





Phytoplankton richness and abundance in response to seasonality and spatiality in a tropical reservoir

Riqueza e abundância fitoplanctônica em resposta à sazonalidade e espacialidade em um reservatório tropical

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Abstract: Aim: Species richness and abundance are important elements in understanding communities' dynamics. In this way we evaluated the spatial and temporal variation of phytoplankton richness and density in a tropical reservoir, and its main drivers. We tested whether the temporal variability of the hydrological cycle influences the phytoplankton, in addition to testing the main environmental variables that influence richness and density. **Methods:** Data from environmental variables and phytoplankton were sampled in different regions of João Leite reservoir, Goiás, Brazil, during a dry and rainy period, and were analyzed by Principal Component Analysis, Student's t-test and Bioenv. **Results:** We recorded distinct environmental scenarios between the dry and rainy period, with temporal differences in richness. Sixty-two taxa were recorded, with cyanobacterial predominance in both hydrological periods and in the lentic reservoir regions. Water temperature, pH, electrical conductivity, dissolved oxygen, turbidity, and nutrient concentrations were the main drivers of phytoplankton richness and density in our study. **Conclusions:** The richness and abundance of species directly reflect the determining factors in the structure of communities, generating important information about ecosystem functions. Therefore, understanding the environmental variability on phytoplankton richness and abundance in tropical reservoirs is essential, since the construction of reservoirs influences aquatic biodiversity and the provision of ecosystem services.

Keywords: Brazil; dam; diversity; impoundment; planktonic algae.

Resumo: Objetivo: A riqueza e abundância de espécies são elementos importantes no entendimento da dinâmica das comunidades. Dessa forma, nós avaliamos a variação espacial e temporal da riqueza e densidade do fitoplâncton em um reservatório tropical e os seus principais direcionadores. Nós testamos se a variabilidade temporal do ciclo hidrológico influencia o fitoplâncton, além de testar as principais variáveis ambientais que influenciam a riqueza e a densidade. **Métodos:** Dados de variáveis ambientais e do fitoplâncton foram amostrados em diferentes regiões do reservatório João Leite, Goiás, Brasil, durante períodos de seca e chuva, e foram analisados por meio de Análise de Componentes Principais, teste-t de Student e Bioenv. **Resultados:** Nós registramos cenários ambientais distintos entre os períodos de seca e chuva, com diferenças temporais na riqueza. Sessenta e dois táxons foram registrados, com predominância de cianobactérias em ambos os períodos hidrológicos e nas regiões



lênticas do reservatório. Temperatura da água, pH, condutividade elétrica, oxigênio dissolvido, turbidez e concentrações de nutrientes foram os principais direcionadores da riqueza e densidade fitoplanctônica em nosso estudo. **Conclusões:** A riqueza e abundância de espécies refletem diretamente os fatores determinantes na estrutura das comunidades, gerando informações importantes sobre as funções do ecossistema. Portanto, o entendimento da variabilidade ambiental sobre a riqueza e abundância do fitoplâncton em reservatórios tropicais é essencial, uma vez que a construção de reservatórios influencia a biodiversidade aquática e o provimento de serviços ecossistêmicos.

Palavras-chave: Brasil; barragem; diversidade; represamento; algas planctônicas.

1. Introduction

Biodiversity is heterogeneously distributed throughout the world, with biological communities vary in space and time (Soininen et al., 2018). Thus, studies have responded to the need to address the extent of biodiversity change and its drivers (Hillebrand et al., 2018). Understanding the dynamics of biological communities is therefore an important step in maintaining ecosystem services, which provide direct and indirect services to humans, and which have only recently received more empirical attention (Rudman et al., 2017).

Species richness has been used to understand community functioning, and the influence of richness has been recognized as an important factor in ecosystem processes and in the dynamics of biological communities (McCann, 2000), as has been verified for the phytoplankton community at both local and regional scales (Bortolini et al., 2014, 2017). Associated with richness, the distribution of phytoplankton species abundance is an accurate indicator of community structure and is especially useful when site data are compared (Borics et al., 2021). Therefore, these measures provide essential information about the organization and structure of the community in relation to the availability of resources and the environmental variability in the aquatic ecosystem.

Thus, phytoplankton richness and abundance can be an important model of this variability, since planktonic algae comprises an extremely diverse group, encompassing diverse phylogeny, sizes, shapes, and adaptive strategies related to their performance to support the environmental variability (Litchman & Klausmeier, 2008; Brasil & Huszar, 2011). Moreover, an important fraction of the primary production of aquatic systems is carried out by planktonic algae, exerting a large influence on trophic interactions and in the ecosystem dynamics, and so these microorganisms play an important role in aquatic environments (Lemke et al., 2017).

In this sense, the remarkable environmental variability in reservoirs directly influences

the phytoplankton community structure, both spatially and temporally (Pivato et al., 2006; Borges et al., 2008; Becker et al., 2009; Moreti et al., 2013; Oliveira et al., 2020). In these ecosystems, changes in the aquatic environment and in the community phytoplankton are recorded, especially after damming (Souza et al., 2016; Jati et al., 2017), due to the delimitation of a spatial gradient with different flow velocities, nutrients, and turbidity, which should directly influence the spatial structure of aquatic communities (Kimmel et al., 1990). In addition, seasonal patterns related to the climatological and hydrological variability act as forcing functions in the longitudinal zoning of reservoirs (Tundisi, 2018), since they influence the conditions of availability of light, water flow, and nutrients, as well as stochastic dispersion processes (Deus et al., 2013; Rodrigues et al., 2018).

Thus, spatial and temporal structure of the phytoplankton richness and abundance strongly reflect the environmental dynamic in these ecosystems, allowing the monitoring of ecosystem services (e.g., water supply) as well as processes of eutrophication and water quality in reservoirs. Since the coupled interaction between fundamental research (e.g., biodiversity studies) and reservoir management is needed to maintain the sustainable use of reservoirs (Tundisi & Matsumura-Tundisi, 2003).

This study evaluated the spatial and temporal variation of phytoplankton richness and abundance in a tropical reservoir in two periods of the hydrological cycle, evaluating the main drivers of this variation. So, we hope that: i) the temporal variability of the hydrological cycle between dry and rainy periods causes changes in the phytoplankton community, with the highest richness and density in the dry season; ii) the spatial variation of reservoir zoning causes differences the distribution of phytoplankton, with higher richness and density in the lentic regions of the reservoir, and lower richness and density in the lotic region; and iii) the environmental conditions related to the

phytoplankton community are different between the hydrological periods, with a higher influence of the nutrient concentrations in the dry period, and turbidity in the rainy period.

