Acta Limnologica Brasiliensia



Spatial and temporal variation of the phytoplankton structure in cascading oligotrophic reservoirs of southeast Brazil

Variação espacial e temporal da estrutura fitoplanctônica em reservatórios oligotróficos em cascata do sudeste do Brasil

Ana Margarita Loaiza-Restano¹ (10), Gisele Carolina Marquardt¹ (10), Carla Ferragut¹ (10) and

Carlos Eduardo de Mattos Bicudo^{1*} 💿

¹Núcleo de Pesquisa em Ecologia, Instituto de Botânica, Av. Miguel Estéfano, 3687, CEP 04301-902, São Paulo, SP, Brasil *e-mail: cbicudo@terra.com.br; carlaferragut@yahoo.com.br

Cite as: Loaiza-Restano, A.M. et al. Spatial and temporal variation of the phytoplankton structure in cascading oligotrophic reservoirs of southeast Brazil. *Acta Limnologica Brasiliensia*, 2020, vol. 32, e12.

Abstract: Aim: Structural changes in phytoplankton was evaluated in one ultraoligotrophic and two oligotrophic cascading reservoirs during two climatic periods (austral winter and summer) of 2014. Changes in phytoplankton biomass, species composition, and codons (functional groups) were evaluated along a vertical and a longitudinal profile. **Methods:** Four sampling sites were selected for the first reservoir in the cascade (Cachoeira do França) and three for each of the other two reservoirs (Cachoeira da Fumaça and Serraria). Samples were collected along a vertical and a longitudinal profile. Species biomass and codons '*sensu*' Reynolds were identified and expressed in terms of biomass. **Results:** 18 codons were identified and associated to the reservoirs' limnological conditions. Composition and biomass of descriptor species changed among seasons. Codon **B** consisting mainly of *Discostella stelligera* was the most frequent in all reservoirs in both climatic seasons. **Conclusions:** Our findings showed that seasonality was the key factor for the species composition and phytoplankton codons changes. However, the cascade effect on phytoplankton structure was shown by the continuous contribution of *Ceratium furcoides* (codon **L**_M) during the winter, and of *Discostella stelligera* (codon **B**) in both sampling periods in all three reservoirs.

Keywords: codon; environmental monitoring; oligotrophic reservoir; phytoplankton; ultraoligotrophic reservoir

Resumo: Objetivo: Mudanças estruturais no fitoplâncton foram avaliadas em três reservatórios em cascata, um ultraoligotrófico e dois oligotróficos, no verão e no inverno de 2014. Avaliou-se a variação da biomassa fitoplanctônica, a composição de espécies e os códons (grupos funcionais) ao longo de um perfil vertical e outro longitudinal. **Métodos:** Foram selecionados quatro locais de amostragem na primeira represa em cascata (Cachoeira do França) e três em cada uma das demais duas (Cachoeira da Fumaça e Serraria). As amostras foram coletadas ao longo dos perfis vertical e longitudinal das represas. Foram determinados o biovolume das espécies e os códons que foram expressos em termos de biomassa. **Resultados:** 18 códons foram identificados e associados às condições limnológicas dos reservatórios. A composição e a biomassa das espécies descritoras mudaram conforme as estações do ano. Códon **B** constituído principalmente por *Discostella stelligera* foi o mais frequente nas três represas e em ambos os períodos de amostragem. **Conclusões:** Os resultados mostraram que a sazonalidade foi um fator importante para as mudanças na composição de espécies e dos códons do fitoplâncton. No entanto, o efeito da cascata sobre a estrutura do fitoplâncton foi demonstrado pela expressiva e constante contribuição de *Ceratium furcoides* (códon **L**_M) no inverno e de *Discostella stelligera* (códon **B**) em ambos os períodos de amostragem nas três represas estudadas.

Palavras-chave: códon; fitoplâncton; monitoramento ambiental; reservatório oligotrófico; reservatório ultraoligotrófico.



1. Introduction

Reservoirs are usually considered synonymous with lakes, however, magnitude and phasing of the forcing functions or driving variables for lakes and reservoirs may be not identical (Thornton et al., 1990). A strong interaction with the hydrographic basin, the multiple uses and the functioning and operating mechanisms make reservoirs complex systems (Tundisi et al., 1999). Cascading reservoirs were first built in sizeable countries with large rivers to provide electric energy, irrigation, and drinking water. Their usual water abundance tends to decrease along the cascade (Straškraba, 1994). The great majority of reservoirs in Brazil are concentrated in the south and southeast regions (Tundisi, 1983), and several rivers were already organized in cascades. Cascading reservoirs are considered complex systems since the first reservoir may affect downriver until the very last one in the series, a fact amplified by the tributary rivers action (Nogueira et al., 2010). Effects and cumulative impacts could completely change the drainage basin biophysical, economic and social features (Tundisi et al., 1999; Nogueira et al., 2006). Such a configuration endorsed the concept of "continuum cascading reservoirs" that, from the ecological point of view states that reservoirs placed in a longitudinal sequence would have a significant interdependence, despite the river's course interruption would affect the structure and functioning of the aquatic communities (Barbosa et al., 1999; Ferreira et al., 2005).

