

RESEARCH ARTICLE

Influence of light and mixing regime on bloom-forming phytoplankton in a subtropical reservoir

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Abstract

The joint influence of local climatic and hydrological conditions on the vertical distribution of bloom-forming phytoplankton was analysed for the Salto Grande Reservoir, a large and enriched subtropical system on the Uruguay River (South America). Threshold of physical factors hindering or impeding blooms was obtained and then contrasted with worldwide observations in reservoirs at similar latitudes. Inflowing discharge, water level, and wind velocity intensity interacted with temperature, producing mixing and light regimes with overriding influence on the vertical distribution of *Microcystis* spp., *Dolichospermum* spp., and *Ceratium furcoides*, hence affecting their maximum abundance and biomass. Cyanobacteria (*Microcystis* > *Dolichospermum*) showed the most heterogeneous distribution in the depth profile during strong thermal stratification, showing surface scums prone to horizontal displacements. *C. furcoides* was evenly distributed in the water column in correspondence to windy periods. Blooms of both Cyanobacteria and dinoflagellates did not occur when inflowing discharge exceeded $10,000 \text{ m}^3 \text{ s}^{-1}$. Nutrient influence on phytoplankton vertical distribution appeared strongly subordinate to the effect of light. Highest microcystin concentrations (>WHO alert Level 2) occurred especially after blooms collapsed during highly turbulent situations.

KEYWORDS

bloom ecology, eco-strategies, physical factors, subtropical reservoirs

1 | INTRODUCTION

The hydrodynamic properties of the aquatic environment resulting from the movements produced by energy transfer (wind stress, heat gain and loss, inflows, and outflows) play a fundamental role in plankton ecology and in the productivity of lakes (Wetzel, 1981). Reynolds (2006) explored the relationship of morphological and functional attributes of phytoplankters with environmental physical properties and described different distributional responses according to their motility and buoyancy capacity. Changes in the turbulence structure of natural waters induce major shifts in species composition but also a change in dominant strategies.

The regulation of rivers through the construction of dams has created numerous reservoirs in regions draining nutrient-rich soils and with high temperatures. Such modification in turbulence regimes enables the development of phytoplankton species that cannot develop in fast flowing waters but will progressively achieve large

populations on behalf of frequently stratified water columns with sufficient nutrients and light conditions. Reservoirs worldwide are inhabited by phytoplankton assemblages dominated by *Microcystis*, *Dolichospermum*, or *Ceratium* species, forming either mixed or single blooms (Cavalcante, Cardoso, Sussella, & Becker, 2016; Crosetti & Bicudo, 2008; Dai, Yang, & Cai, 2008; Hu & Xiao, 2012; Jacoby & Kann, 2007; Matsumura-Tundisi, Tundisi, Luzia, & Degani, 2010; Mwara, Koyo, & Zech, 2004; Oberholster, Botha, & Ashton, 2009; Te & Gin, 2011; Znachor et al., 2006). In South America, the proliferation of cyanobacteria as well as the recent invasion of *Ceratium* is largely a consequence of building cascades of reservoirs on large rivers (Padišák, Vasas, & Borics, 2015). Despite the differences of morphological and physiological features of cyanobacteria and dinoflagellates, reservoirs provide the ecological conditions for their success; the possession of either aerotopes or flagella allows individuals to dominate in these newly created regimes of lower turbulence.

The demise of turbulence imposed by fragmentation of flowing waters will interact with other conditions expected under future global change (Helbling, Banaszak, & Villafañe, 2015). For example, projected enhanced temperature will cause water column stratification and shoaling of the upper mixed layer that will further increase the exposure of planktonic cells to solar radiation. In contrast, expected increases in dissolved organic matter discharge into freshwater systems and greater wind stress will produce more opaque and mixed waters that might negatively affect cyanobacteria. In particular, vertical distribution of microbial communities is strongly influenced by wind affecting the formation and persistence of cyanobacterial blooms (Moreno-Ostos, Cruz-Pizarro, Basanta, & George, 2009); in large shallow lakes, the duration of wind events and their associated hydrodynamics is a key factor for driving spatial community changes (de Souza Cardoso & Marques, 2009; Wu et al., 2013). The effect of the interplay of wind-driven changes and flow on phytoplankton still needs to be understood for reservoirs.

The Salto Grande Reservoir (SGR), emplaced on the Uruguay River, is included in the Río de la Plata Basin, which lodges one of the highest numbers of dam projects on behalf of the growing populations and industrialization needing an increase in energy production (UNESCO, 2006). Summer cyanobacterial blooms are a recurrent phenomenon in this water body with temporal variations primarily dependent on its hydrological regime (Boltovskoy, Correa, Bordet, Leites, & Cataldo, 2013; O'Farrell, Bordet, & Chaparro, 2012). Blooms build-up is favoured by high water retention times under low water levels, especially in closed embayments where stagnant waters and high temperatures lead to the development of strong vertical stratification. Recent observations indicate development of large populations of *Ceratium furcoides* at sites that were previously dominated by bloom-forming Cyanobacteria. In this sense, Meichtry de Zaburlin, Vogler, Molina, and Llano (2016) asserted that the Paraná, Uruguay, and South Atlantic basins have a great risk of invasion, a fact that might account for the species spread toward temperate regions of central and southern Argentina and Uruguay.

The hypotheses of this study are (a) temperature has a joint influence with local meteorological (wind) and hydrological (inflowing discharge and water level) factors on vertical distribution of bloom-forming phytoplankton populations; (b) threshold values of physical variables (wind velocity, river discharge, and water temperature) beyond which blooms are unable to build up differ for assemblages dominated by buoyant cyanobacteria or motile dinoflagellates; and (c) total microcystin concentration is influenced by physical forces affecting the mixing regime (temperature and wind). Our results are compared to mesoeutrophic reservoirs in humid subtropical climates.

2 | METHOD

2.1 | Study area

SGR is a large subtropical river-like reservoir with an area of 750 km², a 144 km length with its major axis running in a NS direction, a mean depth of 6.4 m, and maximum depth of 35 m; this eutrophic water

body is located in the Lower Uruguay River (29°43' to 31°12'S; 57°06' to 57°55'W; Figure 1). The reservoir is polymictic, with short lasting stratification phases that occur under low river discharge conditions. Average yearly water discharge of the Uruguay River is 4,640 m³ s⁻¹ with pronounced seasonal variations, ranging between 216 and 22,000 m³ s⁻¹ in dry (summer time) and rainy (April to November) periods, respectively. SGR has a mean volume of 5,000 hm³; mean water retention time is around 2 weeks, though it may exceed 9 weeks at low water periods. Local winds have a NE direction, with mean monthly velocities between 10 and 12 m s⁻¹; mean annual temperature is 19 °C. This system has multiple purposes: energy production, drinking water, and recreational activities.

