35012234

MCCUNE, B. and MEFFORD, MJ. 1999. PC-ORD. *Multivariate analysis of ecological data*. version 4.0. Gleneden Blach: MjM Software Design.

MCPHADEN, MJ., ZEBIAK, SE. and GLANTZ, MH. 2006. ENSO as an Integrating concept in earth science. *Science*, vol. 314, no. 5806, p. 1740-1745. PMid:17170296. http://dx.doi.org/10.1126/science.1132588

MELO, S. and HUSZAR, VLM. 2000. Phytoplankton in an Amazonian flood-plain lake (Lago Batata, Brasil): diel variation and species strategies. *Journal of Plankton Research*, vol. 22, no. 1, p. 63-76. http://dx.doi.org/10.1093/plankt/22.1.63

NABOUT, JC., NOGUEIRA, IS. and OLIVEIRA, LG., 2006. Phytoplankton community of floodplain lakes of the Araguaia River, Brazil, in the rainy and dry seasons. *Journal of Plankton Research*, vol. 28, no. 2, p. 181-193.

NABOUT, JC., NOGUEIRA, IS., OLIVEIRA, LG. and MORAIS, RR. 2007. Phytoplankton diversity (alpha, beta, and gamma) from the Araguaia River tropical floodplain lakes (central Brazil). *Hydrobiologia*, vol. 575, n. 1, p. 455-461. http://dx.doi.org/10.1007/s10750-006-0393-8

NEIFF, JJ. 1990. Ideas para la interpretacion ecologica del Paraná. *Interciência*, vol. 15, no. 6, p. 424-441.

NEIFF, JJ. 2001. Diversity in some tropical wetland systems of South America. In GOPAL, B., JUNK, WJ. and DAVIS, JÁ., eds. *Biodiversity in wetlands:* assessment, function and conservation. Leiden: Backhuys Publishers. p. 157-186.

NEIFF, JJ. and NEIFF, M. 2003. *PULSO*: software para análisis de fenómenos recurrentes. Buenos Aires. Available from: <http://www. neiff.com.ar>.

NOGUEIRA, IS., NABOUT, JC., IBAÑEZ, MSR. and BOURGOIN, LM. 2010. Determinants of beta diversity: the relative importance of environmental and spatial processes in structuring phytoplankton communities in an Amazonian floodplain. *Acta Limnologica Brasiliensia*, vol. 22, no. 3, p. 247-256. http://dx.doi.org/10.4322/actalb.02203001

OLIVEIRA, MD. and CALHEIROS, DF. 2000. Flood pulse influence on phytoplankton communities of the south Pantanal floodplain, Brazil. *Hydrobiologia*, vol. 427, n. 1, p. 101-112. http://dx.doi.org/10.1023/A:1003951930525

PADISÁK, J., CROSSETTI, LO. and NASELLI-FLORES, EL. 2009. Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. *Hydrobiologia*, vol. 621, no. 1, p. 1-19. http://dx.doi.org/10.1007/s10750-008-9645-0

PASSARINHO, KN., LOPES, MRM. and TRAIN, S. 2013. Diel responses of phytoplankton of an Amazon floodplain lake at the two main hydrological phases. *Acta Limnologica Brasiliensia*, vol. 25, no. 4, p. 361-374. http://dx.doi.org/10.1590/S2179-975X2013000400002

PTACNIK, R., ANDERSEN, T., BRETTUM, P., LEPISTO, L. and WILLEN, E. 2010. Regional species pools control community saturation in lake phytoplankton. *Proceedings of the Royal Society B: Biological Sciences*, vol. 277, no. 1701, p. 3755-3764.

REYNOLDS, CS., HUSZAR, V., KRUK, C., NASELLI-FLORES, L. and MELO, S. 2002. Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, vol. 24, no. 5, p. 417-428. http://dx.doi.org/10.1093/plankt/24.5.417

ROBERTO, MC., SANTANA, NF. and THOMAZ, SM. 2009. Limnology in the Upper Paraná River floodplain: large-scale spatial ad temporal patterns, and the influence of reservoirs. *Brazilian Journal of Biology*, vol. 69, no. 2, p. 717-725. Supplement. PMid:19738977. http://dx.doi.org/10.1590/S1519-69842009000300025

RODRIGUES, LC., TRAIN, S., BOVO-SCOMPARIN, VM., JATI, S., BORSALLI, CCJ. and MARENGONI, E. 2009. Interannual variability of phytoplankton in the main rivers of the Upper Paraná River floodplain, Brazil: influence of upstream reservoirs. *Brazilian Journal of Biology*, vol. 69, no. 2, p. 501-516. Supplement. PMid:19738958. http://dx.doi.org/10.1590/S1519-69842009000300006

SOUZA FILHO, EE. 2009. Evaluation of the Upper Paraná River discharge controlled by reservoirs. *Brazilian Journal of Biology*, vol. 69, no. 2, p. 707-716. Supplement. PMid:19738976. http://dx.doi.org/10.1590/S1519-69842009000300024

STEVAUX, JC., MARTINS, DP. and MEURER, M. 2009. Changes in a large regulated tropical river: The Paraná River downstream from the Porto Primavera Dam, Brazil. *Geomorphology*, vol. 113, no. 3-4, p. 230-238. http://dx.doi.org/10.1016/j.geomorph.2009.03.015

StatSoft, Inc. 2005. *Statistica*: data analysis software system. version 7.1. Tulsa. Available from: <www.statsoft.com>.

STOMP, M., HUISMAN, J., MITTELBACH, GG., LITCHMAN, E. and KLAUSMEIER, C. 2011. Large-scale biodiversity patterns in freshwater phytoplankton. *Ecology*, vol. 92, no. 11, p. 2096-2107. PMid:22164834. http://dx.doi.org/10.1890/10-1023.1

THOMAZ, SM., BINI, LM. and BOZELLI, RL. 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia*, vol. 579, no. 1, p. 1-13. http://dx.doi.org/10.1007/s10750-006-0285-y

TRAIN, S. and RODRIGUES, LC. 2004. Phytoplankton assemblages. In THOMAZ, S. M., AGOSTINHO, AA. and HAHN, NS., ed. *The Upper Paraná river floodplain*: physical aspects, ecology and conservation. Netherlands: Backhuys. p. 103-124.

TRAIN, S., RODRIGUES, LC., BOVO, VM., BORGES, PAF. and PIVATO, BM. 2004. Phytoplankton composition and biomass in environments of the Upper Paraná river. In AGOSTINHO, AA., RODRIGUES, L., GOMES, LC., THOMAZ, SM. and MIRANDA, LE., ed. *Structure and functioning of the Paraná river and its floodplain*. Maringá: EDUEM. p. 63-74.

WARD, JV. and TOCKNER, K. 2001. Biodiversity: towards a unifying theme for river ecology. *Freshwater Biology*, vol. 46, no. 6, p. 807-819. http://dx.doi.org/10.1046/j.1365-2427.2001.00713.x

WANTZEN, KM., JUNK, WJ. and ROTHHAUPT, KO. 2008. An extension of the floodpulse concept (FPC) for lakes. *Hydrobiologia*, vol. 613, no. 1, p. 151-170. http://dx.doi.org/10.1007/s10750-008-9480-3

UTERMÖHL, H. 1958. Zur Vervollkommnung der quantitativen phytoplankton-methodic. *Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie*, vol. 9, p. 1-38.

Received: 20 August 2013
Accepted: 25 August 2014