



Water quality and spatial and seasonal dynamics in the largest water supply reservoir in Brazil and implications for diatom assemblages

Qualidade da água e dinâmica espacial e sazonal no maior reservatório de fornecimento de água do Brasil e implicações para comunidades de diatomáceas

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Abstract: Aim: in this paper we investigated how spatial factors and seasonal dynamics influenced the diatom community in a tropical deep environment of low productivity waters in Brazil. **Methods:** we used physical and chemical characteristics of the water and planktonic diatoms from 9 sampling stations during dry (austral winter) and wet (austral summer) seasons (N = 18) as the outline to identify water quality, spatial and seasonal patterns. To evaluate spatially and temporally integrated events from the recent past (approximately the last 5 years before sampling), and the species from diverse habitats of the system, we used diatoms from the surface sediment (top 2 cm, N = 9). Since we used the top 2 cm of surface sediment containing the dead diatoms that were deposited over recent past of the reservoir, seasonal sampling of the sediment was not needed. **Results:** during the dry season heavily silicified long colonial planktonic diatom species associated mainly with higher mixing depth, pH, and transparency dominated the plankton, whereas in the wet season the reservoir became stratified, favoring planktonic solitary diatoms with high surface volume ratios. For the sediment, a general pattern emerged where planktonic species dominated in the deep sections of the reservoir, and the abundance of benthic species in shallow areas near the tributaries increased. **Conclusions:** the diatom assemblages was mainly influenced by seasonal variations and mixing regime. Surface sediment samples provided longer-term information, and revealed habitat differentiation shaping diatom assemblages. Overall, the small centric planktonic *Aulacoseira tenella* (Nygaard) Simonsen stood out as the most abundant species in the entire reservoir in both, the plankton and the sediment, indicating that size and shape serve as adaptive strategies for buoyancy and nutrient uptake stand as a competitive advantage in deep low productivity environments.

Keywords: Cantareira System; oligotrophic diatom species; phytoplankton; surface sediment; tropical deep reservoir.

Resumo: Objetivos: Neste trabalho investigamos como fatores espaciais e dinâmica sazonal influenciaram a comunidade de diatomáceas em um reservatório tropical, profundo e de baixa produtividade no Brasil. **Métodos:** Nós usamos as características físicas e químicas da água e as diatomáceas presentes no plâncton em 9 estações de amostragem durante os períodos seco (inverno austral) e chuvoso (verão austral) (N = 18) como base para avaliação da qualidade da água, e



das características espaciais e dos padrões sazonais do reservatório. Para avaliar espacialmente e temporalmente os eventos integrados do passado recente (aproximadamente 5 anos antes da data de amostragem), e as espécies provenientes dos diversos habitats do ecossistema, foram analisadas diatomáceas presentes nos sedimentos superficiais (primeiros 2 cm, N = 9). A amostragem sazonal do sedimento não foi necessária, já que os 2 cm de sedimento superficial utilizados contêm as carapaças de diatomáceas depositadas no passado recente do reservatório. **Resultados:** durante a estação seca, diatomáceas longas, coloniais e altamente silicificadas, associadas com aumento da profundidade de mistura, pH e transparência da água, dominaram o ambiente planctônico, enquanto na estação úmida, o reservatório se tornou estratificado, favorecendo diatomáceas planctônicas solitárias com alta razão superfície volume. No sedimento superficial, um padrão geral foi observado, onde espécies planctônicas foram dominantes nas amostras de regiões mais profundas da represa, enquanto a abundância de espécies bentônicas aumentou nas estações mais rasas, próximas aos tributários. **Conclusões:** A assembleia de diatomáceas foi influenciada principalmente pela sazonalidade e regime de mistura. O sedimento superficial forneceu informação de longo prazo, e revelou que a comunidade de diatomáceas é moldada de acordo com a diferenciação de habitats. No geral, a espécie planctônica, cêntrica e pequena *Aulacoseira tenella* (Nygaard) Simonsen destacou-se como a mais abundante do reservatório tanto no plâncton como no sedimento, indicando que tamanho e forma provavelmente servem como estratégias adaptativas favorecendo flutuabilidade e absorção de nutrientes, e representam vantagem competitiva em ambientes profundos de baixa produtividade.

Palavras-chave: Sistema Cantareira; espécies de diatomáceas oligotróficas; fitoplâncton; sedimento de superfície; reservatório tropical profundo.

1. Introduction

The understanding of structure and function of biological communities permit the assessment of an ecosystem's status (Tilman et al., 1997), and especially for diatoms, it is an important tool for environmental monitoring and sustainable exploitation of natural resources (Ndiritu et al., 2003). The diatom community is widely associated with water quality (Liang et al., 2020; Pandey et al., 2018; Poulicková et al., 2004), pH variations (Razumovskii and Razumovskii, 2019; Sienkiewicz and Gąsiorowski, 2019; Dixit et al., 1992), and trophic status (Costa-Böddeker et al., 2012; Besse-Lototskaya et al., 2011; Belling et al., 2006; Bennion, 1995; Fritz et al., 1993). However, other factors may also be important to understand the organization of these communities. Some species of this group are favored by physical factors such as turbulence (Zalat and Vildary, 2007), light availability (Zalat & Vildary, 2005), habitat availability (Telford et al., 2006), and water column mixing regime (Tolotti et al., 2007; Reynolds, 1997; Bailey-Watts, 1986). In deep oligotrophic systems, for example, one of the most important variables influencing diatom communities is the extent and duration of mixing (Salmaso et al., 2003; Vincent, 1983).

Predictions from modeling diatom species distributions suggest that climate related factors are as important as water chemistry and may be stronger drivers determining the distribution of microorganisms (Pajunen et al., 2016; Rühland et al., 2015; Winder et al., 2009). Diatoms

are heavy unicellular organisms characterized by silicon oxide cell walls, abundant in nearly every aquatic habitat (Round et al., 1990). Due to their high sinking rates (Reynolds, 2006) and typically high nutrient requirements in deep water bodies (Litchman et al., 2007), diatoms are adversely affected by changes in the mixing regime. Some diatoms benefit from turbulent waters to remain in a well mixed nutrient-rich euphotic zone (Znachor et al., 2015; Becker et al., 2009; Zalat and Vildary, 2005; Huisman et al., 2004; Huisman & Sommeijer, 2002). Their great variety in size, morphology and life forms allows some species to overcome the complications imposed by deep stratified waters, meaning some characteristics may serve as adaptive strategies facilitating survival in a nutrient-depleted and/or stable surface layer (Hofmann et al., 2020; Lavoie & Raven, 2020; Reynolds, 2006).

Wind-driven mixing can only occur when almost all thermal stratification of the water column has broken down (Wetzel, 2001). The temperature difference of a vertical profile in a stratified tropical lake may be as little as 2°C, but the layering is persistent until dry season cooling lowers temperatures in the surface waters (Kalf, 2002; Lewis, 1996). Thus, during the dry season many tropical lakes will experience a brief period of overturn that re-suspends nutrients (Becker et al., 2009; Lewis, 1996). Unlike high latitude lakes, the growing season does not slacken at this time (Lewis Junior, 1987), providing the opportunity for

different wet season and dry season adaptations to shape communities.

Ecologically, planktonic diatoms exist in an adaptive balance to light attenuation with depth, sinking velocities, and nutrient-rich zones of the water column (Borics et al., 2016). In tropical systems during the wet season light penetration may be relatively high, and nutrients may be scarce but concentrated near the base of the epilimnion (Wetzel, 2001). Adaptations to counter sinking are critically important. Contrastingly, in the dry season mixing promotes nutrient dispersal and diatom re-suspension from the epilimnion (Cao et al., 2018; Reynolds, 2006).