2. Material and Methods

2.1. Study area description

The study was performed in João Leite reservoir, Goiás state, Brazil, located in the Ribeirão João Leite (Figure 1). The region has seasonal tropical climate, with cerrado vegetation and tropical forest ranges, with mean temperature for the state of 23.44 °C (Cardoso et al., 2014). The rainy period in this region is concentrated in spring and summer, between October and March, and the mean annual rainfall ranges from 1200 mm to 1800 mm, while the dry period occurs between May and September, with precipitation values reaching zero (Costa et al., 2012), draining the reservoir flow in north–south, with a maximum flow in the rainy period of 11.2 m³.s⁻¹ and a minimum of 4.0 m³.s⁻¹ in the dry period (Carneiro et al., 2010). The João Leite reservoir comprises an important water supply source of the Goiás state, with an area of approximately 10.4 km², an extension of approximately 15 km, mean width of approximately 800 m, and the maximum depth in

the dam region of approximately 36 meters (Carmo, 2014). Although the Ribeirão João Leite basin is an environmental protection area (EPA), the area is subject to intense human impact, as more than 60% of the land is occupied by cattle ranching, with a coverage of only 30% of native vegetation (Carneiro et al., 2010).

2.2. Sampling and physicochemical analysis

Sampling was performed at seven stations along the reservoir in two distinct periods of the hydrological cycle, being one in September 2018 (dry period) and another in February 2019 (rainy period). Water temperature (°C), pH, electrical conductivity (µS.cm), and turbidity (NTU) were measured using portable digital potentiometers, while the dissolved oxygen (mg.L⁻¹) was measured by the titration method (APHA, 2017). Concentrations of nitrogen (nitrite, nitrate and ammonium – mg.L⁻¹), total phosphorus (mg.L⁻¹), and iron (soluble and total – mg.L⁻¹) were obtained according to APHA (2017). The dissolved inorganic nitrogen (DIN) was estimated from nitrite, nitrate, and ammonium concentrations. Precipitation data (mm) in the study region were provided by Goiás Sanitation Company S/A (Saneago).

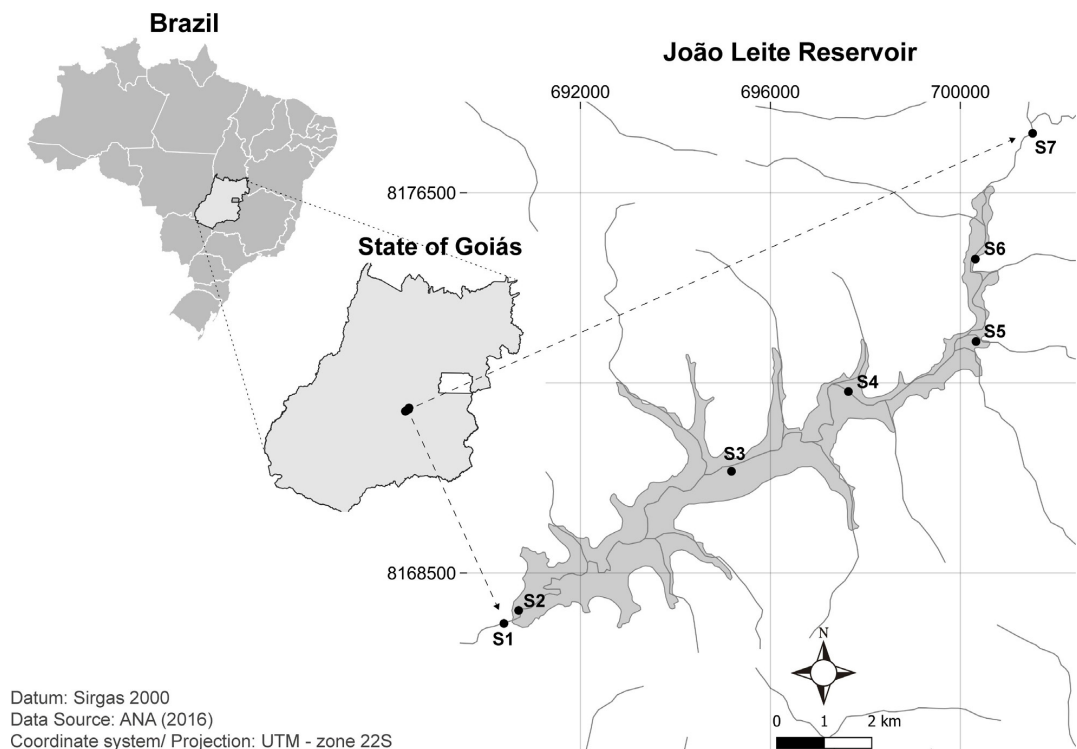


Figure 1. Map of the João Leite reservoir, GO, Brazil, and sampling sites (S1 - downstream; S2, S3 and S4 - lacustrine region; S5 and S6 - intermediate region; S7 - lotic region).

2.3. Sampling and analysis of the phytoplankton community

The phytoplankton samples were taken directly with bottles at the subsurface and fixed in situ with acetic Lugol's solution (Bicudo & Menezes, 2017). Phytoplankton density was estimated using an inverted microscope of Olympus CKX41 model (x 400 magnification), according to the methods by Utermöhl (1958). Density was expressed in individuals (cells, cenobes, colonies or filaments) by milliliters, considering the forms in which algae occur in nature. We considered as species richness the total number of taxa in each sample. The frequency of occurrence (FO) of the taxa in the samples was calculated according to Dajoz (2005), being classified as constant ($FO \geq 70\%$), common ($30\% \geq FO \leq 70\%$), sporadic ($10\% \geq FO \leq 30\%$) or rare ($FO \leq 10\%$).

2.4. Data analysis methods

We performed a Principal Components Analysis (PCA) to summarize the environmental variability and identify the different environmental scenarios along hydrological periods and in spatial extent of the reservoir. The phytoplankton richness of the study area was estimated through nonparametric extrapolator indices. We performed a Student's t-test to verify significant differences between the phytoplankton richness and total density at temporal scale (dry and rainy periods). For this analysis, the assumptions of normality and homoscedasticity were tested. We performed a BioEnv test to assess the relationship between phytoplankton dissimilarity (presence/absence and density of taxa) and environmental variables (water temperature, pH, electrical conductivity, turbidity, dissolved oxygen, total phosphorus, iron soluble, iron total, and dissolved inorganic nitrogen), since this analysis finds the best subset of environmental variables, so that the Euclidean distances of scaled environmental variables have the maximum (rank) correlation with community dissimilarities. The strength of the relation was assessed through the Spearman correlation between the phytoplankton dataset and its best environmental subset, and tested for statistical significance using a permutation procedure (with 999 permutations) by Mantel tests. All analyzes were performed on free software R (R Development Core Team, 2018) using the Vegan (Oksanen et al., 2017), Biodiversity R (Kindt & Coe, 2005), and Ade4 (Bougeard & Dray, 2018) packages.