Composition and abundance of phytoplankton vary spatially and temporally in cascading reservoirs of different rivers (Bonilla, 1997; Padisák et al., 2000; Silva et al., 2005; Saldana-Fabela et al., 2014). In cascading reservoirs, phytoplankton structure may be affected by limnological factors such as nutrient availability and hydrodynamic changes. According to Saldana-Fabela et al. (2014), diatoms occur in places where connectivity is present, whereas there is a clear dominance of Cyanobacteria and chlorophyceans in the non-connected reservoirs related to nutrient enrichment and sewage discharge. In addition, environmental heterogeneity and rain precipitation are likely to impact phytoplankton density and richness, and codons in cascading reservoirs (Moura et al., 2013). Phytoplankton development takes place when the system water retention time is greater if compared to that of lakes, as opposed to its disappearance when water retention time is similar to that of the river (Riera & Morguí, 1990; Roldán, 1992), and its

organization follows a vertical axis established by light attenuation, thermal gradient and algal adaptations (Reynolds, 1997; Wetzel, 2001; Mellard et al., 2011). Exploring such communities will help to understand the aquatic environmental changes, since they are considered fast water quality environmental sensors (Gemelgo et al., 2009) due to their intrinsic characteristics, as for instance their short-term generation time.

In Brazil, ecological research has successfully used phytoplankton as an indicator of changes in the environment quality of cascading reservoirs in the Tietê River Basin (Barbosa et al., 1999; Padisák et al., 2000; Silva et al., 2005; Ferrareze & Nogueira, 2006). Besides changes in species composition, studies showed that the use of codons 'sensu' Reynolds et al. (2002) may be very useful and effective for the evaluation of aquatic environmental changes in cascading reservoirs (Nogueira et al., 2010; Santana et al., 2017). Current assessment of different ecological assemblies in a series of cascading reservoirs emphasizes that the physical and chemical features of water are not the only causes for changes in the communities structure, given that connectivity may have a stronger effect (Santos et al., 2018). In fact, phytoplankton structure may change depending on the limnological and hydrodynamic conditions of cascading reservoirs (e.g. Padisák et al., 2000; Silva et al., 2005). Concerning the three reservoirs in the present study, Marquardt et al. (2018) reported that hydrological connectivity predictor proved to play an utmost role toward explaining the diatom metacommunity dynamics. In this sense, structural changes in phytoplankton was evaluated in three cascading reservoirs, one ultraoligotrophic and two oligotrophic, in two seasons (summer and winter). Changes in phytoplankton biomass, species composition and codons were evaluated along a vertical and a longitudinal profile. Our present main question was whether the taxonomic structure and the codons could be linked to the environmental conditions of each reservoir, or connectivity could have a homogenizing effect on the community.

2. Material and Methods

2.1. Study area

This study was carried out in three interconnected reservoirs of a cascading series, namely Cachoeira do França, Cachoeira da Fumaça and Serraria, located across the Juquiá Guaçu River, Ribeira do Iguape/Southern Litoral Basin, in the state of São Paulo (Figure 1). Cachoeira do França and Cachoeira

da Fumaça are connected to Serraria forming a series of reservoirs across the Juquiá Guaçu River. Ribeira do Iguape/Southern Litoral Basin has a drainage area of 17,068 km² (SÃO PAULO, 2006). Cachoeira do França (23°54'50.81"S, 47°15'31.98"W and 23°56'0.26"S, 47°9'42.99"W) and Cachoeira da Fumaça (23°59'27.79"S, 47°15'59.71"W and 24°0'50.43"S, 47°13'58.85"W) reservoirs border the Jurupará State Park, whereas Serraria (24°06'26.05"S, 47°34'4.14"W and 24°06'55.77"S, 47°31'9.3"W) lies in the Serra do Mar State Park. The three reservoirs are located in secondary Atlantic forest conservation areas. Climate of the region has two very well defined seasons, one warm and rainy (October to March) and the other one cold and dry (April to September) (CBH-RB, 2014). Information on morphometry, trophic state and hydrological characteristics of reservoirs are in Table 1.

2.2. Samplings

Water and phytoplankton samplings were performed during the winter (June and September 2014) and summer (January and February 2014). On the horizontal scale, samples were obtained from four sampling sites in the Cachoeira do França reservoir, and three each in the Cachoeira da Fumaça and Serraria reservoirs. Sampling sites were distributed upstream, central area of reservoir and close to the dam (reservoirs deepest region), thus prioritizing the tributaries entrances. In each sampling site, water column samples were obtained from the subsurface, middle, and bottom strata considering the column mixing and light regime, the surface being the euphotic zone identified by the Secchi disk transparency, middle (interphase), and 1 m above the bottom of reservoir, the aphotic zone.