2.2 | Sampling design

This study was performed at four sites located at the southern area of the SGR: two at the arms Gualaguaycito (S9) and Itapebi (S10) and two at the central channel, upriver (C2) and downriver the arms (C1), close to the dam (Figure 1). Monthly samplings were carried out from mid-winter 2012 to the end of spring 2013. At each site, in situ depth profiles of temperature, pH, conductivity, and dissolved oxygen were obtained with Hydrolab DS5 multiparameter water quality probe; measurements were performed at 0.2 m (subsurface), 1 and 3 m (approximately the euphotic depth, Zeu), and bottom layers, whose mean depth differs among sites (C2 15.5 m, C1 29.7 m, S9 8.05 m, and S10 11.11 m). Samples were obtained at subsurface, Zeu, and bottom layers for chlorophyll *a*, suspended solids and nutrients (only measured at S9 at surface and deep layers), and phytoplankton analysis. Transparency was estimated with a Secchi disc. Samples for dissolved nutrients and chlorophyll *a* analyses were collected and preserved in dark and cold conditions until their filtration through fibreglass filters (Whatman GF/F). Phosphate and nitrate concentrations were analysed following the stannous chloride method and cadmium reduction method, respectively, and ammonia was estimated by nesslerization. Total phosphorus (TP) and nitrogen (TN) were determined from unfiltered samples digestion with persulfate (APHA, 2005). Concentrations of inorganic suspended solids were evaluated by drying the nonfiltrable residue at 550 °C (SS₅₅₀; APHA, 2005) and chlorophyll *a* by spectrophotometry using acetone as solvent (Lorenzen, 1967). Phytoplankton was counted according to Utermöhl (1958); biovolumes were estimated following Hillebrand, Claus-Dieter, Kirschtel, Pollinger, and Zohary (1999). Total microcystin concentration was measured monthly at both arm sites by direct quantification using liquid chromatography coupled with a photodiode array detector; extraction was performed with methanol/water (Lawton, Edwards, & Codd, 1994; PEC.AGROPEC. 098 based on norm ISO 20179; 2005(E)).

Joint Technical Commission of Salto Grande provided daily data of water level, measured at the dam, and the inflow estimated as a mass balance with the outflow and the volume variation. National Meteorological Service made available the wind intensity and rainfall daily data.

2.3 | Statistical analyses

To evaluate the relationships between biotic and abiotic variables, nonparametric Spearman rank correlations were performed.

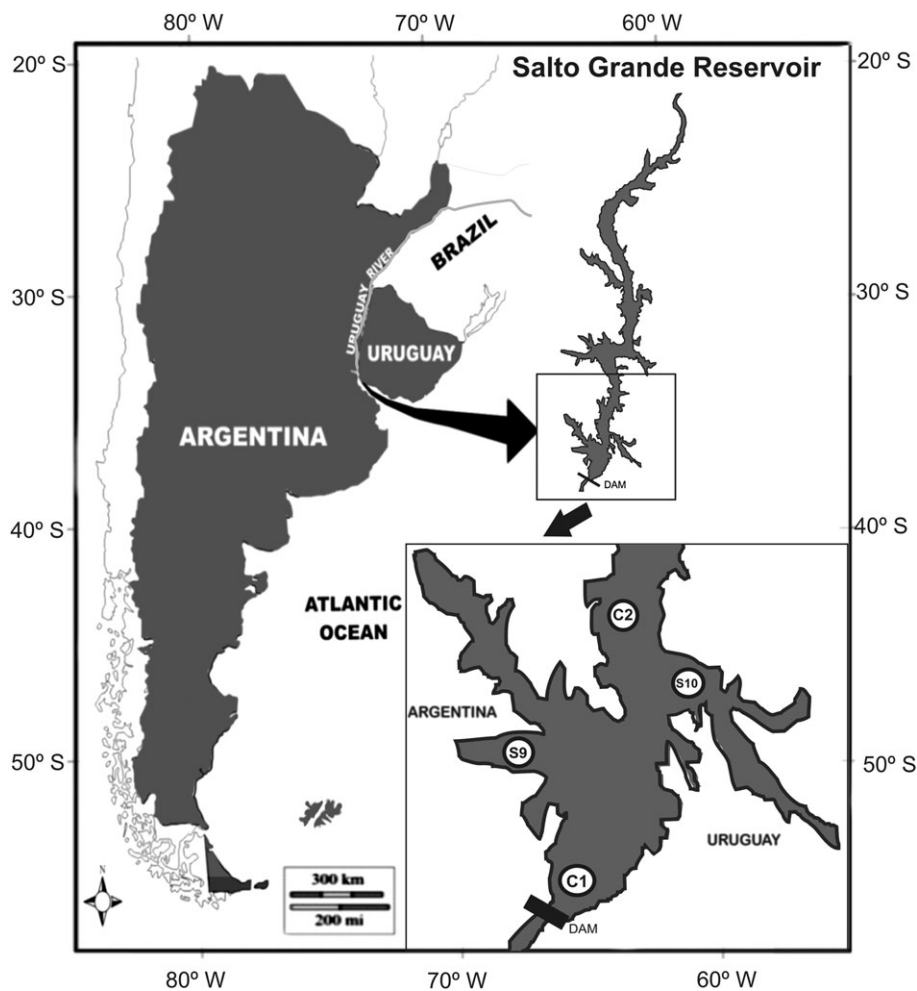


FIGURE 1 Location of the Salto Grande Reservoir with a detail indicating sampling sites

Redundancy analysis (RDA) was performed to assess for significant relationship between environmental and biological variables, because data showed a linear responses in the detrended correspondence analysis previously performed. Environmental parameters that were not highly correlated ($r < 0.7$) and with an inflation factor < 10 were included in the analysis. Biovolumes of species responsible for the blooms in SG were grouped in the genera *Microcystis*, *Dolichospermum*, and *Ceratium* with different eco-strategies (buoyant, buoyant and N-fixer, and motile) and considered as response variables. Forward analysis of variables was used in all cases, considering the explained percentage of the variables and its significance. The Monte Carlo test was used for the statistical validation of the association the ordination values, with 499 interactions and a significance level of $p < .05$ (terBraak & Verdonschot, 1995). Multivariate analyses were performed with the software CANOCO 4.5. A first analysis included data from all sites (S9, S10, C1, and C2), sample dates (16 times), and depths (surface, 3 m, and bottom); a second one was performed with data corresponding to surface and deep layers from S9, where the three dominant genera represented $> 80\%$ of total phytoplankton abundance and nutrient data were available for both depths. The variation coefficients (VC) of the phytoplankton dominant groups in the water column were calculated using the abundances from the three layers (surface, 3 m, and bottom) corresponding to each site and sampling date. Finally, multiple regressions were performed with

the VC weighted with the abundance of each phytoplankton group summed up in the water column, as dependent variable, and difference of water temperature between surface and bottom layers (ΔT), wind, and SS_{550} , as independent environment variables. To test assumptions, we used residual analysis. Homogeneity of variance was tested with Q-Q plot and Shapiro-Wilks test, and homoscedasticity with partial residual graphs, plotting standardized residuals versus predicted Y' values.

For estimating thresholds of physical variables impeding or promoting blooms of the three dominant eco-strategists, such events were matched with the corresponding values of significant variables produced in the RDA performed with data from all four sites. Water temperature, wind velocity, water discharge, and water level (closely related to depth variation) were chosen among significant variables because this information is systematically produced by reservoir managers. Blooms were defined following the criteria of Humbert and Fastner (2017) for mesoeutrophic systems: chlorophyll-*a* concentrations $> 50 \mu\text{g L}^{-1}$ under dominance (80%) of one or two species. Thus, samples were sorted according to decreasing chlorophyll concentrations up to of $50 \mu\text{g L}^{-1}$. The corresponding values of the selected physical variables were extracted for all samples within the high chlorophyll assortment. The dominant eco-strategy was matched to the corresponding physical data of the sample, and hence, a range could be assigned for *Microcystis*, *Dolichospermum*, or *Ceratium*.

