



Climate and hydrological processes explain temporal dissimilarity in the phytoplankton community and favor seasonal dominance of harmful and alien algae in a subtropical reservoir

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Abstract. In phytoplankton communities, dissimilarities in the species composition and abundance can be correlated with environmental variability at different spatial and temporal scales. This environmental variability can ascertain periodic replacements in phytoplankton assemblages, favoring, in some cases, the growth and dominance of specific algae groups. In this study, the occurrence of spatial/temporal dissimilarities (variation in the density of different taxonomic groups) in the phytoplankton community and their correlations with the environmental variability were studied in an artificial reservoir located in southern Brazil. Seasonal alternation of dominant groups was observed, with dominance of potential harmful cyanobacteria (*Aphanizomenon* spp. and *Dolichospermum* spp.) in summer, alien dinoflagellates (*Ceratium* spp.) in autumn/winter and chlorophytes in spring. The variability of the environmental conditions and resources explained a significant portion of the dissimilarity observed in the phytoplankton community among seasons. In the BioEnv analysis, water temperature explained 53% of the phytoplankton dissimilarities. In the same way, the results of RDA approach pointed to water temperature, pH, soluble solids and nutrient availability as the environmental variables that best explained variability in phytoplankton's densities. These results contribute to understanding the influence of the environmental variability on the phytoplankton structure modulation in subtropical freshwater ecosystems. Furthermore, they warn about the need to consider climate variability (e.g. extreme drought and rain events) on management of water quality and control of harmful and alien algal blooms, especially in disturbed ecosystems.

Key words: Freshwater biodiversity, Structure of aquatic communities, Seasonal phytoplankton succession, Biological invasions, Subtropical reservoirs

Resumo: **Processos climáticos e hidrológicos explicam a dissimilaridade temporal na comunidade fitoplanctônica e favorecem a dominância sazonal de algas nocivas e exóticas em um reservatório subtropical.** Nas comunidades fitoplanctônicas, dissimilaridades na composição e abundância das espécies podem estar correlacionadas com a variabilidade ambiental em diferentes escalas espaciais e temporais. Essa variabilidade ambiental pode determinar substituições periódicas nas assembleias fitoplanctônicas, favorecendo, em alguns casos, o crescimento e a dominância de grupos específicos de algas. Neste estudo, a ocorrência de dissimilaridades (variações na densidade dos diferentes grupos taxonômicos) espaciais e

temporais na comunidade fitoplanctônica e suas correlações com a variabilidade ambiental foram estudadas em um reservatório artificial localizado no sul do Brasil. Foram observadas alternâncias sazonais dos grupos dominantes, com predominância de cianobactérias potencialmente nocivas (*Aphanizomenon* spp. e *Dolichospermum* spp.) no Verão, dinoflagelados exóticos (*Ceratium* spp.) no Outono/Inverno e algas verdes na Primavera. Na análise BioEnv, a temperatura da água explicou 53% da dissimilaridade do fitoplâncton. Da mesma forma, os resultados da RDA apontaram temperatura da água, pH, sólidos solúveis e disponibilidade de nutrientes como as variáveis ambientais que melhor explicaram a variabilidade nas densidades do fitoplâncton. Esses resultados contribuem para o entendimento da influência da variabilidade ambiental na estruturação do fitoplâncton em ecossistemas subtropicais de água doce. Além disso, eles alertam para a necessidade de considerar as mudanças climáticas (por exemplo, eventos de seca e chuva extremos) na gestão da qualidade da água e no controle da proliferação de algas nocivas e exóticas, especialmente em ecossistemas perturbados.

Palavras-chave: Biodiversidade de água doce, Estrutura das comunidades aquáticas, Sucessão sazonal do fitoplâncton, Invasões biológicas, Reservatórios subtropicais.

Introduction

Assessing the forces that drive biodiversity in space and time remains a milestone challenge in Community Ecology (Maurer & McGill, 2011). The variability in the structure of the biological communities generally depends on habitat's physical and chemical characteristics, their temporal and spatial variability, and the patterns of biotic interactions at different scales (Bengtsson et al., 1997; Crossetti et al., 2014). The establishment of relationships between the structure of biological communities and the environmental variability can provide a valuable contribution to understand the forces and processes behind biodiversity and ecosystem functioning (Magurran & McGill, 2011).

In aquatic environments, the temporal and spatial variability of the environmental factors are important predictors to explain the dissimilarities in the biotic communities (Reynolds, 2006). In the phytoplankton assemblages, for instance, species diversity may be regulated by stability of the habitat, and the environmental instability can alter the communities' structure in different scales (Hutchinson, 1961). Temporal variability can affect the structure of phytoplankton communities through two main regulatory processes, based on the time scale observed. At short-medium time scale (e.g. days–weeks), extreme meteorological and hydrological events are important drivers, whereas at large time scale (seasons), the climate (e.g. water temperature, insolation, and/or rainfall), nutritional (e.g. phosphorus and/or nitrogen concentrations), and interspecific relationships (e.g. grazing, competition and/or allelopathy) are the most significant forces (Salmaso, 2003). These two temporal scales may provide important

environmental variability, which is essential to supporting the diversity of phytoplankton. Furthermore, in some cases, this environmental variability can favor seasonal blooms of harmful and/or alien species, which may result on local extinction of native species ((Paerl & Huisman, 2009; Wagner & Adrian, 2009; Willame et al., 2009; O'Neil et al., 2012; Paerl & Otten, 2013; Yang et al., 2016a; Haakonsson et al., 2017; Simic et al., 2017).

For man-made lakes (such as artificial reservoirs), the phytoplankton biodiversity and the main environmental features are usually very similar to those observed in natural lakes (Kalff, 2002). These environments integrate many processes that occur throughout the watershed area, which makes them very sensitive to environmental disturbs (Tundisi, 1999; Straškraba & Tundisi, 2013; Pompêo et al., 2015). Particularly tropical and subtropical reservoirs are special aquatic ecosystems, in which the periodic exchange of water by tributaries and the loading of allochthonous resources have a strong influence on physical, chemical and biological characteristics (Thornton et al., 1990). Thus, it is expected that the variability of environmental factors, especially those related to climate change (fluctuations in rainfall and temperature regimes) and human activities in the adjacent areas (deforestation, agriculture, pasture and urbanization) can play an important role in all ecological processes that occur in these dynamic systems, including the structuring of biological communities. Furthermore, environmental disturbances tend to favor biological invasions and the growth and establishment of potentially harmful organisms, which makes artificial reservoirs ecosystems especially susceptible to these processes (Strayer, 2010).

Several ecological studies have been conducted to analyze the relationships between the structure of phytoplankton communities and environmental variability in artificial reservoirs in subtropical regions (Burford et al., 2007; Becker et al., 2010; Lv et al., 2014; Yang et al., 2016b; Yang et al., 2017; Li et al., 2018; Huo et al., 2019). In South American reservoirs, the structuring of phytoplankton and the occurrence of alien and harmful species have been related to climate variability (e.g. rainfall, water temperature and light availability) and hydrological (e.g. water transparency, mixture regime and nutrient availability) factors (Mac Donagh et al., 2005; Beamud et al., 2015; Almanza et al., 2016; Meichtry de Zaburlín et al., 2016; Haakonsson et al., 2017). Specifically in southern Brazil, the temporal variation in water temperature, mixing regime, nutrient availability and water retention time play an important role in structuring phytoplankton communities (Schneck et al., 2011; Cavalcante et al., 2016; Cassol et al., 2017; Beló et al., 2018).

Because of their position at the base of aquatic food webs and their basic nutritional needs, phytoplankton communities provide unique information about the ecosystem's conditions (Rakocevic-Nedovic & Hollert, 2005). Thus, to describe the role of the environmental variability on the structuring of phytoplankton communities is important to understanding spatial and temporal dynamics of freshwater ecosystems, mainly in those highly susceptible to disturbances such as artificial reservoirs. In this sense, we evaluated the occurrence of spatial/temporal dissimilarities, investigated dominance patterns and estimated the influence of the environmental variability on the phytoplankton community of an artificial subtropical reservoir located in southern Brazil. Furthermore, we evaluated the main environmental variables correlated with phytoplankton density in this environment. We hypothesized that the temporal variability of the phytoplankton community of this subtropical artificial reservoir is driven by climate and hydrological processes, as observed in several studies conducted in similar ecosystems (Schneck et al., 2011; Almanza et al., 2016; Cavalcante et al., 2016; Meichtry de Zaburlín et al., 2016; Cassol et al., 2017; Haakonsson et al., 2017; Beló et al., 2018). We believe that our study will contribute to the knowledge about phytoplankton communities' structuring and the main forces behind their temporality and dominance patterns in subtropical freshwater ecosystems, especially in disturbed

environments such as artificial reservoirs.

