Relationship between phytoplankton structure and environmental variables in tropical reservoirs with different trophic states

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ABSTRACT

Phytoplankton structure is influenced by environmental factors, seasonal cycles and the trophic state of the system. The objective of the present study was to identify guilds of phytoplankton species that are representative of seasonality and trophic status. We evaluated phytoplankton biomass and species composition in five tropical reservoirs, with different trophic states and during rainy and dry periods. At most of the sampling sites, total biomass was higher during the rainy season. Moreover, high cyanobacterial biomass was observed in all reservoirs except for one of the mesotrophic reservoirs, which had no significant contribution from the group. Phytoplankton guilds associated with the trophic gradient and seasonality were identified. Additionally, trophic status was determined to be the most important community structure factor. The results emphasize the importance of taxonomic identification when monitoring phytoplankton structure and autoecology. Furthermore, these aquatic organisms are highly sensitive to environmental variations, making them useful tools for evaluating and/or monitoring the ecological condition of aquatic ecosystems.

Keywords: Cyanobacteria, phytoplankton, guild, reservoir, seasonality

Introduction

Phytoplankton are one of the most efficient indicators of changes in the ecological condition of an aquatic ecosystem, participating as primary producers, with a short life cycle and a wide spatial distribution (Padisák *et al.* 2009). In reservoirs, phytoplankton composition depends on a variety of physical, chemical and biological factors (Bouvy *et al.* 2009). For example, natural climatic changes, such as precipitation, wind and/or river flow, as well as anthropogenic changes in nutrient input and water output rates (Chellappa *et al.* 2007) all contribute to variations in the phytoplankton community. The topography of reservoirs creates a longitudinal gradient, caused by water flow over different depths, consequently mixing the euphotic zones and nutrients and consequently resulting in system instability (Borges *et al.* 2008). Along with external factors, water column instability also modulates phytoplankton species richness and diversity (Calijuri *et al.* 2002).

Changes in aquatic community structure occur spatially and temporally, and are due to a combination of factors present at different scales (Heino *et al.* 2015), particularly in the tropical region (Fonseca & Bicudo 2008; Becker *et al.* 2009; Yang *et al.* 2018). In other words, the morphological characteristics of reservoirs can be manipulated by seasonal cycles and environmental factors, as well as the frequency and intensity of anthropogenic practices, culminating in a competitive environment where the best-adapted species prevail (Padisák *et al.* 2010). This competition can be

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detected at the floristic and structural levels, by monitoring changes in algal class biomass distributions (Naselli-Flores *et al.* 2007). The results can be interpreted as population responses, since the aquatic organisms have been exposed to different available resources (Crossetti & Bicudo 2005). Indeed, the composition and structure of phytoplankton are considered to be fundamental components of aquatic ecosystem metabolism (Calijuri *et al.* 2002).

Previous studies demonstrated that phytoplankton structure is affected by the trophic state of the system (Matsumura-Tundisi & Tundisi 2005; Bortolini *et al.* 2014; Salmaso *et al.* 2015; Santana *et al.* 2017). Indeed, the eutrophication of aquatic systems relies heavily on changes in nutrient concentrations, which can influence species selection. This is due to the fact that some species that have a higher requirement for a specific nutrient, allowing these organisms to exploit its enrichment when the opportunity arises, but suffering during low availability (Reynolds 1998). Despite the demonstrated relationship between trophic status and productivity of aquatic systems and its use in the management of water resources (Elser & Goldman 1991), knowledge about this relationship in tropical lakes and reservoirs is still limited.

The coexistence of species is extremely common among phytoplankton (Miyazaki *et al.* 2006). The communities are composed of different species that share and compete for resources, forming guilds (Wilson 1999). Since the intrinsic variability of the ecosystem, due to environmental stress, strongly affects the guild composition, monitoring these communities provides a means to evaluate the ecological condition of aquatic ecosystems (Vandrucci *et al.* 2008). Moreover, knowledge about ecological guilds that use the same resource dimension is important for understanding mechanisms involved in the coexistence of species along a resource gradient (Blondel 2003). The available resources necessary for phytoplankton development vary seasonally (Interlandi & Kilham 2001) and also depend on the trophic state of the lake or reservoir (Reynolds 1998). In the present study, we sought to determine the effect of seasonal variation and trophic state on phytoplankton guild composition, in five tropical reservoirs. More specifically, we attempted to answer two questions: (1) Is there guild formation associated with the trophic status and/or

seasonality? and (2) Which species are most dominant or abundant in these guilds? The answers to these questions will provide a better understanding about the influence trophic state and seasons have on phytoplankton structure in tropical reservoirs.

Materials and methods

Study area

Phytoplankton were evaluated in five reservoirs that are part of the Médio Tietê/Sorocaba watershed, located in a highly urbanized and industrial area (IPT 2008) in the central southeastern part of the state of São Paulo (Fig. 1). The selected reservoirs and trophic status were as follows: Barra Bonita (hypertrophic), Hedberg (eutrophic), Ipaneminha (mesotrophic), Itupararanga (mesotrophic), and Santa Helena (oligotrophic) (Lucinda 2003; Buzelli & Cunha-Santino 2013; CETESB 2013; SAAE 2013). Table 1 summarizes the main features of the five reservoirs studied. Previously, the study area was described as being located in a region of tropical climate of altitude (Conti & Furlan 2008) characterized by two contrasting seasonal periods: high temperatures and precipitation (October–March, 2014 average: 29.6 ºC and 168 mm per month, respectively), and low temperatures and rainfall (April to September, 2014 average: 19.7 ºC and 40.8 mm per month, respectively) (INMET 2018).

Sampling and analyzed variables

For evaluating phytoplankton in reservoirs with different trophic states, samples were collected from five reservoirs, during the dry and rainy periods of 2014. Each location was selected based on Trophic State Index (TSI) and depth (>20 m). The number of sampling sites was determined by taking into account the size, inputs from main tributaries, dam regions and greatest depths of the reservoir, with the goal of achieving the greatest spatial variability, ultimately resulting in a total of 19 sampling sites (Barra Bonita, n=5; Itupararanga, n=5; Hedberg, n=3: Ipaneminha, n=3: and Santa Helena, n=3).

