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ECOLOGY OF SHALLOW LAKES

Blooms of toxic Raphidiopsis raciborskii in Laguna del Sauce (Uruguay): environmental drivers and impacts

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Abstract Laguna del Sauce is a eutrophic shallow lake and the second drinking water source in Uruguay. This ecosystem suffers recurrent blooms of potentially toxic nitrogen-fixing cyanobacteria, mostly during summertime. Here we analyze environmental drivers and potential impacts of blooms of the toxic cyanobacteria Raphidiopsis raciborskii in Laguna del Sauce from 2003 to 2020, and assess its effects on governance and biomonitoring. We registered three blooms of R. raciborskii, in 2004, 2015, and 2020, the last two expressed saxitoxin (lack of toxicity information for 2004). The 2015 bloom occurred in autumn, reaching an absolute biovolume of 104 mm^3 l^{-1}, and had high saxitoxin concentrations (up to 9.8 1g l^{-1}) which continued to be detected even after the bloom collapsed. This was the first saxitoxin register in this ecosystem and drastically affected the drinking water supply. After this massive bloom, a monitoring program was established which continues up to date. The 2020 bloom also occurred in autumn and lasted until winter; it was of lower magnitude (up to 6.3 mm^3 l^{-1}) and had lower saxitoxin concentration (up to 0.9 1g l^{-1}) compared to the 2015 bloom. Blooms of R. raciborskii were associated with a combination of persistent low water level, low water color, and high water transparency, conditions that rarely coincide in this ecosystem. Hence, the programs which started

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after the 2015 bloom, allowed better characterizing the environmental drivers of R. raciborskii blooms in Laguna del Sauce. Furthermore, these implied adapting the ecosystem management and water treatment strategies, and strengthening of academia—stakeholders' interactions.

Keywords Cyanobacterial blooms Saxitoxin Prediction capacity Adaptation Anticipation

Introduction

Eutrophication constitutes the main threat to water quality at a global scale, conditioned by multiple factors such as bad practices of fertilization in food production systems, absence or limitations of wastewater treatment plants, fragmentation or elimination of habitats, biodiversity losses, and climate change (Khan & Ansari, 2005; Moss 2008; Paerl et al., 2016). In eutrophic scenarios, the occurrence of potentially toxic cyanobacterial blooms and their interferences in the support and provision of goods and ecosystem services represents one of the most relevant challenges of the Anthropocene (Rockström et al., 2009; Moss et al., 2011).

Cyanobacteria represent a very diverse group of primary producers with a great capacity to adapt to wide environmental gradients and limited resources (light and nutrients) (Margalef, 1978; Reynolds, 2006; Agawin et al., 2007; Paerl et al., 2019; Wurtsbaugh et al., 2019). Cyanobacteria blooms are predicted to become more frequent in the context of climate change and eutrophication (Paerl & Huisman, 2009), and several cyanobacteria traits provide competitive advantages in the set of Anthropocene transformations (O'Neil et al., 2012). For example, cyanobacteria as a group have a high light efficiency and a low photoinhibition threshold that would favor their fitness in low-light situations (Schwaderer et al., 2011), high-temperature optima (Lürling et al., 2013) that would favor their success in an increasingly warm world (Litchman et al., 2010), and can regulate their position in stratified water columns that would allow regulating their access to resources (Paerl & Huisman, 2009). Among cyanobacteria, the order Nostocales have the capacity to fix atmospheric nitrogen, which can provide competitive abilities under N-limited situations. Indeed, N-fixing cyanobacteria should be favored because of its possibility to compensate for low N levels (Schindler, 1977, 2006). Nevertheless, blooms of N-fixing cyanobacteria can also occur in the absence of fixing behavior (Jacobsen & Simonsen, 1993; González-Madina et al., 2018). Other relevant traits in Nostocales include their capacity to produce dormant cells which allow the perennation of populations under unfavorable situations, and, like other cyanobacteria, can synthesize cyanotoxins which can hinder grazing among and can affect human health (Chorus and Welker 2021).

Raphidiopsis raciborskii (Woloszynska) Aguilera et al. (2018) (Cylindrospermopsis raciborskii recently synonym) is a N-fixing cyanobacteria that develops potentially toxic blooms (cylindrospermopsin and saxitoxin) which can interfere with the water potabilization and recreation (Chorus & Bartram, 1999; Chorus & Welker, 2021). R. raciborskii is considered an invasive species (Padisák & Istvánovics, 1997; Sinha et al., 2012), hence, there is an increasing concern in understanding its performance in nature. This species has been observed as a bloom-forming species in several water systems in Uruguay, showing that it can dominate phytoplankton over a wide range of environmental conditions (Vidal & Kruk 2008; Bonilla et al., 2012). Despite recognized as an invasive species, in our experience R. raciborskii blooms does not occur in multiple systems at the same time, nor does they occur all the time in those systems where it has been observed. The ecological traits of R. raciborskii (growth rate, light and temperature optima) have been thoroughly studied, nevertheless, we still needed to know which combination of environmental drivers determine its presence and toxicity levels.

The shallow lake Laguna del Sauce is the second-largest drinking water source in Uruguay. This lake suffers recurrent cyanobacterial blooms which can represent a challenge for water supply due to their capacity to produce toxins. Cyanobacteria blooms are mostly composed of N-fixing species (Nostocales) within the genera Dolichospermum, Cuspidothrix and Aphanizomenon (González-Madina et al., 2018). In 2015, however, a dramatic water supply crisis was associated with the emergence of a massive and

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persistent (lasted for 3 months) bloom of the N-fixing cyanobacteria R. raciborskii. The bloom produced high concentrations of toxin that demanded a fast and non-anticipated implementation of several modifications and new drinking water treatment alternatives (i.e., activated carbon addition and chlorination in the distribution network). After this crisis, various and large investments in infrastructure at the level of drinking water purification systems and sewage infrastructure in the basin were implemented, as well as the application of several public actions (i.e., controlling the nutrient inputs at basin scale) (Mazzeo et al., 2018).