Material and Methods

Study area: The study was conducted in the Itá Hydroelectric Power Plant reservoir (Itá reservoir), located in the Upper Uruguay River region, southern Brazil (27°16'38"S, 52°23'0"W). The artificial lake was formed in the early 2000's from the construction of the dam in the main course of the Uruguay River, has an area of approximately 141 Km², maximum depth of 125 m (average of 36 m) (Consórcio Itá, 2014) and is located in the subtropical climate zone (Cfa-Cfb) (Alvares et al., 2013). The retention time is 55-60 days, according to the season of the year (Loureiro et al., 2012; de Lima et al., 2017). The landscapes around the reservoir have been historically subject to strong human pressure, mainly regarding the land use and occupation (Miranda et al., 2013). The agricultural activity is characterized predominantly by intensive poultry and pork production, which results in high waste concentrations and consequently in high potential diffuse contamination of surface and groundwater at this region (Miranda et al., 2013; Marchesan et al., 2016).

We established six sampling sites along the reservoir, considering the discharge of important sub-basins of the region: P01 (Rancho Grande River mouth); P02 (Suruvi River mouth); P03 (Queimados River mouth); P04 (Dourado River mouth); P05 (Jacutinga River mouth) and P06 (Novo River mouth) (Fig. 1). All the sampling sites were established at 20 m from the margin. In each site, eight field samplings were conducted quarterly, in February/2017, May/2017, August/2017, November/2017, February/2018, May/2018, August/2018 and December/2018. We considered the entire reservoir as the sampling unit. Therefore, the repetition of samplings conducted quarterly in each site was used as replicates, resulting in N= 48 observations (e.g. 24 per year). For spatial effects, samples of each sampling were grouped for both years (e.g. P01 = data from 2017 and 2018 sampled at site P01; P02 = data from 2017 and 2018 sampled at site P02; and subsequently). For temporal effects, data collected along 2017 and 2018 were grouped according to respective season (e.g. sum/2017 = summer/2017; aut/2017 = autumn/2017; and subsequently).

Environmental variables: Water temperature, pH, dissolved oxygen (DO), electrical conductivity (EC) and total dissolved solids (TDS) were measured in sub-surface (~0.5 m) water, with a high-resolution multiparameter probe (Aquaread AM-200,

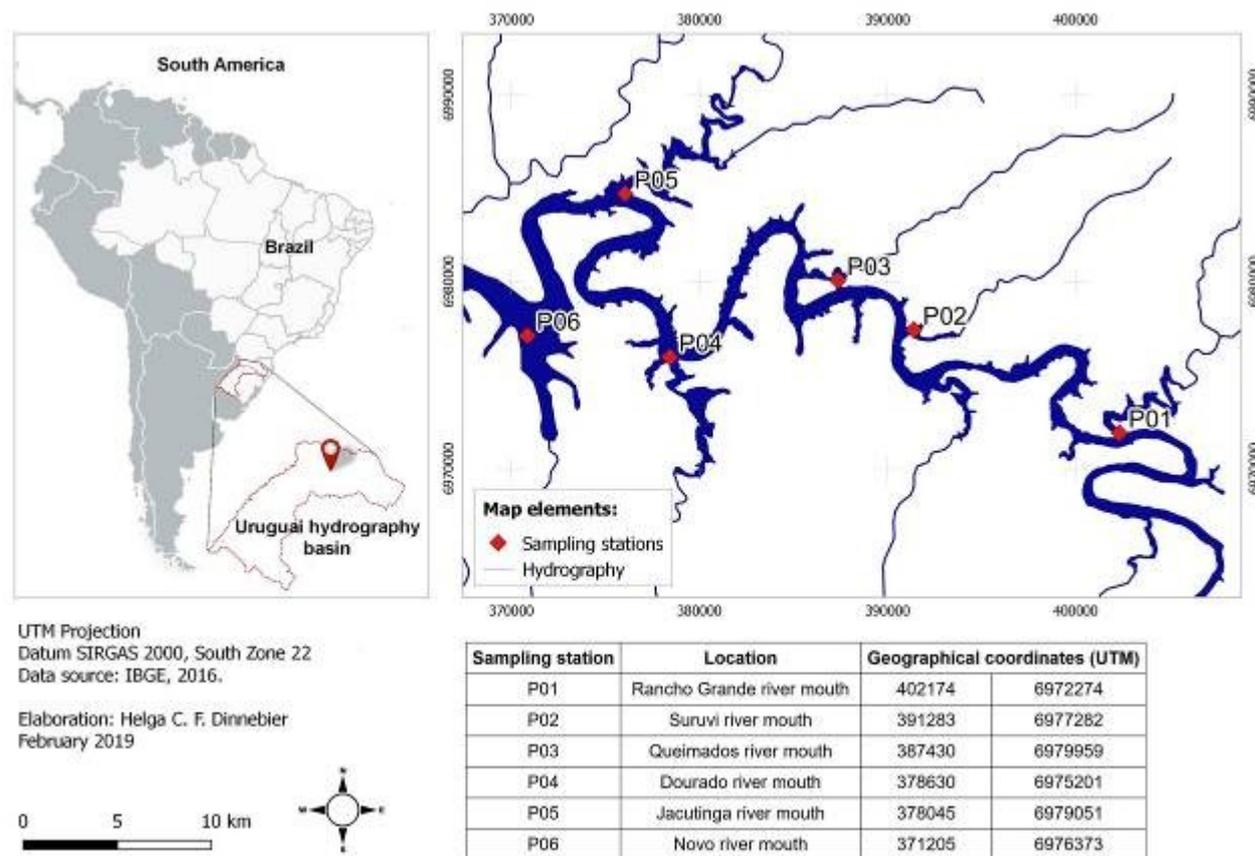


Figure 1. Localization of sampling sites in the Itá Reservoir, upper Uruguay River, southern Brazil. P01 = Rancho Grande river mouth; P02 = Suruvi river mouth; P03 = Queimados river mouth; P04 = Dourado river mouth; P05 = Jacutinga river mouth; P06 = Novo river mouth.

Aquaprobe AP-2000). The transparency of the water column was determined through Secchi disc. Sub-surface (~0.5 m) water samples were collected in 1L sterilized bottles and stored in iceboxes.

In the laboratory, turbidity was determined by the nephelometric method (Hach et al., 1985). The concentrations of nitrate (N-Nitrate - cadmium reduction method) and phosphorus (Total-P - colorimetric method with ascorbic acid digestion and UV spectrophotometer reading) were conducted according (APHA - American Public Health Association, 2017). For total coliforms and *E. coli* evaluation, water samples were submitted to a tenfold serial dilution in saline solution (0.85%) and bacteria were quantified by plate counting method using Petrifilm® system, following the manufacturer instructions (Swanson et al., 2001). Results were expressed as Colony Forming Units per volume (CFU/mL). Monthly insolation, accumulated rainfall and wind intensity were obtained from Embrapa Agrometeorological Station, located about 14 Km from the study area.

Phytoplankton community: The composition of the phytoplankton community and the density of the taxonomic groups were estimated from water samples collected in sub-surface (~0.5 m) by towing a phytoplankton net (20 µm). In this case, due to this sampling strategy used, the data set presents only organisms larger than 20 µm. After trawling, the concentrated samples were conditioned in 50 mL Falcon's tubes and preserved with Lugol acetic solution. In laboratory, we separated 2 mL subsamples, which were placed in sedimentation chambers for 24 hours (Utermöhl, 1958).