Table 1. Characteristics of the reservoirs.

	Hypertrophic	Eutrophic	Mesotrophic	Mesotrophic	Oligotrophic
	Barra Bonita	Hedberg	Ipaneminha	Itupararanga	Santa Helena
Area (Km²)	310[a]	0.13[b]	0.15[c]	30[d]	0.38[d]
Vmax (10^6 m³)	3160[a]	0.5[b]	0.2[c]	302[d]	1.84[d]
Zmax (m)	19.0	5.2	3.2	14.0	9.5
Tret (days)*	255.0	-----	-----	200.0	3.0
Main use	Power generation	Disabled	Public supply	Public supply and Power generation	Power generation

 a: Matsumura-Tundisi & Tundisi 2005; b: Personal communication Flona 2014; c: Personal communication SAAE Sorocaba 2017; d: Personal communication Votorantim Energia 2015

 * Vmax = maximum volume, Zmax = maximum depth and Tret = water residence time. Calculated for the present study.
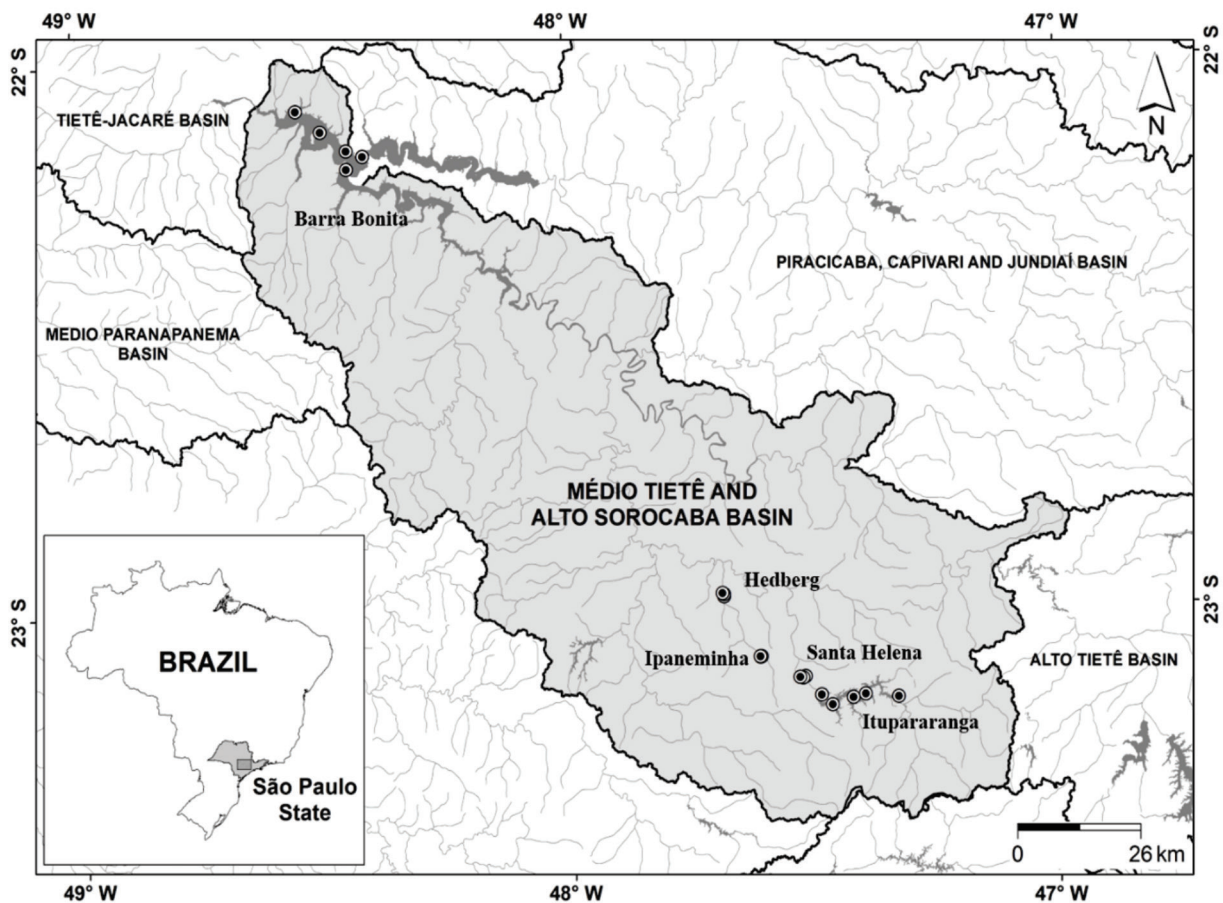
Figure 1. Location of the study reservoirs. Light gray areas represent the reservoir watershed.

Water samples were collected at the subsurface with a van Dorn bottle, and subsequently used for physical and chemical variable determinations (Brandão *et al.* 2011). Water temperature, pH, turbidity, electric conductivity and dissolved oxygen were measured 'in situ' using a Horiba U50 multiparameter probe. Water transparency was measured with a Secchi disk (Cole 1992). The analytical procedures for assessing the other abiotic variables (*i.e.* alkalinity, dissolved oxygen, nitrite, nitrate, ammonium, orthophosphate, total dissolved phosphorus (TDP), total nitrogen (TN), total phosphorus (TP), and soluble reactive silica) were performed according to the standard methods of the American Public Health Association (APHA 2005). Water samples utilized for identification of dissolved nutrients were filtered through a glass-fiber filter (GF/F Whatman) under low pressure, and the concentration of chlorophyll *a* (corrected for phaeophytin) was determined with the 90 % ethanol method (Sartory & Grobbelaar 1984), using the material retained on the filter. As proposed by Carlson (1977) and modified by Lamparelli (2004), the chlorophyll *a* and TP concentrations of the system subsurface were used to calculate the Trophic State Index (TSI).

