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# Rivers affect the biovolume and functional traits of phytoplankton in floodplain lakes

## Rios afetam o biovolume e características funcionais do fitoplâncton em lagos de planície de inundação

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**Abstract: Aim:** We analyzed the temporal distribution (dry and rainy periods) of phytoplankton functional groups (biovolume) from lakes connected to dammed (S1 - Paraná River) and non-dammed rivers (S2 - Baia River and S3 - Ivinhema River) in the upper Paraná River floodplain, Brazil. We also determined the drivers of the phytoplankton community assemblage. **Methods:** Phytoplankton and environmental variables samplings were performed quarterly in dry (2000 and 2001) and rainy (2010 and 2011) periods. We classified the phytoplankton species into seven morphological based functional groups (MBFG). We used analysis of variance to test differences in total phytoplankton biovolume and MBFGs biovolume between lakes and climatic periods. We also used redundancy analysis to determine the MBFGs-environment relation. **Results:** The lake related to the dammed river (S1) presented the lowest species richness. The total phytoplankton biovolume presented differences among the lakes, but we did not register temporal differences associated with water level variation. The lake related to the non-dammed and semi-lentic river (S2) presented the highest biovolume, while S1 (related to the dammed river) and S3 (related to the non-dammed river) exhibited the lowest ones. Filamentous organisms (MBFG III) were associated with poor nutrient conditions and diatoms (MBFG VI) were favored in high water mixing sites. The flagellate groups MBFG II and MBFG V were related to deeper water and lower column mixing conditions, respectively. **Conclusions:** Our results suggest that phytoplankton species with different functional traits drive the primary productivity in the dry and rainy periods. Hence, we highlight the importance of maintaining high functional diversity in lakes to ensure primary productivity. Therefore, we stress the importance of protecting the natural environment such as floodplain lakes because of its contribution to the regional biodiversity and the flow of energy.

**Keywords:** hydrosedimentological regime; dams; functional groups; upper Paraná River; water level.

**Resumo: Objetivo:** Analisamos a distribuição temporal (períodos de seca e chuva) dos grupos funcionais fitoplanctônicos (biovolume) de lagos conectados a rios barrados (S1 - Paraná) e não barrados (S2 - Baia e S3 - Ivinhema) da planície de inundação do alto rio Paraná, Brasil. Além disso, determinamos os fatores que controlam a montagem da comunidade fitoplanctônica. **Métodos:** amostras de fitoplâncton e variáveis ambientais foram coletadas em períodos secos (2000 e 2001) e chuvosos (2010 e 2011). As espécies fitoplanctônicas foram classificadas em sete grupos funcionais baseados na morfologia (MBFG). Aplicamos Análise de Variância para testar diferenças no biovolume total e dos MBFGs entre lagos e períodos. Além disso, usamos Análise de Redundância para determinar a relação entre os MBFGs e as variáveis ambientais. **Resultados:** O lago relacionado com o rio barrado (S1) apresentou a menor riqueza de espécies. O biovolume fitoplanctônico variou entre os lagos, mas não apresentou diferenças temporais associadas à variação do nível hidrométrico. O lago associado ao rio não barrado e de características semi-lênticas apresentou o maior biovolume, e em S1 (relacionado com o rio barrado) e S3 (relacionado com rio não barrado) registramos menores valores. Organismos filamentosos (MBFG III) estiveram associados com condições de poucos nutrientes, e as diatomáceas (MBFG VI) foram favorecidas nos locais com elevada mistura da coluna da água. Os flagelados dos grupos MBFG II e MBFG V estiveram relacionados a condições de maior profundidade e baixa mistura da água, respectivamente. **Conclusão:** Nossos resultados sugerem que espécies fitoplanctônicas com diferentes traços funcionais controlam a produtividade primária em períodos de chuva e de seca. Por isso, ressaltamos a importância de manter a alta diversidade funcional em lagos para garantir a produtividade primária. Enfatizamos a importância da proteção de ambientes naturais como os lagos de planície de inundação devido a contribuição para a diversidade regional e o fluxo da energia.

**Palavras-chave:** regime hidrossedimentológico; reservatórios; grupos funcionais; alto Rio Paraná; nível da água.

## 1. Introduction

Floodplains are fluvial macro-systems (Neiff, 1990) of high functional and structural complexity, formed by aquatic habitats of notable biodiversity, especially in relation to the phytoplankton community (Thomaz et al., 2004; Train & Rodrigues, 2004). Floodplain lakes are important to supply and maintain ecosystem services, such as primary productivity (Beeton, 2002; Junk, 2002; Simões et al., 2015). Moreover, the environmental and biological heterogeneity found in floodplains makes them important conservation areas (Agostinho et al., 2004).