3 | RESULTS

Temperature, rainfall, and wind fluctuations affect the meteorological scenario of the SGR (Figure 2a). Daily mean air temperature markedly differed between winter and summer, with minimum and maximum values of 4.9 and 33.1 °C, respectively. Total annual rainfall in 2012 was higher (1,621.9 mm) than in 2013 (1,232.4 mm) due to heavy spring rainfall. Daily wind intensity produced either totally calm or very windy days (highest daily mean value, 35.2 m s⁻¹): By the end of winter 2012, wind intensity was low, increased by early spring, and decreased once again in summer and autumn 2013 (few windy days) to achieve

fairly constant and strong wind till the end of the year. Hydrological conditions were highly variable (Figure 2b); at the beginning of the study period, the inflowing discharge was mostly below the historical mean with many values about 1,000 m³ s⁻¹, then increased abruptly on October (in response to heavy rainfall) to a maximum of 25,888 m³ s⁻¹ and dropped by the end of 2012. During 2013, discharge fluctuations were weaker and minimum flow fairly higher. Water level ranged between 31.3 and 36.5 m and was correlated to inflowing discharge ($r = 0.696$, $p = .003$), showing less variation due to the water releases performed to ensure the target of energy production.

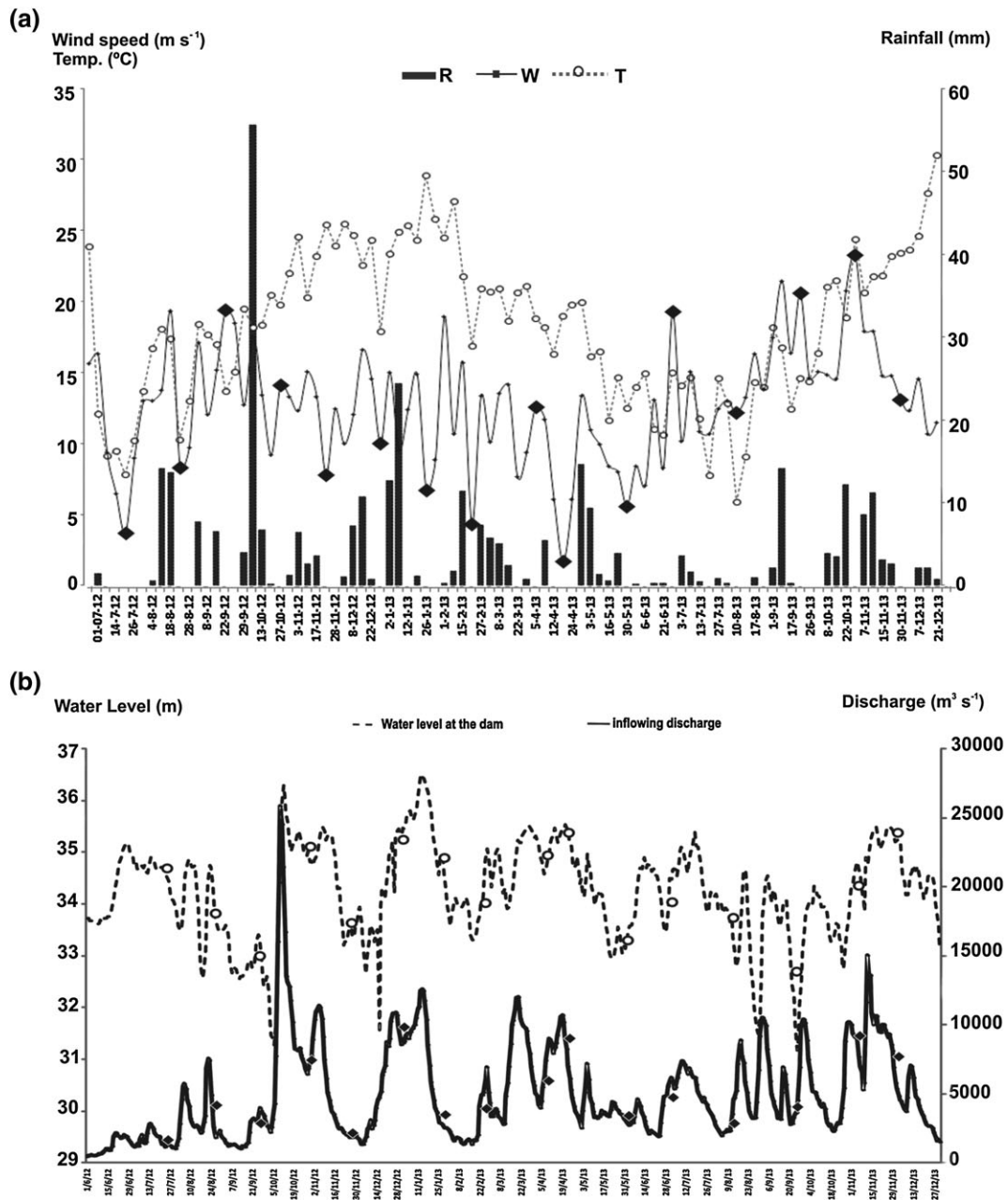


FIGURE 2 Meteorological and hydrological conditions in the study area of the Salto Grande Reservoir. (a) Grey lines indicate mean weekly temperature (T), black lines indicate weekly mean wind speed (W; principal axis), and vertical bars mean weekly rainfall (R; secondary axis). Diamonds correspond to sampling dates. (b) Daily inflowing discharge of the Uruguay River to the Salto Grande Reservoir and water level at the dam over the study period of mid-winter 2012 (July) to the end of spring 2013 (December). Black diamond and white circle: Values corresponding to each sampling date

Table 1 presents the mean values of the physical and chemical variables for three depths at the four sites. Despite temporal differences usually override variability among depths, there were consistent patterns that revealed higher conductivities and SS_{550} concentrations (less light due to higher inorganic turbidity) at the bottom and enhanced pH and dissolved oxygen concentrations at the surface; such gradients were less evident in the main channel. Oxygen diminished to deeper layers, but concentrations never dropped below 4 mg L^{-1} . Discontinuous thermal stratification occurred during the warm season; its onset was registered on November 2012 and lasted till January 2013. The maximum temperature amplitude over depth was recorded at S9 on January ($\Delta T 6.2 \text{ }^\circ\text{C}$; Figure 3). Though this pattern was similar at all sites, enhanced superficial heating during the hottest summer days was more pronounced at the arms and at C1. Zeu/Zmix variations did not coincide with the temporal thermal stratification pattern and mostly reflected the differences between the main channel (<0.1) and the arms (>0.1). Dissolved inorganic nitrogen (DIN) concentrations were quite similar among sites and also between the surface and bottom layers of S9; Soluble Reactive Phosphorus was higher at S9 due to a surface peak of 0.5 mg L^{-1} that coincided with the highest river discharge.

Regarding phytoplankton, Cyanobacteria dominated the assemblages at the arm sites on behalf of the abundance of *Microcystis* and *Dolichospermum* species. Dinoflagellates represented by *C. furcoides*, contributed with quite high abundances at S9 (Figure 4). The main channel also presented a minor contribution of green algae (mostly volvocales) and diatoms (*Aulacoseira* spp.). The arm sites supported phytoplankton densities at least two orders of magnitude higher than in the main channel, where they seldom exceeded $1,000 \text{ cells ml}^{-1}$. An extraordinary surface peak at C1 (*Microcystis* and *Dolichospermum*: $665,000$ and $26,000 \text{ cells ml}^{-1}$, respectively), coinciding with a bloom at S9, was recorded after 3 weeks of sustained drops of inflowing discharge (from $>10,000$ to less $<2,000 \text{ m}^3 \text{ s}^{-1}$) and water level, followed by a sudden withdrawal from the dam outlet on November 28, 2012. Until the onset of winter 2013, densities at S9 usually exceeded $10,000 \text{ cells ml}^{-1}$; at S10, figures were frequently lower. Total phytoplankton abundance at the arms consistently and sharply dropped from the surface layer to the bottom; the same pattern occurred at the main channel though with a slight gradient (Figure 4). Though *Microcystis* dominated at the upper layers, *Ceratium* was evenly distributed in the water column. Biovolume patterns showed the same response in the depth profile (Table 2).