Water collected, with a van Dorn bottle, along the vertical profile of reservoirs (subsurface, mean depth and ± 1.0 m above sediments) was used for phytoplankton analyses. Following collection, individual water samples were immediately pooled into one sample and preserved in a 4 % formalin solution. Taxonomic identification was performed using a binocular optical microscope (Zeiss Axioskop 2). A portion of each sample was prepared for diatom oxidation and permanent slide production, using Naphrax, following the method proposed by the European Commission for Standardization (2003) for taxonomic analyses. For quantitative analysis, samples were fixed with a 0.5 % acetic lugol solution and phytoplankton were counted on an inverted microscope (Zeiss Axio Observer D1, 400× magnification), according to Utermöhl (1958). The counting limit was defined by the minimum count of 100 individuals of the most abundant species, and the species rarefaction curve. Phytoplankton biomass was estimated by calculating the biovolume ($\mu m^3\,ml^{-1} \rightarrow mm^3\,L^{-1}$) of the geometric models, as defined by the shape of the cells (Hillebrand *et al.* 1999). Whenever possible, measurements of 20–30 individuals of each type were taken. Species present with a relative biomass of >5 % were considered descriptive. Abundant species were considered those with biomass values above the mean value of the community, and dominant species accounted for >50 % of the total biomass (Lobo & Leighton 1986).

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Data treatment

Two-way permutational multivariate variance analysis (Two-way PERMANOVA; α = 0.05) was used to identify phytoplankton species composition differences, in the dry and rainy periods and in different trophic states. This analysis was done using Bray-Curtis similarity and PAST 3.01 statistical software (Hammer *et al*. 2001).

Redundancy analysis (RDA) was used to correlate the phytoplankton descriptive species with the environmental variables, using log (x + 1) transformed data and a covariance matrix. Due to the ordering of the species by the DCA (Detrended Correspondence Analysis), this analysis indicated that the length gradient was <2.0, which is indicative of the algal biomass and environmental gradient values being linear (Birks 2010). The six environmental matrix variables included: temperature, conductivity, nitrate, ammonium, TP and TN, and were selected based on the principal component analysis (PCA). Monte Carlo randomization tests were performed, and axes with p<0.05 were considered to be interpretable. Data analyses were conducted using the PC-ORD 6.0 program (McCune & Mefford 2006).

Results

Abiotic variables

Summarized in Table 2, a number of abiotic variables were monitored in the present study. Notably, water transparency and euphotic zone depth were found to be higher during the dry period. Variations in nutrient and chlorophyll *a* concentrations were also detected during the two climatic periods, with the greatest mean values observed during the dry season, at most of the sampling sites. Additionally, dissolved oxygen, electric conductivity, pH, orthophosphate and soluble reactive silica exhibited low temporal variations. The rainy and dry periods also had no effect on the trophic status of the reservoirs.

Phytoplankton

Phytoplankton taxonomic identification revealed 154 taxa, distributed into 10 taxonomic classes, with Chlorophyceae representing 28.6 % of the taxa identified, followed by Euglenophyceae (22.1 %), Bacillariophyceae (15.6 %), Cyanobacteria (12.3 %), Cryptophyceae

Table 2. Limnological variables of the reservoirs, during rainy and dry periods. Hyper: Hypertrophic; Eu: Eutrophic; Meso: Mesotrophic; Oligo: Oligotrophic; BB = Barra Bonita, HB = Hedberg, IP = Ipaneminha, IT = Itupararanga, SH = Santa Helena.