This crisis had important political consequences and induced water governance changes in the area. The study of the resilience of social-ecological systems implies the simultaneous analysis of adaptation and transformation capacities (Folke, 2016), and depends on various attributes and processes that govern the individual and social learning processes, the innovation, and anticipation capacities (Chapin et al., 2009; Biggs et al. 2015). Uruguay has experienced several transformations of the water governance system associated with the transition from command-control to integrated management paradigm since 2004 (Trimble et al., 2021). The water crisis in 2015 determined relevant changes, such as the emergence of a high frequency monitoring program and research projects, supported by the interaction between public agencies and the academic sector. All these strategies focused on increasing the anticipation capacity against adverse events of cyanobacteria blooms (Crisci et al., 2017a; González-Madina et al., 2017; Mazzeo et al., 2019). In addition to the 2015 crisis, another R. raciborskii persistent (lasted for 4 months) bloom occurred in 2020, which could be better handled based on the increased anticipatory capacity (given by investments in infrastructure), and the experience generated during the massive 2015 bloom.

We here combine spatial and temporal approaches to understand the environmental conditions that favor the dominance and persistence of R. raciborskii from 2003–2020 and assess the impacts of the monitoring strategies on drinking water management and interinstitutional interactions. We aimed to answer: Which are the environmental drivers that promote the blooms of R. raciborskii? Is it possible to predict the occurrence of R. raciborskii blooms to better anticipate its consequences and mitigate the adverse effects on water provision?

Materials and methods

Study area

Laguna del Sauce (3443^0 S, 5513^0 W) is located in the Department of Maldonado, Uruguay, and is formed by three connected shallow subsystems: Laguna del Sauce, Laguna de los Cisnes and Laguna del Potrero (Fig. 1). The basin has an area of 722 km^2, and the total area including the three subsystems is 48 km^2. The main tributaries are the Pan de Azúcar (426 km^2) and the Sauce (122 km^2) streams, and the ecosystem drains into the Atlantic Ocean through the Potrero stream (Inda & Steffen, 2010) (Fig. 1). The mean water input is 263.7 hm^3 per year, and the water

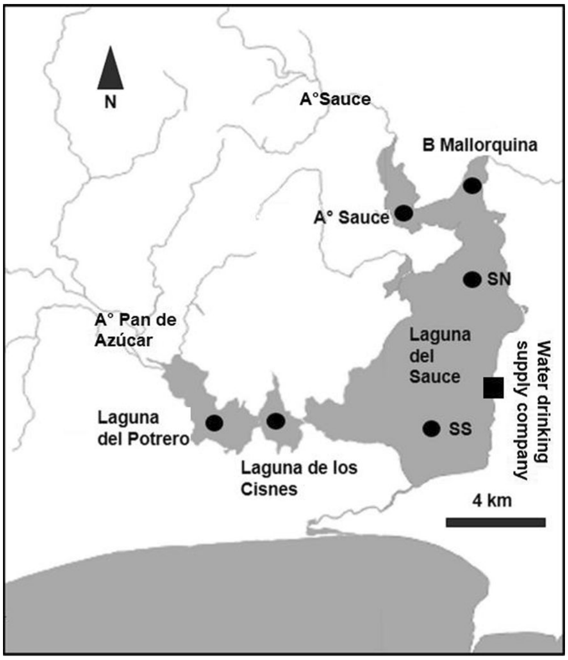

Fig. 1 Laguna del Sauce ecosystem and spatial distribution of the sampling sites (black dots) considered in Program A and D (see research strategy). The study area includes 3 shallow lakes connected: Laguna del Potrero, Laguna de los Cisnes and Laguna del Sauce which are considered subsystems. The main tributaries are Sauce and Pan de Azúcar streams. The zone of water intake of the drinking supply company is located 100 m from the margin (black square, Program B). The system drains to Río de la Plata through the Potrero stream, where a dam constructed in 1947 regulates the water level

output is 88 hm^3, out of which 18 hm^3 corresponds to the water withdrawal posed by the drinking water service administrator (OSE-UGD) (Crisci et al., 2017b). Laguna del Sauce supplies drinking water for approximately 160,000 permanent inhabitants; this figure more than doubles during the summer season when high-income tourists visit Punta del Este beaches (INE, 2011). Laguna del Sauce has a mean residence time of 195 days.

Laguna del Sauce is a eutrophic ecosystem, and among the three subsystems, there are differences in the dominance of primary producers (Rodríguez et al., 2010) and in its depth. Laguna del Sauce subsystem has the highest depth (3.0–5.0 m), lacks submerged vegetation, and is turbid. Contrary, Laguna del Cisne sub-system is shallower (1.6–2.5 m) and has about 20% of its area covered by submerged and free-floating vegetation. Finally, Laguna del Potrero sub-system is the shallowest (1.3–2.2 m) and is dominated by submerged vegetation, mainly Egeria densa (Planch, 1849) and Ceratophyllum demersum (Linneo, 1753) (Mazzeo et al., 2010).

In Laguna del Sauce diatoms (winter and spring) and cyanobacteria (summer) blooms have been observed since the 1960s. Since 2008, cyanobacteria blooms have intensified (higher frequency and higher biomass, wider distribution, increased persistence, and toxic events) (González-Madina et al., 2018). Noteworthy, the basin has been suffering from nutrient inputs due to agricultural activity, growth of cattle production and tourism intensification, and an increase of the urbanization process (Mazzeo et al., 2010).

Research strategy

The study combines four different limnological monitoring approaches (Program A, B, C, and D) in terms of the spatio-temporal scales and observation frequencies used, as follows:

Program A. To characterize the trophic state of Laguna del Sauce system and identify the principal physicochemical and phytoplankton temporal-spatial gradients, we analyzed data from 5 growing seasons (spring to autumn) from the onset of the monitoring program, established in 2015, and up to 2020 (2015–2016, 2016–2017, 2017–2018, 2018–2019, 2019–2020) at 6 sites located in the Laguna del Sauce sub-systems (Fig. 1). Program A, included weekly samplings throughout the growing season (November–April, spring to autumn) at each of the 6 sampling sites. In each date and site, we measured several environmental variables in situ: temperature, conductivity, pH, turbidity, dissolved oxygen, chlorophyll-a, and phycocyanin in vivo using YSI 6600 multiparameter probe, and water transparency using a Secchi disk.