For the most part, studies that have investigated the variability of diatom assemblages in tropical lakes have focused on a single sampling point. Studies that conducted spatial analyses using multiple locations found that inflowing rivers can have a profound effect on the system (Zorzal-Almeida et al., 2018; Talling, 1986). Inlets provide nutrient rich waters, often with different flow velocities during the course of a year, and the adaptations required to exist in these settings can be quite different to those in the slack water where the inflow exerts no impact in the flow velocity (Kennedy & Walker, 1990). Studies of diatom responses to environmental factors in deep tropical water bodies, where stratification is less stable and the mixing season is shorter, are even more scarce although important, especially given the increasing threat from climate change (IPCC, 2015), leading to a less predictable seasonal pattern (Vargas, 2019) and the increase in nutrient input and pollution by human land-use (Green et al., 2015; WWAP, 2009; Dudgeon et al., 2006).

The present study was conducted on Jaguari-Jacaré, a deep reservoir that during the period of study was classified as oligotrophic to ultra-oligotrophic, although its two major supplying rivers that are considered eutrophic and hypereutrophic (CETESB, 2019). We used water chemistry and diatoms from the plankton as the outline to identify spatial and seasonal patterns and water quality, and diatoms from the surface sediment to evaluate spatially and temporally integrated events from the recent past (approximately the last 5 years before sampling), and the species from diverse habitats of the system (Stoermer & Smol, 2010; Bennion, 1995). Instant information of the conditions of an aquatic system at the moment the measurement is done can be achieved by using physical and chemical analysis, whilst the evaluation of biological organisms capture long-term information of

the ecological status of that system. In aquatic sediments, the information provided is of greater prolonged effect, since this compartment constitutes a biogeochemical archive of information, through the deposition of layers that are accumulated in a temporal manner (Stoermer and Smol, 2010).

The goal of this study was to investigate how the reservoir's spatial factors and seasonal dynamics of the water influenced the diatom community in this large oligotrophic water supply reservoir in Brazil. We hypothesized that the species composition and structure of the diatoms present in the sediment would change in response to the differences in flow regime caused by the reservoir's inlets, and that the planktonic diatoms would change in response to the variations in mixing regime caused by seasonality.

2. Material and Methods

2.1. Study area

The Cantareira System is one of the largest public water supply systems in the world. It produces 30 m³/s of water, approximately half of the water consumed by the 20 million inhabitants of the MRSP (Metropolitan Region of São Paulo) (Whately & Cunha, 2007). Jaguari-Jacaré Reservoir, first of the Cantareira System series, is the largest and most important reservoir in this system, contributing over 60% (22 m³/s) of the total water produced by the entire system (Carli et al., 2020). Located in São Paulo State, southeast Brazil, between the coordinates 22°53'20"S and 46°24'49"W (Figure 1), the Jaguari-Jacaré Reservoir comprises two reservoirs, the Jaguari and the Jacaré, connected through a canal with width of 25m and length of 130m, forming one water body. Altogether the reservoir has a drainage area of 1.252 km², volume of 808 hm³ (Sperling, 1999), maximum depth of 50 m (ANA, 2015), and water residence time of 368.5 days (Pompêo et al., 2017). The climate in the region is characterized as tropical, with dry and wet seasons, the average temperature for the hottest month is above 22 °C and for the coldest month is below 18 °C, while average annual rainfall is c. 1400 mm (Miranda et al., 2009).

Regarding its flow regime, the Jaguari-Jacaré Reservoir exhibits a peculiar situation, since it is influenced by two different rivers and dams. High flow velocity, abundant suspended particulate matter and relatively high phosphorus concentrations characterize the riverine zones, where the rivers Jaguari and Jacaré supply the reservoir. The sampling sites 1 and 9 are located in these riverine zones (Figure 1). Within the main

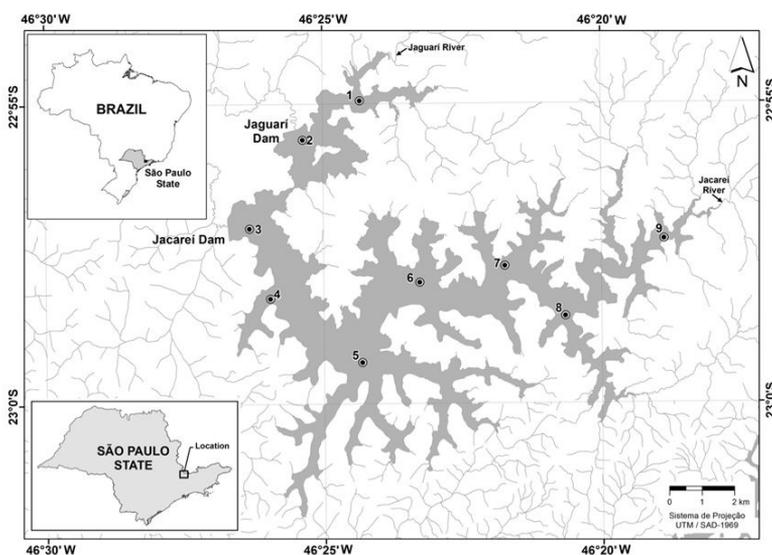


Figure 1. Map showing the location of the state of São Paulo in Brazil with location of Jaguarí-Jacaré Reservoir. Numbers represent sampling sites locations. The sampling sites 1 and 9 receive input from the Jaguarí and Jacaré Rivers and are considered as riverine zones.

body of the reservoir these flows are diminished and the lacustrine zone, characterized by the gradual decrease of suspension particles and nutrient availability, form closer to the dams. Our sampling sites 2 to 8 are located in this lacustrine zone (Figure 1). While the longitudinal gradient in water quality is partly the product of this flow regime, the lack of sewage treatment in the Jaguarí and Jacaré Rivers sub-basins (Hackbart et al., 2015) could enrich waters along this gradient beyond the zone of suspended particle settlement.

2.2. Methods

We collected rainfall and air temperature data for the study period (2010), provided by the company responsible for the water and waste management (Sabesp), and obtained at the Agrometeorological Integrated Information Center (Ciiagro). Wind velocity was obtained from the National Institute of Meteorology (INMET) website for the year of 2010, both located adjacent to the Jaguarí River Dam at Bragança Paulista City, São Paulo.

We defined nine sampling stations within the reservoir, comprising its fluvial, transition and lacustrine zones. Because of the difference in size between both reservoirs, Jaguarí had two sampling stations (sampling sites 1 and 2) and Jacaré seven (sampling sites 3 to 9 - Figure 1). Water samples were obtained during the dry (mixing period - June 2010) and wet (stratification period - December 2010) seasons, with a Van Dorn sampler and stored in 5 liter Polyethylene bottles. One sample

per sampling point was collected per period (N = 18). The water sub-surface temperature, pH, and electrical conductivity were obtained *in situ*, using standard electrodes (Eureka Amphibian, Manta+30, 2010) and water transparency was determined using Secchi disk. In the laboratory, unfiltered samples from all sampling stations were used for the measurement of total nitrogen and total phosphorus (Valderrama, 1981). Samples filtered under low pressure (< 0.5 atm) were used for the measurement of dissolved reactive silica (Golterman, 1978). Total oxygen was measured in laboratory on the same day of the sample collection, from samples fixed *in situ* (Golterman, 1978). Chlorophyll-*a* corrected for phaeophytin was analyzed from the pre calcinated Whatman GF/F filters, within at most one week from the day of sampling using 90% ethanol as the organic solvent (Sartory & Grobbelaar, 1984). The Trophic Status Index (TSI) was calculated based on Secchi disk transparency, total phosphorus and Chlorophyll-*a*, according to that adapted Carlson TSI to tropical reservoirs (Lamparelli, 2004).