3. Results

3.1. Environmental scenarios and environmental variables

A remarkable seasonality was recorded in the study area, with total rainfall in the dry period (September 2018) of 53.6 mm, while in the rainy period (February 2019) the total rainfall was 145.6 mm (Figure 2). The environmental variables measured at the sampling sites in the dry and rainy periods are shown in Table 1.

The Principal Components Analysis explained 70% of the environmental variability, indicating environmental dissimilarity along the spatial extent of the reservoir, as well as between hydrological periods. Therefore, according to PCA, a clear temporal separation was evidenced by distinguishing the dry and rainy period, as well as spatial separation, especially with the distinction of the lotic region (Figure 3). The PCA axis 1 (40%) was positively influenced by WT (0.54), and negatively by turbidity (-0.48), soluble iron (-0.48) and total iron (-0.48). The PCA axis 2 (30%) was positively influenced by conductivity (0.46) and negatively by TP (-0.50).

3.2. Phytoplankton richness and density as a response variable

We identified 62 phytoplankton taxa in our study. According to the Bootstrap richness estimator, the sample sufficiency was well represented and the number of phytoplankton species sampled (62 taxa) represented 91% of the expected taxa according to the estimator (68 taxa). This fact suggests that the sampling and analysis effort was appropriate to characterize the phytoplankton community of the reservoir area (Figure 4).

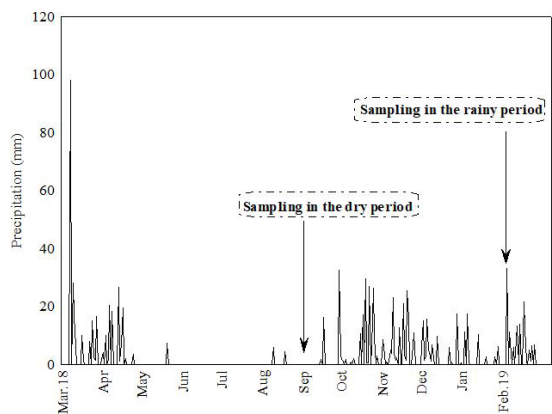


Figure 2. Annual variation of precipitation (mm) in the study region, and sampling during the dry and rainy period.

Table 1. Environmental variables sampled in the João Leite reservoir, GO, Brazil, during a dry and rainy period.

	Dry period							Rainy period						
	S1	S2	S3	S4	S5	S6	S7	S1	S2	S3	S4	S5	S6	S7
WT	22.9	23.9	24.2	24	23.2	21.8	18.1	28.9	28.5	28.4	28.4	27.8	24.5	23.6
TURB	1.5	2.3	1.8	2.8	7.6	2.4	7.2	2.2	1.4	1.9	3.5	8.1	4.9	42.0
pH	6.93	7.55	7.66	7.64	7.61	6.87	6.95	7.28	7.53	7.42	7.44	7.45	6.85	6.79
DO	6.08	7.30	7.41	7.14	6.98	7.02	7.63	7.22	7.47	7.44	7.49	7.17	7.99	7.10
COND	112.8	112.5	113.2	115.5	122	113	126	133	132	132	133	136	132.6	132.6
SI	0.04	0.06	0.06	0.04	0.12	0.07	0.34	0.02	0.01	0.02	0.06	0.14	0.23	0.79
TI	0.08	0.08	0.08	0.16	0.66	0.18	0.69	0.08	0.06	0.1	0.21	0.62	0.56	4.63
TP	2.8	2.8	2.8	2.8	2.8	2.8	2.8	0.027	0.035	0.049	0.04	0.042	0.008	0.048
DIN	0.184	0.148	0.223	0.154	0.230	0.219	0.355	1.736	0.085	0.046	0.037	0.125	0.265	0.601

WT = water temperature; TURB = turbidity; DO = dissolved oxygen; COND = electrical conductivity; SI = soluble iron; TI = total iron; TP = total phosphorus; DIN = dissolved inorganic nitrogen; S1 = downstream; S2, S3 and S4 = lacustrine region; S5 and S6 = intermediate region; S7 = lotic region.

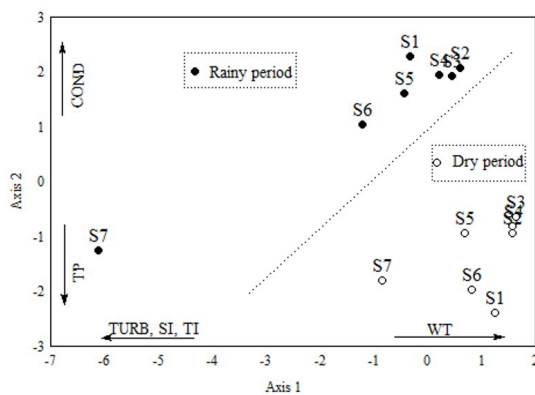


Figure 3. Dispersion of month-sites scores along the first two axes of the Principal Components Analysis performed with environmental variables measured in the João Leite reservoir, GO, Brazil, during a dry and rainy period (TP - total phosphorus; COND - electrical conductivity; WT - water temperature; TURB - turbidity; SI - soluble iron; TI - total iron; S - sampling sites).

In the dry period, 60 taxa were recorded, distributed mainly in Cyanophyceae, Bacillariophyceae, Chlorophyceae, Cryptophyceae, and Mediophyceae. Regarding the occurrence of species, the highest contribution recorded was from sporadic taxa (50%), followed by constants (29%), common (18%), and rare (3%). The taxa *Limnococcus limneticus* Lemmermann, *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerová & Cronberg, *Snowella atomus* Komárek & Hindák, and *Chlamydomonas* sp. were taxa with 100% occurrence in the dry period. According to the spatial distribution of species richness during the dry period, the highest number of taxa was recorded at station S1, downstream of the dam, while the lowest richness was recorded at station S4, lacustrine region. High phytoplankton abundance was registered in this period in all sites (except in

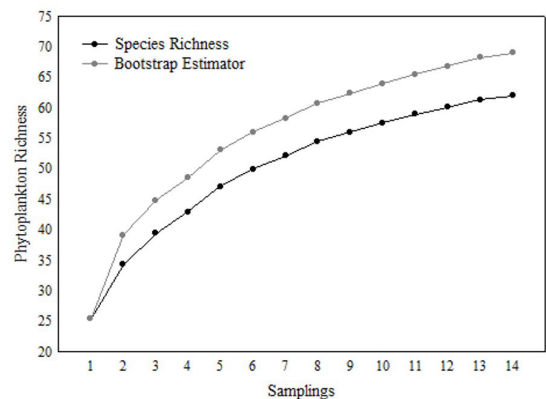


Figure 4. Species accumulation curve and Bootstrap estimator of the phytoplankton richness recorded in the João Leite reservoir, GO, Brazil, during a dry and rainy period.

the lotic region), particularly a high density of *P. limnetica* and *S. atomus* (Figures 5 and 6).