In addition, three integrated samples were collected using a 10-cm-diameter tube by vertically integrating the water column. A fraction of these samples was kept cold and in darkness, and was used for the physical and chemical analysis in the laboratory, including alkalinity (APHA, 1985) and real color (HACH D900), ammonium ($N–NH_4^?$, Koroleff, 1970), nitrate ($N–NO_2^-$, Müller & Wiedemann, 1955), soluble reactive phosphorus (SRP, Murphy & Rilley, 1962), and total nitrogen and phosphorus (TN, TP, Valderrama, 1981). The suspended total solids (STS) and their organic content (SOM) were determined following APHA (1985), inorganic suspended total solids were calculated as the difference between these. Chlorophyll-a was spectrophotometrically determined using the cold ethanol technique (Jespersen & Christoffersen, 1987).

Phytoplankton was quantified using sedimentation chambers using an inverted microscope (Nikon Eclipse 50i) at 9400 magnification (Utermöhl, 1958; Guillard, 1978). Random fields were used (Uhelinger, 1964; Utermöhl, 1985) and at least 100 organisms of the most frequent species were counted (Lund et al., 1958). The organisms were also measured (CMOS 5.0, software Micrometrics Premium Edition), and their volume was calculated according to its geometric form, following Hillebrand et al. (1999). Next, phytoplankton biovolume was calculated as the density multiplied by its volume. We consider a bloom whenever cyanobacteria biovolume surpasses 10 $mm^3 \ l^{-1}$, as suggested by Chorus & Bartram (1999).

Program B. This approach was used to identify the presence of the N-fixing cyanobacteria R. raciborskii in the period between 2003 and 2020, and to determine the environmental conditions associated with the occurrence of such blooms. Data were obtained at the zone of water intake of the potabilization plant (Fig. 1), where the following variables were daily measured: water temperature (LD0101 HACH), conductivity (Orion DuraProbe^{TM}, 4-Electrode Conductivity Cells, model 013010), turbidity (HACH Cat N

47000-88, model 2100 N), real color (HACH D900), and water level. Chlorophyll-a estimated by extraction from GF/F Whatman filter using hot ethanol (90%), according to Nusch (1980) and spectrophotometry (Macherey–Nagel UV/VIS). R. raciborskii abundance and biovolume were estimated following the approach mentioned in Program A.

Program C. According to the results of approach B, we analyzed the R. raciborskii biovolume temporal variation in two critical periods (blooms): April to June 2015, and March to June 2020. R. raciborskii biovolume was quantified as in Program A. We further analyzed the temporal variation of toxins (saxitoxin and cylindrospermopsin), using ELISA methodology. These analyses were run in OSE (the public provider of drinking water) laboratory using commercial kits (ABRAXIS and EUROFINS ABRAXIS).

Program D. We analyzed in detail the spatio-temporal variation throughout the 2019–2020 growing season, across the same 6 sites as in Program A. We also analyzed the composition and biovolume of the phytoplankton community focusing on R. raciborskii. Furthermore, we measured R. raciborskii filament length and identified the presence of heterocytes (cells specialized for nitrogen fixation) and of akinetes (dormant cells) throughout the bloom.

Adaptation and anticipatory capacity

We assessed the adaptation and anticipation capacities (Folke, 2016; Miller et al. 2018; Trimble & Mazzeo, 2020) promoted by the monitoring program. We further assessed the development of predictors models and, the interaction with the decision-making process with the drinking water supply company and public actors involved in the ecosystem stewardship. Specifically, we compared the capacity building during 2015–2020 period, and the responses to R. raciborskii blooms in 2015 and 2020 associated with the above mentioned actors. This was contemplated with the assessment of cooperation agreements between the drinking water supply company, the academic sector, and the Ministry of Environment, since 2015, and the design, implementation, and results of several projects with the active participation of the authors.

Data analysis

First, descriptive statistical attributes were estimated to characterize the mean values, ranges and coefficient of variation among sampling sites and interannual fluctuations (Program A, 2015–2020). Subsequently, indirect ordering analysis (principal component, PCA) was used to identify the main spatial gradients, as well as temporal patterns (Program D, 2019–2020). Before running PCA, highly correlated variables ([0.7) were eliminated. Next, a standardized matrix was used with the selected variables, using a correlation matrix and using the option between groups. Principal components 1 and 2 (PC1 and PC2, respectively) were used later in a Bubble plot, using cyanobacteria and R. raciborskii absolute biovolume as response variables (Program D, 2019–2020).

The ANOSIM test (with post hoc analysis) was used to determine the statistical significance of differences among sampling sites for each growing season from a multivariate water quality perspective (Program A, 2015–2020). For ANOSIM, the input limnologícal matrix (temperature, conductivity, pH, turbidity, real color, water transparency, total and inorganic dissolved nitrogen and phosphorous, dissolved oxygen and phycocyanin and chlorophyll a in vivo) was standardized and the algorithm consid-ered was Pearson correlation.

A combination of Spearman correlation and multiple linear regression was used to determine the relationship between response variables and control factors. In the case of Program A, multiple regression was used to determine the main drivers of pH and water transparency, in order to characterize the system. The same approaches were used to understand the role of the environmental factors that influence the dynamics of phytoplankton biomass during 2003–2020 (Program B) and R. raciborskii biovolume (Program C, 2015 and 2020, and Program D, 2019–2020). The normal distribution of residuals and the homogeneity of variance were verified. The details of the models considered and variables transformations are indicated in the Results section.

With the aim to determine extreme conditions in physical variables throughout the 2003–2020 period (Program B), we calculated confidence bands considering the 5th and 95th empiric percentiles for each variable. At each day, percentiles were obtained considering data from a 7-day window centered in the day and their correlative days on the 17 available years. Hence, for the calculation of each percentile, we had 133 data when there were no missing values. If for a given day, available data was less than 50% (less than 67), quantiles were not calculated. It must be noticed that the quantile bands are the same for each year.

These analyses were run using RStudio (RStudio Team, 2013) and PAST 4 (Hammer & Harper, 2001).