Phytoplankton was identified and counted in a Zeiss® inverted optical microscope (Axiovert A1 MAT) with magnification of 400x (Utermöhl, 1958). The counting of organisms (cells, colonies or filaments) was done in linear transects. All organisms observed in the transect were counted until reaching the minimum number of 100 organisms, a value established to maintain the sample error below 20%, with a 95% confidence coefficient. We counted more than one transect in

chambers with samples where $N < 100$ organisms/transect. The phytoplankton density (organisms/mL) was estimated from the number of organisms counted in each transect multiplied by the correction factor, calculated based on the volume of original 2 mL (Lund et al., 1958). The results were presented as relative density (%), which was calculated from the density of each phytoplankton taxa divided by the total density of the sample considered (e.g. a sampling site or season).

The phytoplankton classification follows specific literature (Komárek & Anagnostidis, 1998; Sant'Anna et al., 2004; Komárek & Anagnostidis, 2005; Hoffmann et al., 2005; Metzeltin & Lange-Bertalot, 2007; Godinho et al., 2010; Rodrigues et al., 2010; Rosini et al., 2012; Rosini et al., 2013b; Rosini et al., 2013a; Cavalcante et al., 2013; Almanza et al., 2016; Campanelli et al., 2017).

Statistical analysis: Shapiro-Wilks test and Levene's test were used to evaluate the normality of distributions and the equality of the variances for all abiotic and biotic data. The non-parametric Kruskal-Wallis analysis was performed to investigate spatial (between different sites) and seasonal (between different seasons) variations of the abiotic predictors, always with a significance level of 5%.

We used distance-based multivariate analysis of variance (Permutational Multivariate Analysis of Variance – PERMANOVA and Analysis of Similarities – ANOSIM - both with 9999 permutations) to test spatial and temporal variations in the phytoplankton assemblages. These analyses were based on a dissimilarity matrix obtained with the Bray-Curtis index (Faith et al., 1987; Legendre & Legendre, 2012), applied to phytoplankton density data (including all species) and using sampling sites (P01-P06) and seasons (sum/2017, aut/2017, win/2017, spr/2017, sum/2018, aut/2018, win/2018 and spr/2018) as the grouping variables.

The BioEnv approach (Clarke & Ainsworth, 1993) was used to evaluate potential relationships between the dissimilarities in the phytoplankton community structure and dissimilarities in the environmental variables. This analysis correlates dissimilarity matrices of all possible combinations of environmental variables (computed using Euclidean distance) with the biotic dissimilarity matrix (generated using the Bray-Curtis index on phytoplankton density data), and selects the subset of environmental variables that shows the best correlation with the biotic data. We used the variance inflation factor (VIF) to identify co-linearity between environmental variables, and only variables

with $VIF < 10$ were used in the environmental matrix. The quality of the relationships between biotic and environmental dissimilarities was assessed through the Spearman's rank correlation, and the statistical significance of the biotic matrix and its best environmental subset was tested using the Mantel test (with 9999 permutations).

To reduce the limitations of the dissimilarity-based approaches discussed by Warton et al. (2012), we performed a constrained analysis (Redundancy Analysis - RDA), by using the same biotic and environmental matrices applied in the BioEnv. The quality of the RDA model adjusted and the ability of each environmental variable to explain the variance in phytoplankton were tested using ANOVA for redundancy analysis (function `anova.cca` in the Vegan R package, under 999 permutations), and the variables were considered to be significant when $p < 0.05$.

All analyses were conducted in R environment (R Core Team, 2020) using the Vegan (Oksanen et al., 2013) package. In both BioEnv and RDA approaches, the phytoplankton density matrix was previously subjected to Hellinger transformation to correct the asymmetry of the data (Borcard et al., 2011). All other analyses were conducted without data transformation.

Results

No significant spatial variations were observed for abiotic variables (Kruskal-Wallis > 0.05 for all variables; Table A-I). Seasonally, most of the environmental predictors varied significantly, highlighting low water temperatures in win/2017 and win/2018, high pH values in summer and spring at both years, decreased rainfall and increased water transparency in the cold seasons (Table A-II Annex I).

The phytoplankton community was composed by 34 taxa, distributed in 6 divisions, 9 classes, 15 orders and 21 families (Table I). Aphanizomenonaceae (*Aphanizomenon* sp. and *Dolichospermum* spp.), Ceratiaceae (exclusively *Ceratium* spp.), Scenedesmaceae (*Coelastrum* spp.) and Sphaerocystidaceae (*Sphaerocystis* sp.) (Fig. 2) were the most representative families in all sampled sites. However, no significant spatial dissimilarities were observed in the phytoplankton community structure (Fig. 3). The results of PERMANOVA and ANOSIM analyses showed significant temporal dissimilarities in the phytoplankton community (Fig. 4). Again, Aphanizomenonaceae, Ceratiaceae, Scenedesmaceae and Sphaerocystidaceae were the

Table I. Taxonomic groups of phytoplankton recorded in Itá Reservoir, upper Uruguay River, southern Brazil, between February 2017 and December 2018. All samples were conducted with a 20µm phytoplankton net. Due to this sampling strategy used, the data set presents only organisms larger than 20 µm.

Division	Family	Taxa	
Bacillariophyta	Fragilariaceae	<i>Fragillaria</i> (Lyngbye 1819) spp.	
	Surirellaceae	<i>Surirella</i> (Turpin 1828) spp. Bacillariophyceae (Haeckel 1878) spp.	
	Aulacoseiraceae	<i>Aulacoseira</i> (Thwaites 1848) spp. <i>Aulacoseira granulatta</i> (Ehrenberg) (Simonsen 1979)	
	Melosiraceae	<i>Melosira varians</i> (Agardh 1827) <i>Melosira</i> (Agardh 1824) spp.	
	Thalassiosiraceae	<i>Thalassiosira</i> (Cleve 1873) spp.	
Charophyta	Closteriaceae	<i>Closterium</i> (Nitzsch) (Ralfs 1848) spp.	
	Desmidiaceae	<i>Staurastrum</i> (Ralfs 1848) spp. <i>Staurastrum</i> (Ralfs 1848) sp.1 <i>Staurastrum</i> (Ralfs 1848) sp.2	
	Zygnemataceae	<i>Mougeotia</i> (Agardh 1824) spp.	
Chlorophyta	Goniaceae	<i>Gonium</i> (Müller 1773) spp.	
	Sphaerocystidaceae	<i>Sphaerocystis</i> (Chodat 1897) spp.	
	Volvocaceae	<i>Volvox</i> (Linnaeus 1758) spp.	
	Hydrodictyceae	<i>Pediastrum</i> (Meyen 1829) spp. <i>Sorastrum spinulosum</i> (Nägeli 1849)	
	Scenedesmaceae	<i>Coelastrum indicum</i> (Turner 1892) <i>Coelastrum microporum</i> (Nägeli 1855) <i>Coelastrum reticulatum</i> var. duplex (Compère 1970)	
		Chlorellaceae	<i>Chlorella</i> (Beyerinck [Beijerinck] 1890) spp.
Oocystaceae		<i>Oocystis</i> (Nägeli) (Braun 1855) spp.	
Cyanobacteria	Microcystaceae	<i>Sphaerocavum brasiliense</i> (De Azevedo & Sant' Anna 2003) Chroococcales (Schaffner 1922) spp.	
	Aphanizomenonaceae	<i>Aphanizomenon</i> (Morren) (Bornet & Flahault 1886 '1888') spp. <i>Dolichospermum solitarium</i> (Klebahn) (Wacklin et al. 2009) <i>Dolichospermum</i> (Ralfs ex Bornet & Flahault) (Wacklin et al. 2009) sp.1 <i>Dolichospermum</i> (Ralfs ex Bornet & Flahault) (Wacklin et al. 2009) sp.2	
		Pseudanabaenaceae	<i>Pseudanabaena</i> (Lauterborn 1915) spp.
		Euglenaceae	<i>Euglena</i> (Ehrenberg 1830) spp.
Euglenozoa	Phacaceae	<i>Lepocinclis acus</i> (Müller) (Marin & Melkonian 2003) <i>Phacus pleuronectes</i> (Müller 1841)	
	Miozoa	Ceratiaceae	<i>Ceratium</i> (Schrank 1793) spp.

most representative families, with a clear alternation of these groups in the different seasons. Aphanizomenonaceae was the most representative family in summer/2017 (45.22% of total phytoplankton density) and summer/2018 (49.75% of total phytoplankton density). *Ceratium* spp. (Family Ceratiaceae) were the most representative species in the cold seasons, representing more than 91% of total phytoplankton density in winter/2017 and more than 94% in winter/2018. Green algae of the Scenedesmaceae (49.9%) and Sphaerocystidaceae (31.5%) families dominated spring/2017. *Coelastrum* spp. (Family Scenedesmaceae) were the most abundant algae also in spring/2018, where they represented more than 53% of total phytoplankton density (Fig. 4).