In floodplain systems, the hydrosedimentological regime is the main driving force controlling the flow of matter and energy (Neiff, 1990, 1996). This regime presents high water periods in which there is high connectivity between the main channel and adjacent environments, and low water periods in which the adjacent environments become more isolated (Neiff, 1990, 1996). The connectivity between biotopes and the main river helps to maintain the biodiversity in floodplains because it favors the exchange of materials and the dispersion of species (Neiff, 1990; Train & Rodrigues, 1998; Bovo-Scomparin & Train, 2008; Borges & Train, 2009). Although water level variation of the main channel influences the dynamic of the whole floodplain, the effect on the associated lakes and rivers depends on the size, position and the level of connection of these environments (Junk et al., 1989).

However, dam construction in the main channels affects the natural water level fluctuation in floodplains (Souza Filho et al., 2004). In fact, impoundments are among the major anthropogenic impacts affecting freshwater ecosystems (Nilsson et al., 2005; Winemiller et al., 2016) because they cause habitat fragmentation and loss of biological diversity (Agostinho et al., 2004; Bovo-Scomparin et al., 2013). Dams, mainly when built in cascade, affect the hydrodynamics and the environmental conditions of both upstream and downstream regions (Souza Filho et al., 2004; Souza Filho, 2009; Roberto et al., 2009; Bovo-Scomparin et al., 2013). Reservoirs retain sediments and nutrients causing oligotrophization in downstream regions (Ward & Stanford, 1983). The lentic conditions and high nutrient concentration of the lacustrine zone of reservoirs also favor the development of cyanobacteria that are dispersed to downstream regions (Bortolini et al., 2017). In addition, extreme climatic events such as El Niño and La Niña cause anomalies in the precipitation regime and influence the variation of water level in the main channel, affecting the phytoplankton distribution (Train & Rodrigues, 2004; Rodrigues et al., 2009; Bortolini et al., 2016).

Phytoplankton species of floodplain lakes connected to rivers are sensitive to both the water level variation and river input. River input may cause dilution in lakes and drive the phytoplankton biomass dynamics (Walks & Cyr, 2004). Thus, in periods with high hydrometric level and high river water flow (i.e. rainy periods), lakes could present low phytoplankton biomass because of a higher dilution effect. In addition, the negative effect of washout on phytoplankton community of lakes could be higher in rivers located downstream the dams, because of its low contribution to diversity and poor nutrient input to the lakes (Bovo-Scomparin et al., 2013; Bortolini et al., 2017). However, morphometric characteristics of lakes like a larger area or a longer connectivity channel to the river can reduce the effect of the river input on planktonic communities (Walks & Cyr, 2004).

Phytoplankton is an important primary producer in floodplain lakes and because of its short generation time, an excellent indicator of environmental conditions (Reynolds, 2006). Phytoplankton is a practical model of study in community and ecosystem ecology (Weithoff, 2003). Moreover, phytoplankton presents functional features easily measured and related to environmental factors and ecological processes (Litchman & Klausmeier, 2008). Size, for example, is related to nutrient uptake, as smaller cell sizes are advantageous under limiting nutrient conditions (Chisholm, 1992). In this way, similar phytoplankton species may present similar responses to environmental changes. Hence, species can be grouped according to shared morphological and functional traits, and this grouping is not necessarily limited to phylogenetic groups (Reynolds, 2002; Kruk et al., 2010).

Morphology-based functional groups allow the understanding and prediction of distribution patterns of the phytoplankton community, as has been successfully tested in lentic environments of subtropical and tropical regions (e.g., Kruk et al., 2010, 2011). In this work, by using morphology-based functional groups (Kruk et al., 2010) we aim to analyze the temporal variation (dry and rainy periods) in the structure (biovolume) of the phytoplankton community of three shallow lakes from different sub-basins in the floodplain of the upper Paraná River. In addition, we were interested in determining the factors driving the structure (biovolume) of the phytoplankton community of each lake. We tested the hypothesis that the temporal variation of the hydrometric level influences the phytoplankton biovolume in floodplain lakes. Accordingly, we expected a higher biovolume in the period of extreme drought because rivers present a lower dilutive effect on lakes in this period. In addition, we investigated if dammed rivers have a higher negative effect on the development of the phytoplankton than not-dammed rivers. Thus, we expected lower biovolume in the lake associated with the dammed river. Finally, we expected higher cyanobacteria biovolume in the lake associated with the dammed river because of the export of cyanobacteria inocula from upstream reservoirs.