In the rainy period, 42 taxa were recorded, also mainly distributed in Cyanophyceae, Chlorophyceae, Bacillariophyceae, Cryptophyceae, and Mediophyceae. Regarding the occurrence of species, the highest contribution was recorded from rare taxa (32%), followed by sporadic (27%), constant (24%), and common (16%) taxa. The taxa *Cyanodictyon imperfectum* Cronberg & Weibull, *Cyanodictyon planctonicum* B. A. Mayer, *P. limnetica*, *Chlamydomonas* sp., *Monoraphidium pusillum* (Printz) Komárková-Legnerová, *Dinobryon sertularia* Ehrenberg, *Chroomonas acuta* Utermöhl, *Cryptomonas brasiliensis* A. Castro, C. Bicudo & D. Bicudo, and *Cryptomonas marssonii* Skuja were taxa with 100% occurrence in the rainy period. According to the spatial distribution of species richness during the rainy period, the highest value recorded was in station S2, lacustrine region,

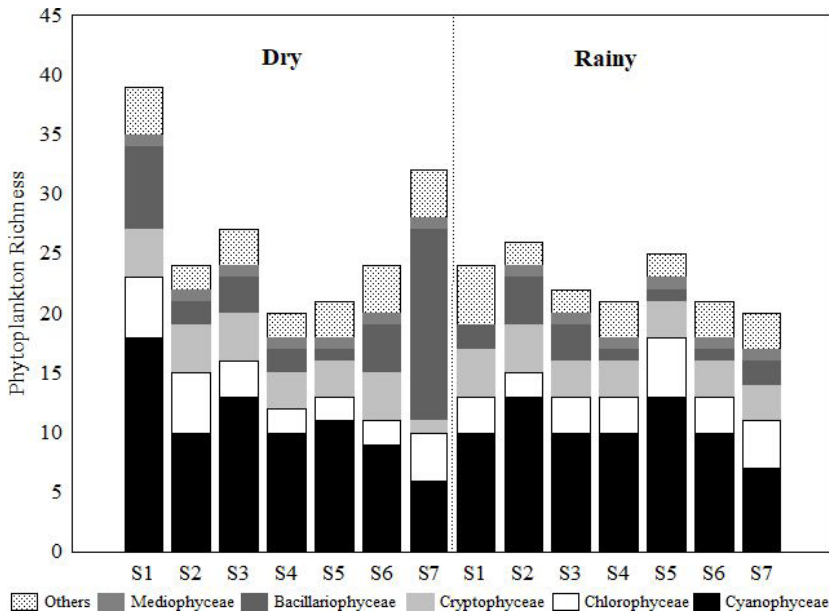


Figure 5. Spatial and temporal variation of the phytoplankton richness in the João Leite reservoir, GO, Brazil during a dry and rainy period.

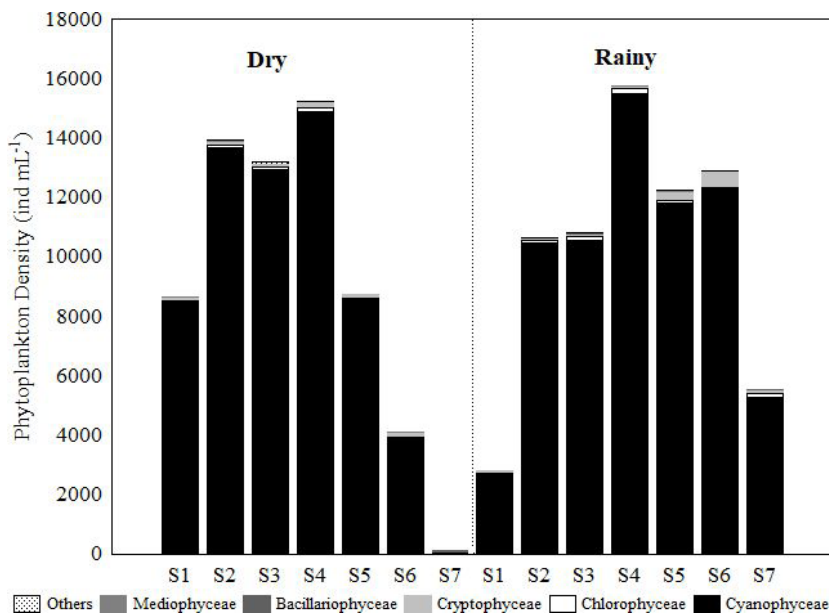


Figure 6. Spatial and temporal variation of the phytoplankton density in the João Leite reservoir, GO, Brazil during a dry and rainy period.

while the lowest species richness was verified in station S7, lotic region. However, the distribution of richness among the sampled sites seems to be more homogeneous than in the dry period. In this period, high phytoplankton abundance was also registered, mainly in lentic regions, with high density of *C. imperfectum*, *P. limnetica*, and *S. atomus* (Figures 5 and 6).

According to t-test, phytoplankton richness differed significantly between hydrological periods ($t = 1.9$; $p = 0.04$). Regarding the total

density of each sampling site, differences not found between hydrological periods ($t = -0.36$; $p = 0.63$).

BioEnv indicated that the variables correlated with phytoplankton presence/absence in the dry period were water temperature, pH, iron concentrations and dissolved oxygen ($r = 0.813$; $p = 0.03$), while in the rainy period, the variables correlated were water temperature, turbidity, soluble iron, dissolved inorganic nitrogen and electrical conductivity ($r = 0.641$; $p = 0.008$) (Table 2).

Table 2. Results of the BioEnv for phytoplankton presence/absence during a dry and rainy period in the João Leite reservoir.