The RDA performed with the dominant bloom-forming species grouped in three genera revealed that distribution was strongly affected by temporal fluctuations of physical conditions, namely, water temperature ($r = -0.44/0.53$ with Axes 1 and 2, respectively), SS_{550} ($r = 0.42$ with Axis 1), wind velocity ($r = -0.47$ with Axis 2), and depth ($r = 0.67/0.54$ with Axes 1 and 2, respectively; Figure 5). The cumulative percentage variance of the species–environment relation explained between the first two axes is 99.5%. Samples are arranged in the plot following a seasonal pattern from winter to spring–summer (right to left in the plot) along the first axis in association to increasing temperature and to decreasing depth and SS_{550} . The second axis is related to seasonal, meteorological, and hydrological conditions, and thus, samples plotted in the lower panel correspond to windy days and periods of high discharge and low temperature and water level;

TABLE 1 Mean and standard deviations of physical and chemical variables analysed for the depth profile (surface, 3 m, and bottom) at four study sites (C2, C1, S9, and S10) in Salto Grande Reservoir

		Temp. ($^\circ\text{C}$)	DO (mg L^{-1})	pH	Cond. ($\mu\text{s cm}^{-1}$)	Secchi (m)	SS_{550} (mg L^{-1})	Chlorophyll ($\mu\text{g L}^{-1}$)	SRP (mg L^{-1})	TP (mg L^{-1})	TN (mg L^{-1})	DIN (mg L^{-1})
C2	S	21.2 ± 7.3	8.7 ± 2.6	7.65 ± 1.9	55.5 ± 16.3	0.4 ± 0.1	7.6 ± 3.4	5.0 ± 3.3	0.02 ± 0.01	0.03 ± 0.02	0.85 ± 0.49	0.57 ± 0.26
	3 m	20.6 ± 6.9	8.2 ± 2.6	7.33 ± 1.8	55.8 ± 16.8	ND	8.3 ± 4.7	3.9 ± 1.7	ND	ND	ND	ND
	B	20.5 ± 6.8	8.1 ± 2.5	7.30 ± 1.8	57.6 ± 17.8	ND	14.5 ± 12.7	4.6 ± 3.2	ND	ND	ND	ND
C1	S	21.8 ± 5.6	9.2 ± 1.8	7.83 ± 0.6	57.3 ± 8.9	0.47 ± 0.12	5.8 ± 3.3	10.2 ± 17.1	0.02 ± 0.01	0.04 ± 0.02	1.00 ± 0.67	0.56 ± 0.20
	3 m	20.8 ± 7.0	8.3 ± 2.5	7.45 ± 1.8	56.1 ± 16.4	ND	7.1 ± 4.8	5.2 ± 3.2	ND	ND	ND	ND
	B	20.4 ± 6.8	8.1 ± 2.4	7.38 ± 1.8	56.8 ± 17.0	ND	21.1 ± 31	4.5 ± 3.3	ND	ND	ND	ND
S9	S	21.5 ± 5.5	10.4 ± 1.7	8.47 ± 0.6	55.6 ± 7.1	0.47 ± 0.09	5.4 ± 2.4	64.9 ± 35.7	0.06 ± 0.12	0.06 ± 0.03	1.11 ± 0.55	0.56 ± 0.25
	3 m	20.3 ± 4.9	8.6 ± 1.4	7.77 ± 0.2	54.4 ± 7.3	ND	5.9 ± 2.8	42.5 ± 53.6	ND	ND	ND	ND
	B	19.9 ± 4.7	8 ± 2.0	7.47 ± 0.2	56.9 ± 9.3	ND	7.0 ± 3.1	21.9 ± 21.0	0.02 ± 0.01	0.04 ± 0.02	0.83 ± 0.44	0.56 ± 0.25
S10	S	20.7 ± 5.4	9.4 ± 1.5	7.92 ± 0.5	61.9 ± 11.5	0.47 ± 0.11	6.0 ± 5.4	24.8 ± 40.3	0.03 ± 0.02	0.09 ± 0.10	1.02 ± 0.60	0.56 ± 0.26
	3 m	19.9 ± 4.9	8.8 ± 1.4	7.62 ± 0.3	62.9 ± 12.2	ND	9.5 ± 3.1	6.9 ± 3.6	ND	ND	ND	ND
	B	19.6 ± 4.8	8.6 ± 1.5	7.53 ± 0.2	65.2 ± 13.1	ND	16.7 ± 10.7	7.2 ± 4.4	ND	ND	ND	ND

Note. Nutrient deep layer data are only available for S9. TP = total phosphorus; TN = total nitrogen. ND = No Data

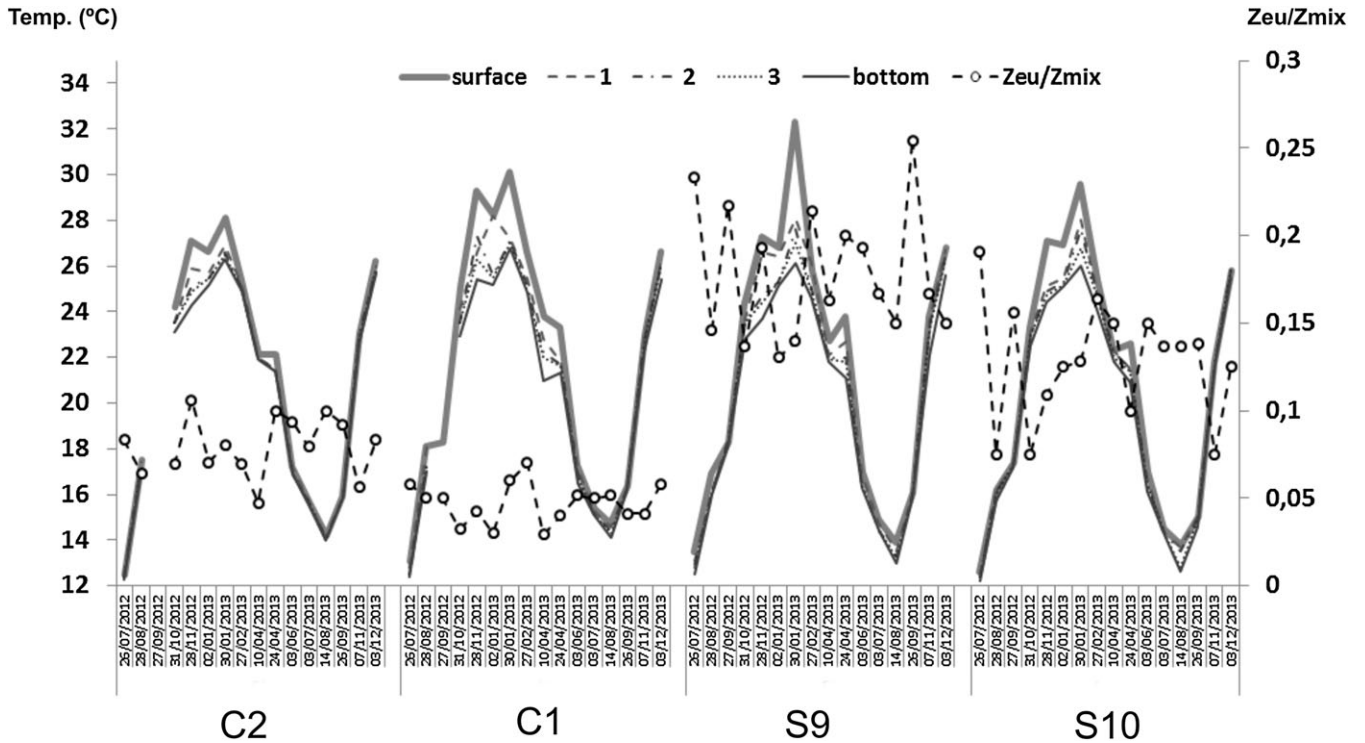


FIGURE 3 Depth temperature profile (surface, 1m, 2m, 3m) at the four sampling sites from mid-winter 2012 (July) to late spring 2013 (December), indicating the variation of Zeu/Zmix ratio