For the diatom analysis, sampling method integrated the water above the mean depth of the water column which ranged from 4 to 25 m, depending on location and time of year. The integration was realized according to the mixing regime and light. In the presence of stratification, equal volume samples were taken from 2 to 3 depths of each strata (epilimnion and hypolimnion, calculated based on Dadon (1995)) depending on the depth of the water column on the sampling

station, until the mean depth of water column was reached, then integrated. In the absence of stratification, because the reservoir is deep, 3 depths of equal volume from the euphotic zone, plus the mean depth of the water column were integrated. A fraction of 150 ml from the integrated sample was fixed with neutral Lugol's solution and used for the analysis of the diatom planktonic community. Samples from the surface sediment (top 2 cm) were obtained during the dry season (June 2010) with a gravity corer (UWITEC, Mondsee, Austria). One sample was collected per point (N = 18) and preserved in a refrigerator. All diatom samples were digested according to standard procedures using concentrated hydrogen peroxide (H₂O₂ 35%) (Battarbee et al., 2001), and then mounted on microscope slides using Naphrax (refractive index 1.7). Quantitative analysis was performed according to Battarbee et al. (2001) using a Zeiss (Axioskop 2 plus) light microscope equipped with a DC500 high-resolution digital camera, under a 1000× magnification. At least 400 valves were counted per slide and until reaching 90% in counting efficiency, according to Pappas & Stoermer (1996). Species abundances were expressed as a percentage of the total diatom counts per sample. Diatom names were coded according to the OMNIDIA software (Lecointe et al., 1993).

Multivariate Principal Components Analysis (PCA) was used to ordinate the samples (sites 1 to 9) and seasons in relation to the abiotic environmental data (called here PCA abiotics), and to ordinate sampling units (sediment and plankton), and seasons in relation to the species abundances data (called here PCA species). Although we measured water temperature, the data was not included in the PCA analysis to avoid collinearity. Since the sediment samples represent spatially and temporally integrated events from the recent past (approximately the last 5 years before sampling), and the species from the diverse habitats of the system (Stoermer & Smol, 2010; Bennion, 1995), the PCA analysis of the species was performed using both the plankton and the sediment samples altogether. Canonical Correspondence Analysis (CCA) was to analyze the distribution of the diatom community in relation to environmental variables. Because the results of the CCA depend upon input from a second matrix of variables that can only predict species responses when also measuring those explanatory variables, we excluded the sediment data from this analysis. The only environmental variables evaluated in this study that were not used

in the CCA analysis were temperature and trophic state, since both affect and are affected by the other variables. The diatom abundances were transformed using cosine square root and the environmental variables were log-transformed to approximate the linear relationship assumed for all analysis. Data transformation and multivariate analysis were carried out using PC-ORD program, version 5.15 (McCune & Mefford, 1999; McCune & Mefford, 1997).

3. Results

Surface water temperature followed seasonal changes, with the average of 18.9 °C and 24.9 °C for the dry and wet season, respectively, and dry season rainfall accounted for just 15% of the total rain received during the wet season. The average monthly precipitation was 1.24 mm during the dry period, with no rain registered in the 10 days previously to sampling. During the rainy period the average monthly precipitation was 9.48 mm and a total precipitation of 69.8 mm was registered in the 10 days previously to sampling. Operation of water level by the company responsible for the water and waste management (Sabesp) resulted in the Jaguari-Jacaréí having a greater volume during the dry season (801.9 hm³) than during the wet season (621.2 hm³). Depth of mixing reached the bottom in all the sampling stations during the dry season and in sampling sites of the lacustrine zone (sites 2 to 8) during the wet season. At the lacustrine zone in the wet season, the depth of the epilimnion ranged from 6 to 30 m. Water transparency (Secchi disk) was lower at areas located at the riverine region, near the Jaguari and Jacaréí rivers (sites 1 and 9) in both study seasons (Table 1). Little variation in transparency was found among the lacustrine sampling stations (sites 2-8). Light attenuation was always higher during the wet season. The pH levels ranged from slightly acidic (6.5 to 6.8) in the dry season to neutral or slightly alkaline (7.4 to 8.0) in the wet season. Electrical conductivity was always low (32 to 41 µS.cm⁻¹). Total nitrogen was highest during the dry season (average of 297 µg.L⁻¹), especially in the Jaguari side of the reservoir (sites 1 and 2, Table 1), whilst in the wet season (average of 189 µg.L⁻¹), the sampling stations 4 (lacustrine) and 9 (riverine) also presented high values. Total phosphorus was always low (average of 10 µg.L⁻¹ in the dry season and 14 µg.L⁻¹ in the wet season), reaching a maximum of 37.2 µg.L⁻¹ at the riverine sampling station receiving water from the Jaguari River (site 1). Chlorophyll-*a* concentrations were

Table 1. Limnological data from Jaguari-Jacaré Reservoir analyzed during dry and wet seasons of 2010.

Cumulative monthly rainfall/ Average monthly wind velocity	Sampling station	Zmax (m)	Zepi (m)	TRAN (m)	TEMP (°C)	COND ($\mu\text{S}\cdot\text{cm}^{-1}$)		TN ($\mu\text{g}\cdot\text{L}^{-1}$)	TP ($\mu\text{g}\cdot\text{L}^{-1}$)	DRS ($\mu\text{g}\cdot\text{L}^{-1}$)	Chlo-a ($\mu\text{g}\cdot\text{L}^{-1}$)	Trophic status
							pH					
21 mm/ 1.60 m.s ⁻¹ Dry season	1 (R)	12.0	12.0	2.4	17.7	32.8	6.6	464.3	15.7	5.5	3.1	M
	2 (L)	45.0	45.0	3.0	18.3	33.1	6.5	368.4	13.6	5.9	4.2	O
	3 (L)	46.0	46.0	3.5	19.2	33.5	6.8	217.7	13.7	5.0	< 2.0	O
	4 (L)	41.0	41.0	3.6	19.3	33.8	6.6	360.2	< 4.0	4.0	2.9	O
	5 (L)	40.0	40.0	4.3	19.3	34.1	6.5	243.8	< 4.0	4.0	6.3	O
	6 (L)	37.0	37.0	4.2	19.3	34.5	6.5	228.8	11.6	3.9	< 2.0	U
	7 (L)	31.3	31.3	4.5	19.4	34.1	6.6	203.5	11.6	4.2	< 2.0	U
	8 (L)	24.3	24.0	4.0	19.1	34.6	6.6	269.4	< 4.0	4.0	2.7	U
	9 (R)	10.5	10.5	2.6	18.9	34.9	6.7	321.5	18.5	3.7	8.3	M
Average	-	32.0	31.8	3.5	18.9	33.9	6.6	297.5	10.7	4.4	3.7	-
316 mm/ 1.73 m.s ⁻¹ Wet season	1 (R)	7.0	7.0	1.5	25.1	40.0	8.0	344.8	37.2	4.3	4.6	M
	2 (L)	40.0	30.0	2.7	24.2	39.0	7.3	366.6	21.2	4.4	4.4	O
	3 (L)	33.0	11.0	3.2	24.8	35.0	7.4	89.3	12.1	3.4	< 2.0	U
	4 (L)	17.0	9.5	3.3	24.4	35.0	7.4	228.3	13.8	3.2	< 2.0	O
	5 (L)	35.0	13.0	3.1	25.5	35.0	7.4	156.0	15.9	3.4	4.8	O
	6 (L)	28.0	6.0	2.9	25.1	35.0	7.8	89.0	< 4.0	2.6	< 2.0	O
	7 (L)	27.0	27.0	3.2	24.5	36.0	7.7	106.2	< 4.0	2.7	< 2.0	U
	8 (L)	21.0	7.0	3.0	25.1	36.0	7.5	67.2	< 4.0	2.8	< 2.0	U
	9 (R)	5.5	5.5	1.9	25.5	41.0	7.6	258.1	21.4	2.5	5.6	M
Average	-	23.0	12.9	2.7	24.9	36.88	7.5	189.5	14.3	3.2	3.2	-