Results

Main physical, chemical, and phytoplankton features in Laguna del Sauce (Program A, 2015–2020)

All 5 growing periods assessed (Table 1) were characterized by a similar temperature range (22–24 C), reaching maximum values in January (ca. 28 C). Conductivity presented a variation between 0.16–0. 18 mS cm^{-1}, with low variability among periods and sampling sites (\ 20%) (Table 1). Conductivity and alkalinity were strongly correlated (rS = 0.92, P \ 0.001). pH values ranged between 6.18 and 9.15; its temporal and spatial variability was low (Table 1) and were statistically related to conductivity, temperature, cyanobacteria abundance and photosynthetic activity-oxygen levels- [multiple regression, adjusted R^2 = 0.47, P \ 0.001, variables transformed ln (x ? 1): conductivity (betha = 0.24, P = 0.07), dissolved oxygen levels (betha = 0.12, P \ 0.001), temperature (betha = 0.09, P \ 0.01) and phycocyanin in vivo (betha = 0.03, P \ 0.001)].

Mean water transparency was low, less than 1 m of Secchi depth (Table 1). However, a considerable range (0.30–2.5 m) in transparency was observed. Water transparency was statistically associated [multiple regression, adjusted R^2 = 0.56, P \ 0.001, variables transformed ln (x ? 1)] with: suspended total solids (STS) (betha = - 0.35, P \ 0.001) and color (betha = - 0.48, P \ 0.001). STS and inorganic STS were correlated (rS = 0.86, P \ 0.001). In periods with the absence of blooms, water transparency depended on inorganic turbidity and color. During turbid periods the euphotic layer represented 38% of the water column in Laguna del Sauce subsystem (i.e., 4/4/2020, maximum depth 4.0 m) and 100% of the water column during clear water conditions (i.e., 11/2/2020, maximum depth 4.3 m).

In periods without light limitation by inorganic turbidity or color, high levels of chlorophyll-a and phycocyanin in vivo were registered. Temporal variability for chlorophyll a and phycocyanin was 21 and 81%, respectively. The spatial variability was higher than 20% for both pigments (Table 1).

TP and TN values corresponded to eutrophic conditions, and TN concentrations showed a higher temporal variability (40. 9%) (Table 1). Spatial variability for both total nutrients was low (less than 20%). The N:P ratios (molar ratio) in this system were lower than 10 in several periods of the growing season (Table 1). The temporal variability of N:P ratio was 62.3% while the spatial heterogeneity was lower than 20%. Soluble dissolved nutrients showed a higher temporal variability (49% SRP, 48% N–$NO_2^-$and 90% N–$NH_4^?$); spatial variability of N–$NH_4^?$ was greater than N–NO_2^- (Table 1).

The water level was highly fluctuating between the growing seasons (Table 1); it was lowest in the first and last growing periods (2015–2016 and 2019–2020). The periods with a higher water level correspond to a lower spatial variability of limnological features, reflected on a lower CV (Table 1).

ANOSIM results confirmed a significant difference among sampling sites in all growing periods assessed, except for 2018–2019 (rA = - 0.02, P = 0.97). The higher differences were observed during 2015–2016 and 2019–2020 (rA = 0.17, P \ 0.001; rA = 0.20, P \ 0.001, respectively). In the case of periods with significant differences, the sampling sites located within the Laguna del Sauce subsystem were like each other.

Main physical, chemical, and phytoplankton features in Laguna del Sauce (Program D, 2019–2020)

The PCA analysis allowed us to identify the main spatial gradients observed for the different subsystems. The nutrient gradients (except ammonium) and turbidity were positively correlated with axis 1 (PCA1), showing similar spatial and temporal patterns during period 2019–2020. In this sense, PCA1 explained 54% of the total variance. The PCA 2 (variance explained: 37%) was directly correlated with phycocyanin in vivo and chlorophyll-a

Table 1 Average (in bold), minimum and maximum (in parentheses) of the limnological attributes surveyed in the field and in the laboratory for the growing seasons between 2015 and 2020 (Program A)

	2015–2016 (15)	2016–2017 (18)	2017–2018 (19)	2018–2019 (22)	2019–2020 (23)	Temporal CV
T (C)	24.04 (19.73; 27.65)	24.22 (20.56; 28.51)	23.38 (18.32; 27.17)	22.51 (16.31; 27.82)	22.25 (16.49; 27.42)	3.8
	0.9	1.5	0.76	0.64	1.17	
Conductivity (ms cm^{-1})	0.18 (0.15; 0.27)	0.15 (0.13; 0.20)	0.16 (0.11; 0.21)	0.14 (0.08; 0.211)	0.16 (0.12; 0.23)	9.39
	12.18	11.67	9.1	10.1	14.43	
Alkalinity (mg $CaCO_3$ l^{-1})				50.62 (18; 90)	59.45 (42; 92)	11.35
				16.33	19.43	
pH	7.71 (6.95; 8.94)	7.47 (6.73; 8.52)	8.08 (6.29; 9.02)	7.31 (6.18; 8.18)	7.46 (6.53; 9.15)	4.42
	2.57	1.61	1.22	2.83	3.53	
Turbidity (NTU)	14.27 (1.28; 47.15)	19.45 (3.82; 38.47)	12.9 (3.84; 26.14)	12.09 (2.44; 29.11)	13.3 (0.82; 48.52)	20.34
	41.31	36.63	24.4	21.06	19.88	
Real Color (lg Pt l^{-1})				167.81 (69; 385)	116.27 (17; 260)	25.66
				4.7	11.13	
Secchi depth (cm)	78.30 (30; 200)	63.69 (30; 125)	80.2 (45; 130)	91.63 (45; 190)	89.33 (26; 250)	13.72
	35.32	19.73	15.26	11.46	15.89	
Chlophyll-a in vivo (lg l^{-1})	8.34 (2.97; 33.36)	5.91 (1.06; 19.45)	5.56 (0; 16.64)	6.12 (3.32; 13.94)	8.93 (0.73; 64.78)	22.17
	34.2	32.35	18.46	4.21	27.41	
Phycocianine in vivo (cell.ml^{-1})	3830.15 (809.75; 26,116.20)	2113.27 (823.33; 14,775)	2079.86 (804.2; 9369.11)	2217 (1001.67; 14,543)	9150.75 (1053; 64,579)	78.33
	46.95	61.6	21.74	16.26	44.37	
TP (lg l^{-1})	79.06 (24.22; 161.61)	87.99 (41.10; 118.49)	72.19 (16.74; 178.53)	65.91 (17.58; 175.16)	40.61 (7.49; 97.17)	25.94
	16.42	7.68	4.13	5.48	14.92	
SRP (lg l^{-1})	25.64 (0.24; 80.19)	51.96 (0.10; 84.77)	44.94 (0.85; 93.26)	38.75 (2.23; 85.44)	9.46 (0; 46.84)	49.37
	29.7	24.77	3.40	6.01	30.33	
TN (lg l^{-1})	714.26 (433.81; 1362.41)	519.94 (286.40; 945.90)	199.55 (87.26; 530.35)	381.88 (102.70; 711.07)	511.09 (159.46; 1422.27)	40.86
	18.71	3.49	5.74	2.47	6.73	
NO_3^-–N (lg l^{-1})	173.95 (100.21; 286.76)	257.26 (104.13; 569.56)	70.28 (6.25; 223.21)	95.30 (1.36; 342.90)	172.96 (10.58; 361.08)	48.04
	11.03	21.03	10.07	13.76	7.16	
$NH_4^?$–N (lg l^{-1})	106.81 (5.92; 843.20)	41.78 (5.02; 149.55)	20.70 (0; 162.24)	16.37 (0; 62.97)	23.97 (0; 135;52)	89.53
	32.16	21.99	39.86	18.56	28.85	
N:P (mol)	21.9 (9.33; 61.53)	13.26 (6.27; 25.21)	6.70 (1.51; 29.46)	15.42 (3.39; 69.17)	37.87 (5.64; 171.39)	62.26
	9.51	10.99	6.73	10.08	17.12	