Figure 1. Study area at the Ribeira do Iguape/Southern Litoral Basin, São Paulo, SP, Brazil. Small maps show sampling sites in each reservoir.

 Table 1. Main limnological characteristics of the connected reservoirs Cachoeira do França, Cachoeira da Fumaça and Serraria.

| Reservoir | Construction (year) | Area (km²) | Volume (10 ⁶ m ³) | Main reservoir use | TSI* (annual mean) | WRT* (days) (annual mean) |
|------------------------|------------------------|---------------|---|-----------------------|-----------------------|------------------------------|
| Cachoeira do França | 1954 | 12.7 | 135.2 | Power generation | Oligotrophic | 76.4 |
| Cachoeira da Fumaça | 1964 | 6.92 | 53.5 | Power generation | Ultraoligotrophic | 42.5 |
| Serraria | 1978 | 2.2 | 37.6 | Power generation | Oligotrophic | 10 |
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*Abbreviations: TSI (Trophic State Index) and WRT (Water Retention Time).

2.3. Climate, hydrological and abiotic variables

Rainfall, air temperature and water flow rate data were obtained from the CBA, Brazilian Aluminum Company. Maximum depth (Z_{max}) was measured with a portable depth device. Water temperature, pH, turbidity and electric conductivity were measured 'in situ' with a multiparameter probe (Horiba U-53). Water transparency was obtained with a Secchi disk and the euphotic zone (Z_{ev}) according to Cole (1983). Mixing zone (Z_{mix}) was identified by the vertical temperature profile. To assess light availability, Z_{eu}/Z_{max} and Z_{eu}/Z_{mix} ratios were calculated. The following variables were also measured: dissolved oxygen (DO) (Golterman et al., 1978), HCO_3 , free CO_2 , nitrite $(NO_2^{-}-N)$ and nitrate (NO₃⁻-N) (Mackereth et al., 1978), ammonium (NH_4^+-N) (Solorzano, 1969), soluble reactive phosphorus (PO4-3-P) (Strickland & Parsons, 1960), total phosphorus (TP) and total nitrogen (TN) (Valderrama, 1981), and soluble reactive silica (SRS) (Golterman et al., 1978). Water samples for identification of dissolved nutrients were filtered under low pressure using glass-fiber filters (GF/F Whatman). Chlorophyll-a corrected for phaeophytin was measured within at most one week from the sampling day, with 90% ethanol as the organic solvent (Sartory & Grobbelaar, 1984). Trophic State Index (TSI) was calculated based on the subsurface chlorophyll-a concentration and total phosphorus value (Lamparelli, 2004).

2.4. Biological variables

Phytoplankton samples were collected with a van Dorn bottle and fixed with 1% lugol acetic solution for the quantitative analyses. Cyanobacteria and algae were quantified using an inverted Zeiss Axio Observer D1 microscope at 400x, following Utermöhl (1958). The counting limit was determined by the species rarefaction curve. Algal biovolume was estimated by multiplying each species' density by the mean volume of its representative individuals, and whenever possible measuring the cell or coenobium dimensions of at least 10 specimens of each species according to its geometric formulae following Hillebrand et al. (1999) and Napiórkowska-Krzebietke & Kobos (2016). Biovolume was expressed as biomass (mg L-1). Species were classified into codons 'sensu' Reynolds (Reynolds et al., 2002; Padisák et al., 2009). Dominant species were selected upon 50% of the relative abundance in each sample.

2.5. Data treatment

Permutational multivariate analysis of variance (two-way PERMANOVA; $\alpha = 0.05$) was used to analyze the influence of seasonality (Past 4.02, Hammer et al. 2001). Redundancy Analysis (RDA) was used to evaluate the relationship between environmental variables, phytoplankton descriptive species ($\geq 5\%$ of total algal biomass) and codons. Environmental variables were chosen based on principal component analysis (PCA). Logarithm-transformed biological and abiotic data were used, except for pH. A randomization test was carried out to determine interpretable axes (p < 0.05). RDA and PCA analysis were run using PC-ORD 6.0 program (McCune & Mefford, 2011).

3. Results

3.1. Climate, abiotic variables and TSI

During the summer, precipitation ranged from 150 mm (Cachoeira do França) to 521.5 mm (Serraria), the highest values registered in February at all reservoirs' sites. Mean air temperature for the period ranged from 20-38°C (Serraria) to 16-46°C (Cachoeira do França). During the winter, precipitation ranged from 49.5 mm to 144.25 mm (Cachoeira da Fumaça). Mean air temperature values ranged from 6-36°C (Cachoeira do França) to 8-27°C (Serraria).