Zmax: maximum depth, Zepi: epilimnion depth, TRAN: transparency, Temp: water temperature, COND: electrical conductivity, TN: total nitrogen, TP: total phosphorus, DRS: dissolved reactive silica, Chlo-a: Chlorophyll-a, @: Riverine, (L): Lacustrine, M: mesotrophic, O: oligotrophic, U: ultraoligotrophic, <: bellow the method detection limit.

low in both climatic seasons, reaching the maximum value of $8.3 \mu\text{g}\cdot\text{L}^{-1}$ at the riverine sampling station influenced by the Jacaré River (site 9). According to the Trophic Status Index (TSI), the Jaguari-Jacaré Reservoir was ultraoligotrophic to oligotrophic. However, the riverine sampling stations (sites 1 and 9) were classified as mesotrophic.

Overall, 66 infrageneric diatom taxa belonging to 32 genera were found. From those 57 infrageneric taxa were reported in phytoplankton, and 59 in surface sediment assemblages. Three rare (occurring bellow 5% abundance) infrageneric taxa were exclusive from the phytoplankton and 5 from the sediment. Only 13 and 14 species, respectively, occurred in abundances $\geq 5\%$, in the plankton and surface sediments. Although none of the abundant species was exclusive of one particular compartment (plankton or sediment), their abundances differed within these compartments and are presented in Figures 2 and 3. Therefore, the species with abundance above 5% in the plankton during the dry season were *Aulacoseira ambigua* (Grunow) Simonsen, *Aulacoseira granulata* var. *angustissima* (O. Müller) Simonsen, *Aulacoseira*

granulata (Ehrenberg) Simonsen var. *granulata*, *Aulacoseira tenella* (Nygaard) Simonsen, *Cyclotella meneghiniana* Kützing, *Discostella stelligera* (Cleve et Grun.) Houk & Klee, *Fragilaria crotonensis* Kitton, *Nitzschia amphibia* Grunow, and *Spicaticribra rudis* (Tremarin, Ludwig, Becker & Torgan) Tuji et al. During the wet season, the abundant species were the same ones observed during the dry season with the addition of *Achnantheidium tropicocatenatum* G.C. Marquardt, C.E. Wetzel & Ector, *Brachysira microcephala* (Grunow) Compère, and *Fragilaria vaucheriae* (Kütz) Petersen. For the sediment the species occurring at abundances above 5% were *Aulacoseira ambigua* (Grunow) Simonsen, *Aulacoseira granulata* (Ehrenberg) Simonsen var. *granulata*, *Aulacoseira tenella* (Nygaard) Simonsen, *Achnantheidium tropicocatenatum* G.C. Marquardt, C.E. Wetzel & Ector, *Cyclotella meneghiniana* Kützing, *Discostella stelligera* (Cleve et Grun.) Houk & Klee, *Encyonema silesiacum* (Bleisch in Rabh.) D.G. Mann, *Eunotia botulitropica* Wetzel & Costa, *Gomphonema parvulum* (Kützing) Kützing, *Humidophila contenta* (Grunow) Lowe et al., *Luticola ectorii* Levkov, Metzeltin & Pavlov,

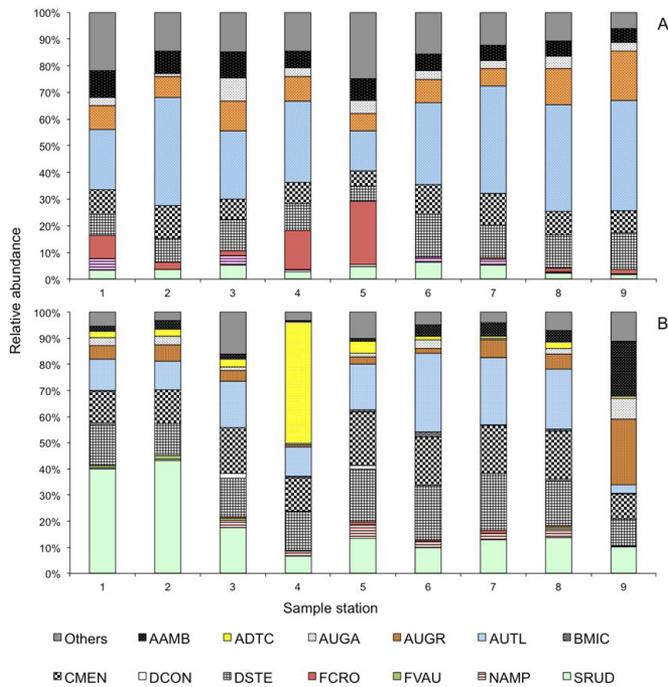


Figure 2. Relative abundance of 13 planktonic diatom taxa (abundant) during the dry (A) and wet (B) dry season in Jaguari-Jacareí Reservoir. Species codes - AAMB: *Aulacoseira ambigua*, ADTC: *Achnanthisdium tropicocatenatum*, AUSA: *Aulacoseira granulata* var. *angustissima*, AUGR: *Aulacoseira granulata*, AUTL: *Aulacoseira tenella*, BMIC: *Brachysira microcephala*, CMEN: *Cyclotella meneghiniana*, DSTE: *Discostella stelligera*, FCRO: *Fragilaria crotonensis*, FVAU: *Fragilaria vaucheriae*, HUCO: *Humidophila contenta*, NAMP: *Nitzschia amphibia*, SRUD: *Spicaticribra rudis*.

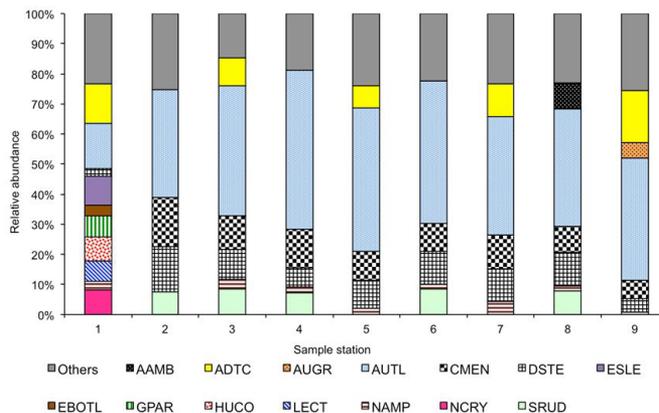


Figure 3. Relative abundance of 14 surface sediment diatom taxa (abundant) in Jaguari-Jacareí Reservoir. Species codes - AAMB: *Aulacoseira ambigua*, ADTC: *Achnanthisdium tropicocatenatum*, AUGR: *Aulacoseira granulata*, AUTL: *Aulacoseira tenella*, CMEN: *Cyclotella meneghiniana*, DSTE: *Discostella stelligera*, ESLE: *Encyonema silesiacum*, EBOTL: *Eunotia botulitropica*, GPAR: *Gomphonema parvulum*, HUCO: *Humidophila contenta*, LECT: *Luticola ectorii*, NAMP: *Nitzschia amphibia*, NCRY: *Navicula cryptocephala*, SRUD: *Spicaticribra rudis*.