## 2. Material and Methods

### *2.1. Study area*

The upper Paraná River floodplain (Figure 1) is actually 230 Km long and 5-20 Km wide, with flooded areas covering active and semi-active channels, floodplain lakes, elongated lowlands associated with paleochannels, and backwaters (Agostinho et al., 2004). This floodplain is located between the Porto Primavera and Itaipu Reservoirs, being the last stretch of this river free of impoundments, and fundamental to the maintenance of biodiversity in the region. The flooding regime in this system has been deeply altered by the operation of upstream dams that increase the flood pulse frequency and decrease the flood magnitude (Souza Filho et al., 2004).

In this area, the rainy season (November-March) presents the highest water level and the dry season (June-August) the lowest. To guarantee high contrast between high and low water level periods, we used data from extreme drought seasons in 2000 and 2001 (hereafter dry period) and from high water seasons in 2010 and 2011 (hereafter rainy period) (Figure 2). The influence of the Paraná River in the associated environments starts when the water level surpasses 3.5 m (Souza Filho, 2009). The flood reaches the environments associated with the Baia and Ivinhema Rivers when the water level exceeds 4.6 m (Souza Filho, 2009).

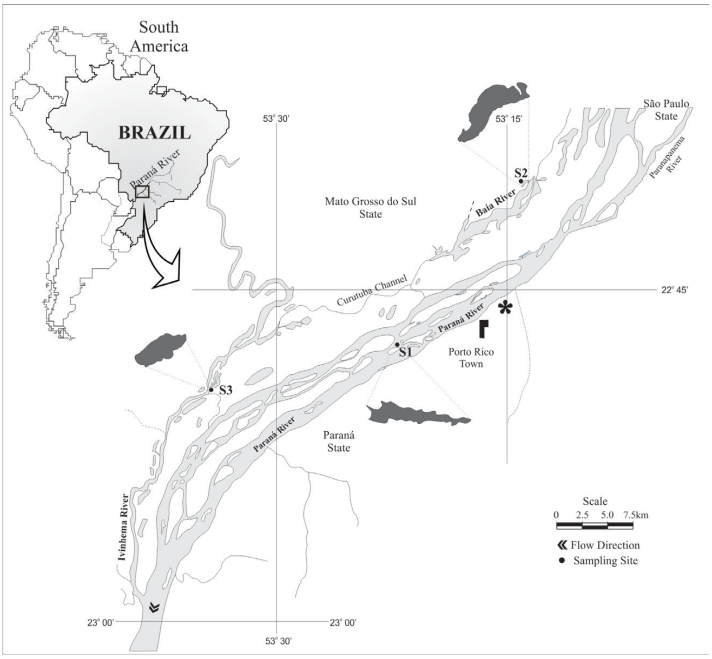

**Figure 1.** Map and location of sampling sites in the upper Paraná River floodplain. S1, lake related to the dammed river (Paraná River); S2 and S3, lakes related to the non-dammed rivers ( Baia and Ivinhema River).

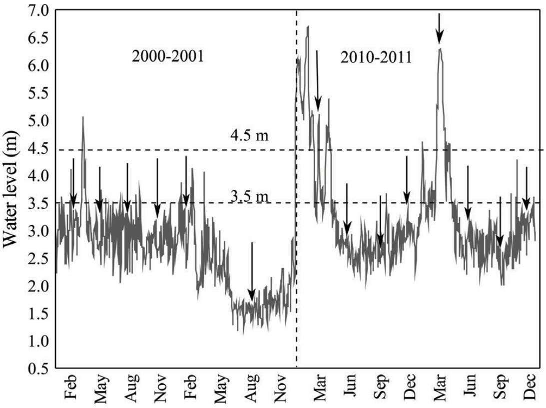

**Figure 2.** Variation of the water level of the Paraná River in the years of 2000, 2001, 2010 and 2011 (The arrows correspond to the sampling days).

We realized samplings in three subtropical floodplain lakes, each one belonging to a different sub-basin (Figure 1) in the upper Paraná River floodplain: the Paraná River, the Baia River, and the Ivinhema River. The rivers are permanently connected to the lakes, and only the Paraná is dammed. The lake connected to the Paraná River (S1 - 22°47'55.92"S, 53°21'32.58"W), is 180 m in length and 0.61 ha in area, has a perimeter of 2,579 m, and an average depth of 3.3 m. This lake connects to the Paraná River by a channel of approximately 7.0 m in length.

The lake connected to the Baia River (S2 - 22°40'30.18"S, 53°13'11.16"W) is 693.3 m in length and 14.7 ha in area, with a perimeter of 2,579 m and an average depth of 3.3 m. It connects to the Baia River by a channel of approximately 3 m in length. The lake connected to Ivinhema River (S3 - 22°50'5.76" S, 53°33'56.88" W) is 334.5 m in length and 2.3 ha in area, has a perimeter of 786.2 m, and an average depth of 3.6 m. It connects to the Ivinhema River by a channel of approximately 5 m in length and 10 m in width (Figure 1).