Table 1 continued

	2015–2016 (15)	2016–2017 (18)	2017–2018 (19)	2018–2019 (22)	2019–2020 (23)	Temporal CV
Water level (m)	-0.1 (-0.46; 1.35)	0.55 (0.39; 0.73)	0.33 (0.07; 0.75)	0.56 (0.32; 1.25)	0.08 (-0.2; 0.56)	102

The value located below the mean indicates the coefficient of spatial variation (among the 6 sampling stations indicated in Fig. 1). The last column on the right shows the coefficient of temporal variation observed in among the 5 growing seasons considered. The number of field monitoring occasions during each growing season is indicated (in parentheses)

determined spectrophotometrically, pH and inversely related to SRP, N–NO$_3^-$ and water color.

The main gradients from Laguna del Potrero to Laguna del Sauce (Fig. 2) included a decrease in conductivity, alkalinity, pH, water transparency, turbidity, water color, TN and TP. Arroyo Sauce showed lower values of conductivity, alkalinity and pH in comparison with the Laguna del Sauce subsystem (Fig. 2). Arroyo Sauce and Laguna del Sauce had higher ammonium concentrations than Laguna del Potrero and Laguna del Cisne. The second axis of the PCA suggests that Laguna del Cisne (Green) and Laguna del Sauce (red) had higher concentrations of

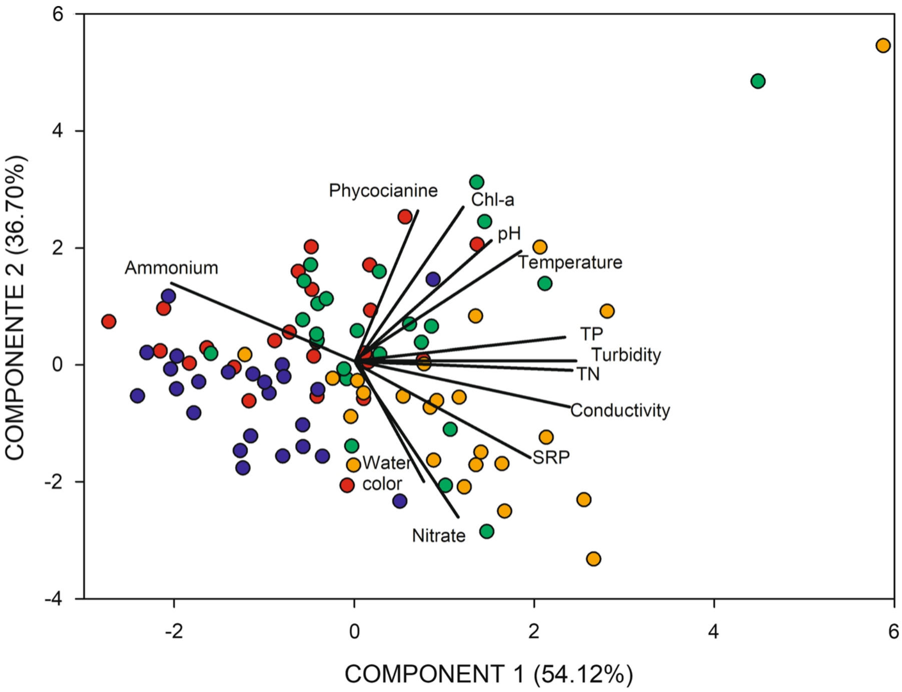

Fig. 2 Indirect ordination (Principal Component Analysis) for the 6 sampling sites across growing periods clustered by color according with the main subsystems described in Fig. 1. The sampling ordination include the period 2019–2020 (Program D) as example of temporal variation and spatial distribution of Raphidiosis raciborskii blooms. Laguna del Potrero: Orange; Laguna del Cisne: Green; Laguna del Sauce: red; Arroyo Sauce: blue. The bidimensional plot includes the first two components that account 54.1 and 36.7%, respectively, of the total variance explained. The main spatio-temporal gradients and its relationship with the main components can be visualized with the arrows. The variables used were: Ammonium, phycocyanin (phyco), Chlorophyll a (Chla), pH, Temperature (Temp), Total phosphorus (TP), Total Nitrogen (TN), Turbidity (Turb), Conductivity (Cond), soluble reactive phosphorus (SRP), Water color (color) and nitrate

phycocyanin and chlorophyll than Laguna del Potrero (Orange) and Arroyo Sauce (blue), respectively.

Raphidiopsis raciborskii blooms throughout 2003–2020 (Program B)

Laguna del Sauce showed an important temporal variability of chlorophyll-a (Fig. 3a). Chlorophyll-a exhibited an inverse correlation with color (rS = - 0.6, P \ 0.001) and turbidity (rS = - 0.5, P \ 0.001). Moreover, a multiple linear regression model of chlorophyll-a (adjusted $R^2 = 0.32$, P \ 0.001) was explained by color (betha = - 1.21, P \ 0.001), turbidity (betha = - 0.12, P \ 0.01) and water level (betha = - 1.12, P \ 0.05). Turbidity and water color variation were directly correlated (rS = 0.8, P \ 0.001), but there was absence of correlation between water level and turbidity. Contrary, water level and color presented a positive correlation (rS = 0.2, P \ 0.001).