Models Sizes		Models	Correlation
<i>Dry period</i>			
1	WT		0.6905
2	SI+DO		0.7762
3	WT+SI+DO		0.8217
4	WT+SI+COND+DO		0.8152
5	WT+pH+SI+TI+DO		0.8223
6	WT+pH+SI+DIN+COND+DO		0.8081
7	WT+TURB+pH+SI+ DIN+COND+DO		0.7665
8	WT+TURB+pH+SI+ TI+DIN+COND+DO		0.7437
<i>Rainy period</i>			
1	DIN		0.5067
2	TURB+DIN		0.6255
3	TURB+TI+DIN		0.6645
4	TURB+TI+DIN+COND		0.6976
5	WT+ TURB+SI+DIN+COND		0.7087
6	WT+ TURB+SI+DIN+COND		0.6996
7	WT+ TURB+pH+SI+DIN+COND		0.6658
8	WT+ TURB+SI+TI+TP+DIN+COND+DO		0.4820

WT = water temperature; TURB = turbidity; DO = dissolved oxygen; COND = electrical conductivity; SI = soluble iron; TI = total iron; TP = total phosphorus; DIN = dissolved inorganic nitrogen.

Table 3. Results of the BioEnv for phytoplankton density during a dry and rainy period in the João Leite reservoir.

Models Sizes		Models	Correlation
<i>Dry period</i>			
1	WT		0.7922
2	WT+DO		0.8377
3	WT+SI+DO		0.8636
4	WT+ pH+SI+DO		0.8169
5	WT+pH+SI+DIN+DO		0.8104
6	WT+pH+SI+DIN+COND+DO		0.7935
7	WT+TURB+pH+SI+ TI+DIN+DO		0.7065
8	WT+TURB+pH+SI+ TI+DIN+COND+DO		0.6727
<i>Rainy period</i>			
1	DIN		0.7831
2	TURB+DIN		0.8403
3	SI+TI+DIN		0.8545
4	TURB+SI+TI+DIN		0.8481
5	TURB+ pH+SI+TI+DIN		0.8234
6	WT+TURB+ pH+SI+TI+DIN		0.7857
7	WT+ TURB+pH+SI+TI+DIN+COND		0.6675
8	WT+ TURB+pH+SI+TI+TP+DIN+DO		0.5740
9	WT+ TURB+pH+SI+TI+TP+DIN+COND+DO		0.5140

WT = water temperature; TURB = turbidity; DO = dissolved oxygen; COND = electrical conductivity; SI = soluble iron; TI = total iron; TP = total phosphorus; DIN = dissolved inorganic nitrogen.

BioEnv indicated that the variables correlated with phytoplankton density in the dry period were water temperature, soluble iron and dissolved oxygen ($r = 0.9362$; $p = 0.007$), while in the rainy period, the variables correlated were iron concentrations and inorganic dissolved nitrogen ($r = 0.6669$; $p = 0.003$) (Table 3).

4. Discussion

Our results demonstrate how the seasonality between dry and rainy periods, as well as the spatiality in a tropical reservoir, influences phytoplankton richness and abundance. In fact, environmental variability is an important structuring factor of the

phytoplankton community in tropical reservoirs, influencing ecosystem metabolism (Figueredo & Giani, 2001; Calijuri et al., 2002; Silva et al., 2005; Borges et al., 2008; Xiao et al., 2016; Oliveira et al., 2020). Despite environmental variability, the remarkable seasonality in the study region can be an important driving factor at a regional scale (Nabout & Nogueira, 2011), while environmental variability in the reservoir can be an important factor at a local scale (Rodrigues et al., 2018), associated with variations in nutrient concentrations, turbidity, water flow, and retention time in each zone (Kimmel et al., 1990; Thornton et al., 1990).

During the rainy period a more homogeneous distribution of richness can be verified, probably associated with the homogenization effect that occurs in this period, reducing the spatial variation in the reservoir and promoting greater dispersion of taxa. Conversely in the dry period, the low water flow due to lower rainfall can decrease the dispersal capacity of organisms, promoting greater heterogeneity in the distribution of taxa, especially between the more lotic and lentic regions of the reservoir. This pattern of variation has been recorded by other authors in a reservoir in the same biogeographic region (Rodrigues et al., 2018). In addition, nutrient conditions, turbidity, temperature, electrical conductivity, pH, and dissolved oxygen appear to be important factors on a local scale and that influence the community organization during the hydrological periods.

Despite the taxonomic richness, we clearly evidenced a higher contribution from cyanobacteria, green algae, and diatoms. These phytoplankton groups are common components in these ecosystems (Borges et al., 2008). However, the dynamics of each reservoir can be an important factor affecting the community (Silva et al., 2005), as verified in our study by a clear distribution of distinct taxonomic groups along the different zones of the longitudinal axis of the reservoir.

In addition to an important contribution to species richness, cyanobacteria were dominant in density in both hydrological periods, as well as in the downstream and lentic regions of the reservoir. Cyanobacteria are cosmopolitan and important components of phytoplankton (Paerl, 2017) with a wide distribution in freshwater environments, usually associated with higher temperatures and high nutrient concentrations, exhibiting a wide diversity of traits and ecophysiological strategies to explore these environments (Paerl & Otten, 2013). Some taxa, such as *P. limnetica*, *S. atomus*, and

C. imperfectum, that were dominant in density are common taxa and can succeed in deep or shallow waters, oligo to eutrophic (Padisak et al., 2009). Therefore, they can be favored in reservoirs with conditions suitable for their development, as we registered.

The hydrodynamic conditions (e.g. low mixing of the water column), especially in the lacustrine and intermediate regions, associated with nutrient availability and higher temperature, tend to favor the group, and then these organisms can be transported downstream of the dam through unidirectional flow, as evidenced in our study. Even if the downstream conditions are unideal, the constant mass flow may have ensured inoculum input, contributing to the richness and density of these organisms in this site. Thus, hydrological conditions, over-enrichment, and water temperature are major drivers of cyanobacteria proliferation and persistence (Cha et al., 2017; Burford et al., 2020). Therefore, such conditions seem to favor cyanobacteria, since density dominance was registered in both hydrological periods.

Green algae, mainly represented by nanoplankton chlorophytes, have wide variability in morphological traits and are common in tropical waters due their ability to develop in a wide variety of habitats, mainly by a combination of nutrient availability and light intensity in the aquatic environment that favor these algae (Kruk et al., 2010; Kruk & Segura, 2012). In our study, green algae were important contributors to the species richness in the different regions of the reservoir in both hydrological periods. However, they presented a low contribution in density.