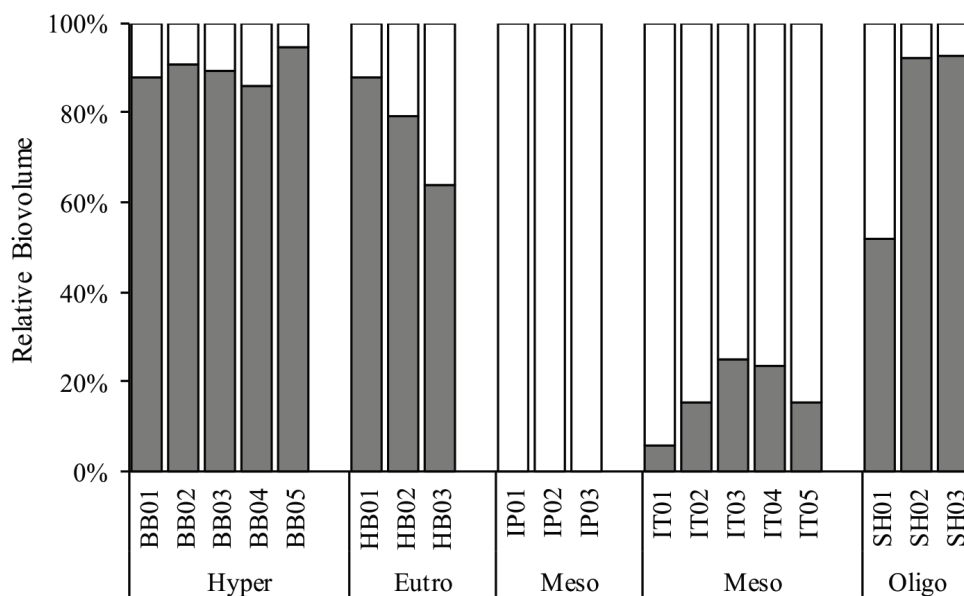|	Rainy Period					Dry Period				
	Hyper	Eu	Meso	Meso	Oligo	Hyper	Eu	Meso	Meso	Oligo
	BB	HB	IP	IT	SH	BB	HB	IP	IT	SH
Water transparency (m)	0.7 ± 0.3	0.3 ± 0.1	0.5 ± 0.1	0.9 ± 0.2	1.1 ± 0.1	1.4 ± 0.3	0.8 ± 0.2	0.7 ± 0.1	1.1 ± 0.4	1.7 ± 0.1
Euphotic zone depth (m)	2.0 ± 0.8	1.0 ± 0.2	1.4 ± 0.2	2.6 ± 0.6	3.0 ± 0.2	3.8 ± 0.7	2.2 ± 0.6	2.1 ± 0.3	3.1 ± 1.0	4.8 ± 0.4
Water temperature (°C)	27.7 ± 0.7	23.6 ± 1.0	23.6 ± 0.1	25.8 ± 0.7	25.6 ± 1.0	18.6 ± 0.3	20.0 ± 0.2	23.6 ± 0.8	25.8 ± 1.0	25.6 ± 1.0
Conductivity ($\mu S\ cm^{-1}$)	323 ± 28.4	113 ± 3.6	160.6 ± 2.5	94 ± 6.8	100.3 ± 5.7	385 ± 56.6	155.6 ± 1.5	165 ± 9.5	102.6 ± 7.5	99.6 ± 2.3
pH	8.9 ± 0.5	6.7 ± 0.3	6.7 ± 0.1	7.4 ± 0.7	7.1 ± 0.1	7.5 ± 0.3	9 ± 0.4	7.4 ± 0.1	6.9 ± 0.3	7.1 ± 0.4
Dissolved Oxygen ($mg\ L^{-1}$)	6.9 ± 1.2	6.2 ± 2.0	3.9 ± 0.4	6.2 ± 1.3	6.6 ± 0.5	6 ± 2.3	8.9 ± 1.0	10.3 ± 1.3	7.2 ± 0.5	6.9 ± 1.4
NH_4^+-N ($\mu g\ L^{-1}$)	666.5 ± 832.8	42.4 ± 38.8	69.8 ± 17.9	34.7 ± 24.8	153.9 ± 34.9	1724.6 ± 2224.3	71.7 ± 15.3	316.3 ± 22.4	102.9 ± 56.1	193.3 ± 7.3
NO_2^--N ($\mu g\ L^{-1}$)	324.2 ± 245.2	27.7 ± 1.7	28.1 ± 2.5	5.0 ± 0.0	9.4 ± 1.1	162.4 ± 24.3	68.2 ± 22.6	32.8 ± 0.9	5.3 ± 0.7	9.4 ± 1.0
NO_3^--N ($\mu g\ L^{-1}$)	1689.2 ± 917.5	218.4 ± 1.7	71.9 ± 6.9	8.0 ± 0.0	33.4 ± 1.1	1687.2 ± 184.9	777.7 ± 109.2	32.8 ± 0.9	59.5 ± 65.1	170.5 ± 5.8
TN ($\mu g\ L^{-1}$)	6162.6 ± 3470.6	892.5 ± 356.5	526.0 ± 71.5	565.0 ± 114.2	487.7 ± 55.2	4506.3 ± 2148.9	1704.8 ± 188.4	1311.0 ± 33.7	965.8 ± 128.8	601.2 ± 90.4
PO_4^{-3}-P ($\mu g\ L^{-1}$)	41.6 ± 34.4	27.9 ± 5.6	4.0 ± 0.0	4.0 ± 0.0	4.0 ± 0.0	183.5 ± 141.8	15.6 ± 9.1	5.9 ± 0.4	4.0 ± 0.0	4.0 ± 0.0
TDP ($\mu g\ L^{-1}$)	67.5 ± 43.5	42.4 ± 2.6	13.3 ± 1.0	5.7 ± 4.0	4.2 ± 0.2	211.1 ± 144.8	28.4 ± 10.1	11.3 ± 1.4	7.6 ± 0.9	7.3 ± 0.6
TP ($\mu g\ L^{-1}$)	319.6 ± 224.6	117.7 ± 57.2	33.2 ± 0.9	21.7 ± 18.0	11.4 ± 1.4	247.3 ± 133.2	82.9 ± 13.9	35.1 ± 3.9	30.5 ± 8.3	16.4 ± 3.0
Chlorophyll-*a* ($\mu g\ L^{-1}$)	112.2 ± 50.0	36.1 ± 28.9	10.9 ± 6.3	15.4 ± 13.4	6.7 ± 4.7	53.5 ± 21.1	56.1 ± 84.7	14.3 ± 5.4	20.8 ± 19.0	2.2 ± 1.2
TN:TP molar ratio	60.2 ± 19.1	19.9 ± 3.8	36.2 ± 4.4	268.3 ± 454.5	100.3 ± 18.9	50.7 ± 13.6	47.3 ± 8.2	85.6 ± 8.6	77.7 ± 18.9	79.0 ± 10.3
Free CO_2 ($mg\ L^{-1}$)	0.3 ± 0.4	14.0 ± 7.3	21.0 ± 5.6	3.4 ± 2.0	4.5 ± 1.0	6.0 ± 5.5	0.1 ± 0.1	4.3 ± 1.2	7.4 ± 3.3	7.0 ± 7.5
Trophic State Index (TSI)	69.1	62.5	56.8	57.8	51.8	67	61.1	55.1	57.3	50.6

(5.2 %), Trebouxiophyceae (5.2 %), Zygnematophyceae (3.9 %), Xanthophyceae (3.9 %), Dinophyceae (2.6 %) and Chrysophyceae (0.6 %).

The relative biovolume of Cyanobacteria varied in the reservoirs depending on climatic period. Notable increases in biovolume were detected during the rainy period at most of the sampling sites, with the only exceptions being the mesotrophic reservoirs, of which the Ipaneminha reservoir presented almost no seasonal variability. Additionally, despite Cyanobacteria contributing to >50 % of the relative biovolume at some of the mesotrophic Itupararanga sampling sites during the dry period, this group did not contribute

significantly to the biovolume of mesotrophic reservoirs. In contrast, Cyanobacteria was found to contribute heavily to the community structure of the hypertrophic and oligotrophic reservoirs during the rainy period, when the relative biovolume exceeded 90 %. (Fig. 2).