Limnological data are shown in Table 2. During the summer, Cachoeira do França reservoir had neutral to alkaline pH, whereas Cachoeira da Fumaça and Serraria reservoirs had acidic to slightly alkaline pH. PO₄-3-P concentrations dropped usually below the method detection limit in most sampling sites. NH4+-N, TN, TP, free CO₂ and NO₃⁻-N concentrations, as well as electric conductivity vertical distribution pattern in the water column were more homogeneously distributed at the lower depths of reservoirs, especially during the summer, unlike the dissolved oxygen whose highest concentrations were detected near the reservoirs' subsurface. Secchi disk depth was greater during the winter than in the summer, especially at Serraria reservoir that also showed the lowest turbidity values. In the three reservoirs, the highest depth of the mixing (Z_{mix}) and euphotic (Z_{eu}) zones were found during the winter. $Z_{eu} : Z_{mix} > 1$ was detected during the summer and winter in the studied reservoirs.

Spatial and temporal variation...

Table 2. Mean values of limnological variables and the standard deviation, in parenthesis, in Cachoeira do França, Cachoeira da Fumaça and Serraria reservoirs during summer and winter. Modified from Marquardt et al. (2018).

| Variable | Cachoeira do França | | Cachoeira da Fumaça | | Serraria | | |
|--|---------------------|--------------|---------------------|--------------|---------------|---------------|--|
| | Summer | Winter | Summer | Winter | Summer | Winter | |
| Chlorophyll-a (µg L-1) | 1.8 (±1.1) | 10.4 (±14.7) | 1.5 (±1.4) | 1.5 (±1.1) | 2.1 (±2.6) | 2.1 (±2.4) | |
| Conductivity (µS cm ⁻¹) | 27.6 (±10.1) | 26.0 (±1.4) | 26.7 (±2) | 27.2 (±0.7) | 29.6 (±11.9) | 27.9 (±1.3) | |
| DO (mg L ⁻¹) | 5.4 (±1.9) | 6.7 (±1.4) | 4.9 (±2.3) | 7.0 (±1.1) | 4.8 (±2.4) | 7.3 (±1.7) | |
| Free CO ₂ (mg L ⁻¹) | 0.5 (±0.9) | 10.1 (±13) | 26.8 (±42.2) | 30.0 (±30.1) | 31.5 (±37.9) | 27.0 (±44.7) | |
| HCO ₃ (mg L ⁻¹) | 11.4 (±2.2) | 10.5 (±0.6) | 10.7 (±2.2) | 10.6 (±0.3) | 11.7 (±3.7) | 14.1 (±1.4) | |
| NH₄+-N (μg L-1) | 33.7 (±24.0) | 27.2 (±14.8) | 73.7 (±57.9) | 23.7 (±16) | 22.3 (±21.4) | 15.9 (±17.8) | |
| NO ₃ ⁻ -N (µg L ⁻¹) | 20.2 (±20.2) | 31.8 (±32.7) | 59.9 (±50.9) | 85.2 (±10.9) | 109.1 (±92.7) | 138.1 (±50.4) | |
| рН | 7.6 (±0.5) | 6.5 (±0.9) | 6.0 (±0.6) | 6.0 (±0.4) | 6.0 (±0.8) | 6.3 (±0.9) | |
| PO ₄ - ⁻³ -P (µg L ⁻¹) | 5.3 (±1.0) | 4.1 (±0.3) | <4.0 | <4.0 | 5.2 (±3.7) | <4.0 | |
| Turbidity (NTU) | 15.5 (±13.4) | 15.2 (±27.2) | 10.7 (±9.3) | 4.1 (±2.5) | 4.8 (±8.5) | 2.5 (±2.9) | |
| Secchi Disk (m) | 1.7 (±0.1) | 1.8 (±0.2) | 1.7 (±0.2) | 3.4 (±0.7) | 2.9 (±0.2) | 5.0 (±0.3) | |
| Silicate (mg L ⁻¹) | 1.9 (±0.6) | 3.5 (±0.3) | 1.5 (±0.3) | 3.2 (±0.1) | 2.0 (±0.9) | 4.8 (±0.5) | |
| Total Phosphorus (µg L ⁻¹) | 14.0 (±6.4) | 4.8 (±1.1) | 6.8 (±1.5) | 4.6 (±1.1) | 5.6 (±1.7) | 10.1 (±1.8) | |
| Total Nitrogen (µg L-1) | 307.2 (±176) | 258 (±65.1) | 407.1(±138.6) | 136 (±23) | 186.7(±192.3) | 243.1 (±47.5) | |
| Temperature (°C) | 25.6 (±3.0) | 16.9 (±1.2) | 25.2 (±3.6) | 18.0 (±1.4) | 24.7 (±5.1) | 19.2 (±1.5) | |
| Z _{eu} :Z _{max} | 0.34 (±0.09) | 0.41 (±0.1) | 0.20 (±0.06) | 0.39 (±0.05) | 0.26 (±0.4) | 0.56 (±0.1) | |
| Z _{eu} :Z _{mix} | 1.4 (±0.08) | 1.3 (±0.7) | 1.8 (±0.6) | 1.7 (±2.3) | 4.8 (±2.1) | 9.1 (±7.5) | |
| Z _{eu} | 4.6 (±0.1) | 4.9 (±0.7) | 4.4 (±0.7) | 9.0 (±2.1) | 7.8 (±0.6) | 13.5 (±0.8) | |
| Z _{max} | 13.6 (±2.1) | 13.7 (±2.0) | 27.0 (±6.1) | 29.3 (±6.5) | 30.0 (±6.6) | 26.9 (±5.8) | |
| Z _{mix} | 3.2 (±0.2) | 5.2 (±3.9) | 2.8 (±1.1) | 18.0 (±0.7) | 1.8 (±0.7) | 10.0 (±16) | |