Despite the low contribution to species richness and density, the constant frequency of some cryptophytes is probably associated with the opportunistic character of the taxa, broad physiological plasticity (such as the development of myxotrophy), and high metabolic rates (Reynolds et al., 2002; Padisák et al., 2009). This allows its occurrence in the most diverse aquatic environments, including tropical reservoirs and, in our case, especially in the intermediate and lotic regions during rainy period, where light intensity was smaller due the higher turbidity. Taxa such as *C. acuta*, *C. marssonii*, and *C. brasiliensis* have been recognized as important plankton constituents in aquatic ecosystems (Bortolini et al., 2017). Their development can be limited due to zooplankton predation pressure (Jati et al., 2017), since these

organisms are particularly favored in environments with low predation rates (Padisak et al., 2009).

Regarding the diatom, it was possible to observe a greater contribution of taxa, mainly by richness, in the dry period, and especially in the lotic region. This record is in line with that proposed by Reynolds et al. (2002), who associated the occurrence of the group with more turbulent and lotic environments. The most frequent taxon was *Achnanthes minutissimum* (Kützing) Czarnecki, which is considered one of the most common species in the world (PotaPoVa & Hamilton, 2007). In addition, the centric diatoms, represented by the genera *Discostella* and *Cyclotella*, which are common in plankton, were also frequent in our study. Diatoms also appear to be strongly associated with environmental variability, in addition to spatial extent in reservoirs (Zorzal-Almeida et al., 2017). Although diatoms contributed to the phytoplankton richness in the reservoir (especially in the lotic region) they showed low density.

We recorded other taxonomic groups in our study, but with lesser contributions to both phytoplankton richness and density. For example, the occurrence of euglenophyceans, especially in the rainy periods, may be related to the increased turbidity of water in some sites, occasioned by carrying of organic matter, especially from the margins, and favoring the group. On the other hand, although chrysophyceans also presented few taxa for richness and density, a high frequency of *D. sertularia* was recorded, which is a chrysophycean that can develop heterotrophy and form resistance cysts (Segura et al., 2013). The other taxonomic groups such as Trebouxiophyceae (green algae), Conjugatophyceae (desmidis), Synurophyceae (chrysophyceans), and Klebsormidiophyceae (green algae), despite having low contributions to the richness and density of reservoir, were important for diversity of community traits.

Our results suggest that the environmental variability of the different environmental scenarios in the dry and rainy period, as well as the spatial zonation, were important drivers of phytoplankton richness and abundance in our study. Thus, our first question that the temporal variability of the hydrological cycle between dry and rainy periods cause changes in the phytoplankton community, with the highest richness and density in the dry season, was partially corroborated, since the phytoplankton density did not differ between the hydrological periods. Our second question that the spatial variation of reservoir zoning cause

differences the distribution of phytoplankton, with higher richness and density in the lentic regions of the reservoir and lower in the lotic region, was evidenced. Our third question that the environmental conditions related to the phytoplankton community are different between the hydrological periods, with higher influence of the nutrient concentrations in the dry period and higher influence of turbidity in the rainy period, was partially corroborated, since temperature, pH, electrical conductivity, and dissolved oxygen were also important in the sets of variables selected as drivers of phytoplankton.

Species richness and abundance plays a key role in understanding biodiversity, generating important information on conservation and maintenance of ecosystem functions, since the construction of reservoirs influences aquatic biodiversity (Nilsson et al., 2005). In addition, reservoirs are increasingly common and understanding the functioning of these aquatic ecosystems is essential to establish monitoring strategies and use priorities, especially for the important ecosystem services they provide, such as water supply, food, hydroelectricity, irrigation, recreation, navigation, among others (Tundisi et al., 2008; Carneiro & Bini, 2020).

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References

- AMERICAN PUBLIC HEALTH ASSOCIATION – APHA. *Standard methods for the examination of water and wastewater*. Washington: APHA, 2017.
- BECKER, V., HUSZAR, V.L.M. and CROSSETTI, L.O. Responses of phytoplankton functional groups to the mixing regime in a deep subtropical reservoir. *Hydrobiologia*, 2009, 628(1), 137-151. <http://dx.doi.org/10.1007/s10750-009-9751-7>.
- BICUDO, C.E.M. and MENEZES, M. *Gêneros de algas de águas continentais do Brasil: chave para identificação e descrições*. São Carlos: Rima, 2017.
- BORGES, P.A.F., TRAIN, S. and RODRIGUES, L.C. Spatial and temporal variation of phytoplankton in two subtropical Brazilian reservoirs. *Hydrobiologia*, 2008, 607(1), 63-74. <http://dx.doi.org/10.1007/s10750-008-9367-3>.
- BORICS, G., ABONYI, A., SALMASO, N. and PTACNIK, R. Freshwater phytoplankton diversity: models, drivers and implications for ecosystem properties. *Hydrobiologia*, 2021, 848(1), 53-75.