The BioEnv analysis indicated water

temperature as the environmental variable best correlated with the phytoplankton dissimilarity matrix ($r = 0.530$; Table II). The Mantel test showed significant correlations between the environmental and biotic matrices (Mantel statistic $r = 0.233$; $p < 0.001$), indicating that the dissimilarity in the selected environmental variables led to significantly dissimilar phytoplankton structures. The results for other BioEnv models are show in Table II.

In the RDA analysis, the first two axes of the abiotic variables explained, together, more than 81% of the data variance in the phytoplankton densities. The first axis (RDA1 = 63.48%) was related mainly to pH and water temperature and the second axis (RDA2 = 17.68%) included mainly nutrients and TDS concentrations (Fig. 5). The tests of significance showed significant results for both axes

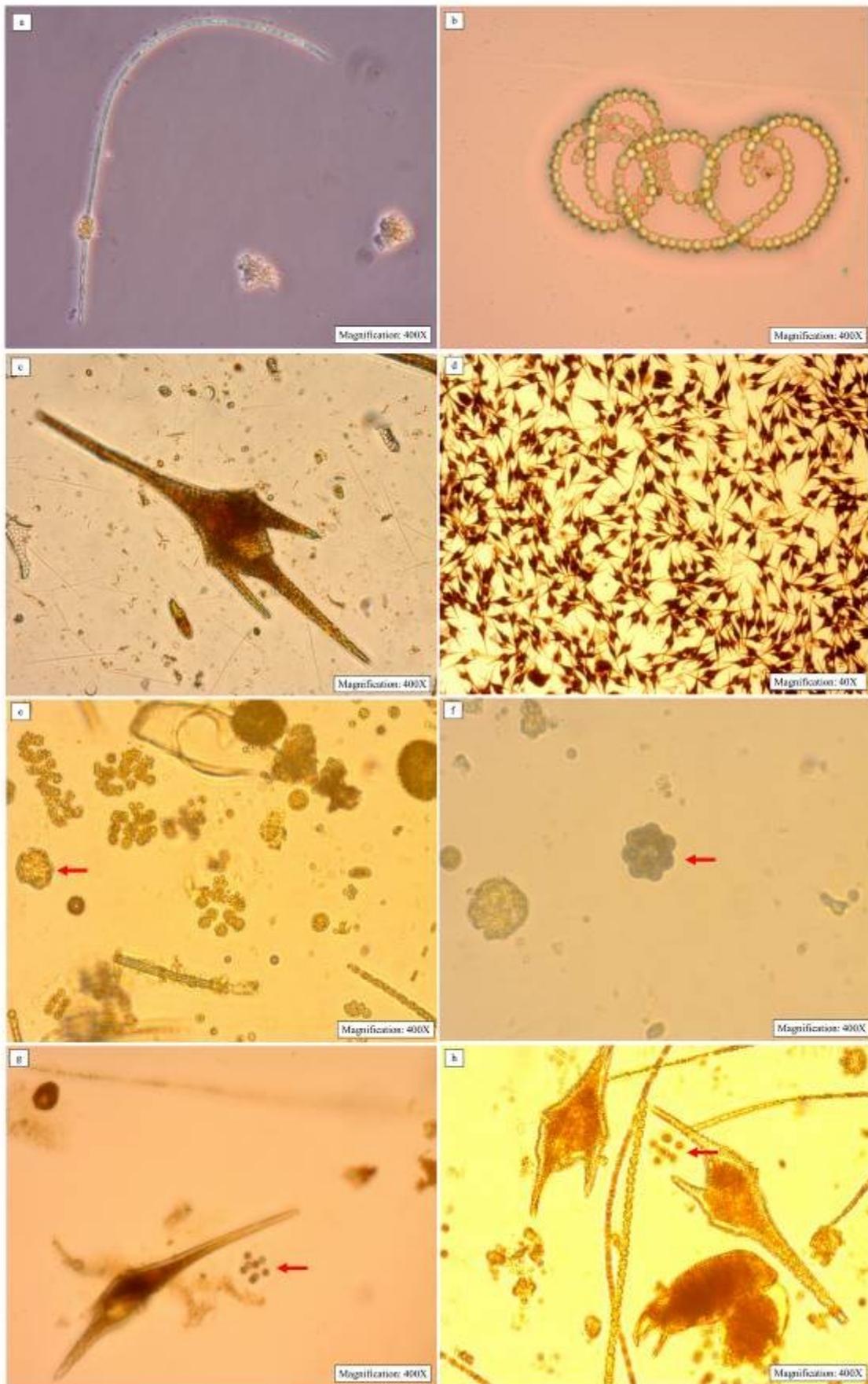


Figure 2 (previous page). Main phytoplankton taxonomic groups recorded in Itá Reservoir, upper Uruguay River, southern Brazil, between February 2017 and December 2018. Family Aphanizomenonaceae: (a) *Aphanizomenon* sp.; (b) *Dolichospermum* spp.; Family Ceratiaceae: (c-d) *Ceratium* spp.; Family Scenedesmaceae: (e-f) *Coelastrum* spp.; Family Sphaerocystidaceae: (g-h) *Sphaerocystis* spp.