Navicula cryptocephala Kützing, *Nitzschia amphibia* Grunow, and *Spicaticribra rudis* (Tremarin, Ludwig, Becker & Torgan) Tuji et al.

These species accounted for more than 70% of the total abundance of the community in each sample. For the plankton, during the dry season

Aulacoseira tenella was the most abundant species at all sampling sites, except the lacustrine site 5, ranging from 14% (site 5) to 41% (lacustrine sites 2 and 7 and riverine site 9) of the total abundance (Figure 2a). At site 5, *Fragilaria crotonensis* Kitton was the most abundant species, comprising 23% of

the flora, with *A. tenella* as the next most abundant species. During the wet season, *Spicaticribra rudis* (Tremarin, Ludwig, Becker & Torgan) Tuji et al. was the most abundant diatom in the riverine site 1 and lacustrine site 2, accounting for 40-43% of the total abundance (Figure 2b). In the lacustrine sampling sites 3, 6, 7 and 8, species distributions were more heterogeneous, and *A. tenella* was the most abundant ranging from 17 to 30% of the diatom abundance. At other sampling stations, *Achnantheidium tropicocatenatum* G.C. Marquardt, C.E. Wetzel & Ector, (lacustrine site 4: 46%), *Cyclotella meneghiniana* Kützing (lacustrine site 5: 20%) and *Aulacoseira granulata* (Ehrenberg) Simonsen var. *granulata* (O. Müller) (riverine site 9: 24%) were the most abundant taxa (Figure 2b). For the surface sediment, *A. tenella* was the most abundant species in all samples, with values ranging

from 15% (lacustrine site 1) to 53% (riverine site 4) of the diatom sum (Figure 3).

The ordination of abiotic environmental data using PCA based on 8 abiotic environmental data of the water (PCA abiotics) revealed two interpretable axes that accounted for 69.9% of the variation (Table 2, Figure 4a). Samples collected during the dry season occupied positive positions on Axis 1, mainly associated with higher values of transparency, epilimnion depth, total nitrogen and Chlorophyll-*a* (Table 3). Samples with a negative relationship to Axis 1 were associated with higher values of pH, conductivity and dissolved reactive silica. The second axis separated most of the riverine from the lacustrine sites. Riverine sites were associated with higher values of dissolved reactive silica, total nitrogen and Chlorophyll-*a*. This way, the PCA analysis highlighted that the samples were primarily organized according to seasonality (axis

Table 2. PCA and CCA synthesis performed from, abiotic analysis, plankton and surface sediment assemblages in Jaguari-Jacaré Reservoir.

Synthesis	PCA abiotics		CCA		PCA species	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	6.32	3.13	0.061	0.030	0.900	0.768
Broken-stick Eigenvalue	3.49	2.36	-	-	0.686	0.490
% of variance	46.8	23.1	30.7	15.2	25.5	21.7
% accumulated variance	46.8	69.9	30.7	45.8	25.5	47.2
Pearson Correlation	-	-	0.954	0.870	-	-
Kendall Correlation	-	-	0.804	0.712	-	-
Species-environment Correlation	-	-	0.009	-	-	-

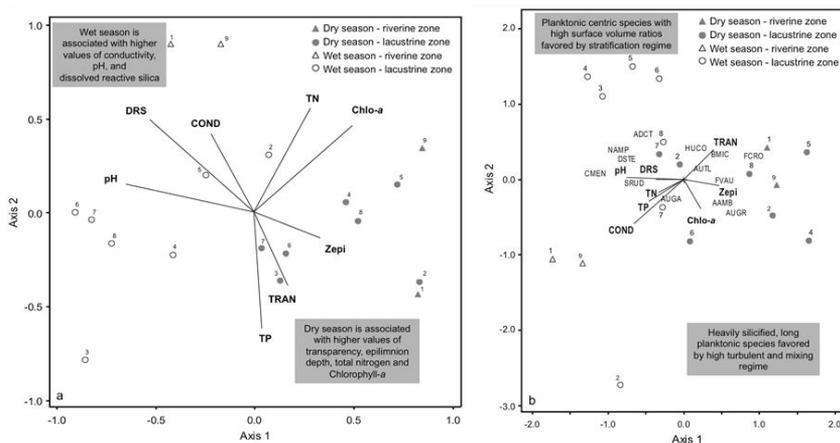


Figure 4. Principal Component Analysis (PCA abiotics) based on 8 abiotic environmental data of the water of Jaguari-Jacaré Reservoir (a). Environmental variables codes: Zepi: epilimnion depth, TRAN: transparency, COND: electrical conductivity, TN: total nitrogen, TP: total phosphorus, DRS: dissolved reactive silica, Chlo-*a*: Chlorophyll-*a*. Canonical Correspondence Analysis (CCA) based on the 13 abundant (above 5%) diatom taxa from plankton in Jaguari-Jacaré Reservoir (b). Numbers indicate the sampling station. Species codes - AAMB: *Aulacoseira ambigua*, ADTC: *Achnantheidium tropicocatenatum*, AUGA: *Aulacoseira granulata* var. *granulata*, AUGR: *Aulacoseira granulata*, AUTL: *Aulacoseira tenella*, BMIC: *Brachysira microcephala*, CMEN: *Cyclotella meneghiniana*, DSTE: *Discostella stelligera*, FCRO: *Fragilaria crotonensis*, FVAU: *Fragilaria vaucheriae*, HUCO: *Humidophila contenta*, NAMP: *Nitzschia amphibia*, SRUD: *Spicaticribra rudis*.

1) and secondarily with the compartment in which they were sampled (axis 2).

The evaluation of the community in relation to the environmental variables using CCA revealed one interpretable axis of variation from the 13 taxa (abundant) found in phytoplankton assemblages. This axis accounted for 30.7% of the total variation with correlation between diatom species and environment ($p = 0.009$) (Table 2, Figure 4b). Samples from the dry season of the planktonic assemblages occupied positive positions on Axis 1, ordered mainly *Aulacoseira* species and *Fragilaria crotonensis* associated with higher values of chlorophyll-a, transparency and depth of epilimnion. Samples from the wet season presented a negative relationship to Axis 1, presenting higher abundances of *Discostella stelligera* (Cleve e Grunow) Houk & Klee, *Cyclotella meneghiniana* and *Spicaticribra rudis* and associated with higher concentrations of nutrients (TN, TP and DRS), pH and conductivity (Table 4). The CCA then evidenced the relationship between certain species from the planktonic habitat with mixing regime and pH.

The ordination of the species using PCA (PCA species) revealed two interpretable axes of

variation from the 18 taxa (abundant) found in phytoplankton and surface sediment assemblages. These axes accounted for 47.2% of the variation (Table 2, Figure 5). Samples from the surface sediment assemblages occupied positive positions on Axis 1, mainly associated with *Achnanthisidium catenatum* and *Humidophila contenta* (Grunow) Lowe et al. Samples with a negative relationship to Axis 1 were rich in *Aulacoseira* spp. [*A. ambigua* (Grunow) Simonsen and *A. granulata*], *Discostella stelligera* (Cleve e Grunow) Houk & Klee and *Spicaticribra rudis* (Table 3). The second axis separated samples rich in *Aulacoseira* spp. (*A. granulata*, *A. tenella* and *A. ambigua*) and *Fragilaria crotonensis*, from those rich in *S. rudis*. Results of the PCA highlighted that diatom assemblages were mainly organized according to compartment in which they were sampled, so the planktonic habitat and surface sediment (PC1), and secondarily, the species occurring on the planktonic habitat were organized by seasonality (PC2).