- <http://dx.doi.org/10.1007/s10750-020-04332-9>. PMID:32836348.
- BORTOLINI, J.C., BOVO-SCOMPARIN, V.M., PAULA, A.C.M., MORESCO, G.A., REIS, L.M., JATI, S. and RODRIGUES, L.C. Composition and species richness phytoplankton in a subtropical floodplain lake: a long-term study. *Acta Limnologica Brasiliensia*, 2014, 26(3), 296-305. <http://dx.doi.org/10.1590/S2179-975X2014000300009>.
- BORTOLINI, J.C., TRAIN, S. and RODRIGUES, L.C. The variability in the hydrosedimentological regime supports high phytoplankton diversity in floodplain: a 12-year survey of the Upper Paraná River. *Journal of Limnology*, 2017, 76(3), 591-604. <http://dx.doi.org/10.4081/jlimnol.2017.1509>.
- BOUGEARD, S. and DRAY, S. Supervised multiblock analysis in R with the ade4 package. *Journal of Statistical Software*, 2018, 86(1), 1-17. <http://dx.doi.org/10.18637/jss.v086.i01>.
- BRASIL, J. and HUSZAR, V.L.M. O papel dos traços funcionais na ecologia do fitoplâncton continental. *Oecologia Australis*, 2011, 15(4), 799-834. <http://dx.doi.org/10.4257/oeco.2011.1504.04>.
- BURFORD, M.A., CAREY, C.C., HAMILTON, D.P., HUISMAN, J., PAERL, H.W., WOOD, S.A. and WULFF, A. Perspective: Advancing the research agenda for improving understanding of cyanobacteria in a future of global change. *Harmful Algae*, 2020, 91, 101601. <http://dx.doi.org/10.1016/j.hal.2019.04.004>. PMID:32057347.
- CALIJURI, M.C., SANTOS, A.C.A. and JATI, S. Temporal changes in the phytoplankton community structure in a tropical and eutrophic reservoir (Barra Bonita, S.P., Brazil). *Journal of Plankton Research*, 2002, 24(7), 617-634. <http://dx.doi.org/10.1093/plankt/24.7.617>.
- CARDOSO, M.R.D., MARCUZZO, F.F.N. and BARROS, J.R. Classificação climática de Köppen Geiger para o estado de Goiás e o Distrito Federal. *Acta Geográfica*, 2014, 8(16), 40-55.
- CARMO, E.J.S. *Cianobactérias planctônicas do reservatório do Ribeirão João Leite (Goiás) durante a fase de enchimento: florística e floração*. [Dissertação de mestrado em Botânica]. Goiânia: Departamento de Botânica; Universidade Federal de Goiás, 2014, p.119.
- CARNEIRO, F.M. and BINI, L.M. Revisiting the concept of longitudinal gradients in reservoirs. *Acta Limnologica Brasiliensia*, 2020, 32, e8. <http://dx.doi.org/10.1590/s2179-975x1319>.
- CARNEIRO, F.M., BINI, L.M. and RODRIGUES, L.C. Influence of taxonomic and numerical resolution on the analysis of temporal changes in phytoplankton communities. *Ecological Indicators*, 2010, 10(2), 249-255. <http://dx.doi.org/10.1016/j.ecolind.2009.05.004>.
- CHA, Y., CHO, K.H., LEE, H., KANG, T. and KIM, J.H. The relative importance of water temperature and residence time in predicting cyanobacteria abundance in regulated rivers. *Water Research*, 2017, 124, 11-19. <http://dx.doi.org/10.1016/j.watres.2017.07.040>. PMID:28734958.
- COSTA, H.C., MARCUZZO, F.F.N., FERREIRA, O.M. and ANDRADE, L.R. Espacialização e Sazonalidade da Precipitação Pluviométrica do Estado de Goiás e Distrito Federal. *Revista Brasileira de Geografia Física*, 2012, 01(1), 87-100. <http://dx.doi.org/10.26848/rbgf.v5i1.232785>.
- DAJOZ, R. *Princípios de ecologia*. Porto Alegre: Artmed, 2005.
- DEUS, R., BRITO, D., KENOV, I.A., LIMA, M., COSTA, V., MEDEIROS, A., NEVES, R. and ALVES, C.N. Three-dimensional model for analysis of spatial and temporal patterns of phytoplankton in Tucuruí reservoir, Pará, Brazil. *Ecological Modelling*, 2013, 253, 28-43. <http://dx.doi.org/10.1016/j.ecolmodel.2012.10.013>.
- FIGUEREDO, C.C. and GIANI, A. Seasonal variation in the diversity and species richness of phytoplankton in a tropical eutrophic reservoir. *Hydrobiologia*, 2001, 445(1/3), 165-174. <http://dx.doi.org/10.1023/A:1017513731393>.
- HILLEBRAND, H., BLASIUS, B., BORER, E.T., CHASE, J.M., DOWNING, J.A., ERIKSSON, B.K., FILSTRUP, C.T., HARPOLE, W.S., HODAPP, D., LARSEN, S., LEWANDOWSKA, A.M., SEABLOOM, E.W., VAN DE WAAL, D.B. and RYABOV, A.B. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. *Journal of Applied Ecology*, 2018, 55(1), 169-184. <http://dx.doi.org/10.1111/1365-2664.12959>.
- JATI, S., BORTOLINI, J.C. and TRAIN, S. Mixotrophic species influencing phytoplankton community structuring during the filling phase of a subtropical reservoir. *Brazilian Journal of Botany*, 2017, 40(4), 933-941. <http://dx.doi.org/10.1007/s40415-017-0407-y>.
- KIMMEL, B.L., LIND, O.T. and PAULSON, L.J. Reservoir primary production. In: K.W. RYCHNTON, B.L. KIMMEL and F.E. PAYNE, eds. *Reservoir limnology: ecological perspectives*. New York: Wiley, 1990.
- KINDT, R. and COE, R. *Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies*. Nairobi: World Agroforestry Centre (ICRAF), 2005.
- KRUK, C. and SEGURA, A.M. The habitat template of phytoplankton morphology-based functional groups. *Hydrobiologia*, 2012, 698(1), 191-202. <http://dx.doi.org/10.1007/s10750-012-1072-6>.