As shown in Figure 3, total phytoplankton biovolume was found to be increased at most sampling sites during the rainy period. The samples from the mesotrophic Itupararanga sites presented the highest biovolume values, followed by the hypertrophic reservoir. Samples with the lowest biovolume values were collected from three sites in the mesotrophic Ipaneminha reservoir.
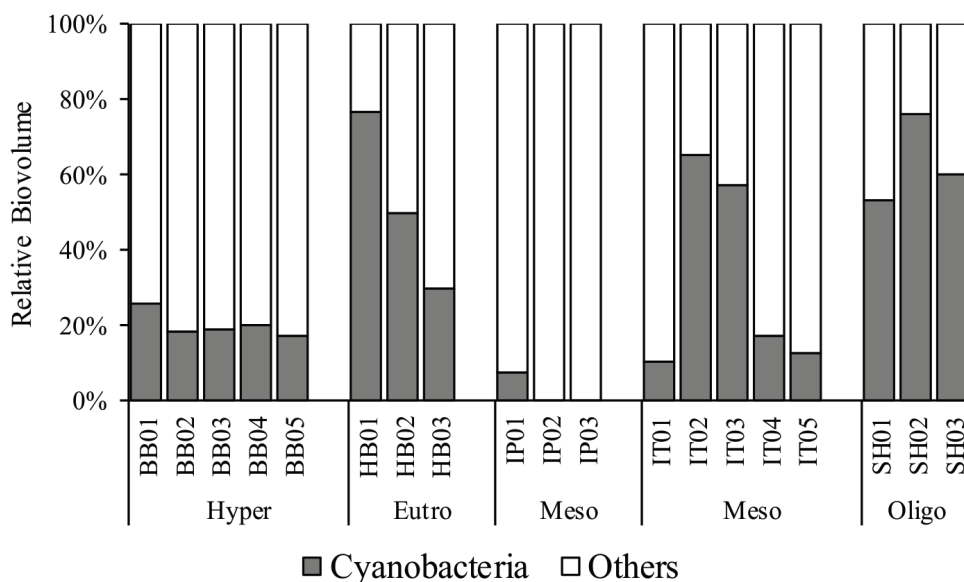
Figure 2. Relative biovolume of Cyanobacteria from reservoirs with different trophic states, during rainy and dry periods. Abbreviations: Hyper = hypertrophic; Eutro = eutrophic; Meso = mesotrophic; Oligo = oligotrophic.

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During the rainy period (Fig. 4, column A), the cyanobacteria *Microcystis aeruginosa* was dominant in the hypertrophic reservoir, accounting for 68-91 % of the relative biovolume, at all sampling sites. In the eutrophic and oligotrophic reservoirs, the dominant cyanobacteria was *Dolichospermum solitarium* (45-87 % of relative biovolume). With regards to the mesotrophic sites, *Trachelomonas volvocinopsis* (12-22 % relative biovolume) and *Mougeotia* sp. (69-83 % relative biovolume) were the most abundant phytoplankton in the Ipaneminha, and Itupararanga reservoirs, respectively.

Interestingly, during the dry period (Fig. 4, column B), the hypertrophic sites had a higher abundance of the diatom *Aulacoseira granulata* (18-54 %) and the Dinophyceae *Ceratium furcoides* (17-36 %). While the eutrophic reservoir contained an abundance of the cyanobacteria *Oscillatoria tenuis* (20-53 %). In the mesotrophic Ipaneminha reservoir, the diatom *Discostella stelligera* (25-35 %) and the Euglenophyceae *Euglena granulata* (34-60 %) were found in the highest abundance, whereas the most dominant and abundant phytoplankton at the Itupararanga sites were *Mougeotia* sp. (82 %) and the cyanobacteria *Dolichospermum planctonicum* (48-53 %), respectively. Furthermore, temperature and precipitation had no effect on the species dominance in the oligotrophic reservoir, since *Dolichospermum solitarium* (53-76 %) remained the most abundant species.

Results from the two-way PERMANOVA suggested that phytoplankton species composition during different climatic periods was significantly altered (F = 3.1; *p* = 0.02),

and that it was expressively influenced by trophic state (F = 5.7; *p* = 0.001).

As shown in Figure 5, RDA was performed using 40 species and six environmental variables (Fig. 5). The eigenvalues for Axes 1 (λ = 5.03) and 2 (λ = 3.52) accounted for 21.4 % of the total data variation. A correlation between species abundance and environmental factors was high for Axes 1 (*r* = 0.93) and 2 (*r* = 0.93), indicating a strong relationship between species distribution and environmental variables. The Monte Carlo randomization test showed that Axes 1 and 2, were significant (*p* = 0.001). The most important variables for Axis 1 ordination were nitrate and electric conductivity (*r* > 0.8). Axis 1 represented the trophic gradient, ordering the sample units from oligotrophic to hypertrophic status. The sampling sites from the oligotrophic and mesotrophic reservoirs were localized to the negative side of Axis 1, conditions associated with the lowest nutrient concentrations and conductivity values. In contrast, sampling sites from the eutrophic and hypertrophic reservoirs were positioned on the positive side Axis 1.

The most important variable for Axis 2 (seasonality) ordination was determined to be water temperature (*r* > 0.8), with most of the sampling sites during the rainy period being positioned on the positive side of Axis 2, which was associated with the highest water temperature and lowest water transparency values. On the negative side of axes 2 ordered the dry season sampling stations associated with the lowest values of the same variables above.

Considering the species correlation with the axes and their proximity to the sample unit, two guilds were formed: (1) five
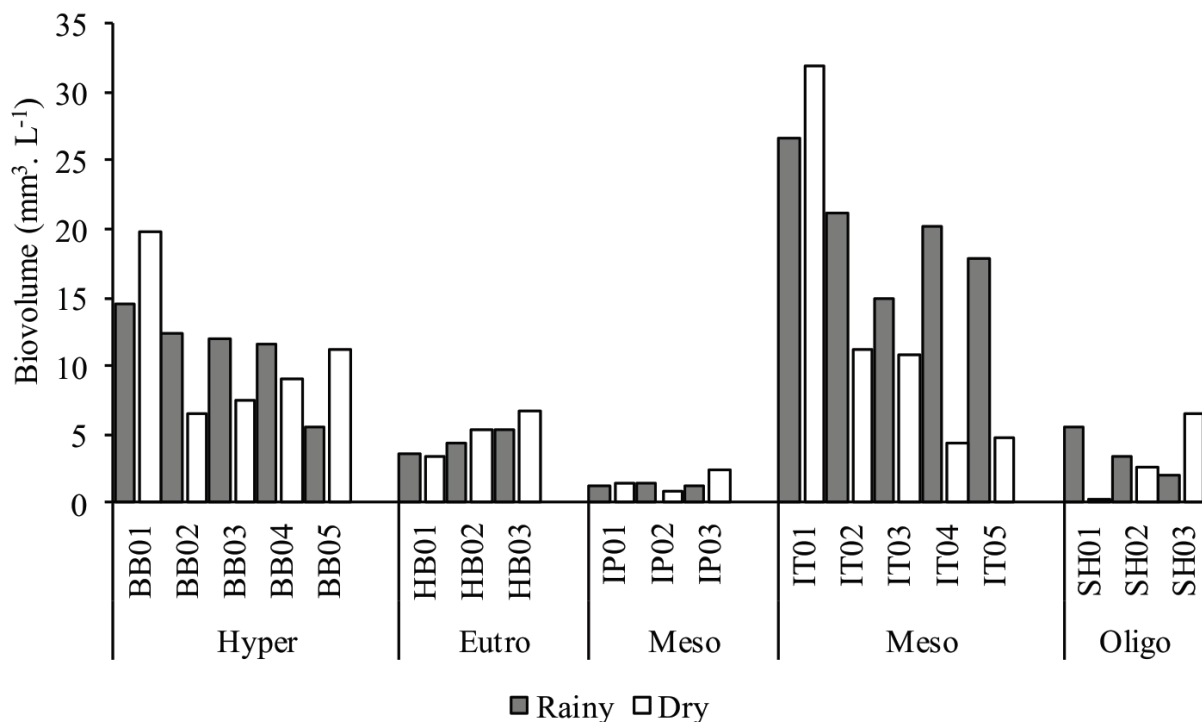