3.2. Phytoplankton

Comparatively, the largest phytoplankton biomass was found in the upstream reservoir Cachoeira do França (Figure 2). The highest total phytoplankton biomass was found during the winter in the three studied reservoirs. During the summer, all three reservoirs showed greater biomass at their subsurface and middle layers, except for Cachoeira do França that site 2 bottom layer presented the greatest value.

Based on the descriptive species, no significant differences were found in the phytoplankton structure among reservoirs, but among seasons (two-way PERMANOVA: F = 5.06, p = 0.0002). The most constant species with higher relative biomass in all three reservoirs and all three layers of each reservoir were Discostella stelligera (Cleve & Grunow) Houk & Klee and Aphanocapsa delicatissima W. West & G.S. West with lower relative biomass (Figure 3). Ceratium furcoides (Levander) Langhans was more present during the winter in the entire water column, and Cosmarium tinctum Ralfs was exclusively found at the bottom layer of Cachoeira do França reservoir. Considering phytoplankton structure of each reservoir, based on biomass significant difference was found only between seasons (two-way PERMANOVA: França,







Figure 2. Phytoplankton total biomass (mg L⁻¹) in three strata (S subsurface, M middle, B bottom layers) and sampling sites (1, 2, 3, 4) during the winter and summer at the three cascading reservoirs.



Figure 3. Relative biomass of phytoplankton dominant species in the three strata (S subsurface, M middle, B bottom layers) and sampling sites (1, 2, 3, 4) during the winter and summer at the three cascading reservoirs.

F = 3.50, *p* = 0.0011; Fumaça, F = 6.62, *p* = 0.0001; Serraria: F = 2.25, *p* = 0.031).

Codon **B** was practically found throughout the three reservoirs and at all three strata in both seasons, but presented lower relative biomass during the winter and towards the sampling station FR4 of Cachoeira do França reservoir, which is the closest site to the entry of the Juquiá Guaçu river (Figure 4). On the contrary, codon L_M presented the higher relative abundance at this site and both seasons. Codon L_M was more present during the winter at the subsurface and medium layers in the Serraria reservoir, basically due to *Ceratium furcoides*. It was observed that during



 $\blacksquare A \blacksquare B \blacksquare E \blacksquare F \blacksquare K \blacksquare LM \blacksquare LO \blacksquare NA \blacksquare X1 \blacksquare X2 \blacksquare Y \Box Others$

Figure 4. Phytoplankton codons relative biomass (%) in the three strata (S subsurface, M middle, B bottom layers) and sampling sites (S1, S2, S3, S4) during the winter and summer at the three cascading reservoirs.

the stratification period (summer), the bottom layer showed dominance of one codon, whereas at both the subsurface and intermediate layers several codons dominated. On the other hand, during mixing period (winter) one codon tended to dominate the whole water column, mainly *Ceratium furcoides*.

RDA was performed using 37 phytoplankton species biomass and five environment variables (Figure 5, Table 3). Monte Carlo permutation test was significant for both axes 1 and 2 (p = 0.001). Axes 1 ($\lambda = 4.71$) and 2 ($\lambda = 2.31$) eigenvalues explained 18.9% of the total variability of data in both axes. Pearson Correlation Coefficient (PCC) species-environment for axes 1 (0.850) and 2 (0.825) indicated a strong relationship



Figure 5. Redundancy analysis of phytoplankton species biomass (37 species) and environment variables (5 variables) in the three studied reservoirs. Abbreviations: capital letters indicate reservoir (FR Cachoeira do França, FU Cachoeira da Fumaça, SE Serraria), number indicates sampling site (1, 2, 3, 4), lowercase letter indicates sampling depth (s subsurface, m intermediate layer, b 1 m above bottom), and last capital letter indicates season of the year (S Summer, W Winter). Vectors: NO3 Nitrate, Secchi Secchi Disk, Temp Temperature, TP total phosphorus, TN Total Nitrogen.