- KRUK, C., HUSZAR, V.L.M., PEETERS, E.H.M., BONILLA, S., COSTA, L., LURLING, M., REYNOLDS, C.S. and SCHEFFER, M. A morphological classification capturing functional variation in phytoplankton. *Freshwater Biology*, 2010, 55(3), 614-627. <http://dx.doi.org/10.1111/j.1365-2427.2009.02298.x>.
- LEMKE, M.J., PAVER, S.F., DUNGEY, K.E., VELHO, L.F.M., KENT, A.D., RODRIGUES, L.C., KELLERHALS, D.M. and RANDLE, M. Diversity and succession of pelagic microorganism communities in a newly restored Illinois River floodplain lake. *Hydrobiologia*, 2017, 804(1), 35-58. <http://dx.doi.org/10.1007/s10750-017-3327-8>.
- LITCHMAN, E. and KLAUSMEIER, C.A. Trait-Based Community Ecology of Phytoplankton. *Annual Review of Ecology Evolution and Systematics*, 2008, 39(1), 615-639. <http://dx.doi.org/10.1146/annurev.ecolsys.39.110707.173549>.
- MCCANN, K.S. The diversity-stability debate. *Nature*, 2000, 405(6783), 228-233. <http://dx.doi.org/10.1038/35012234>. PMID:10821283.
- MORETI, L.O.R., MARTOS, L., BOVO-SCOMPARIN, V.M. and RODRIGUES, L.C. Spatial and temporal fluctuation of phytoplankton functional groups in a tropical reservoir. *Acta Scientiarum. Biological Sciences*, 2013, 35(3), 359-366. <http://dx.doi.org/10.4025/actascibiolsci.v35i3.12998>.
- NABOUT, J.C. and NOGUEIRA, I.S. Variação temporal da comunidade fitoplanctônica em lagos urbanos eutróficos. *Acta Scientiarum. Biological Sciences*, 2011, 33(4), 383-391. <http://dx.doi.org/10.4025/actascibiolsci.v33i4.5955>.
- NILSSON, C., REIDY, C.A., DYNESIUS, C. and REVENGA, M. Fragmentation and flow regulation of the world's large river systems. *Science*, 2005, 308(5720), 405-408. <http://dx.doi.org/10.1126/science.1107887>. PMID:15831757.
- OKSANEN, J., BLANCHET, F.G., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGLINN, D., MINCHIN, P.R., O'HARA, R.B., SIMPSON, G.L., SOLYMOS, P., HENRY, M., STEVENS, H., SZOECIS, E. and WAGNER, H. *Vegan: Community Ecology Package. R package version 2.4-5* [online]. Vienna: R Foundation for Statistical Computing, 2017 [viewed 22 Dec. 2019]. Available from: <http://CRAN.R-project.org/package=vegan>
- OLIVEIRA, S.A., FERRAGUT, C. and BICUDO, C.E.M. Relationship between phytoplankton structure and environmental variables in tropical reservoirs with different trophic states. *Acta Botanica Brasiliensis*, 2020, 34(1), 83-93. <http://dx.doi.org/10.1590/0102-33062019abb0207>.
- PADISÁK, J., CROSSETTI, L.O. and NASELLI-FLORES, L. Use and misuse in the application of the phytoplankton functional classification: a critical review with updates. *Hydrobiologia*, 2009, 621(1), 1-19. <http://dx.doi.org/10.1007/s10750-008-9645-0>.
- PAERL, H.W. and OTTEN, T.G. Harmful cyanobacterial blooms: causes, consequences, and controls. *Microbial Ecology*, 2013, 65(4), 995-1010. <http://dx.doi.org/10.1007/s00248-012-0159-y>. PMID:23314096.
- PAERL, H.W. Controlling harmful cyanobacterial blooms in a climatically more extreme world: management options and research needs. *Journal of Plankton Research*, 2017, 39(5), 763-771. <http://dx.doi.org/10.1093/plankt/fbx042>.
- PIVATO, B.M., TRAIN, S. and RODRIGUES, L.C. Dinâmica nictemeral das assembléias fitoplanctônicas em um reservatório tropical (reservatório de Corumbá, Estado de Goiás, Brasil), em dois períodos do ciclo hidrológico. *Acta Scientiarum. Biological Sciences*, 2006, 28(1), 19-29.
- POTAPOVA, M. and HAMILTON, P. Morphological and ecological variation within the *Achnantheidium minutissimum* (Bacillariophyceae) species complex. *Journal of Phycology*, 2007, 43(1), 561-575. <http://dx.doi.org/10.1111/j.1529-8817.2007.00332.x>.
- R DEVELOPMENT CORE TEAM. *R: a language and environment for statistical computing* [online]. Vienna: R Foundation for Statistical Computing, 2018 [viewed 22 Dec. 2019]. Available from: <http://www.R-project.org/>
- REYNOLDS, C.S., HUSZAR, V.L.M., KRUK, C., NASELLI-FLORES, L. and MELO, S. Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, 2002, 24(5), 417-428. <http://dx.doi.org/10.1093/plankt/24.5.417>.
- RODRIGUES, L.C., PIVATO, B.M., VIEIRA, L.C.G., BOVO-SCOMPARIN, V.M., BORTOLINI, J.C., PINEDA, A. and TRAIN, S. Use of phytoplankton functional groups as a model of spatial and temporal patterns in reservoirs: a case study in a reservoir of central Brazil. *Hydrobiologia*, 2018, 805(1), 147-161. <http://dx.doi.org/10.1007/s10750-017-3289-x>.
- RUDMAN, S.M., KREITZMAN, M., CHAN, K.M.A. and SCHLUTER, D. Ecosystem Services: Rapid Evolution and the Provision of Ecosystem Services. *Trends in Ecology & Evolution*, 2017, 32(6), 403-415. <http://dx.doi.org/10.1016/j.tree.2017.02.019>. PMID:28336183.
- SEGURA, A., KRUK, C., CALLIARI, D. and FORT, H. Use of a morphology-based functional approach to model phytoplankton community succession in a shallow subtropical lake. *Freshwater Biology*, 2013, 58(1), 504-512. <http://dx.doi.org/10.1111/j.1365-2427.2012.02867.x>.
- SILVA, C.A., TRAIN, S. and RODRIGUES, L.C. Phytoplankton assemblages in a Brazilian subtropical

- cascading reservoir system. *Hydrobiologia*, 2005, 537(1), 99-109. <http://dx.doi.org/10.1007/s10750-004-2552-0>.
- SOININEN, J., HEINO, J. and WANG, J. A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology and Biogeography*, 2018, 27(1), 96-109. <http://dx.doi.org/10.1111/geb.12660>.
- SOUZA, D.G., BUENO, N.C., BORTOLINI, J.C., RODRIGUES, L.C., BOVO-SCOMPARIN, V.M. and SOUZA FRANCO, G.M. Phytoplankton functional groups in a subtropical Brazilian reservoir: responses to impoundment. *Hydrobiologia*, 2016, 779(1), 47-57. <http://dx.doi.org/10.1007/s10750-016-2798-3>.
- THORNTON, K.W., KIMMEL, B.L. and PAINE, F.E. *Reservoir limnology: ecological perspectives*. New York: Wiley, 1990.
- TUNDISI, J.G. and MATSUMURA-TUNDISI, T. Integration of research and management in optimizing multiple uses of reservoirs: the experience in South America and Brazilian case studies. *Hydrobiologia*, 2003, 500(1-3), 231-242. <http://dx.doi.org/10.1023/A:1024617102056>.
- TUNDISI, J.G. Reservoirs: new challenges for ecosystem studies and environmental management. *Water Security*, 2018, 4-5, 1-7. <http://dx.doi.org/10.1016/j.wasec.2018.09.001>.
- TUNDISI, J.G., MATSUMURA-TUNDISI, T. and TUNDISI, J.E.M. Reservoirs and human well being: new challenges for evaluating impacts and benefits in the neotropics. *Brazilian Journal of Biology = Revista Brasileira de Biologia*, 2008, 68(4, Suppl.), 1133-1135. <http://dx.doi.org/10.1590/S1519-69842008000500020>. PMID:19197483.
- UTERMÖHL, H. Zur Vervollkommnung der quantitativen phytoplankton-methodic. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, 1958, 9, 1.
- XIAO, L., HU, R., PENG, L., LEI, L., FENG, Y. and HAN, B. Dissimilarity of phytoplankton assemblages in two connected tropical reservoirs: effects of water transportation and environmental filtering. *Hydrobiologia*, 2016, 764(1), 127-138. <http://dx.doi.org/10.1007/s10750-015-2400-4>.
- ZORZAL-ALMEIDA, S., BINI, L.M. and BICUDO, D.C. Beta diversity of diatoms is driven by environmental heterogeneity, spatial extent and productivity. *Hydrobiologia*, 2017, 800(1), 7-16. <http://dx.doi.org/10.1007/s10750-017-3117-3>.

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