The Baia River is a tributary of the right bank of the upper Paraná River in the state of Mato Grosso do Sul. This river has semi-lotic characteristics (Thomaz et al., 2004) and its hydrometric level is influenced by the management of the Porto Primavera dam because of its subterranean connection with the Paraná River (Souza Filho et al., 2004). It has a depth: width ratio of 18:1 and considerable flow variations during the different phases of the hydrological cycle. During the rainy season, its flow decreases and can be reversed at the entrance of the Paraná River (Train & Rodrigues, 1998). The discharge of Baia River varies between 9.9 m.s$^{-1}$ (May) and 102.2 m.s$^{-1}$ (March).

The Ivinhema River, the main tributary of the upper Paraná River on its right bank in this section of the floodplain, it is not affected by dams and is inserted in the Ivinhema River State Park (Agostinho et al., 2004). This sub-basin is 270 Km length with an area of 38,200 Km$^2$. The Ivinhema River presents a lotic characteristic with a meandering pattern and ratio of width and depth of 22:1, with high current velocity (approximately 0.85 m.s$^{-1}$).

### *2.2. Sampling and data analysis*

Samples of phytoplankton and environmental variables were taken quarterly in 2000 and 2001 (except in 2001, when only two samples were taken) and 2010-2011, directly with bottles at the subsurface, in the limnetic zone of the lakes. Phytoplankton samples were fixed with 5% Lugol solution and were counted following the method of Utermöhl (Utermöhl, 1958), at 400 x magnification. Phytoplankton density was estimated using an inverted microscope. Counting was performed randomly, by fields, following the Utermöhl (1958) and (Lund et al., 1958). Density was calculated according to APHA (2005), and the result was expressed in individuals (cells, coenobium, colonies, filaments) per milliliter. Population biomass was estimated as biovolume and calculated as the individual volume of the species multiplied by their respective abundance. Cell volume was estimated according to the geometric shape (Sun & Liu, 2003). We considered as richness the total number of taxa registered in each site. Phytoplankton species were classified into morphology-based functional groups (MBFG) following Kruk et al. (2010) and Kruk & Segura (2012).

We measured water temperature (WT, °C), pH, electrical conductivity (EC, µS cm$^{-1}$), and dissolved oxygen (DO, mg L$^{-1}$) using digital portable potentiometers. Water column transparency (m) was obtained using a Secchi disk, and the euphotic zone ($Z_{eu}$, m) was calculated as 2.7 times of the Secchi depth (Cole, 1994). We measured the maximum depth ($Z_{max}$, m), and the depth of the mixing zone ($Z_{mix}$, m) was estimated from the thermal profile. We used the $Z_{eu}$:$Z_{max}$ ratio to evaluate the light availability in the water column, and the $Z_{mix}$:$Z_{max}$ ratio to evaluate the stability of the water column. Concentrations of total phosphorus (TP, µg L$^{-1}$), soluble reactive phosphorus (SRP, µg L$^{-1}$), alkalinity (Alk, µEq L$^{-1}$), total nitrogen (TN, µg L$^{-1}$) were also determined. The dissolved inorganic nitrogen (DIN, µg L$^{-1}$) was calculated as the sum of the concentrations of N-$NH_4$, N-$NO_2$, and N-$NO_3$. Details of the methods employed for determining limnological variables can be found in Roberto et al. (2009). National Water Agency (ANA) provided data of the water level (WL, m) of the Paraná River. We ran a principal component analysis (PCA) to characterize the environmental variability among sites and climatic periods.

A Variance Analysis (two-way ANOVA) was applied to test for differences in total phytoplankton biovolume and MBFGs biovolume between lakes and climatic periods. Normality and homogeneity of variance assumptions were met. Redundancy Analysis (RDA) was performed (Legendre & Legendre, 1998) to determine the MBFGs-environment relation in both the sampling sites and climatic periods. Prior to RDA, the MBFGs biovolume data were Hellinger-transformed. The multicollinearity of the explanatory variables was examined by the variance inflation factor (VIF). We removed those variables with VIF > 10. The environmental variables used in the analysis were $Z_{max}$, $Z_{eu}$, $Z_{mix}$, WL, DIN, WT, EC, DO, pH, Alk, SRP. Previously to the analysis, the environmental variables were log-transformed (x+1), except pH. All analyses were performed in R software (R Development Core Team, 2016) using the Vegan package (Oksanen et al., 2012).