Figure 3. Total biovolume in the reservoirs with different trophic states during rainy and dry periods. Abbreviations: Hyper = hypertrophic; Eutro = eutrophic; Meso = mesotrophic; Oligo = oligotrophic.
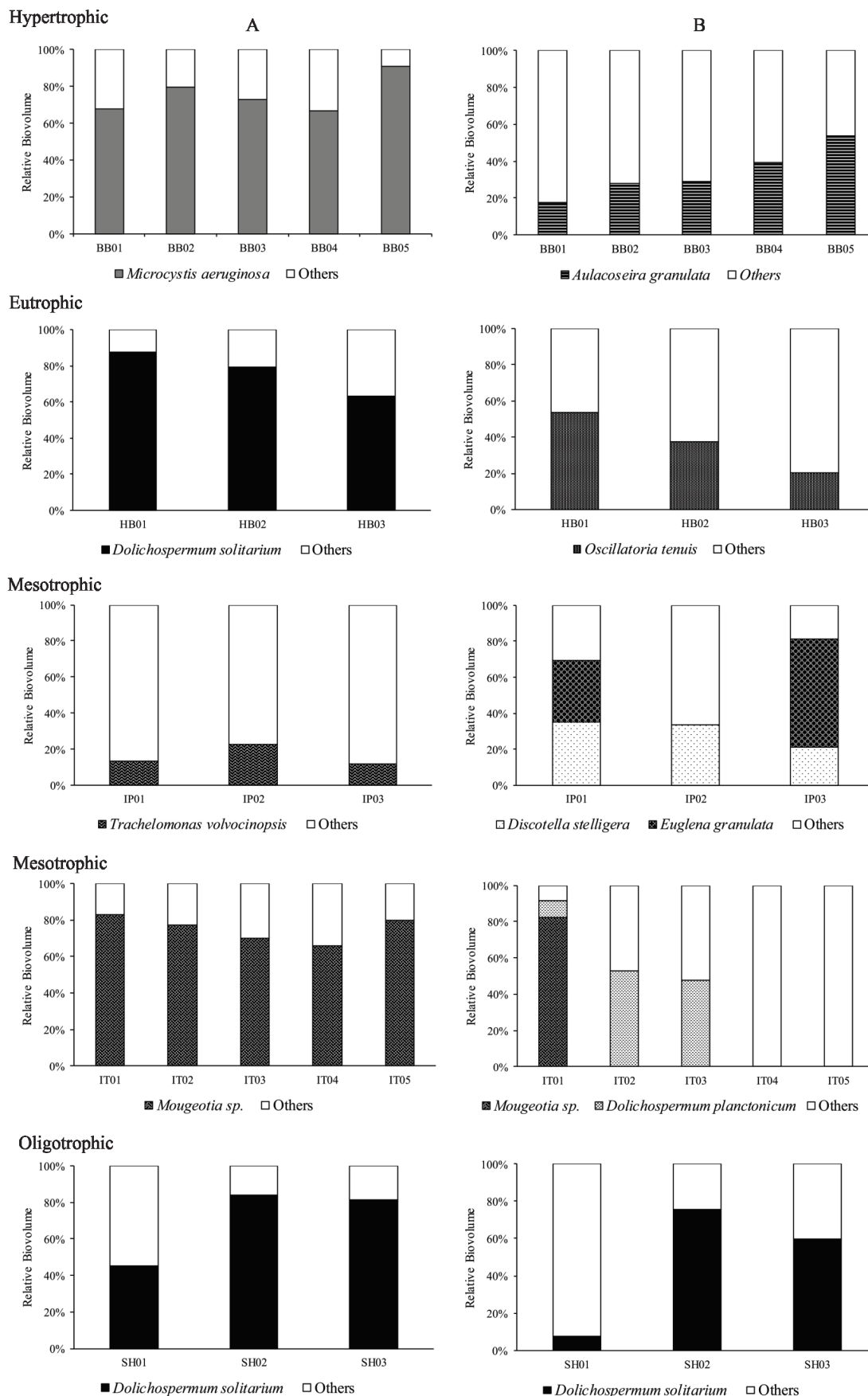
Figure 4. Relative biovolume of dominant and/or abundant species in the rainy (column A) and dry (column B) periods.