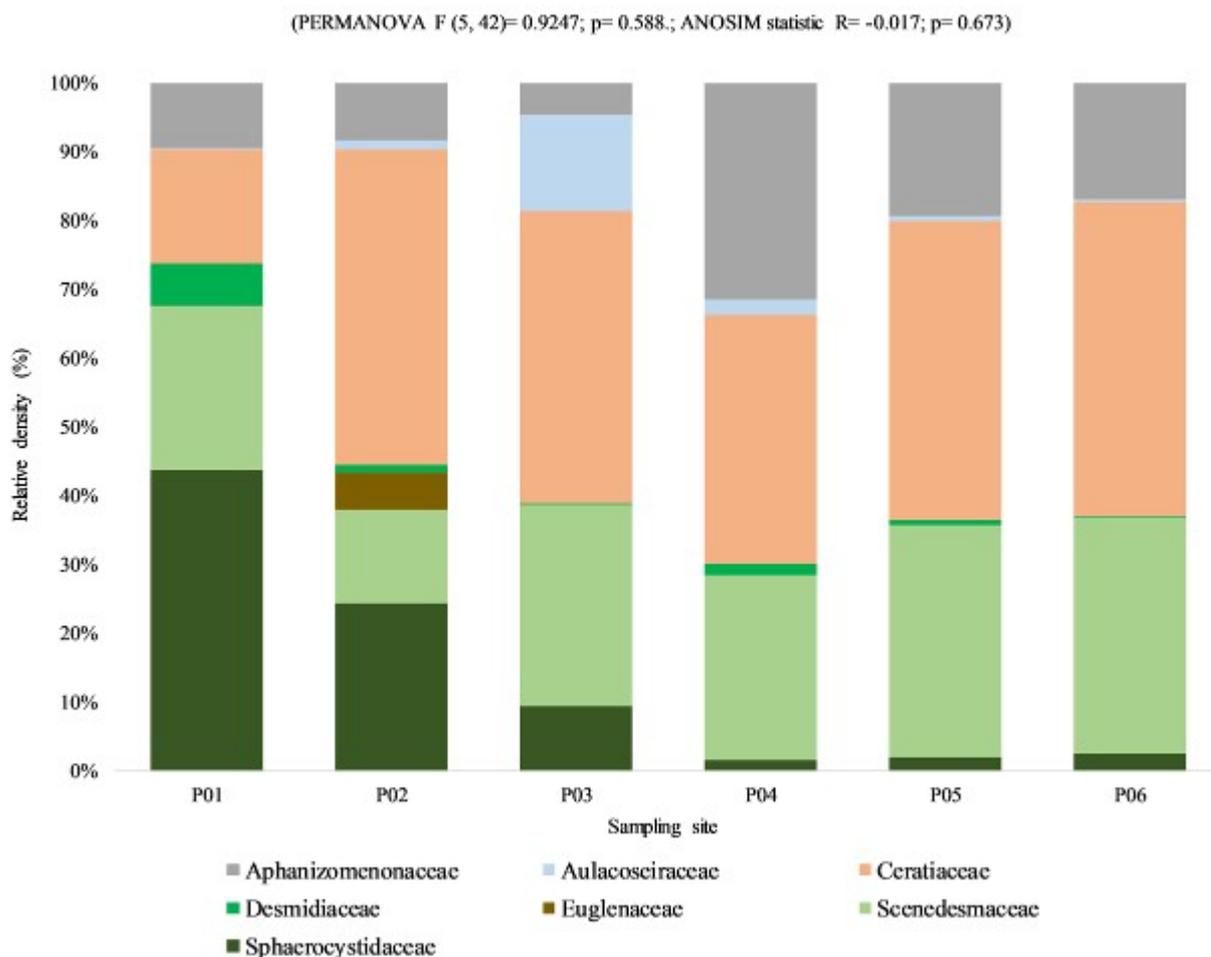


Figure 3. Relative spatial density (percentage in relation to total density in each sampled site) of most representative phytoplankton families recorded in the Itá Reservoir, upper Uruguay river, southern Brazil, between February 2017 and December 2018. Only families with relative density $\geq 5\%$ at least one sampling site were included in the figure. Results of the PERMANOVA and ANOSIM analyses are showed in the figure.

(Table III) and included monthly rainfall, pH, nutrients concentrations, TDS and water temperature among the most critical abiotic factors driving the dissimilarity in the phytoplankton (Table IV), corroborating the results of the BioEnv approach.

Discussion

The main result of this study was that there is a significant temporal dissimilarity in the phytoplankton community in the Itá reservoir, and that such dissimilarity was significantly correlated to the seasonal variability of the environmental

predictors. Furthermore, we observed three seasonal density peaks in the phytoplankton community: (i) dominance of potential harmful cyanobacteria (*Aphanizomenon* sp. and *Dolichospermum* spp.) in summer; (ii) dominance of alien dinoflagellates (*Ceratium* spp.) in autumn/winter; and (iii) increase in the density of green algae (*Coelastrum* spp. and *Sphaerocystis* sp.) in spring.

Our results support the hypothesis that seasonal variability of some climate (e.g. rainfall and water temperature) and hydrological (e.g. nutrient availability, pH and TDS) variables would explain a

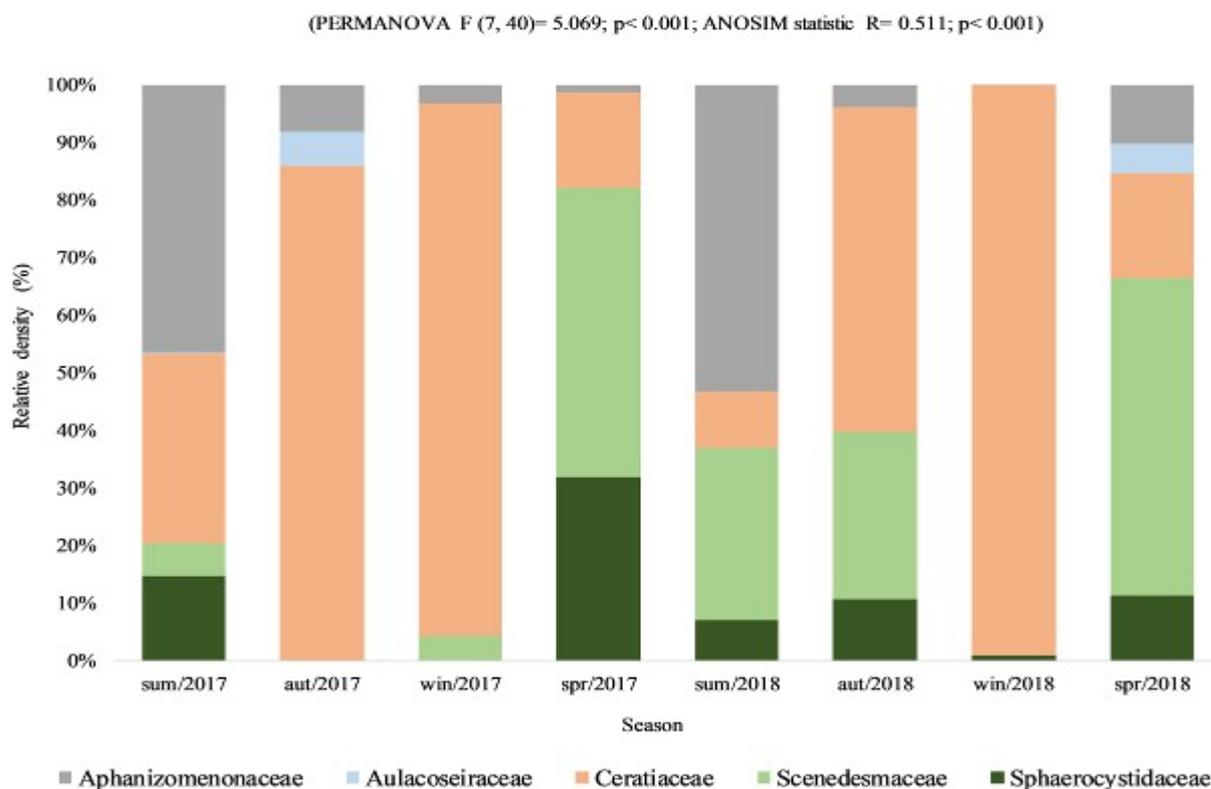


Figure 4. Relative seasonal density (percentage in relation to total density in each season) of most representative phytoplankton families recorded in the Itá Reservoir, upper Uruguay river, southern Brazil, between February 2017 and December 2018. Only families with relative density $\geq 5\%$ at least one season were included in the figure. Results of the PERMANOVA and ANOSIM analyses are showed in the figure.

Table II. BioEnv analysis for the relationship between phytoplankton community and environmental variables in Itá Reservoir, upper Uruguay River, southern Brazil, between February 2017 and December 2018. All taxonomic groups were included in the biotic matrix, whereas only non-correlated variables (Variance Inflation Factor $VIF < 10$) were used in the environmental matrix. DO = Dissolved Oxygen (mg/L); EC = Electronic conductivity ($\mu S/cm$); mont.rainfall = monthly rainfall (mm); nitra = N-Nitrate concentration (mg/L); TDS = Total Dissolved Solids (mg/L); total. p = Total Phosphorus concentration (mg/L); turb = turbidity (NTU); water. temp = water temperature ($^{\circ}C$); water. transp = water transparency. Spearman correlation for the best-adjusted model is show in bold type.

Model size	Model	Spearman correlation
1	water.temp	0.530
2	mont.rainfall + water.temp	0.418
3	mont.rainfall + nitra + water.temp	0.392
4	mont.rainfall + nitra + pH + water.temp	0.383
5	mont.rainfall + nitra + pH + total.p + water.temp	0.351
6	mont.rainfall + nitra + pH + total.p + water.temp + water.transp	0.310
7	mont.rainfall + nitra + pH + TDS + total.p + water.temp + water.transp	0.260
8	EC + mont.rainfall + nitra + pH + TDS + total.p + water.temp + water.transp	0.231
9	EC + mont.rainfall + nitra + pH + TDS + total.p + turb + water.temp + water.transp	0.206
10	DO + EC + mont.rainfall + nitra + pH + TDS + total.p + turb + water.temp + water.transp	0.178

significant portion of the temporal phytoplankton dissimilarities in this ecosystem. Similar sets of environmental variables have been pointed out as key factors driving spatial and temporal dissimilarities in the phytoplankton communities and favoring the occurrence of harmful and alien algae in several subtropical reservoirs (Mac Donagh et al., 2005; Lv et al., 2014; Beamud et al., 2015; Almanza et al., 2016; Yang et al., 2016; Meichtry de Zaburlín et al., 2016; Haakonsson et al., 2017; Yang et al., 2017; Li et al., 2018; Huo et al., 2019). In southern Brazil, seasonal variation of the rainfall was pointed out as the most important process structuring phytoplankton communities in the Dona Francisca reservoir, Jacuí river, where high dissimilarity in the phytoplankton assemblages was observed during the rainy period (Schneck et al., 2011). Similarly, in the same river basin, rainfall regime and hydrodynamics (water mixture and residence time) were included as the key factors controlling phytoplankton community structure in the Ernestina and Itaúba reservoirs (Cassol et al., 2017). The land-use features in the watershed and the nutrient settlement were important structuring factors of phytoplankton biomass in Segredo reservoir (Iguaçu river) and Capivari reservoir (Capivari river) (Borges et al., 2008).