## 3. Results

### *3.1. Environmental characterization*

We registered low temporal variation and high spatial variability of the environmental variables (Figure 3). The lake connected to the dammed river (S1) was related to higher alkalinity, conductivity, pH, nitrogen concentration and transparency. The lakes connected to the non-dammed rivers

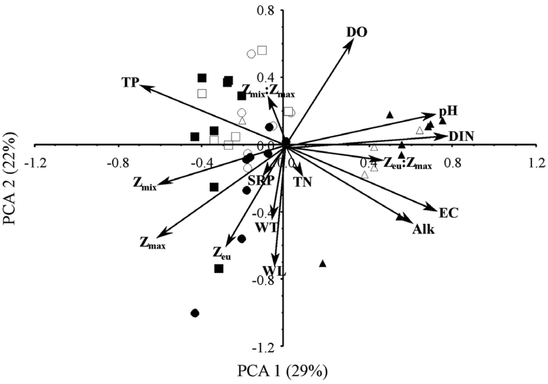

**Figure 3.** Principal components analysis showing the most related variables to the lakes associated with the dammed river (S1 - Paraná River) and non-dammed ones (S2 - Baia River and S3 - Ivinhema River), in the dry (black) and rainy (white) periods. Water temperature (WT, °C), maximum depth ($Z_{max}$, m), euphotic zone ($Z_{eu}$, m), depth of the mixing zone ($Z_{mix}$, m), $Z_{eu}$:$Z_{max}$ ratio, $Z_{mix}$:$Z_{max}$ ratio, dissolved oxygen (DO, mg L$^{-1}$), pH, electrical conductivity (EC, µS cm$^{-1}$), alkalinity (Alk, µEq L$^{-1}$), soluble reactive phosphorus (SRP, µg L$^{-1}$), total nitrogen (TN, µg L$^{-1}$), dissolved inorganic nitrogen (DIN, µg L$^{-1}$), total phosphorus (TP, µg L$^{-1}$).

(S2 and S3) were associated with high phosphorous concentration, water-column mixing, and depth. Most sites and periods showed high variability (coefficient variation higher than 30%) in the depth of the euphotic zone, soluble reactive phosphorus, and dissolved inorganic nitrogen (Table 1).

### *3.2. Phytoplankton community*

We found 288 taxa. Chlorophyceans (76 taxa), diatoms (60 taxa), euglenoids (51 taxa), cyanobacteria (42 taxa), and zygnematophyceans (25 taxa) were best represented. Other groups also contributed to the richness, as chrysophyceans (12 taxa), xanthophyceans (9 taxa), dinoflagellates (7 taxa), cryptophyceans (5 taxa), and raphidophyceans (1taxon). The lake connected to Ivinhema River (S3) presented the highest number of taxa (182), followed by lake connected to Baia River (S2) (177) and Paraná River (S1) (123). High biovolume values (> 2 $mm^3L^{-1}$) were registered in both dry and rainy periods (Figure 4). We found significant differences in total biovolume among the lakes (F=5.87; $p<0.05$). The highest biovolume was observed in S2 and the lowest in S1 and S3. We did not register significant differences between hydrological periods.

We registered the seven MBFG. Non-significant temporal differences were registered in biovolume among the MBFG in S1, but the MBFG V was the most representative, with a greater contribution of the genus *Peridinium* (Figure 5a). In S2 the MBFGs presented significant temporal differences in biovolume (F=9.791; $p<0.05$). In this site, organisms with large filaments and aerotopes (MBFG III), and non-flagellated organisms with siliceous exoskeletons (MBFG VI) presented the highest biovolume, with the dominance of *Dolichospermum planctonicum* (Brunnthaler) Wacklin et al. and *Aulacoseira granulata* (Ehrenberg) Simonsen var. *granulata*, respectively (Figure 5b). Temporal differences in MBFG biovolume were also registered in S3 (F=2.433; $p<0.05$). Flagellates from medium to large size (MBFG V) represented by *Peridinium*, and the MBFG III (mainly *Dolichospermum spiroides* [Klebhan] Wacklin et al.) showed the highest biovolume in S3 (Figure 5c).

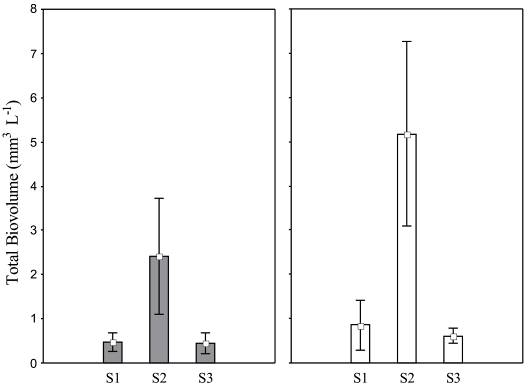

**Figure 4.** Mean values and standard error (bars) of the total phytoplankton biovolume in the lakes related to the dammed river (S1 - Paraná River) and non-dammed ones (S2 - Baia River and S3 -Ivinhema River), in the dry (gray) and rainy (white) periods.