4. Discussion

The chemical signatures and diatom assemblage from the main body of the Jaguari-Jacaréi Reservoir

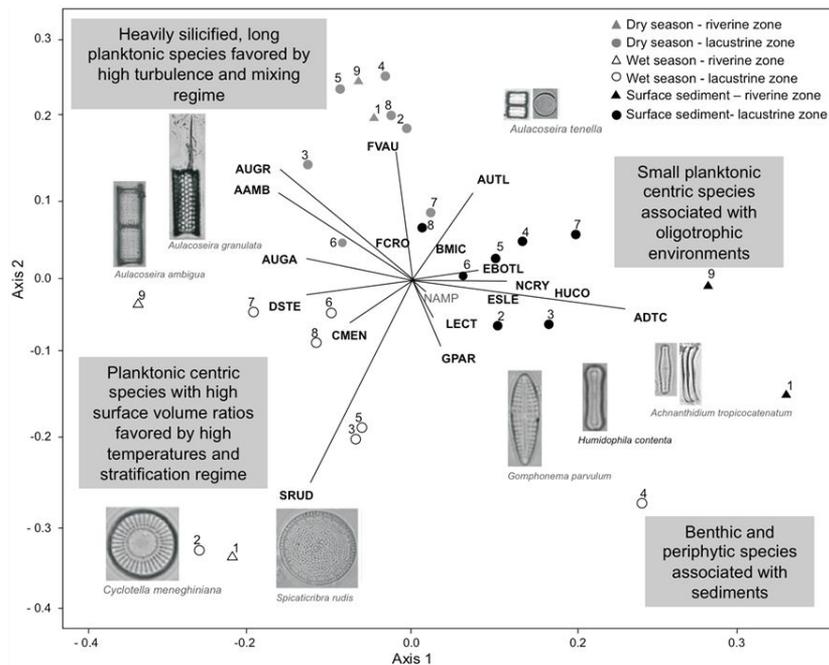


Figure 5. Principal Component Analysis (PCA species) based on the 18 abundant (above 5%) diatom taxa from plankton and surface sediment in Jaguari-Jacaréi Reservoir. Numbers indicate the sampling station. Species codes - AAMB: *Aulacoseira ambigua*, ADTC: *Achnanthisidium tropicocatenatum*, AUGA: *Aulacoseira granulata* var. *granulata*, AUGR: *Aulacoseira granulata*, AUTL: *Aulacoseira tenella*, BMIC: *Brachysira microcephala*, CMEN: *Cyclotella meneghiniana*, DSTE: *Discostella stelligera*, ESLE: *Encyonema silesiacum*, EBOTL: *Eunotia botulitropica*, FCRO: *Fragilaria crotonensis*, FVAU: *Fragilaria vaucheriae*, GPAR: *Gomphonema parvulum*, HUCO: *Humidophila contenta*, LECT: *Luticola ectorii*, NAMP: *Nitzschia amphibia*, NCRY: *Navicula cryptocephala*, SRUD: *Spicaticribra rudis*.

Table 3. PCA abiotics loadings and CCA canonic coefficient and intraset correlations of the environmental variables from the plankton on the first two principal components.

Enviromental Variables	PCAabiotics		Canonic Coefficient		Intraset Correlations	
	Axis 1	Axis 2	Axis 1	Axis 2	Axis 1	Axis 2
<i>Zepi</i>	0.161	-0.619	0.266	-0.908	0.463	-0.072
<i>TRAN</i>	-0.421	0.170	0.794	1.338	0.394	0.353
<i>COND</i>	-0.434	0.565	-0.488	-0.834	-0.645	-0.521
<i>TN</i>	0.79	0.304	-0.060	0.144	-0.330	-0.155
<i>pH</i>	-0.844	0.289	-0.820	1.325	-0.749	0.023
<i>TP</i>	0.048	0.645	-0.549	-0.042	-0.449	-0.258
<i>DRS</i>	0.723	-0.282	0.300	-0.815	-0.365	0.001
<i>Chlo-a</i>	0.626	0.696	0.259	0.350	0.225	-0.341

Environmental variables codes: *Zepi*: epilimnion depth, *TRAN*: transparency, *COND*: electrical conductivity, *TN*: total nitrogen, *TP*: total phosphorus, *DRS*: dissolved reactive silica, *Chlo-a*: Chlorophyll-a.

Table 4. PCA species, CCA loadings and occurrence in abundances above 5% of the 18 abundant diatom taxa from plankton and surface sediment on the first two principal components.

Species	Codes	PCA species		CCA	
		Axis 1	Axis 1	Axis 1	Axis 2
<i>Achnanthisdium tropicocatenatum</i> G.C. Marquardt, C.E. Wetzel & Ector	ADCT	0.779	-0.286	-0.264	0.70
<i>Aulacoseira ambigua</i> (Grunow) Simonsen	AAMB	-0.636	0.498	0.543	0.295
<i>Aulacoseira granulata</i> var. <i>angustissima</i> (O. Müller) Simonsen	AUGA	-0.547	0.222	0.213	0.046
<i>Aulacoseira granulata</i> (Ehrenberg) Simonsen var. <i>granulata</i>	AUGR	-0.618	0.527	0.424	0.179
<i>Aulacoseira tenella</i> (Nygaard) Simonsen	AUTL	0.406	0.496	0.438	0.192
<i>Brachysira microcephala</i> (Grunow) Compère	BMIC	0.204	0.270	0.174	0.225
<i>Cyclotella meneghiniana</i> Kützing	CMEN	0.418	-0.363	-0.654	0.427
<i>Discostella steligera</i> (Cleve et Grun.) Houk & Klee	DSTE	-0.568	-0.226	-0.580	0.336
<i>Encyonema silesiacum</i> (Bleisch in Rabh.) D.G. Mann	ESLE	0.450	-0.164	-	-
<i>Eunotia botulitropica</i> Wetzel & Costa	EUSP	0.416	0.140	-	-
<i>Fragilaria crotonensis</i> Kitton	FCRO	-0.219	0.588	0.874	0.764
<i>Fragilaria vaucheriae</i> (Kütz) Petersen	FVAU	-0.123	0.279	0.386	0.149
<i>Gomphonema parvulum</i> (Kützing) Kützing	GPAP	0.273	-0.432	-	-
<i>Humidophila contenta</i> (Grunow) Lowe et al.	HUCO	0.515	-0.104	0.172	0.030
<i>Luticola ectorii</i> Levkov, Metzeltin & Pavlov	LACD	0.229	-0.333	-	-
<i>Navicula cryptocephala</i> Kützing	NCRY	0.442	-0.062	-	-
<i>Nitzschia amphibia</i> Grunow	NAMP	0.006	-0.040	-0.99	0.010
<i>Spicaticribra rudis</i> (Tremarin, Ludwig, Becker & Torgan) Tuji et al.	SRUD	-0.544	-0.761	-0.771	0.594

P = Plankton, S = Sediment.

indicate an unproductive water body. Our findings are consistent with previous descriptions provided by the monitoring agency that classified the reservoir as ultra-oligotrophic to oligotrophic during the year of the study (Whately & Cunha, 2007). A single species (*Aulacoseira tenella*) stood out for its almost ubiquitous abundance in both seasons in the plankton and in surface sediment assemblages.