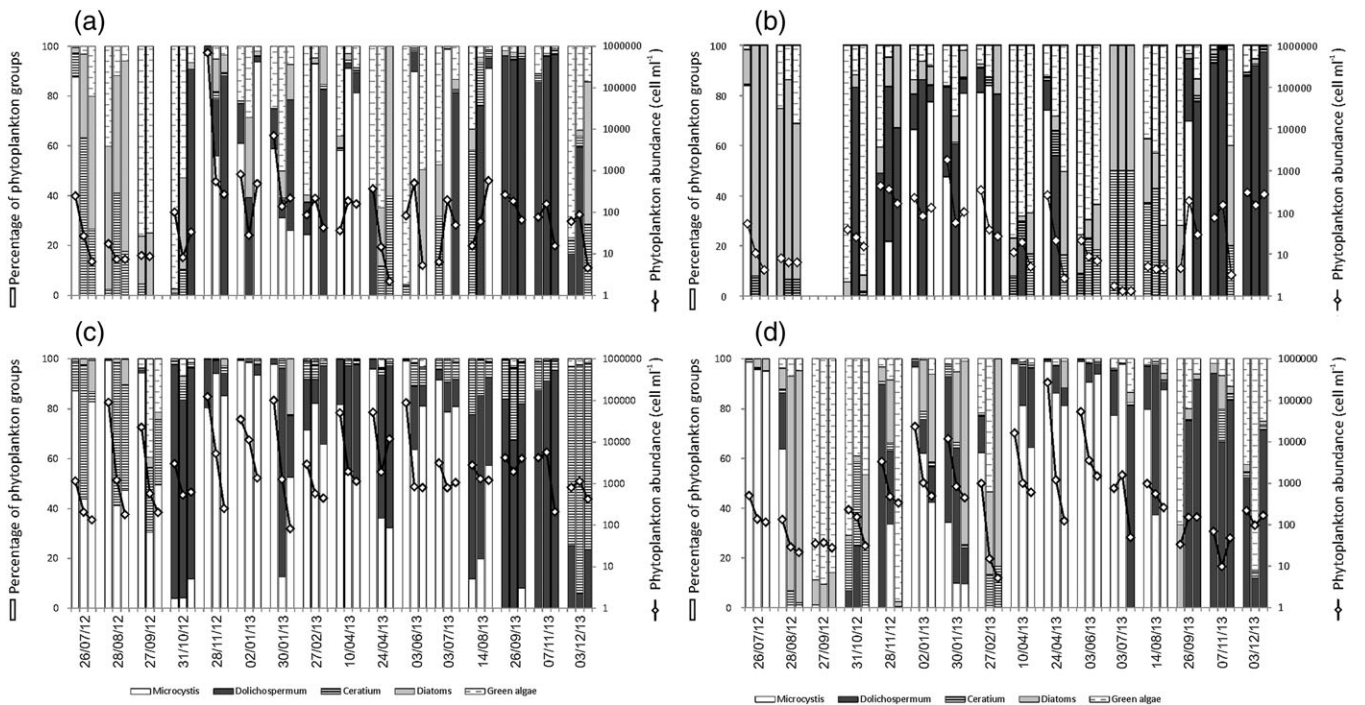


FIGURE 4 Vertical distribution of total phytoplankton abundance (lines) indicating the percentage of bloom-forming eco-strategists and other phytoplankton groups (bars) over the study period at the four sites (a = C2; b = C1; c = S9; d = S10)

opposite conditions are associated to samples in the upper panel. Many deep layer samples are displayed at the right quadrant due to their higher SS_{550} content and lower temperatures as compared to their corresponding surface samples. The dominant groups are clearly separated: *Ceratium* appears related to stronger winds, shorter water columns, and lower temperatures (winter and spring 2013), and both

Microcystis and *Dolichospermum* to deeper water columns at low discharge periods, under higher temperatures, and fairly calm days (spring 2012 to summer 2013).

The RDA performed solely with S9 data (Figure 6), shows a distinction between both surface and deep layers according to the first axis (57.3% of the percentage variance of species-environment

TABLE 2 Mean and standard deviations of biovolume ($\mu\text{m}^3 \text{ml}^{-1}$) of the bloom-forming eco-strategists for the depth profile (surface, 3 m, and bottom) at four sites (C2, C1, S9, and S10) in Salto Grande Reservoir

		C2	C1	S9	S10
S	<i>Microcystis</i>	$2.93 \cdot 10^4 \pm 7.31 \cdot 10^4$	$1.35 \cdot 10^7 \pm 5.34 \cdot 10^7$	$1.07 \cdot 10^7 \pm 1.28 \cdot 10^7$	$7.34 \cdot 10^6 \pm 2.28 \cdot 10^7$
	<i>Dolichospermum</i>	$4.06 \cdot 10^4 \pm 8.37 \cdot 10^4$	$8.16 \cdot 10^5 \pm 3.05 \cdot 10^6$	$1.51 \cdot 10^6 \pm 2.83 \cdot 10^6$	$4.10 \cdot 10^5 \pm 9.12 \cdot 10^5$
	<i>Ceratium</i>	$3.00 \cdot 10^4 \pm 2.57 \cdot 10^4$	$8.04 \cdot 10^4 \pm 1.35 \cdot 10^5$	$5.48 \cdot 10^6 \pm 5.05 \cdot 10^6$	$8.19 \cdot 10^5 \pm 2.78 \cdot 10^6$
3 m	<i>Microcystis</i>	$4.52 \cdot 10^3 \pm 1.20 \cdot 10^4$	$2.75 \cdot 10^4 \pm 4.49 \cdot 10^4$	$4.16 \cdot 10^5 \pm 9.26 \cdot 10^5$	$1.58 \cdot 10^5 \pm 2.93 \cdot 10^5$
	<i>Dolichospermum</i>	$2.41 \cdot 10^4 \pm 3.21 \cdot 10^4$	$1.81 \cdot 10^4 \pm 2.76 \cdot 10^4$	$3.40 \cdot 10^5 \pm 5.99 \cdot 10^5$	$5.24 \cdot 10^4 \pm 6.57 \cdot 10^4$
	<i>Ceratium</i>	$1.95 \cdot 10^4 \pm 1.72 \cdot 10^4$	$9.18 \cdot 10^4 \pm 1.31 \cdot 10^5$	$5.15 \cdot 10^6 \pm 6.86 \cdot 10^6$	$2.22 \cdot 10^5 \pm 3.47 \cdot 10^5$
B	<i>Microcystis</i>	$6.15 \cdot 10^3 \pm 1.24 \cdot 10^4$	$2.77 \cdot 10^4 \pm 5.46 \cdot 10^4$	$1.85 \cdot 10^5 \pm 3.07 \cdot 10^5$	$4.99 \cdot 10^4 \pm 1.21 \cdot 10^5$
	<i>Dolichospermum</i>	$1.32 \cdot 10^4 \pm 3.34 \cdot 10^4$	$1.82 \cdot 10^4 \pm 2.96 \cdot 10^4$	$3.81 \cdot 10^5 \pm 9.40 \cdot 10^5$	$2.19 \cdot 10^4 \pm 2.85 \cdot 10^4$
	<i>Ceratium</i>	$1.80 \cdot 10^4 \pm 2.45 \cdot 10^4$	$4.36 \cdot 10^4 \pm 8.12 \cdot 10^4$	$2.17 \cdot 10^6 \pm 3.94 \cdot 10^6$	$6.80 \cdot 10^4 \pm 7.76 \cdot 10^4$