R. raciborskii blooms occurred 3 times throughout the 2003–2020 period: in 2004 (max biovolume: 36.7 mm^3 l^{-1}), 2015 (max biovolume: 104.1 mm^3 l^{-1}) and 2020 (max biovolume: 10.01 mm^3 l$^{-1)}$ (Fig. 3b). These periods exhibited a particular combination of environmental conditions:

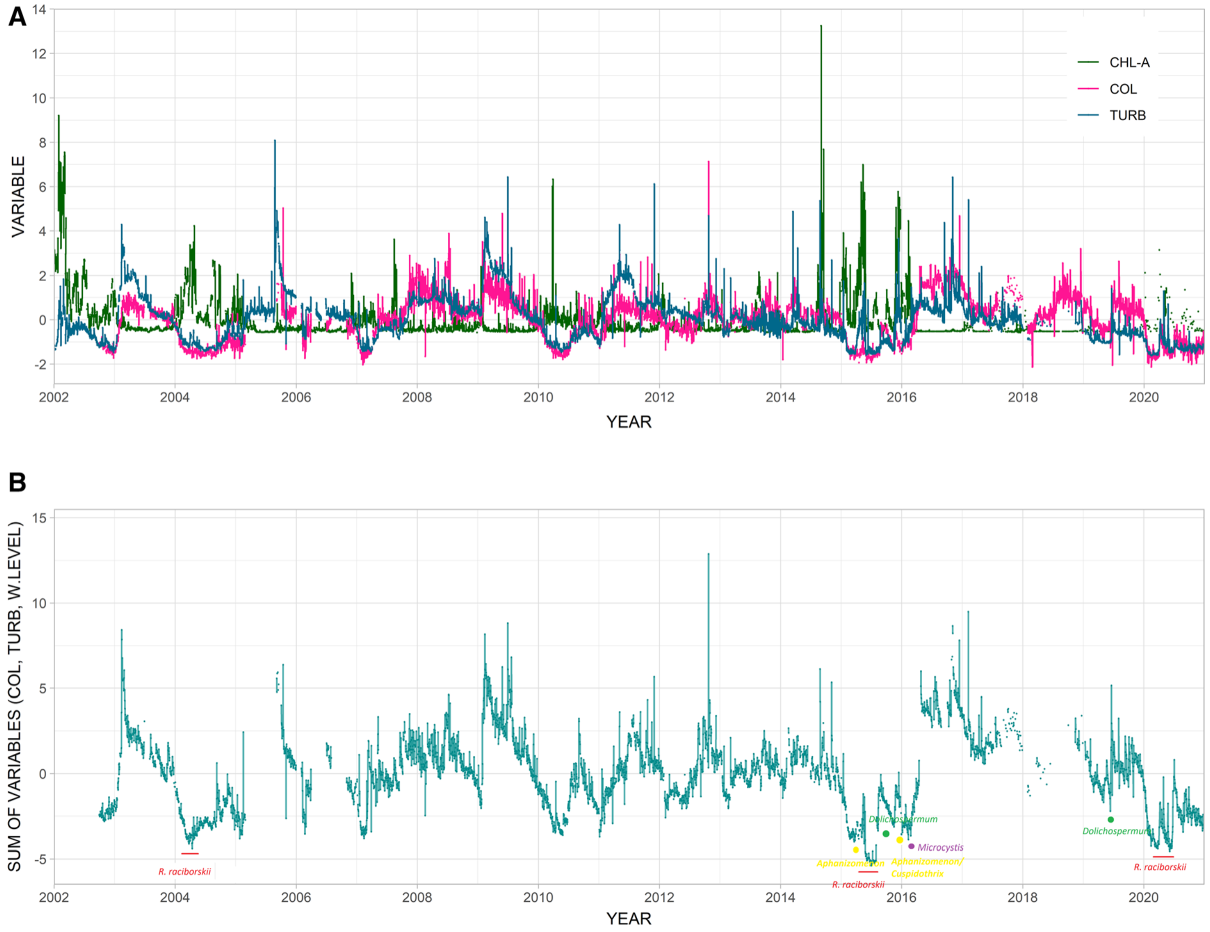

Fig. 3 Temporal variation of chlorophyll a (Chla), water color and turbidity during the period 2003–2020 in the area close to the water caption of the drinking water supply company. Variables were standardized (a). Additive contribution and its temporal fluctuation of turbidity, water color and water level (b). The sum includes the standardized (minus mean divided by standard deviation) values of each environmental driver. The time series comprise the period between 2003 and 2020 and the sampling frequency was daily (Program B). From 2015–2020 (Program A), we identified 2 blooms of R. raciborskii (horizontal bars, 3–4 months long); other cyanobacteria blooms lasted for shorter periods (up to one month, dots). From 2003 to 2015 we lacked information about cyanobacteria blooms, except for the bloom of R. raciborskii in 2004

persistent low water level (associated with dry periods), low turbidity and low water color, as observed by the sum of these three variables (Fig. 3b). This combination was only observed 3 times in the data set. Moreover, all three variables reached the 5% limit of the confidence bands throughout several days in 2004, 2015 and 2020 (Fig. 4a–c).

Raphidiopsis raciborskii 2015 and 2020 blooms (Program C)

Between 2015 and 2020, six N-fixing cyanobacteria blooms ([10 mm^3 l^{-1}) were registered in the Laguna del Sauce subsystem, composed either by Dolichospermum, Raphidiopsis, Cuspidothrix, and Aphanizomenon (Fig. 3b). The blooms with the highest persistence were the ones of R. raciborskii, which lasted 3–4 months each, and started at the onset of autumn. All other N-fixing cyanobacteria blooms occurred in summer and lasted for up to 1 month. In this period also a non-N-fixing cyanobacteria bloom happened (ej. chroococcales, Microcystis) (Fig. 3b). Blooms other than R. raciborskii developed in non-extreme situations (within the 5th–95th percentiles) of water depth and water transparency (turbidity and color) (Fig. 4a–c).