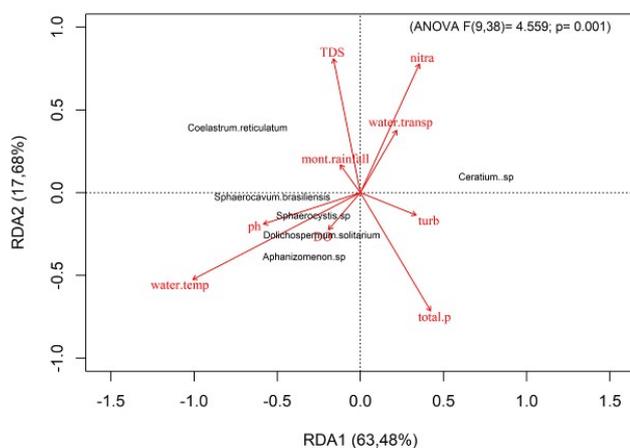


Figure 5. Redundancy Analysis (RDA) ordination of the phytoplankton density and the environmental variables in the Itá Reservoir, upper Uruguay River, southern Brazil, between February 2017 and December 2018. All taxonomic groups were included in the biotic matrix, but only taxonomic groups classified in the most representative phytoplankton families (Aphanizomenonaceae, Ceratiaceae, Scenedesmaceae and Sphaerocystidaceae) are showed in the figure. Only non-correlated variables (Variance Inflation Factor $VIF < 10$) were used in the environmental matrix. The result of ANOVA permutation test (function `anova.cca` in the Vegan R package, under 999 permutations) indicating the significance of the adjusted model is showed in the figure.

Table III. Summary statistics for the test of significance (function `anova.cca` in the Vegan R package, under 999 permutations) for the first two axes of Redundancy Analysis (RDA) on the phytoplankton densities and abiotic variables in the Itá Reservoir, upper Uruguay River, southern Brazil, between February 2017 and December 2018. All taxonomic groups were included in the biotic matrix, whereas only non-correlated variables (Variance Inflation Factor $VIF < 10$) were used in the environmental matrix. Significant p values are show in bold type.

	RDA axis 1	RDA axis 2
Eigenvalues	0.129	0.036
Explained variance (%)	63.48	17.68
Significance (ANOVA)	F= 26.052; p= 0.001	F= 7.256; p= 0.002

Table IV. Results of the ANOVA Permutation Analysis (function `anova.cca` in the Vegan R package, under 999 permutations) performed from the Redundancy Analysis (RDA) for the relationship between phytoplankton density and environmental variables in Itá Reservoir, upper Uruguay River, southern Brazil, between February 2017 and December 2018. All taxonomic groups were included in the biotic matrix, whereas only non-correlated variables (Variance Inflation Factor $VIF < 10$) were used in the environmental matrix. DO = Dissolved Oxygen (mg/L); mont.rainfall = monthly rainfall (mm); nitra = N-Nitrate concentration (mg/L); TDS = Total Dissolved Solids (mg/L); total.p = Total Phosphorus concentration (mg/L); turb = turbidity (NTU); water.temp = water temperature ($^{\circ}\text{C}$); water.transp = water transparency. Significant p values are show in bold type.

Environmental variable	F	p
DO	2.485	0.038
mont.rainfall	2.936	0.019
nitra	5.493	0.001
pH	5.518	0.002
TDS	4.231	0.005
total.p	2.429	0.049
turb	1.173	0.277
water.temp	14.410	0.001
water.transp	2.358	0.057

The variability of the environmental predictors may create periodic conditions that may promote significant alternations in the phytoplankton community, favoring the establishment and growth of specific algal groups, which could explain the seasonal dominance peaks observed in the Itá

reservoir. The seasonal variability of water temperature, for instance, may explain the higher density of cyanobacteria (*Aphanizomenon* sp. and *Dolichospermum* spp.) in the warm seasons. In a review compiling data of different kinds of ecosystems around the world, O'Neil et al. (2012) suggested that rising temperatures will change many of the physical-chemical features of freshwater environments, favoring the establishment, rapid growth and dominance of different species of cyanobacteria. Higher temperatures may decrease surface water viscosity (Vogel, 1996), which promotes the sinking of larger and non-motile cells (e.g. diatoms and chlorophytes). With the sinking of these organisms, the interspecific competition in the superficial layers is reduced, favoring the growth of organisms better adapted to buoyancy. In this case, the presence of morphological adaptations (as the gas vesicles observed in some cyanobacteria species) allow an important advantage (Paerl & Huisman, 2009). Warmer water may also change the availability of different forms of carbon (e.g. CO₂ and carbonates) and modify the diffusion of some nutrients (e.g. soluble Phosphorus and Nitrogen) towards the cell surface, both crucial processes, mainly in nutritionally poor environments (Vogel, 1996; Peperzak, 2003). Again, cyanobacteria can take advantage in this scenario, mainly due to their physiological adaptations, as optimization of nutrient fixing and carbon uptake (O'Neil et al., 2012).

Several studies conducted in different freshwater ecosystems have been demonstrating that the increase of water temperature, combined with the reduction of nutrients and inorganic carbon inflow (as a consequence of more constant and lasting drought periods, with the decrease of nutrient loading, for example) might favor the occurrence of cyanobacterial blooms (Brock, 1973; Shapiro, 1973; López-Archilla et al., 2004; Viney et al., 2007; Carvalho et al., 2011; Dziallas & Grossart, 2011; Okello & Kurmayer, 2011; Kosten et al., 2012; O'Neil et al., 2012; Paerl & Otten, 2013; Dao et al., 2016; Simić et al., 2017; Haakonsson et al., 2017). Increased water temperature was the most important factor favoring cyanobacteria dominance in the Tingxi reservoir, located in subtropical southeast China (Lv et al., 2014). In four subtropical reservoirs also located in southeast China, Yang et al. (2016a) observed that the decline in water level during dry seasons modified the internal nutrient loading regimes, boosting the cyanobacteria dominance in these reservoirs. Tucci & Sant'Anna (2003)

observed the highest densities of the cyanobacteria *Cylindrospermopsis raciborskii* during periods with higher water temperature and low water transparency in Lago das Garças reservoir, southeast Brazil. In the same way, cyanobacterial blooms were related to decrease of water level and increase of water temperature in Alagados reservoir, located in Tibagi river, southern Brazil (Beló et al., 2018).

Harmful cyanobacteria dominance may result in serious consequences for human drinking and irrigation water supplies, fisheries, recreational resources and maintenance of natural ecosystems (Paerl & Huisman, 2009). In most current water management protocols, cyanobacterial blooms control is based on the reduction of nutrient inputs. However, as we show here, cyanobacterial bloom can also be observed in mesotrophic and oligotrophic environments, stimulated mainly by climate conditions in these cases (Paerl & Otten, 2013). Thus, besides the nutrient input control, water authorities must consider the hydrological and physical-chemical effects of climatic change in their management strategies, with a special focus on surface water heating, stratification and availability of inorganic carbon.