Aulacoseira tenella is a very small planktonic colonial centric species, with the valve diameter between 5 and 6.2 μm and mean mantle height between 1 and 1.8 μm with colonies form very short chains with frustules joined by small spines. It has been reported in acidophilus (Camburn & Charles, 2000), oligotrophic to oligomesotrophic (Siver & Kling, 1997), low conductivity waters (Raupp et al.,

2006). Overall, *A. tenella* is a good indicator of low nutrient conditions (Bicudo et al., 2016), which endorses the idea that planktonic organisms of small body size present high nutrient uptake efficiency (Irwin et al., 2006; Litchman et al., 2007). Additionally, due to the combination of its colonial life form, shape and size we infer that *A. tenella* probably sinks slowly, and has the potential for a high population growth rate (Reynolds, 2006). In lakes from arctic, temperate and alpine regions, the association between small-sized and centric-shaped diatoms and high lake depth has been observed (Pla et al., 2005; Rühland et al., 2015). It is conceivable that the morphometric characteristics of *A. tenella* serve as adaptive strategies, favoring buoyancy, reproduction and survival in the deep oligotrophic waters of Jaguari-Jacaréi.

4.1. Competitive advantages and seasonality

Heavily silicified, long centric diatoms, forming filaments e.g. *Aulacoseira* species (*A. granulata* and *A. ambigua*), and long non-centric colonial planktonic species, joined in large ribbon-like colonies, e.g. *Fragilaria crotonensis* characterize plankton assemblages in the dry season (Figure 2). Although these three species are usually associated with a broad range of trophic status (Bicudo et al., 2016; Li et al., 2011; Manoylov et al., 2009), they require well-mixed water columns to keep them suspended (Znachor et al., 2015; Costa-Böddeker et al., 2012; Padisák et al., 2009; Tolotti et al., 2007; Zalat and Vildary, 2007; Bailey-Watts, 1986). Because the Jaguari-Jacaréi Reservoir is oligotrophic and has low phosphorus concentrations (10–14 $\mu\text{g}\cdot\text{L}^{-1}$ in average), we suggest that the high abundances of *F. crotonensis*, *A. ambigua* and *A. granulata* are associated with greater turbulence and water-mixing as thermal stratification dissipates, characteristic of the dry season. In fact, the CCA analysis shows that these species were mainly associated with higher epilimnion depth (mixing) and transparency.

Despite during the dry season water transparency was higher, the mixed layer had less light availability (due to low Zeup:Zepi ratio), which explains why *Aulacoseira* species and *F. crotonensis* are more important during dry season (Reynolds, 2006). These findings are in agreement with modeled relationships in which heavier planktonic outcompete smaller species in deeper systems when the system experiences high turbulence (Portalier et al., 2016). The high occurrence of *A. ambigua* and *A. granulata* as a result of water column mixing in Jaguari- Jacaréi Reservoir has also

been recorded in other deep reservoirs in the South of Brazil caused by the mixing regime as well as eutrophication, in particular nitrogen (Becker et al., 2009; Borges et al., 2008). During the wet period, *F. crotonensis*, *A. ambigua* and *A. granulata* occurred in most sites, but at lower abundances compared with the dry period.

While much of the lake stratified during the wet season, near the inlets, the inflow of water led to local turbulence that maintained a mixed water column. Sites 1, 7 and 9 remained mixed, and consequently supported larger, heavier diatoms. In the most extreme case was site 9, where *A. ambigua* and *A. granulata* were extremely abundant, confirming the association of these species with turbulence in this system. Sites 1 and 9 also presented low epilimnion depth, transparency and high total phosphorus, possibly as a response to the water turbulence.

Still during the wet season, but in the riverine zone of the reservoir, planktonic solitary centric diatoms, particularly *Spicaticribra rudis*, *Discostella stelligera* and *Cyclotella meneghiniana*, characterized plankton assemblages in the wet season (Figure 2). *Spicaticribra rudis* (ex *Thalassiosira rudis*) was first described in Brazil from reservoirs and rivers in the states of Paraná, Rio Grande do Sul and Bahia (Ludwig et al., 2008). Since then, *S. rudis* has been reported in good quality waters of reservoirs from the State of São Paulo (Fontana & Bicudo, 2009) (AcquaSed Project dataset). Overall, *S. rudis* is a member of planktonic assemblages in rivers and reservoirs of tropical and subtropical regions (Tuji et al., 2012; Fontana & Bicudo, 2009; Johansen et al., 2008; Ludwig et al., 2008), forming blooms during the spring and summer of nutrient-rich waters (Ludwig et al., 2008). *Discostella stelligera* and *C. meneghiniana* occur across a wide range of nutrient concentrations (Faustino et al., 2016; Saros & Anderson, 2015; Potapova & Charles, 2003), making it difficult to relate these species with nutrients. Both, *D. stelligera* and *C. meneghiniana*, however, are sensitive to the onset of thermal stratification (Malik & Saros, 2016; Saros & Anderson, 2015; Saros et al., 2012; Padisák et al., 2009), being capable of remaining suspended within the metalimnion (Tolotti et al., 2007). The commonality between *C. meneghiniana*, *S. rudis* and *D. stelligera* is their planktonic solitary life form, centric shape with low height mantle, which promotes high surface area to volume ratio, thus increasing resistance force against water (Reynolds, 2006). The three

species are characteristic of the stratified waters of Jaguari-Jacarei during the wet season implying that high surface area volume ratio plays important role in the effective buoyancy of these centric diatoms. Using sediment cores from three lakes in the southern Ecuador, Michelutti et al. (2015) linked the unprecedented increase in thalassiosiroid diatoms, specially *Discostella stelligera* with warming and/or enhanced water column stratification. The response of *D. stelligera* to seasonality and enhanced water column stratification observed in our work, is then a topic of great interest due to its potential to indicate global warming in oligotrophic lakes.

The element pH also showed great differences between studied periods and it was strongly related to our first axis of the CCA. Being one of the main factors affecting diatom distribution, temporal changes and this variable can affect the composition of diatom communities (Soininen et al., 2016; Birks et al., 1990). The dry season presented overall lower pH (6.5-6.8) when compared with the wet season (7.3-8.0). In an evaluation of the ecological preferences and distribution of *Aulacoseira* species in Brazilian reservoirs, a study found that *A. ambigua* and *A. granulata* occurred at optimal pH of 6.7-6.8 (Bicudo et al., 2016). Meanwhile along the Polish-German border, over 100 post-mining lakes infer that species of *Discostella*, including *D. stelligera*, and of *Cyclotella* occurred at optimal pH above 7 (Sienkiewicz & Gąsiorowski, 2017), which agrees with the distribution observed in Jaguari-Jacarei. Unfortunately, the correlation between pH, nutrient and thermal regimen in this reservoir makes it difficult to conclude what were the exact drivers of this community.

4.2. Spatially and temporally integrated characterization of the diatom distribution

The distribution of diatom species in surface sediment was influenced by the major tributaries and the diatom abundance in the plankton and littoral areas (Figure 3). Thus, the sampling site under Jaguari River influence (sampling station 1) showed association with five different species (*Humidophila contenta*, *Encyonema silesiacum*, *Gomphonema parvulum*, *Navicula cryptocephala* and *Luticola acidoclinata*). Of these, only *Encyonema silesiacum* and *Luticola acidoclinata* occurred in high abundances in the sampling station under influence of Jacarei River (sampling station 9).