Both R. raciborskii blooms in 2015 and 2020 were preceded by other N-fixing cyanobacteria bloom and their subsequent collapse (Aphanizomenon in 2015 and Dolichospermun in 2020) (Fig. 3b). The first massive bloom in 2015 started in April (22 C) and finished in June (11.5 C), the maximum biovolume reached was 104.1 mm^3 l^{-1} and it occurred on May 23rd (Fig. 5a). The second massive bloom started in March (24 C) and finished in June 2020 (12 C), the maximum biovolume recorded was 10.01 mm^3 l^{-1} (March 29th) (Fig. 5b); one order of magnitude lower biomass than the 2015 bloom. R. raciborskii relative biovolume in both blooms mostly represented 80% of total phytoplankton biovolume and sometimes even reached up to 100% of the phytoplankton biovolume (during short periods of one to a couple of weeks) (Online Resource 1).

In the 2015 and 2020 blooms we detected saxitoxin concentration, but we did not detect cylindrospermopsin. During the first months in both blooms, saxitoxin concentration followed the biovolume pattern (e.g. April and May, 2015, and March and April, 2020); in the subsequent months, however, either high R. raciborskii biovolume had low saxitoxin (May 2020) or toxin was detected even after R. raciborskii collapsed (Fig. 5a, b). Saxitoxin concentration was one order of magnitude higher during the first bloom (2015, maximum of 9.8 lg l^{-1}) than in 2020 (maximum of 0.9 lg l^{-1}) (Fig. 5a, b). Remarkably, saxitoxin presence was detected, at low concentrations in the water, even 4–5 months after the bloom collapsed: in 2015 the bloom collapsed in June yet saxitoxin was detected until November (0.03 lg l^{-1}), and in 2020 the bloom ended at mid-May yet saxitoxin was detected until September (0.06 lg l^{-1}). The fact that both blooms expressed saxitoxin suggests that future blooms would be able to express toxicity too.

Morphological characterization and spatial heterogeneity in 2020 Raphidiopsis bloom (Program D)

Throughout the 2019–2020 growing period, two blooms of cyanobacteria were observed: at the beginning of January a bloom composed of several species of the genera Dolichospermum, and in March the R. raciborskii bloom started (Fig. 6a, b). Both blooms developed mostly in Laguna del Sauce and Laguna de los Cisnes subsystems (Fig. 6a, b), and the highest biovolume of R. raciborskii was observed in Laguna de Sauce subsystem (Fig. 5b). The PCA analysis showed that all Laguna del Sauce sampling sites (averaged according to the ANOSIM results) were in an intermediate position of the main environmental gradients associated with the first axis of PCA (Fig. 2). Higher values of ammonium were recorded in Laguna del Sauce. In the case of the second axis, the higher biomass and lower SRP and $N–NO_2^-$ of Laguna del Sauce sampling sites conditioned the spatial distribution in the bidimensional graph (Figs. 2, 6).

During the 2020 bloom (Program D), the key environmental drivers that explained the temporal variability of R. raciborskii (multiple linear regression, adjusted $R^2 = 0.78$, P \ 0.001) were: inorganic suspended matter (betha = 0.02, P [0.05), water color (betha = 0.14, P [0.05), water temperature (betha = - 0.62, P \ 0.05) and water level (betha = - 1.01, P \ 0.001). In this period, filaments were long: mean trichome length ranging from 158.8 to 198.3 lm. All R. raciborskii trichomes were straight and the number of heterocytes per trichome varied from 0 to 1 (note that the maximum possible number of