The seasonal variability of water temperature may also be the underlying factor behind the dominance of the alien dinoflagellate *Ceratium* spp. in the autumn/winter seasons in Itá reservoir. The genus *Ceratium* Schrank is considered an alien/invasive taxa in South American freshwaters (Boltovskoy et al., 2013). Since the 90s, species of this genus have been recorded in Chile and Argentina (Mac Donagh et al., 2005; Boltovskoy et al., 2013). Ten years later, the genus was recorded in rivers and reservoirs from the southeastern (Santos-Wisniewski et al., 2007; Matsumura-Tundisi et al., 2010) to the northeastern (Oliveira et al., 2011) Brazil. In southern Brazil, the first record of the genus as an alien organism was reported in 2013 (Cavalcante et al., 2013).

Ceratium species are considered good competitors among freshwater phytoplankton, due to intrinsic features, mainly due to excellent swimming performance, low predation pressure, tolerance to wide water temperature range and potential mixotrophy (Heaney & Talling, 1980; Heaney et al., 1988; Xie et al., 1998; Salmaso, 2003; Reynolds, 2006; Cardoso et al., 2010; Cavalcante et al., 2016). Our results showed that, in the cold seasons, the average surface water temperature (around 22°C in autumn and 19°C in winter) remained very close to the optimum temperature for the growth of

Ceratium spp. [between 15 and 25°C (Heaney & Talling, 1980; Butterwick et al., 2005)]. Furthermore, the decrease of rainfall in winter/2017 and winter/2018 may reduce the discharge of tributaries, limiting the runoff of nutrients and organic matter and resulting in a low mixing and highly transparent water column in these seasons. In this case, surface water may become severely deficient in nutrients, while, in the deeper layers, nutrient availability is richer, but there is a low light condition for primary production and growth of autotrophic organisms. One of the most advantageous adaptive strategies in this scenario is to be able to make substantial vertical migrations between the two water column compartments, a very evident ability in *Ceratium* species (Reynolds, 2006). Furthermore, the poor nutrient availability in the cold/dry seasons may favor organisms that can exploit alternative resources. In this case, the potential mixotrophy capacity that some *Ceratium* species have is an important advantage compared to others phytoplankton species.

The effect of water temperature and nutrient limitation has been discussed in several studies that report *Ceratium* spp. invasions in subtropical lakes and reservoirs (Hart & Wragg, 2009; Silverio et al., 2009; Almanza et al., 2016; Meichtry de Zaburlín et al., 2016; Morales, 2016; Crossetti et al., 2019). In the Furnas reservoir (southeast Brazil), Silva et al. (2012) reported a better development of *Ceratium furcoides* during the highly transparent water observed in the cool/dry months. The abundance of *C. furcoides* revealed inverse correlations with temperature and insolation in an artificial urban lake located in the city of Porto Alegre, southern Brazil (da Silva et al., 2019). High organic-matter content, nutrient availability, well-oxygenated water and temperatures from 15 to 25 °C were cited as the main environmental conditions that contribute to the establishment of *C. furcoides* in Faxinal and Maestra reservoirs, southern Brazil (Cavalcante et al., 2016).

Despite being a non-toxic genus, high biomasses of *Ceratium* spp. may be harmful to other aquatic organisms (especially to ichthyofauna), mainly due to oxygen depletion (Smayda, 1997). Moreover, in watersheds destined for public consumption, extreme bloom events may cause odor and taste in drinking water, besides clogging of filters during water treatment (Ewerts et al., 2013). Our results warned to the possibility of increased *Ceratium* spp. blooms in future climate scenarios with more severe drought and/or extreme freezing periods, mainly during ENSO events (Barros et al.,

2002). This highlights the need to consider the effects of these climatic disturbances on the physical-chemical forces that control the structure and dynamic of the phytoplankton communities, especially in disturbed ecosystems susceptible to biological invasions.

Finally, the higher nutrient and TDS concentrations and low light availability during the water column mixture seem to be a determining factor for the dominance of green algae in the spring and early summer. Our results showed increased precipitation and decreased water transparency, suggesting a well-mixed water column in these seasons. This scenario is usually good for phytoplankton development (Moura et al., 2013). However, for some species, increased water mixture is a critical factor, mainly due to water transparency reduction, which reduces light availability and photosynthesis efficiency, and species that can settle in low-light conditions have advantages in these conditions. In the functional classification of the freshwater phytoplankton proposed by Reynolds et al. (2002) and revised by Kruk et al. (2017), the groups “F”, “G” and “J” include green algae species with rapid growth in low-light and well-mixed habitats. Therefore, in the Itá reservoir, the dominance of chlorophytes included in these functional groups (e.g. *Coelastrum* spp. and *Sphareocystis* sp.) in the spring and early summer can be explained by their adaptive capacity, mainly the tolerance to restrictive physical factors, which results in advantages for their growth and establishment in these seasons. Spring blooms of chlorophytes have been described in several lakes and subtropical reservoirs (de Almeida & Melo, 2011; Wu et al., 2013; Moura et al., 2013; Moreti et al., 2013; Xiao et al., 2016; Li et al., 2018; Yang et al., 2019; Bortolini et al., 2019), supporting our results.

Conclusion

The approaches used in this study proved to be useful not only to assess the existence of correlations between phytoplankton dissimilarities and environmental variability, but also to determine the set of environmental variables that best explain the dissimilarities in algal communities in subtropical freshwater environments. We recommend that future studies on phytoplankton ecology within subtropical reservoirs or in similar ecosystems, could also: i) consider a sampling design with several replicates at each sampling site at the same sampling date. These adjustments would

probably result in more robust spatial (between sites) and temporal (between seasons) comparisons; ii) for phytoplankton, the Size-Density Relationship (the smaller the organism, the greater its abundance in the environment) presents an important factor in structuring communities. Thus, we recommend using a less selective sampling method to record the phytoplankton samples; iii) we used organisms/individuals instead of cells or biovolume as a phytoplankton density metric. We understand that using cells/mL instead of organisms/mL would only change the density of colonial or filamentous organisms. In this case, we would be mainly changing the densities of cyanobacteria (e.g. *Dolichospermum* spp. and *Aphanizomenon* spp.), endorsing the dominance of these organisms in samples where they are already dominants. The density based on the organism shows clearly the structure of the phytoplankton community and, if we count cell by cell, we will only reinforce these results, increasing the cyanobacteria densities in warm seasons. Furthermore, the use of organisms/individuals as a density metric has been supported as a good tool to evaluate phytoplankton population and community dynamics, especially in studies which aim to evaluate spatial and temporal variability of the community structure, ecological succession and biological invasions (da Silva et al., 2005, 2018; Becker et al., 2009; Schneck et al., 2011; Moura et al., 2013; Lv et al., 2014; Almanza et al., 2016; Bortolini et al., 2016; Simić et al., 2017; Li et al., 2018). Anyway, we encourage the use of cells/L or biovolume as density metrics, especially for studies that consider energy flux, primary production and trophic relationships involving phytoplankton communities.

Our results showed that the temporal dissimilarities in the phytoplankton structure in the Itá Reservoir were significantly related to environmental dissimilarities, which are directly associated with the temporal variability of conditions and resources, especially the climatic and hydrological factors that present well-established seasonal variations in this environment. The climate and hydrological conditions also seem to play a key role in the establishment and dominance of potentially toxic (*Aphanizomenon* spp. and *Dolichospermum* spp.) and alien (*Ceratium* spp.) species. This alerts about the need for more careful investigations regarding the influence of these factors on the phytoplankton communities structuring and their influence on favoring potential periodic blooms of harmful and alien algae in the

subtropical freshwater ecosystems. These investigations become even more urgent if we consider the anthropic disturbances in the watershed area (such as deforestation, agricultural activities and urbanization), besides climatic changes (e.g. extreme drought and rain events) in local and regional scales.

Considering the importance of the phytoplankton communities in the ecological processes at different environments, mainly as a base of the trophic networks, our results may provide valuable additional information on algal life strategies, sensitivities, and tolerances. This is important to understand phytoplankton dynamics and its implications in the ecosystem's functioning, and can greatly contribute to the understanding of fundamental issues in freshwater ecology, as community succession, colonization and dominance patterns, pulse effects, biological invasions and growth/establishment of harmful and alien organisms, especially in disturbed ecosystems, such as artificial reservoirs.