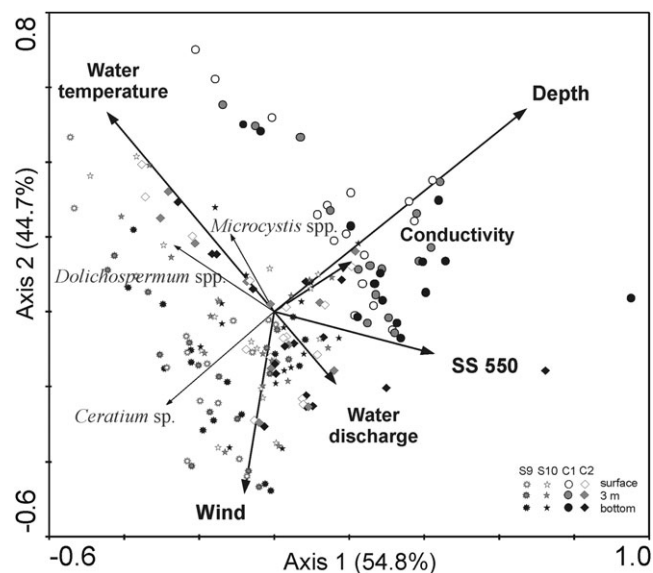


FIGURE 5 Redundancy detrended analysis plots based on the ordination performed with physical and chemical variables corresponding to all sites from surface, 3 m, and deep layers

relation), directly correlated with DIN ($r = 0.49$), organic N ($r = 0.44$), and inversely with SS_{550} ($r = -0.38$). The second axis explained 32.5% of the variance and was correlated inversely with wind intensity ($r = -0.67$) and directly with temperature ($r = 0.54$), depth ($r = 0.45$), and DIN ($r = 0.39$). Accordingly, surface samples from warm periods mostly appear to the right side of the plot or to the right of its corresponding bottom sample; bottom or surface samples from windy days at colder periods are located to the lower side of the plot. The second axis is positively correlated to DIN and associated to high cyanobacterial biomass. Thus, the most intense blooms of *Microcystis* and *Dolichospermum* were associated to high N and water temperature and low wind and discharge conditions, whereas *Ceratium* to windy days and colder situations.

When matching the occurrence of blooms (*sensu* Humbert & Fastner, 2017) of the three dominant eco-strategists with the magnitudes of each one of the selected physical variables that were significant in the RDA (wind velocity, discharge, water level, and temperature), it is clear that biomass exceeding $50 \mu\text{g L}^{-1}$ of chlorophyll *a* did not build up at inflowing discharges $>9,900 \text{ m}^3 \text{ s}^{-1}$ nor at water levels $>35 \text{ m}$. Cyanobacterial blooms occurred at water temperatures $>16.5 \text{ }^\circ\text{C}$ (mean: $23.8 \text{ }^\circ\text{C}$), as long as wind intensity was $<12.5 \text{ m s}^{-1}$ and the bloom was preceded by a suite of calm days. As

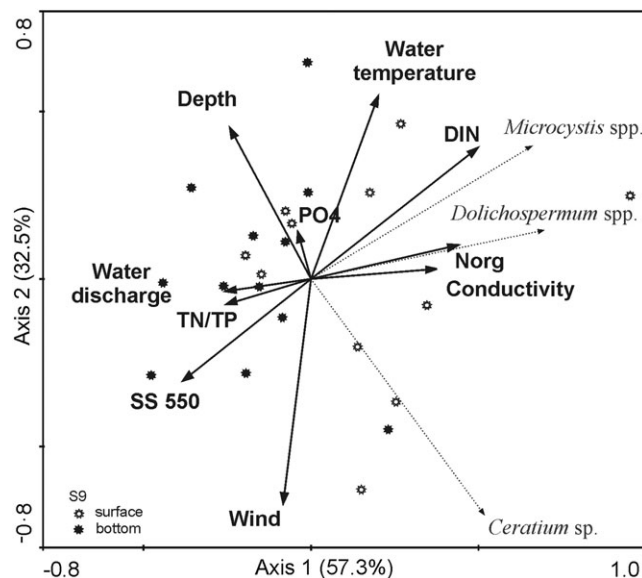


FIGURE 6 Redundancy detrended analysis with S9 surface and bottom samples and the corresponding physical and chemical (nutrient data are included). DIN = dissolved inorganic nitrogen

for dinoflagellates, within the environmental conditions here analysed, *Ceratium* blooms were registered at water temperatures over $16 \text{ }^\circ\text{C}$ (mean: $20.5 \text{ }^\circ\text{C}$), and under quite strong winds ($>12 \text{ m s}^{-1}$).

The VC of phytoplankton abundance among the three depths is here considered a proxy of the stratification of the assemblages. Cyanobacteria showed the highest variation among depths (*Microcystis* $>$ *Dolichospermum*), whereas diatoms (fully entrained by turbulence) evidenced a higher homogenization in the water column; *Ceratium* and chlorophytes had an intermediate response (Figure 7). VC values were quite similar among sites. VC of total Cyanobacteria was inversely correlated with wind intensity; the stronger correlations were registered at S9 ($r = -0.41$), revealing how calm days benefitted the efficient buoyancy regulation of *Microcystis*. When weighting the VC with the abundance of each complex in the water column, only *Microcystis* abundance could be predicted:

$$\text{VC} * \text{Microcystis abundance} = 28,288.68 \Delta T - 14,375.05 \text{SS}_{550} \\ (R^2 = 0.57, p < .05)$$

Microcystis were detected at S9 before the onset of spring 2012 and persisted up to late autumn 2013; at S10, positive analyses were recorded during summer and early autumn 2013. Negative results