| Species | С | Code | Axis 1 | Axis 2 |
|--|----------------|-------|--------|--------|
| Aulacoseira tenella (Nygaard) Simonsen | Α | Aten | 0.270 | -0.235 |
| Urosolenia eriensis (H.L.Smith) Round & R.M.Crawford | Α | Ueri | 0.562 | 0.034 |
| Discostella stelligera (Cleve & Grunow) Houk & Klee | в | Dste | 0.271 | 0.414 |
| Fragilaria billingsii Wengrat, C.E.Wetzel & Morales | в | Fbil | 0.608 | 0.068 |
| Bicosoeca petiolata (F.Stein) E.G.Pringsheim | Е | Bico | -0.141 | -0.141 |
| Mallomonas fresenii Kent | Е | Mfre | 0.065 | -0.057 |
| Botryococcus braunii Kützing | F | Bbra | -0.384 | -0.362 |
| Keratococcus obtusus (Koršikov) Hindák | F | Kobt | -0.180 | 0.487 |
| <i>Oocystis lacustris</i> Chodat | F | Olac | 0.002 | 0.240 |
| Radiococcus planktonicus J.W.G.Lund | F | Rpla | -0.114 | 0.659 |
| Dolichospermum planctonicum (Brunnthaller) Wacklin et al. | H1 | Dpla | 0.375 | -0.017 |
| Hariotina reticulata P.A.Dangeard | J | Hret | 0.035 | 0.163 |
| Tetraedriella jovetti (Bourrelly) Bourrelly | J | Tjov | 0.532 | 0.110 |
| Aphanocapsa delicatissima W.West & G.S.West | К | Egle | -0.277 | 0.320 |
| Epigloeosphaera glebulenta (Zalessky) Komárková-Legnerová | ĸ | Adel | -0.282 | 0.435 |
| Ceratium furcoides (Levander) Langhans | L _M | Cfur | 0.242 | -0.054 |
| Microcystis aeruginosa (Kützing) Kützing | L _M | Maer | -0.080 | 0.533 |
| Gymnodinium fuscum (Ehrenberg) Stein | Lo | Pinc | 0.389 | 0.040 |
| Parvodinium inconspicuum Lemmermann | Lo | Gfus | 0.152 | -0.074 |
| Cosmarium majae Strøm | N _A | Cmaj | 0.454 | 0.130 |
| Cosmarium tinctum Ralfs | N _A | Ctin | -0.140 | 0.030 |
| Staurodesmus ralfsii (West) Tomaszewicz | N _A | Staur | 0.059 | -0.057 |
| Eunotia waimiriorum C.E.Wetzel | MP | Ewai | 0.708 | 0.112 |
| Closterium acutum Brébisson var variabile (Lemmermann) Willi Krieger | Р | Cacu | 0.751 | -0.143 |
| Staurastrum tetracerum Ralfs ex Ralfs | Р | Stet | 0.479 | 0.117 |
| Consider from 2 Born alda Carder & latter for an arise successivity | | | | |

C: codon 'sensu' Reynolds, Code: 4 letters for species recognition.

Table 3. Continued...

| Species | С | Code | Axis 1 | Axis 2 |
|--|----------------|-------|--------|--------|
| Planktothrix isothrix (Skuja) Komárek & Komárková | S1 | Piso | -0.041 | 0.185 |
| Raphidiopsis raciborskii (Woloszýnska) Aguilera et al. | S _N | Crac | 0.751 | 0.117 |
| Trachelomonas volvocina (Ehrenberg) Ehrenberg | W2 | Tvolv | 0.096 | 0.374 |
| Trachelomonas volvocinopsis Svirenko | W2 | Tvolp | -0.023 | -0.082 |
| Monoraphidium minutum (Nägeli) Komárková-Legnerová | X1 | Mmin | 0.437 | 0.184 |
| Chlamydomonas debaryana Goroschankin | X2 | Cder | -0.119 | -0.257 |
| Cryptomonas brasiliensis Castro et al. | X2 | Cbra | -0.592 | 0.272 |
| Hemiselmis simplex Butcher | X2 | Hsim | -0.223 | -0.218 |
| Pedinomonas minutissima Skuja | X2 | Pedi | -0.163 | 0.028 |
| Rhodomonas lacustris Pascher & Ruttner | X2 | Rlac | -0.229 | 0.228 |
| Cryptomonas erosa Ehrenberg | Y | Cero | -0.227 | 0.146 |
| Cryptomonas marssonii Skuja | Y | Cmar | -0.034 | 0.092 |

C: codon 'sensu' Reynolds, Code: 4 letters for species recognition.