Humidophila contenta, *Encyonema silesiacum*, *Navicula cryptocephala* and *Luticola acidoclinata* are species that usually occur in benthic or subaerial

habitats (Lowe et al., 2014; Round et al., 1990; Cox, 1995) and ecosystems with low nutrient concentrations (Costa-Böddeker et al., 2012; Fontana & Bicudo, 2012; Poulicková et al., 2004; Lange-Bertalot, 1996; Van Dam et al., 1994). *Gomphonema parvulum* seems to occur in different types of environments and habitats, but is most commonly found attached to some kind of substrate (Tremarin et al., 2009; Wojtal, 2003; Sayer & Roberts, 2001; Moro & Fürstenberger, 1997; Dawson, 1972). Therefore, in sampling sites under the tributaries influence, occurred mainly benthic species that were probably brought dead or alive from the rivers and decanted so there was flow decrease (at riverine or intermediate zone).

The other sampling sites from the surface sediment compartment were mostly associated with *Aulacoseira tenella* (most abundant species), *Aulacoseira ambigua*, *A. granulata*, *Cyclotella meneghiniana*, *Discostella stelligera* and *Spicaticribra rudis*, as already discussed, associated to planktonic habitat. Therefore, in most of the surface sediment riverine sampling sites, the diatom composition is explained by the dominance of the species occurring in the plankton habitat.

4.3. Threats and cautions

While the deep-water of the reservoir appears to be a high-quality water body, the peripheral areas are a cause of concern. In this study, we revealed that the riverine zones (sites 1 and 9) were mesotrophic, with relatively higher TN and TP concentrations. Although expected, this is important, since it may have influenced the reservoir's water quality over time. The riverine zones, near the Jaguari River influence (site 1) and the Jacarei River influence (site 9), also presented differences in terms of diatom composition, and were strongly associated with benthic and periphytic species, and the planktonic species *Achnathidium tropicocatenatum*. Site 1 had an assemblage rich in *Humidophila contenta*, *Encyonema silesiacum*, *Gomphonema parvulum*, *Navicula cryptocephala* and *Luticola acidoclinata*. Of these taxa, *G. parvulum* and *N. cryptocephala* are known to be tolerant to organic pollution, and *H. contenta* and *L. acidoclinata* are both aerophilic species. Similarly site 9 has the aerophiles, but does not have such a strong representation of the indicators of pollution, *G. parvulum* and *N. cryptocephala*. Evidently there was enough water movement at these riverine sites to prevent an algal bloom in the water column, although enough nutrients to completely alter the benthic ecology.

Achnathidium tropicocatenatum was highly associated with surface sediments in riverine zones (sites 1 and 9), and with the plankton at site 4 during the wet season. The type population of *A. tropicocatenatum* was observed in the Cachoeira do França reservoir in alkaline waters with low conductivity, low levels of nitrate, total nitrogen, total phosphorus, and phosphate concentrations and high pH (Marquardt et al., 2017). The high representation of this taxon in sampling station 4 may indicate a limnological change given the greatest difference in depth between the dry and wet seasons (24 m). Yet, the large difference in water depth between wet and dry seasons observed in only one sampling site could be the result of sampling at a different location in the wet season, in an uneven bottom of the reservoir. Attributing the relatively high abundance of *A. tropicocatenatum* to changes in water level remains uncertain.

When a river flows into a lake there can be a series of natural gradients, such as decreasing flow rates, decreasing sensitivity to peak discharges, increasing dilution, and increasing depth (Zanata & Espíndola, 2002; Armengol et al., 1999; Thomaz et al., 1997). The decrease in total phosphorus towards the dam can occur due to factors such as progressive dilution and adsorption to inorganic particulates, which results in sedimentation and burial. Such processes may be proportionally affected by residence time (Kennedy & Walker, 1990), and could be substantial in systems with a long residence time such as the Jaguari-Jacaré Reservoir (368.5 days).

A more disturbing, and not mutually exclusive possibility is that as an oligotrophic system is loaded with P or N, the capacity to buffer its impact moves progressively downstream. A classic example is the Florida Everglades where P loading is causing the progressive eutrophication spreading outwards from point source discharges (Childers et al., 2003). Over ten years, the loading has caused floral and algal ecosystems to change radically. At the start of the study, the broadleaf cattail, *Typha latifolia*, a perennial plant indicative of eutrophied marsh, replaced the natural component of this ecosystem, the sawgrass plant, *Cladium jamaicense*, as far as 2 km downstream of the known point source. Ten years later, the eutrophied marsh extended 4 km from the source (Childers et al., 2003). Thus, any untreated sewage and agricultural run-off entering the Jaguari-Jacaré Reservoir could load the system, impacting water quality and extending further into the main body over time (Hackbart et al., 2015; Whately & Cunha, 2007), inducing ecological

thresholds of lowered water quality, that over time will progressively extend further into main body of the reservoir. Should this occur, blooms of blue-green algae are likely to replace the existing plankton.

The case of Guarapiranga reservoir in São Paulo is another example. In a longer sedimentary record (>100 years), the eutrophication history of Guarapiranga reservoir shows a shift in diatom assemblages began ~1975, and by the early 1980s the reservoir had become eutrophic, in response to an explosive increase in human population in the watershed (Fontana et al., 2014). By 1980s, cyanobacterial blooms became common in this then eutrophic to hyper-eutrophic system (Beyruth, 2000). Since 1990s, copper sulfate is used to control those blooms, but untreated sewage from the drainage basin is still discharged in the reservoir.

It seems that the water quality in Jaguari-Jacaré worsen in 2016, being classified as oligotrophic to mesotrophic (CETESB, 2019). During the years of 2013 and 2014 (three years after the period of study), southeastern Brazil suffered what was called 'drought of the century', certainly the worst in 80 years of record-keeping. This rainfall deficiency has generated water shortages and a water crisis that have affected population and local economies in the metropolitan region of Sao Paulo, the largest megacity in South America. By January 2015, main reservoirs had reached storage levels of only 5% of their 1.3 billion m³ capacity (Nobre et al., 2016). This drought caused a 77% reduction in usable water volume in the Cantareira system, and Jaguari-Jacaré Reservoir underwent a catastrophic regime change in which its operational capacity was completely depleted in July 2014 (Coutinho et al., 2015). The vulnerability of this system to drought may increase its susceptibility to depletion and increase in nutrients coming from its major rivers Jaguari and Jacaré, that are still untreated and classified as eutrophic and hypereutrophic, respectively (Carli et al., 2020).

5. Conclusions

In this deep oligotrophic reservoir, the diatom communities responded both to seasonal variations in mixing regime and to pH. In the dry season, the water-mixing regime favored heavily silicified, long, colonial planktonic diatoms of low pH optimal, whereas in the wet season, solitary centric planktonic diatoms with high surface volume ratios were favored by stratification and higher pH. Benthic species were only found in the surface sediment

of peripheral settings, especially near tributaries. A small centric colonial planktonic species, *Aulacoseira tenella*, was the most abundant species in the entire reservoir, indicating that its centric shape and small size represent a competitive advantage by facilitating buoyancy and nutrient uptake in deep environments with low productivity waters.

Until 2011, the Jaguari-Jacaré Reservoir still maintained high water quality and low productivity and could be classified as ultra-oligotrophic to oligotrophic. Nevertheless, a longitudinal gradient of diminished water quality exists where input from the tributaries enriched water to the system. The fact that the two main tributaries of the Jaguari-Jacaré Reservoir are sources of untreated sewage is of concern, and the system hold is not likely to be regarded as in equilibrium with current nutrient loading. Steps to manage effluent from current and future communities would help safeguard this vital water supply.

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