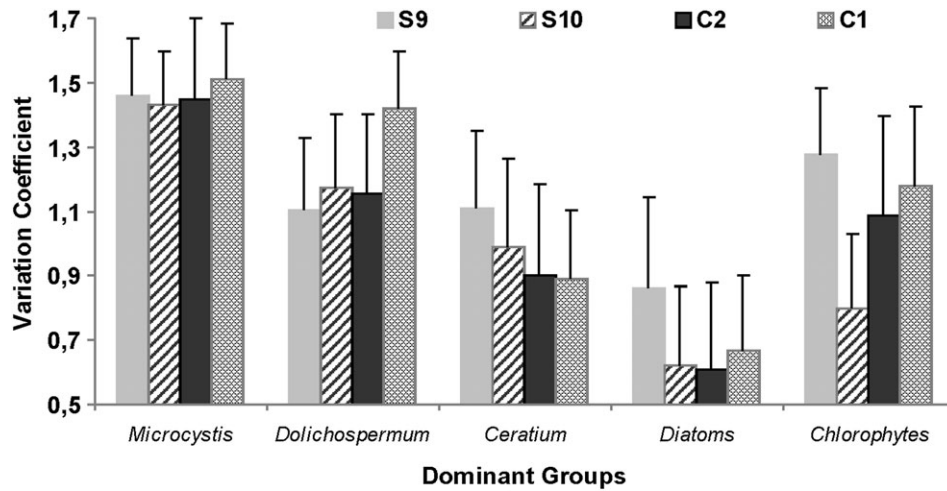


FIGURE 7 Mean variation coefficient among depths (surface, 3 m, and bottom) in the depth profile at each site for dominant groups in Salto Grande Reservoir

characterized winter and spring 2013 at both sites (Figure 8). The maximum concentration ($621 \mu\text{g L}^{-1}$) was measured at S9 and did not coincide with maximum Cyanobacteria abundance; just like the second peak registered ($96 \mu\text{g L}^{-1}$), it was preceded by sustained abundances of *Microcystis* ($>20,000 \text{ cells mL}^{-1}$). Interestingly, both toxin peaks occurred on warm but not highly stratified water columns, as evidenced by temperature profiles and by the drop of the *Microcystis* VC. Total microcystin concentration was correlated to the *Microcystis* and *Dolichospermum* abundances integrated in the water column ($r = 0.53$ and $r = 0.48$, $p < .05$, respectively), and among physical factors to temperature ($r = 0.54$, $p < .05$) and wind intensity ($r = 0.56$, $p < .05$, considering only S10 samples).

4 | DISCUSSION

The build-up of blooms in SGR was affected jointly by wind velocity, river discharge, water level, and temperature conditions. Massive development of either buoyant cyanobacteria or swimming

dinoflagellates over the 16-month survey occurred under different ranges of the interplaying physical variables. Total microcystin concentration increased with water temperature, just as cyanobacterial biomass, but otherwise peaked under mixed water column of windy days.

4.1 | Temporal pattern

Microcystis has steadily increased its abundance since the filling of the reservoir in 1979 (O'Farrell & Izaguirre, 2014), and only recently, *Ceratium* achieved high abundances, such as the here registered blooms at S9. *Ceratium hirundinella* and *C. furcoides* have been recognized as invasive in South America (Meichtry de Zaburlin et al., 2016) associated to higher stability of the water column (da Silva, Leone, Santos-Wisniewski, Peret, & Rocha, 2012). *C. hirundinella* was first observed in SGR, but more recently, it has been replaced by *C. furcoides*. Seasonally, the build-up of cyanobacterial algal biomass increases during periods of low water discharge and decreases under high water regimes, as described for the past decade in long-term

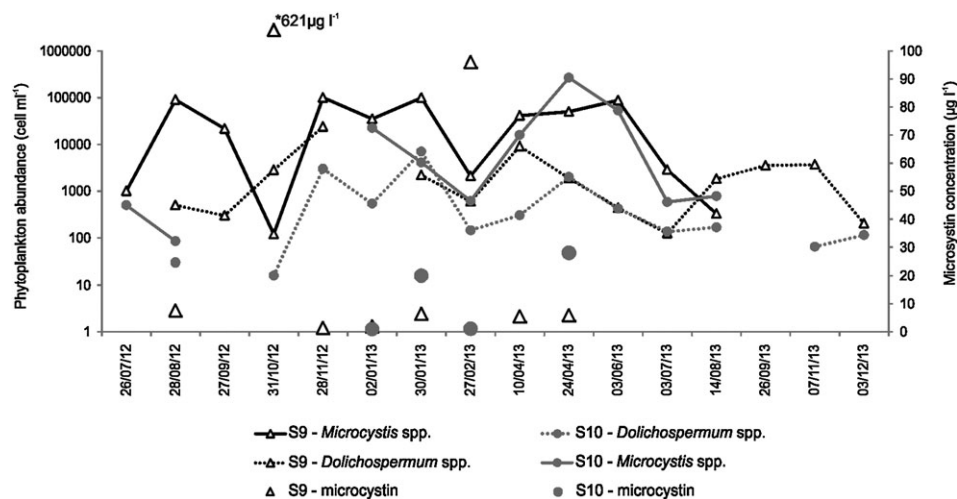


FIGURE 8 Surface microcystin concentrations at S9 (triangles) and S10 (circles) and temporal dynamics of the corresponding abundance of *Microcystis* and *Dolichospermum* complexes

surveys (Boltovskoy et al., 2013; O'Farrell et al., 2012). Accordingly, no cyanobacteria or dinoflagellate blooms were able to build up during the study period at inflowing discharges exceeding $10,000 \text{ m}^3 \text{ s}^{-1}$, even in sheltered areas.

4.2 | Spatial pattern

In SGR, enhanced cyanobacterial bloom frequency and intensity was associated to sites prone to experience vertical stratification; blooms thrived in the arms and especially in beaches of sheltered areas with high values of Z_{eu}/Z_{mix} (O'Farrell et al., 2012). The 2012–2013 results are in agreement with previous observations as blooms strongly developed in the shallow arms (S9 and S10) but did not occur in the deeper main channel; the only exception was a bloom located near the dam that probably drifted from the arms after sudden water withdrawal from the reservoir. *C. furcoides* solely bloomed at S9 (Gualeguaycito Stream); just like in Yacyretá Reservoir (River Paraná), the arms lodging dinoflagellates correspond to streams with extended floodplains, lowered residence time, and high nutrient availability (Meichtry de Zaburlín, Boltovskoy, Costigliolo-Rojas, & Rodríguez, 2014).

4.3 | Vertical pattern

Vertical structure in reservoirs is determined by temperature and wind action but is also affected by river inflows and outflows modifying mixing processes and nutrient loadings, hence inducing changes in the dominant phytoplankton assemblages (Rigosi & Rueda, 2012; Roelke, 2011). Despite many lakes in warm temperate or subtropical climates are reservoirs, few studies have quantified and analysed the suite of physical agents affecting thermal stratification and phytoplankton (Bormans, Ford, & Fabbro, 2005; Fabbro & Duivenvoorden, 2000; Grover & Chrzanowski, 2006; Hambright & Zohary, 2000; Roelke, Buyukates, Williams, & Jean, 2004); many of these works integrate the depth profile losing information on species distribution (Table S1).