Figure 6. RDA codons ordination (*'sensu'* Reynolds) and 4 abiotic variables at Cachoeira do França (FR), Cachoeira da Fumaça (FU) and Serraria (SE) reservoirs. Abbreviations: capital letters indicate reservoir (FR Cachoeira do França, FU Cachoeira da Fumaça, SE Serraria), number indicates sampling site (1, 2, 3, 4), lowercase letter indicates sampling depth (s subsurface, m intermediate layer, b 1 m above bottom) and last capital letter the climatic season (S Summer, W Winter). Vectors: Secchi Disk, Temp Temperature, TP Total Phosphorus, TN Total Nitrogen.

between species distribution and environment variables. Most Cachoeira do França and Cachoeira da Fumaça scores during the summer and Serraria in both seasons were located on the negative side of axis 1. These sample units were correlated with the highest temperature (r = -0.7) and TP (r = -0.6) values. The opposite was observed during the winter at Cachoeira do França and Cachoeira da Fumaça reservoirs. Such ordination showed the temporal change in the phytoplankton taxonomic structure at both Cachoeira do França and Cachoeira da Fumaça reservoirs, but seasonality had a lower weight at the Serraria reservoir. Several species were associated with the winter environmental conditions at Cachoeira do França and Cachoeira da Fumaça reservoirs, mainly *Eunotia waimiriorum* Wetzel, *Closterium acutum* Brébisson var. *variabile* (Lemmermann) Krieger, and *Raphidiopsis raciborskii* (Woloszýnska) Aguilera et al. (= *Cylindrospermopsis raciborskii* (Woloszýnska) Seenayya & Subba Raju) (r > 0.7).

RDA was performed using biomass of 18 codons and four environmental variables (Figure 6). Monte Carlo permutation test was significant for both axes 1 and 2 (p = 0.001). Eigenvalues of axes 1 ($\lambda = 3.08$) and 2 ($\lambda = 1.23$) explained 23.9% of both axes total data set variability. Temperature and TP ($r \ge 0.7$) were the highest weight variables in the ordination. Most Cachoeira do França and Cachoeira da Fumaça reservoir's summer scores and those for both seasons at Serraria reservoir were ordered on the negative side of axis 1. However, Cachoeira do França and Cachoeira da Fumaça reservoirs were ordered in the winter on the positive side of axis 1 ($r \ge 0.66$). Codons **A**, **P**, **S**_N and **MP** were associated with lower temperatures and TP in winter in both Cachoeira do França and Cachoeira da Fumaça reservoirs ($r \ge 0.66$).

4. Discussion

Our findings showed little change in the phytoplankton structure among cascading reservoirs, the highest changes being detected among climatic seasons. The most abundant descriptive species Discostella stelligera and Ceratium furcoides, and codons **B** and L_{M} were predominant in all reservoirs. In addition, phytoplankton total biomass was not cumulative along the cascading reservoirs. In relation to the temporal scale, climatic periods were typical for the region with a rainy summer and high temperatures, the opposite occurring during the winter. According to the Trophic State Index, sampling sites ranged from ultraoligotrophic to oligotrophic. In a previous study, Marquardt et al. (2018) showed that hydrological connectivity played an utmost role in the dispersion processes of the community structure, playing an important part in explaining the variation of the diatom metacommunities. Therefore, our results suggest that connectivity was the determinant factor for phytoplankton structure during the winter and summer, consequently reinforcing the system spatial homogeneity.

Descriptive species did not change drastically with cascading both in the vertical and the longitudinal profiles, as well as among reservoirs. Descriptive species changed, however, among seasons. Thus, seasonality influenced the phytoplankton structure in the ultraoligotrophic and the two oligotrophic reservoirs. Influence of seasonality on phytoplankton structure was clearly evident in the first two cascading reservoirs (Cachoeira do França and Cachoeira da Fumaça), but it was not very noticeable in the third reservoir (Serraria). The most evident feature of Serraria reservoir was that during the summer, the subsurface layer behaved differently than the rest of the water column, when it was more affected by the high transparency, codon F being more associated to

this condition. Consequently, although some studies have shown that changes in downstream reservoirs may be predicted from characteristics of changes upstream (Armengol, 1977; Straškraba, 1994), our findings show that other factors may also affect phytoplankton structure. For example, in cascading reservoir systems phytoplankton structure was noticed to be highly affected by hydrodynamic changes (Padisák et al., 2000; Silva et al., 2005).

In the vertical profile, the relative biomass of Ceratium furcoides was usually greater at the subsurface and intermediate layers during the winter, and its greatest relative biomass was detected at the Cachoeira do França reservoir. Ceratium furcoides was already recorded for several reservoirs in Brazil (Santos-Wisniewski et al., 2007; Matsumura-Tundisi et al., 2010; Crossetti et al., 2019) as well as in cascading lotic systems of the Paranapanema River Basin (Ferrareze & Nogueira, 2006). Currently, Ceratium furcoides is becoming a problem for the water quality of reservoirs in South America, and high temperature seems to promote its invasion (Meichtry-de-Zaburlín et al., 2016). Ceratium species was found throughout the year even at low densities in tropical reservoirs (Silva et al., 2012), though other studies reported winter dominance of Ceratium hirundinella (Müller) Dujardin in a temperate reservoir (Pérez-Martínez & Sánchez-Castillo, 2002). In a eutrophic tropical reservoir, establishment of Ceratium furcoides was associated with disturbance events, which changed the water column stability and transparency (Crossetti et al., 2019). Present study showed that cascading reservoir oligotrophic conditions favor dominance of Ceratium furcoides, especially during the winter, which is a warning sign. Ceratium furcoides is an invasive species in South American freshwater ecosystems, and its bloom can be harmful to several organisms due to oxygen depletion, besides causing serious problems in water treatment (Matsumura-Tundisi et al., 2010; Meichtry-de-Zaburlín et al., 2016).