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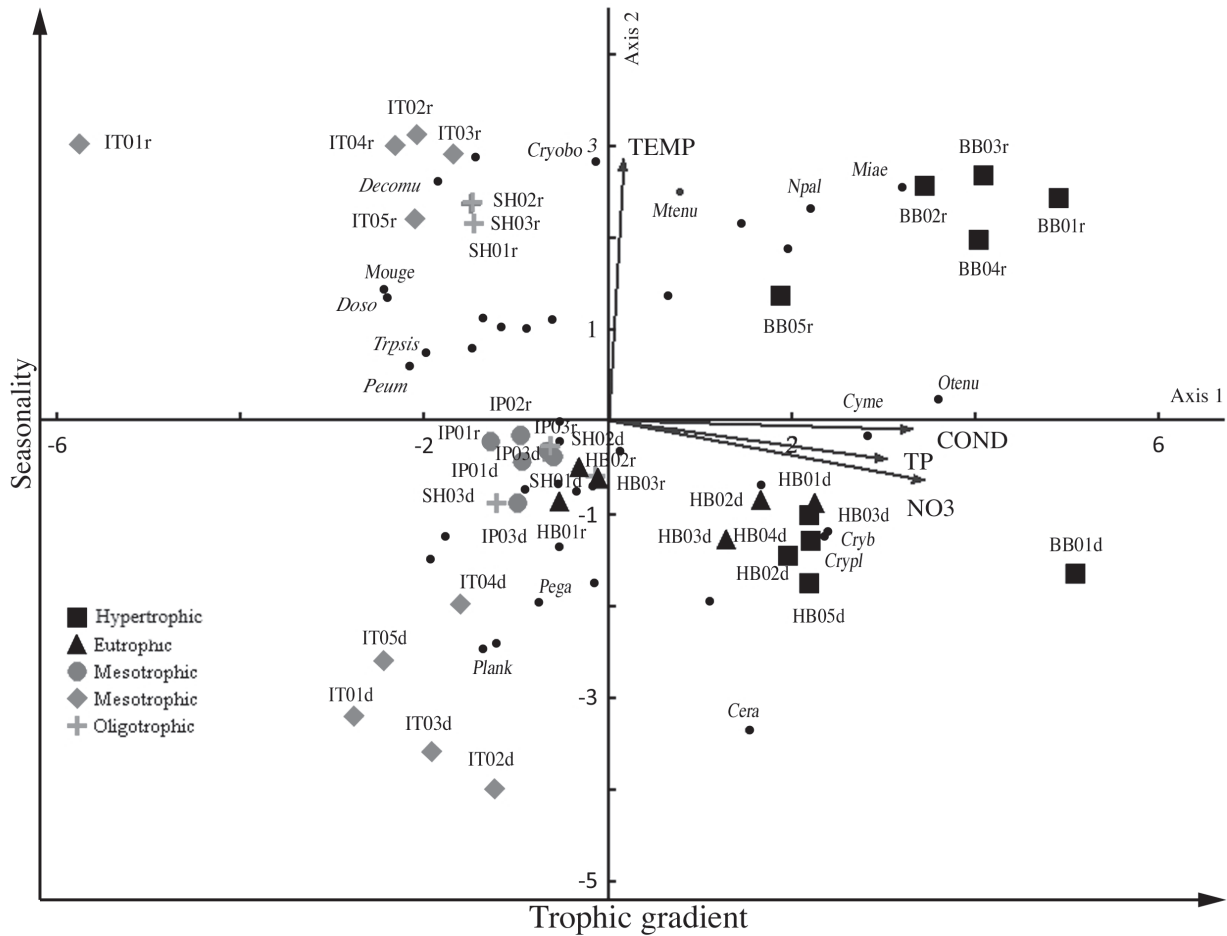and Carlos Eduardo de Mattos Bicudo

Figure 5. Ordination according to the RDA of 40 descriptive species and six environmental variables. The graph only displays the codes of species (*r* > 0.5 along Axis 1) and the environmental variables (*r* > 0.6 correlation between axes) considered interpretable. Abbreviations: Temp = water temperature; Cond = conductivity; NO₃ = nitrate; TP = total phosphorus; d = dry; r = rainy. Species correlation with Axes 1 and 2 and species codes are provided in Table 3.

Table 3. Pearson correlation of phytoplankton species.

Taxa	Code	Axis 1	Axis 2
Ceratium furcoides (Levander) Langhans	Cera	0.32	-0.61
Cryptomonas brasiliensis A.Castro, C.Bicudo & D.Bicudo	Cryb	0.60	-0.19
Cryptomonas platyuris Skuja	Crypl	0.50	-0.17
Cryptomonas obovata Skuja	Cryobo	0.48	0.50
Cyclotella meneghiniana Kützing	Cyme	0.64	0.01
Desmodesmus communis (E.Hegewald) E.Hegewald	Decomu	0.50	0.58
Dolichospermum solitarium (Klebahn) Wacklin, L.Hoffmann & Komárek	Doso	-0.51	0.27
Merismopedia tenuissima Lemmermann	Mtenu	0.29	0.51
Microcystis aeruginosa (Kützing) Kützing	Miae	0.72	0.42
Mougeotia sp.	Mouge	-0.53	0.37
Nitzschia palea (Kützing) W.Smith	Npal	0.50	0.37
Oscillatoria tenuis C.Agardh *ex* Gomont	Otenu	0.85	0.07
Parvodinium cf. *umbonatum* (F.Stein) Carty	Peum	-0.50	0.10
Peridinium gatunensis Nygaard	Pega	-0.12	-0.50
Planktothrix agardhii (Gomont) Anagnostidis & Komárek	Plank	-0.25	-0.56
Trachelomonas volvocinopsis Svirenko	Trpsis	-0.51	0.15

Species with values of r > 0.5 along axes 1 and 2 of the RDA

species associated with the oligotrophic and mesotrophic reservoirs (*r* > 0.5; *Desmodesmus communis*, *Dolichospermum solitarium*, *Mougeotia* sp., *Parvodinium* cf. *umbonatum* and *Trachelomonas volvocinopsis*), on the negative side of Axis 1, and (2) six species associated with the hypertrophic and eutrophic reservoirs (*r* > 0.6; *Cryptomonas brasiliensis*, *Cryptomonas platyuris*, *Cyclotella meneghiniana*, *Microcystis aeruginosa*, *Nitzschia palea* and *Oscillatoria tenuis*) on the positive side of Axis 1. With regards to Axis 2, two other guilds were identified. The first, on the positive side, is composed of three species associated with the rainy period (*r* > 0.5; *Desmodesmus communis*, *Cryptomonas obovata* and *Merismopedia tenuissima*), and another guild, on the negative side, is composed of three species associated with the dry period (*r* > 0.5; *Ceratium furcoides*, *Peridinium gatunensis* and *Planktothrix agardhii*).