**Table 1.** Mean values and coefficient of variation in parentheses (%) of the measured environmental factors. S1, lake related to the dammed river (Paraná River); S2 and S3 lakes related to the non-dammed rivers Baia and Ivinhema respectively.

| Site | S1 | | S2 | | S3 | |
|---|---|---|---|---|---|---|
| Period | Dry | Rainy | Dry | Rainy | Dry | Rainy |
| WT | 25.8 (19) | 24.5 (14) | 24 (17) | 24.3 (19) | 24.3 (19) | 24.4 (18) |
| $Z_{max}$ | 2.4 (86) | 2.1 (64) | 3.0 (21) | 3.9 (38) | 3.7 (14) | 4.6 (23) |
| $Z_{eu}$ | 1.5 (39) | 1.9 (59) | 2.3 (35) | 2.3 (48) | 1.4 (29) | 3.0 (65) |
| $Z_{mix}$ | 1.2 (44) | 1.8 (80) | 3.0 (23) | 3.2 (11) | 3.0 (10) | 3.6 (55) |
| $Z_{eu}$:$Z_{max}$ | 0.8 (44) | 1.0 (8) | 0.8 (29) | 0.6 (30) | 0.4 (25) | 0.6 (37) |
| $Z_{mix}$:$Z_{max}$ | 0.9 (28) | 0.9 (30) | 1.0 (0.0) | 0.9 (20) | 1.0 (59) | 0.7 (39) |
| DO | 5.4 (34) | 7.5 (12) | 6.2 (28) | 6.3 (36) | 6 (0.0) | 4.6 (53) |
| pH | 6.8 (7) | 7.1 (5) | 6.5 (8) | 6.4 (8) | 6.5 (8) | 6.8 (7) |
| EC | 62.6 (8) | 59.6 (7) | 26.7 (17) | 24.3 (45) | 41 (14) | 43.9 (23) |
| Alk | 393.4 (27) | 389.1 (19) | 128.2 (52) | 131.9 (61) | 271.2 (44) | 309.9 (27) |
| SRP | 3.8 (70) | 8.6 (49) | 4.7 (70) | 6.8 (44) | 6.2 (96) | 10.6 (34) |
| TN | 413.4 (45) | 866.0 (16) | 439.7 (39) | 938.0 (18) | 357.2 (39) | 745.0 (32) |
| DIN | 147.6 (97) | 303.1 (19) | 34.7 (168) | 10.9 (80) | 42.3 (56) | 62.3 (81) |
| TP | 22.8 (48) | 16.3 (33) | 48.3 (33) | 44.5 (29) | 36.8 (28) | 37.8 (42) |

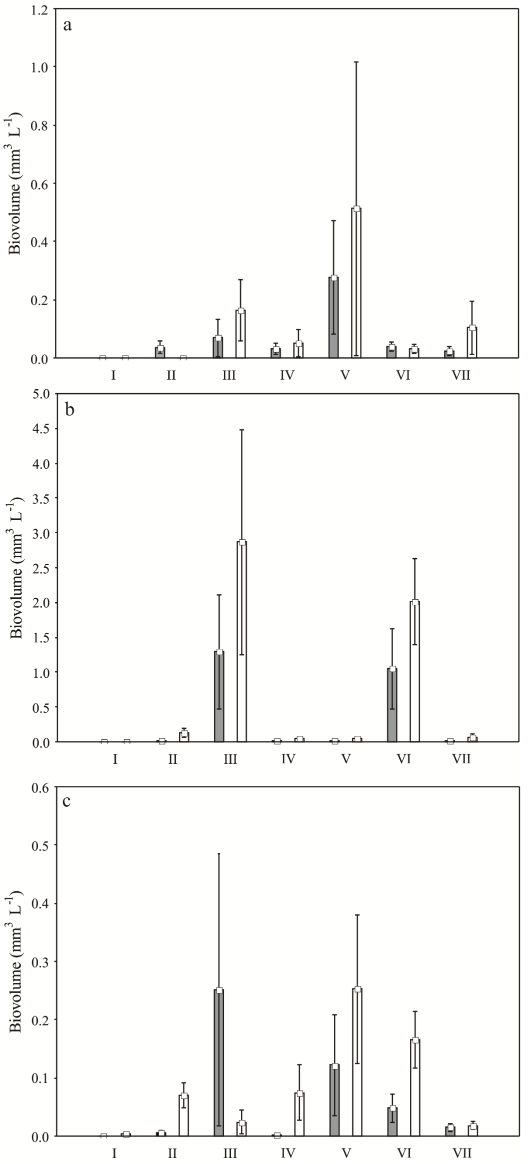

**Figure 5.** Mean values and standard error (bars) of the MBFGs biovolume in the lakes associated with the rivers: Paraná (a), Baia (b) e Ivinhema (c), in the dry (gray) and rainy (white) periods.