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Climate and hydrological processes explain temporal dissimilarity in the phytoplankton community and favor seasonal dominance of harmful and alien algae in a subtropical reservoir

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ANNEX

Table A-I. Mean (\pm standard deviation) and results of Kruskal-Wallis test for main environmental variables recorded in different sampling sites (P01-P06) in Itá Reservoir, upper Uruguay River, southern Brazil, between February 2017 and December 2018. DO = Dissolved Oxygen; EC = Electronic Conductivity; N-Nitrate = Nitrate concentration; TDS = Total Dissolved Solids; Total-P = total Phosphorus concentration. Monthly insolation, rainfall and wind intensity were not spatially compared because the values recorded are repeated in all the different sampled sites.

Environmental variable	P01	P02	P03	P04	P05	P06	Kruskal-Wallis Chi ²	df	p
	Mean \pm SD								
DO (mg/L)	7.674 \pm 1.317	7.600 \pm 0.809	7.575 \pm 0.817	8.000 \pm 1.156	8.093 \pm 1.105	8.199 \pm 1.323	5.176	5	0.394
EC (μ S/cm)	75.585 \pm 16.757	72.821 \pm 14.178	80.379 \pm 14.387	71.919 \pm 21.563	79.715 \pm 14.012	74.066 \pm 11.878	4.671	5	0.457
<i>Escherichia coli</i> (CFU/mL)	1.000 \pm 2;291	0.375 \pm 0.992	0.750 \pm 1.639	1.750 \pm 2.384	0.000 \pm 0.000	0.625 \pm 1.653	6.664	5	0.246
Monthly insolation (sunny hours)	–	–	–	–	–	–	–	–	–
Monthly precipitation (mm)	–	–	–	–	–	–	–	–	–

Environmental variable	P01	P02	P03	P04	P05	P06	Kruskal-Wallis Chi ²	df	p
	Mean±SD	Mean±SD	Mean±SD	Mean±SD	Mean±SD	Mean±SD			
Monthly wind intensity (m/s)	–	–	–	–	–	–	–	–	–
N-Nitrate (mg/L)	0.738±0.213	0.576±0.210	0.816±0.170	0.671±0.142	0.781±0.159	0.644±0.397	6.408	5	0.268
pH	7.669±0.576	7.760±0.704	7.681±0.581	8.004±0.728	8.222±0.761	8.218±0.828	4.868	5	0.432
TDS (mg/L)	48.105±12.944	45.979±10.79 3	51.133±11.519	47.963±10.957	49.796±10.785	46.838±9.670	3.991	5	0.550
Total coliforms (CFU/mL)	26.625±32.472	20.250±25.19 7	27.000±35.103	34.500±43.055	11.250±12.607	20.625±24.565	2.408	5	0.790
Total-P (mg/L)	0.196±0.089	0.157±0.074	0.160±0.082	0.135±0.059	0.141±0.062	0.140±0.069	2.498	5	0.776
Turbidity (NTU)	6.018±2.620	5.024±3.065	5.628±3.480	5.325±2.725	4.674±2.536	6.211±3.758	0.955	5	0.966
Water temperature (°C)	22.549±3.365	22.583±3.405	22.700±3.478	23.195±3.062	23.960±3.104	23.725±3.437	1.679	5	0.891
Water transparency (m)	1.700±0.729	1.640±0.617	1.825±0.758	1.776±0.673	1.950±0.947	1.658±0.668	1.073	5	0.956

Effects of abiotic factors in algal community

Table A-II. Mean (\pm standard deviation) and results of Kruskal-Wallis test for main environmental variables recorded seasonally in Itá reservoir, upper Uruguay River, southern Brazil, between February 2017 and December 2018. DO = Dissolved Oxygen; EC = Electronic Conductivity; N-Nitrate = nitrate concentration; TDS = Total Dissolved Solids; Total-P = total Phosphorus concentration. Significant *p* values are show in bold type

Environmental variables	2017				2018				Kruskal-Wallis Chi ²	df	<i>p</i>
	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring			
DO (mg/L)	8.506 \pm 1.142	6.696 \pm 0.333	8.426 \pm 0.486	8.381 \pm 0.310	8.031 \pm 0.191	5.656 \pm 0.322	8.541 \pm 0.354	8.611 \pm 0.142	31.426	7	<0.01
EC (μ S/cm)	47.641 \pm 1.476	84.833 \pm 3.337	54.666 \pm 15.18 4	82.333 \pm 4.459	87.000 \pm 3.958	81.666 \pm 5.849	80.500 \pm 3.452	87.333 \pm 8.279	30.998	7	<0.01
<i>Escherichia coli</i> (CFU/mL)	0.000 \pm 0.000	0.333 \pm 0.745	2.500 \pm 2.600	0.833 \pm 1.863	2.166 \pm 2.794	0.000 \pm 0.000	0.166 \pm 0.373	0.000 \pm 0.000	15.643	7	0.028
Monthly insolation (sunny hours)	176.333 \pm 6.94 4	113.000 \pm 21.95 4	202.667 \pm 8.01 3	210.000 \pm 35.05 2	178.667 \pm 19.36 2	161.000 \pm 48.25 6	141.000 \pm 16.67 3	168.000 \pm 52.94 0	11.774	7	0.108
Monthly rainfall (mm)	137.000 \pm 23.5 37	254.667 \pm 127.0 20	59.667 \pm 55.07 1	184.000 \pm 73.92 3	163.000 \pm 47.76 2	66.333 \pm 21.545	116.666 \pm 62.76 0	229.000 \pm 85.05 6	12.427	7	0.058
Monthly wind intensity (m/s)	1.103 \pm 0.225	1.437 \pm 0.231	1.327 \pm 0.302	1.370 \pm 0.412	1.027 \pm 0.230	1.313 \pm 0.065	1.420 \pm 0.188	1.250 \pm 0.071	5.765	7	0.567
N-Nitrate (mg/L)	0.395 \pm 0.178	0.863 \pm 0.077	0.823 \pm 0.222	0.814 \pm 0.333	0.485 \pm 0.214	0.758 \pm 0.083	0.673 \pm 0.060	0.821 \pm 0.118	27.318	7	<0.01
pH	8.706 \pm 0.677	7.426 \pm 0.086	7.013 \pm 0.204	8.318 \pm 0.336	7.776 \pm 0.454	7.163 \pm 0.082	8.105 \pm 0.335	8.900 \pm 0.129	37.239	7	<0.01
TDS (mg/L)	23.917 \pm 0.778	55.167 \pm 2.266	38.000 \pm 4.864	52.000 \pm 2.828	56.167 \pm 2.671	53.000 \pm 4.654	51.833 \pm 1.462	56.633 \pm 5.343	32.856	7	<0.01
Total coliforms (CFU/mL)	68.833 \pm 28.37 5	4.667 \pm 8.673	4.500 \pm 2.986	24.333 \pm 15.129	69.333 \pm 26.240	1.833 \pm 1.572	1.167 \pm 1.462	12.333 \pm 4.819	37.864	7	<0.01
Total-P (mg/L)	0.229 \pm 0.003	0.230 \pm 0.042	0.234 \pm 0.037	0.1505 \pm 0.012	0.115 \pm 0.009	0.0973 \pm 0.022	0.091 \pm 0.002	0.089 \pm 0.108	34.091	7	<0.01
Turbidity (NTU)	6.725 \pm 2.217	4.347 \pm 0.756	11.593 \pm 1.475	3.940 \pm 0.593	3.252 \pm 0.436	2.620 \pm 0.609	4.265 \pm 0.475	7.097 \pm 3.512	34.069	7	<0.01
Water temperature ($^{\circ}$ C)	28.667 \pm 0.256	20.958 \pm 0.456	18.388 \pm 0.558	23.602 \pm 1.084	26.423 \pm 0.550	22.825 \pm 0.234	19.300 \pm 1.023	24.785 \pm 0.832	44.373	7	<0.01
Water transparency (m)	1.267 \pm 0.260	1.500 \pm 0.001	2.003 \pm 0.290	1.500 \pm 0.001	1.500 \pm 0.001	3.000 \pm 0.001	2.895 \pm 0.590	1.450 \pm 0.170	38.678	7	<0.01