Discussion

There is a well-established relationship between nutrient concentrations and the taxonomic composition of phytoplankton (Becker *et al.* 2009), and it is known that changes in the community structure are related to differences in nutrient absorption and storage, as well as population growth and loss rates (Watson *et al.* 1997). Herein, we demonstrated that the phytoplankton structure is also influenced by seasonality, characterized by fluctuations in water temperature and nutrient concentrations during rainy and dry periods, resulting in higher biomass in most of the reservoir sampling sites studied. Indeed, the influence of seasonality on phytoplankton has been reported in tropical reservoirs (*e.g.* Calijuri *et al.* 2002; Borges *et al.* 2008; Dantas *et al.* 2008), and in temperate lakes and reservoirs (*e.g.* Grover & Chrzanowski 2006; Butts & Carrick 2017).

Moreover, we identified a phytoplankton guild representative of eutrophic-hypertrophic reservoirs and another for oligo-mesotrophic reservoirs. In the latter, *Dolichospermum solitarium* and *Mougeotia* sp. were dominant, and *Trachelomonas volvocinopsis* was abundant, constituting the most representative species of this guild. The cyanobacteria *Dolichospermum solitarium* would subsist due to the presence of akinetes and heterocytes in environments with low to high nutrient concentrations (Sant'Anna *et al.* 2008). Additionally, the Zygnematophyceae *Mougeotia* sp. prefers higher temperatures and favors oligo-mesotrophic conditions (Kálmán *et al.* 2015), similar to the Euglenophyceae *Trachelomonas volvocinopsis*, a typical species found in shallow and mesotrophic environments (Alves-da-Silva *et al.* 2013). In the guild associated with eutrophic and hypertrophic reservoirs, *Microcystis aeruginosa* was found to be dominant in the hypertrophic reservoir, and *Oscillatoria tenuis* was abundant in the eutrophic sites. Both of these cyanobacterial species form blooms that are potentially toxic (Herry *et al.* 2008). *M. aeruginosa* blooms are commonly observed in freshwater ecosystems, and this type of bloom has been recorded constantly in Brazil (Sant'Anna *et al.* 2008; Silva-Stenico *et al.* 2011). Due to its worldwide distribution and

frequent toxin production, *M. aeruginosa* has been the focus of many studies (Straub *et al.* 2011). In comparison, *Oscillatoria tenuis* blooms are reported less often (Werner *et al.* 2015), and appear as metaphyton, present at low water depths (< 6 m). Taken together, the results show that there is one guild typical of eutrophic environments and another composed of phytoplankton species typical of environments with moderate nutrient concentrations.

Furthermore, we also identified a guild associated with seasonality, with temperature being a determinant factor in phytoplankton structure. Phytoplankton species, in the guilds associated with seasonality, have a great ecological range (Padisák *et al.* 2009) and trophic tolerance, allowing these organisms to adapt to different water depths (Reynolds *et al.* 2002).

Planktothrix agardhii and *Ceratium furcoides* prefer the high nutrient availability conditions characteristic of hypertrophic to eutrophic environments (Kokociński *et al.* 2010; Cavalcante *et al.* 2016). In highly eutrophic reservoirs, *Planktothrix agardhii* grow well and possibly produce toxic blooms, even at low temperatures in the winter (Kokociński *et al.* 2010). With regards to *C. furcoides*, the species is considered invasive and non-toxic, but may affect the taste and smell of drinking water, and can clog water treatment filters, thus classifying it as harmful when monitoring water intended for public consumption (Ewerts *et al.* 2013).

Of the five reservoirs studied, Cyanobacteria were the most successful taxonomic group identified, an observation that was independent of the trophic state, and most apparent during the rainy period when biomass was the highest. At temperatures above 25 °C, these organisms exhibit rapid growth rates (Chu *et al.* 2007), exceeding those reported for algae (Coles & Jones 2000; Butterwick *et al.* 2005). According to Dantas *et al.* (2008) and Sperling *et al.* (2008), Cyanobacteria is the dominant group in eutrophic and hypertrophic reservoirs. We expected to observe low Cyanobacteria biomass in oligo-mesotrophic reservoirs, but these sampling sites contained high *Dolichospermum solitarium* and *Dolichospermum planctonicum* biomass (>50 % of the total abundance) and are species that commonly form blooms (Paerl *et al.* 2011). Thus, despite the low nutrient availability and low trophic state, there are species present that could disturb the balance of the system.

With regards to the mesotrophic reservoirs, the Itupararanga presented high cyanobacterial biomass and higher total biomass, mainly due to *Mougeotia* sp presenting numerous long filaments that increase the relative biomass of this species. Previous studies have associated this species with oligo-mesotrophic environments (Pacheco *et al.* 2010; Santana *et al.* 2018). It should be pointed out that monitoring the phytoplankton community structure, at the taxonomic level, is very sensitive at detecting environmental changes and is representative of the trophic state of the ecosystem, which is not always the case with total biomass. This proposal is further corroborated by the redundancy

analysis, in which the mesotrophic reservoirs descriptor species were associated with the mesotrophic condition. Furthermore, it is plausible that changes in the trophic state of the Itupararanga reservoir will occur.

Based on the results of the redundancy analysis (*i.e.* Axis 1 ordinance), the phytoplankton structure was mainly defined by the trophic state of the reservoirs, evidenced by heterogeneity in the community distribution along the trophic gradient. Moreover, the results of the present study showed that phytoplankton guild formation is associated with the trophic state of the aquatic environment and seasonality, with the former having the greatest impact on phytoplankton structure. Although the identified guilds included species of different groups, high Cyanobacteria biomass was present in all of the reservoirs studied, including those classified as oligo-mesotrophic. This corroborates the results of Galvão *et al.* (2008) that also revealed the weakness of the system. In addition, our findings show that phytoplankton species identification is more representative of trophic state than total biomass, and that population responses are highly sensitive to environmental changes. In conclusion, trophic state and seasonality are determinant factors of phytoplankton taxonomic structure. These results provide a better understanding of the dynamics and factors that modulate phytoplankton communities in tropical reservoirs with different trophic states, and demonstrated that phytoplankton guilds could be used to monitor the ecological quality of tropical reservoirs.

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