The RDA indicated that the environmental factors influenced the distribution of the MBFG biovolume. The two first axes of RDA were significant ($p < 0.05$), and explained 35% of the data variance. This analysis showed high spatial variability and low temporal variation of the MBFG biovolume (Figure 6). The site S1 was associated with high pH, high biovolume of MBFG IV, and low biovolume of diatoms (MBFG VI) and flagellates with siliceous exoskeleton (MBFG II). The site S2 presented the highest biovolume of filamentous algae with aerotopes (MBFG III) and MBFG VI. The biovolume of MBFG III was positively related to dissolved oxygen and negatively related to phosphorus (SRP), alkalinity and conductivity. The biovolume of MBFG VI was positively associated with the depth of the mixing zone. In the site S3, MBFG II and large mucilaginous colonies (MBFG VII) were favored, which were positively related to light availability and depth (Figure 6).

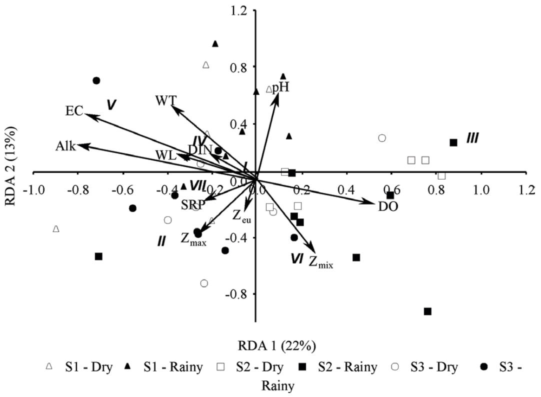

**Figure 6.** Redundancy analysis (RDA) plot showing the spatial and temporal relationship between the phytoplankton morphology-based functional groups (in bold) and the environmental variables in the studied sites. S1, lake related to the dammed river (Paraná River); S2 and S3, lake related to non-dammed Baia and Ivinhema Rivers respectively. We included only the environmental variables with VIF < 10. $Z_{max}$, maximum depth; $Z_{eu}$, euphotic zone; $Z_{mix}$ mixing zone; WL, water level; WT, water temperature; DO, dissolved oxygen; pH; EC, electrical conductivity; Alk, alkalinity; SRP, soluble reactive phosphorus; DIN, dissolved inorganic nitrogen.

## 4. Discussion

Our results show that environmental factors affect the distribution of phytoplankton functional traits in floodplain lakes, and highlight the importance of niche-associated processes to the assemblage of the phytoplankton community.

The total phytoplankton biovolume did not present differences between climatic periods as we expected. Surely, the hydrometric variation drives important changes in the floodplain landscape, as it increases the connectivity among environments (Thomaz et al., 2007) and the dilutive effect of rivers on lakes in rainy periods (Neiff, 1996; Train & Rodrigues, 1998). In our case, however, the temporal variation of water level on total phytoplankton biovolume was negligible, probably because the studied lakes are permanently connected to the rivers. On the other hand, the water level variation was probably not enough to cause temporal differences in the dilution effect of rivers in the lakes to be reflected by the total phytoplankton biovolume.

We expected higher biovolume of cyanobacterial algae in the lake associated with the dammed river (S1). However, the MBFG III and VII associated with large filamentous and colonial cyanobacteria did not present the highest biovolume at this site. Although the inocula exported by reservoirs can increase the phytoplankton biovolume of near downstream sites (Bovo-Scomparin et al., 2013; Bortolini et al., 2017), in our case, we believe the distance between the lake and the reservoir is far enough to avoid the influence of inocula export in the increase of the MBFG III and VII. In addition, local processes related to phosphorus availability, dissolved oxygen, and pH seem to be de main drivers of the filamentous and colonial algae in the studied sites (See MBFG III and VII in Figure 6).

The high phytoplankton richness and biovolume registered in the studied lakes are typical of floodplain lakes (Moresco et al., 2017). Floodplain lakes present high water retention time and, in our case, high nutrients and light availability that favor the establishment and development of several phytoplankton species. In fact, the lakes of the upper Paraná floodplain present a high phytoplankton diversity, with more than 1000 registered species (Train & Rodrigues, 1998, 2004; Bovo-Scomparin & Train, 2008; Bovo-Scomparin et al., 2013). Moreover, the high spatial and temporal environmental heterogeneity in the upper Paraná floodplain offer a large number of niches that can be occupied by the species (Agostinho et al., 2004). Therefore, our results show that the variety of lake morphometries and relations between lakes and rivers increase the environmental heterogeneity, and thus also the phytoplankton diversity.