Hu and Xiao (2012) asserted that the *Microcystis*–*Ceratium* group reflects the unique habitat of reservoirs compared to lakes: “strong and persistent disturbance caused by a deep outlet and relatively stagnant eutrophic surface layer.” The question is which conditions promote or hinder massive development of dominant eco-strategists, either positively buoyant Cyanobacteria or motile dinoflagellates. Despite Z_{eu}/Z_{mix} is a sensitive indicator of bloom occurrence, ratios >0.1 evidenced massive development but showed no further distinction between eco-strategies. According to the RDA, *Microcystis*, *Dolichospermum*, and *Ceratium* are related to different environmental conditions. Cyanobacterial blooms were frequent and intense under stratified water columns occurring in spring–summer due to high water temperature and low values of wind intensity, river discharge, and water level. *Microcystis* displayed stronger association with warmer, transparent ($<SS_{550}$), deeper, and stratified waters under low river discharge, whereas *Dolichospermum* developed under relatively higher incoming river flows, as long as water level was not very high. Our findings are in agreement with the fact that buoyancy regulation held by aerotopes action is more

efficient in colonial than in filamentous cyanobacteria (Visser, Ibelings, Bormans, & Huisman, 2016). Colonies floating at S9 could then be displaced by water withdrawal from the dam when low river inflow and wind velocity conditions prevailed, as evidenced by the scum at C1 on November 28, 2012. Contrarily, increasing wind intensities did not affect so much *Ceratium* populations, which appeared in shorter water columns tolerating more mixed and turbid ($>SS_{550}$) conditions and favoured by lower water temperature than Cyanobacteria. Likewise, Naselli-Flores and Barone (2003) found that *Ceratium* high biomasses occurring under fully mixed waters, and hence low light availability, shifted to *Microcystis* dominance with the onset of summer thermal stratification. Matsumura-Tundisi et al. (2010) and Tundisi et al. (2010) attributed the appearance of *Ceratium* blooms in a reservoir dominated by Cyanobacteria to cold fronts associated to strong winds that increased mixing with consequent light decline, nutrient replenishment, and removal of cysts from the sediments. Van Ginkel, Hohls, and Vermaaket (2001) described a comparable replacement by *Ceratium* when water overturn took place at lower temperatures. The influence of stability/mixing processes is clearly depicted by the response distribution of either positively buoyant colonies or filaments and of unicellular vertically migrating flagellates in the depth profile, as shown in the RDA analyses and then synthesized in the VC plot.

The inclusion of nutrients in the RDA performed with S9 data reveals that the scheme describing the influence of temperature, wind, and discharge on dominant phytoplankton groups is not altered. Despite Rangel, Silva, Rosa, Roland, and Huszar (2012) recognized that in several tropical reservoirs phytoplankton biomass was mainly controlled by phosphorus and modulated by hydrology, our results coincide with Forbes et al. (2008) idea that in reservoirs, nutrient controls on phytoplankton production are weak and subordinate to physical factors. The epilimnion of reservoirs may be nutrient depleted when stratification is persistent, and those eco-strategists able to exploit the upper layer for light and the deep one for nutrient will succeed over other plankters (Merino-Ibarra et al., 2008). The association of *Microcystis* and *Dolichospermum* with high DIN and organic N contents dismisses the latter cause, and such elevated N levels are probably consequence of nutrient regeneration from within the plankton community (Paerl & Otten, 2016). Our results are in line with observations in stratified Australian systems where vertical distribution response was related either to light or to the dynamics of the mixed layer (Bormans, Sherman, & Webster, 1999). Likewise, Cao, Kong, Yang, and Zhang (2006) found no correlations between nutrients and vertical profiles in Lake Taihu. Under relatively low wind intensities, where *Microcystis* thrived associated to higher temperature and a good light climate, we recorded a clear distinction between deep and surface layers. *Microcystis* abundance showed a marked vertical heterogeneity (highest VC), significantly predicted in terms of ΔT and S_{550} , reflecting the competitive advantage with respect to *Dolichospermum* and *Ceratium* in gaining access to optimal light conditions under strong stratified water columns. Moreover, Whittington, Sherman, Green, and Oliver (2000) found no evidence of downward migration of *C. hirundinella* to access nutrients in subtropical Chaffey Reservoir and explained the even distribution in the surface mixed layer as a response to escape inhibiting irradiance.

4.4 | Comparison with other subtropical reservoirs

Despite most studies found in the literature recognize the paramount role of temperature, wind, and flow on the occurrence of bloom-forming populations in reservoirs, their influence is separately addressed and mostly speculative (Dai et al., 2008; Li et al., 2010; Naselli-Flores & Barone, 2003; Oberholster et al., 2009; Sotero-Santos, Garcia Carvalho, Dellamano-Oliveira, & Rocha, 2008; Te & Gin, 2011; Wang, Qian, Han, Luo, & Hamilton, 2012). Some researchers focus on the combined effect of temperature and wind on cyanobacterial blooms, as determinants of both water column stability affecting buoyancy regulation of organisms (Fonseca & Bicudo, 2008; Merino-Ibarra et al., 2008) and horizontal displacement of blooms (Li et al., 2010; Oberholster et al., 2009; Sotero-Santos et al., 2008). Threshold of physical factors hindering build-up of cyanobacterial blooms in SGR differs from other reservoirs on behalf of their meteorological, hydrological, and morphological characteristics. The water temperature threshold (16 °C) is lower than the optimal growth value of *Microcystis* (25 °C; Davis, Berry, Boyer, & Gobler, 2009), probably in response to favourable flow and wind conditions. Rahman, Al Bakri, Ford, and Church (2005) indicated similar wind and temperature threshold values undergoing thermal stratification over a comparable period. The lower critical wind intensity (3 ms⁻¹) encountered elsewhere (Cao et al., 2006; George & Edwards, 1976; Ramírez & Bicudo, 2002; Webster & Hutchinson, 1994) corresponds to differences in lake morphologies such as lower depth and longer fetches. Our data are also in agreement with conditions associated to dinoflagellate appearance. Matsumura-Tundisi et al. (2010), Tundisi et al. (2010), and Van Ginkel et al. (2001) described the replacement of Cyanobacteria by *Ceratium* at 15–25 °C under mixed columns. Likewise, *Ceratium* seasonal dynamics was well represented by a niche response model based on temperature alone with an optimum of 21 °C (Grover & Chrzanowski, 2006). Cavalcante et al. (2016) reviewed the autoecology of *C. furcoides* in subtropical reservoirs confirming this growth temperature range.

4.5 | Microcystin concentrations

Physical factors also affect the dynamics of total microcystin concentrations. The weak correlation between cell abundance and toxin occurrence is similar to other reservoirs (Dai et al., 2008; Te & Gin, 2011). Toxins usually have similar spatial distribution as cyanobacteria when maintained intracellular (Falconer, 2005), but partitioning of toxins between particulate and dissolved phases changes as population density declines and dissolved concentrations increase. Li et al. (2010) and El Herry, Fathalli, and Rejeb AJ-BBouaïcha B. (2008) found that most of the toxins were located within the cells and when the bloom collapsed, significant amounts were found dissolved in the water. In SGR, the collapse of blooms is shown in the RDA by the inversion of the trajectory predictable by seasonality and evidenced by enhanced inorganic turbidity caused by strong wind, rainfall, or flow on previous days. Management stakeholders of subtropical reservoirs, typically affected by strong and frequent meteorological events, should take into consideration that cell counting is not sufficient to establish efficient and safe water policies. Microcystins in SGR were positively

correlated with water temperature in agreement to other reservoirs (Amé, Diaz, & Wunderlin, 2003; Joung, Oh, Ko, & Ahn, 2011). Anyhow, coexistence of toxic and non-toxic genotypes (Bittencourt-Oliveira, 2003; Joung et al., 2011; Te & Gin, 2011) cannot be dismissed. Despite Nostocales require multiple toxin analyses in comparison to *Microcystis* (Paerl & Otten, 2016), in SGR as in most reservoirs in the region only, microcystins are quantified evidencing a subestimation of blooms toxicity.

5 | CONCLUSION

The joint influence of temperature, meteorological, and hydrological conditions on light and mixing regimes affects the distribution of the dominant components of phytoplankton, revealing a differential response to the prevailing force or to their combination. The effects of local climate and hydrological conditions on thermal regime may be modelled (Wang et al., 2012) and then correlated to dominant assemblages, thus obtaining habitat-dependent threshold values promoting or impeding blooms with different eco-strategies. Such ecological approach provides the right guidelines for controlling blooms and discussing adequate measures in reservoirs.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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