Another species with high biomass in the present reservoirs was *Discostella stelligera* that showed greater total biomass at the subsurface and intermediate layers during the winter, probably because reservoirs were not stratified on the sampling day. In fact, depth of Cachoeira do França during the winter was lower than those of Cachoeira da Fumaça and Serraria reservoirs. *Discostella stelligera*, a common species in freshwater plankton communities (Spaulding & Edlund, 2009), like many other diatoms depends on the turbulence to maintain its buoyancy in the upper layers of the water column. Besides being commonly present in tropical reservoirs, *Discostella stelligera* is also found in surface sediments and plankton (Zorzal-Almeida et al., 2017).

Considering the codons 'sensu' Reynolds, codons MP, P and S_{N} altogether reflected the conditions prevalent at the sampling sites of Cachoeira do França and Fumaça reservoirs during the winter due to mixing, with low TN, TP, temperature and transparency values. Codon MP, mainly Eunotia waimiriorum is a colonial planktonic diatom associated with shallow turbid waters, a typical species of the oligotrophic-pristine-high-sedim ent of Branco River in the Brazilian Amazons (Wetzel et al., 2010). In the current study, presence of that species matched with low values of transparency during the winter present in all sampling sites at Cachoeira do França reservoir, probably due to the turbulence induced by the entrance of tributary rivers, since this reservoir is shallower than the other two.

Codon S_N represented by nitrogen fixing Cyanobacteria is sensitive to flushing and is typical from warm mixed environments. According to Soares et al. (2013), Cylindrospermopsis raciborskii (= Raphidiopsis raciborskii) is a species related to systems with annual mixing. In the present study, one of the characteristics exhibited in the winter by Cachoeira do França and Cachoeira da Fumaça reservoirs was the thermal mixing, which implies that mixing is an important feature irrespective of the season. This process qualified typical co-dominance pointed out by Soares et al. (2013) of colonial Chroococcales with filamentous N2fixing Nostocales, codons H1, S_N and L_M (partially Microcystis aeruginosa (Kützing) Kützing) during the winter season in these reservoirs.

Codon **P**, likewise, is typical of continuous or semi-continuous mixed layer of 2-3 m in thickness in higher trophic state reservoirs, which is another feature of Cachoeira do França in the winter, being eutrophic in the sub-surface layer, mainly at site 4. This sampling site is the corridor of the Juquiá Guaçu River. Although annual monitoring by Brazilian water agencies report the Juquiá Guaçu River as having good water quality, it seems that there are obscure sources of allochtonous material that could be the cause of the increased trophy in this sampling site, thus increasing P and N and development of several species, in the same way as for *Ceratium furcoides* (L_M).

5. Conclusions

While **E**, **F**, **K**, **S1**, **X2** and **Y** were considered the summer codons, the winter codons were made up of **A**, **B**, **H1**, **J**, **L**_o, **MP**, **N**_A, **P** and **W2**. It was evident that seasonality played a major influence in the codons' composition in two reservoirs, Cachoeira do França and Cachoeira da Fumaça, and that Serraria reservoir could be influenced by other factors like hydrodynamic changes. We therefore conclude that seasonality was the determinant factor of the phytoplankton structure, and that connectivity acted as a homogenizing factor, mainly due to the continuous contribution of *Ceratium furcoides* (codon L_M) and *Discostella stelligera* (codon **B**) at all reservoirs studied.

Acknowledgements

We acknowledge CNPq, Conselho Nacional de Desenvolvimento Científico e Tecnológico for a doctoral fellowship granted to AMLR (Process nº 155376/2014-4). This study was carried out within the framework of the AcquaSed project (Baseline diagnosis and reconstruction of anthropogenic impacts in the Guarapiranga Reservoir, focusing on sustainability in water supply and water quality management in reservoirs of the Upper Tietê and surrounding basins) financially supported by FAPESP, Fundação de Amparo à Pesquisa do Estado de São Paulo (Project nº 2009/53898-9). We also thank all students and technicians involved in the field and laboratory work at the Instituto de Botânica's Ecology Department. We deeply appreciate the valuable assistance of the Votorantim Energia staff for the logistic support during the fieldwork. We are finally grateful to Prof. William de Queiróz (Geoprocessing Laboratory, Universidade de Guarulhos) for the study area illustration.

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Received: 08 November 2018 Accepted: 30 April 2020

Associate Editors: Antonio Fernando Monteiro Camargo