The lakes in the Paraná floodplain present different relations with the main channel (Souza Filho & Stevaux, 1997), and the processes driving the phytoplankton community in each case can vary. For instance, although the three studied lakes have a short connection channel to the rivers, the effect of wash-out on phytoplankton community could vary among lakes. In S1 and S3, the wash-out effect could be higher than in S2 because of the higher flow of those rivers. In addition, the connection between S2 and the Baia River presents lentic characteristics, hence decreasing the biovolume losses due to wash-out, and could explain the higher total biovolume on this site. Furthermore, the high area of S2 could have reduced the dilutive effect of Baia River in both climatic periods, decreasing the phytoplankton losses associated with the wash-out and favoring the phytoplankton development.

Our results also suggest that the rivers influenced the total phytoplankton biovolume in the lakes regardless if they are dammed or not. For instance, S1 (related to the dammed river) and S3 (related to the non-dammed river) showed the lowest biovolumes, despite presenting high nutrient concentration and high availability of light. As mentioned above, the lakes can be influenced by constant river wash-out that difficults the phytoplankton development. Furthermore, most of the phytoplankton species that we registered are not adapted to river conditions, and the water flux velocity negatively affects their development because it decreases the time available for their populations to increase, as they are rapidly being carried downstream (Salmaso & Braioni, 2008).

However, the fact that a river is dammed seems to affect the phytoplankton richness. We evidenced lower richness in the site associated with the Paraná River (dammed) than in the sites related to the non-dammed rivers (S2 and S3). In that sense, Rodrigues et al. (2009, 2015) demonstrated that after the construction of the Porto Primavera dam the phytoplankton richness in upper Paraná River decreased. Dams can reduce the richness in downstream regions because it prevents the arrival of new species from upstream regions. In addition, dams affect the water level of downstream regions, reduce the connectivity among environments, and difficult the exchange of phytoplankton inocula (Abrahams, 2008; Leira & Cantonati, 2008).

Although it may be difficult to establish distribution patterns for microorganisms (e.g., Nabout et al., 2009), our results show that the functional features of phytoplankton are associated with the environmental conditions of the upper Paraná floodplain lakes. In some cases, we could observe temporal changes in the dominance of functional groups. For example, in the lake connected to Baia River (S2), periods with the highest water-column mixing favored diatoms (MBFG VI), which depend on high water-column mixing because they present high sedimentation rate (Reynolds, 1998). On the other hand, periods with low nutrient concentration and high dissolved oxygen favored filamentous algae with aerotopes (MBFG III) (Figure 6). These organisms predominate in lentic environments with low resource availability because they exhibit high surface:volume ratio that enhances their nutrient uptake (Margalef, 1978). Moreover, in our study, the MBFG III was mainly represented by *Dolychospermum planctonicum* (Brunnthaler) Wacklin et al., a species with fixing nitrogen ability (Kruk & Segura, 2012).

Flagellated organisms with siliceous exoskeleton (MBFG II, mainly *Dinobryon sertularia* Ehrenberg and *Dinobryon divergen* Imhof) were favored in higher depth and light availability. These organisms are commonly found in oligotrophic environments with high availability of light (Kruk & Segura, 2012), and its high biovolume registered in the deeper environments was probably favored by low to moderate sinking losses. In the case of the MBFG V, their distribution was possibly favored by low water-column mixing. The maximum biovolume value recorded in the rainy period in the lake associated with the Ivinhema River (S3) was related to the large size dinoflagellate *Peridinium* sp. This taxon can tolerate reduced nutrient conditions because it is capable of facultative heterotrophy (Reynolds et al., 2002). Thus, the predominance of this group in S3 suggests high organic material concentration.

Our work showed that the phytoplankton richness, biovolume, and functional traits responded to environmental variation in the upper Paraná floodplain lakes. In addition, we highlight the importance of non-dammed rivers to the maintenance of microorganisms diversity in floodplains. We evidenced that the seasonal variation of the hydrometric level affected the distribution of the functional groups but not, as we expected, the total phytoplankton biovolume. This suggests that phytoplankton species with different functional traits drive the primary productivity in the studied lakes in dry and rainy periods. Thus, our results highlight the importance of maintaining a high functional diversity to enhance the use of the resources and ensure primary productivity. Our results also suggest that the morphometry of lakes (e.g., area) influences the wash-out effect of rivers, and favors the development of phytoplankton biomass. Finally, in a scenario in which the natural dynamics have been affected, as is the case of the upper Paraná floodplain, we want to highlight the importance of the development of strategies to protect the natural environments with great importance to the regional biodiversity and the flow of energy.

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