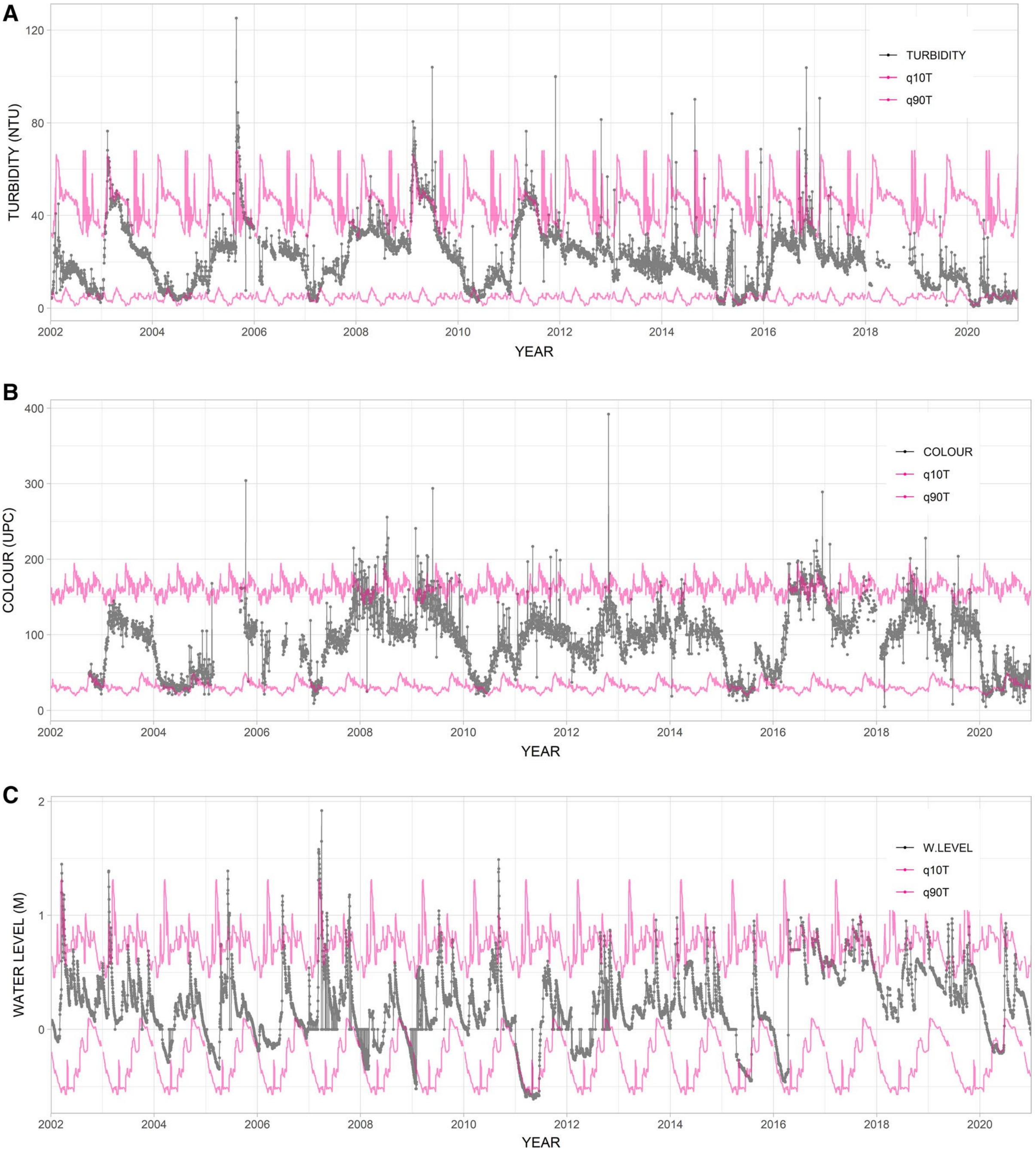

Fig. 4 The graphs (a, b and c) include the confidence bands calculated considering the 5th and 95th empiric percentiles (see "Materials and methods" section) for turbidity, water color, and water level in the area close to the water caption of the drinking water supply company. The time series comprise the period between 2003 and 2020 and the sampling frequency was daily (Program B)

heterocytes per filament is 2), with lots of filaments without differentiated cells (heterocytes). Filaments with akinetes were observed towards the end of the bloom.

Main impacts (2015–2020)

The 2015 crisis led to drinking water treatment improvements such as the inclusion of additional

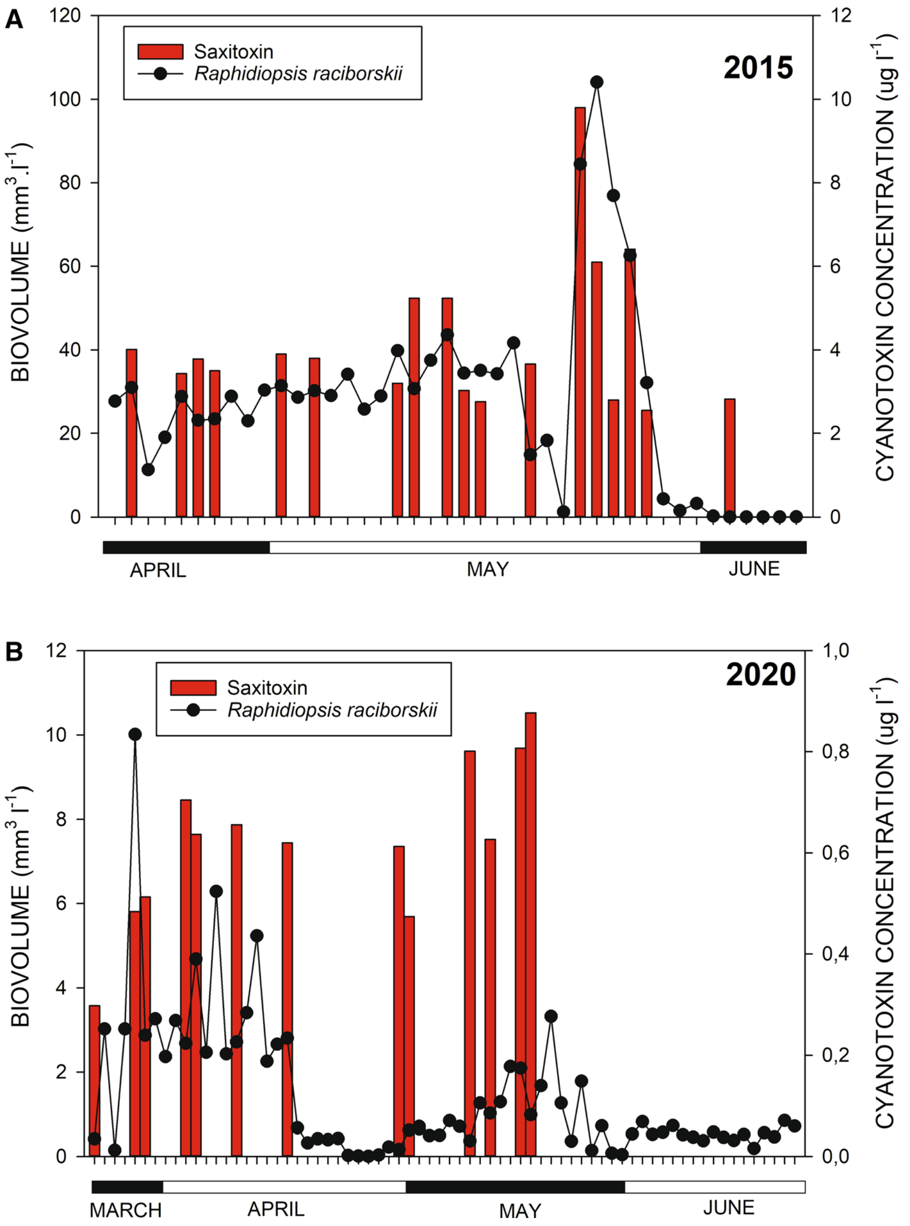

Fig. 5 Temporal variation of Raphidiosis raciborskii biovolume (mm^3 l^{-1}) and saxitoxin concentration (lg l^{-1}) in the area close to water caption of the drinking water supply company for 2015 (A) and 2020 bloom (B) (Program C)

tanks with activated carbon, the construction of an ozone system, and the addition of biological filters as a complement to traditional flocculation and flotation systems. The 2015 crisis also determined the implementation of a new field monitoring program (Program A, 2015-today), the design of research projects related to the creation of long term databases (i.e., Program B, 2003–2020), the development of predictive models using machine learning techniques (i.e., Crisci et al., 2017a, b), and the establishment of inter-institutional cooperation agreements. In this sense, the 2015 crisis represented a window of opportunity that promoted a closer collaboration between actors linked to ecosystem management, drinking water supply, and academia.

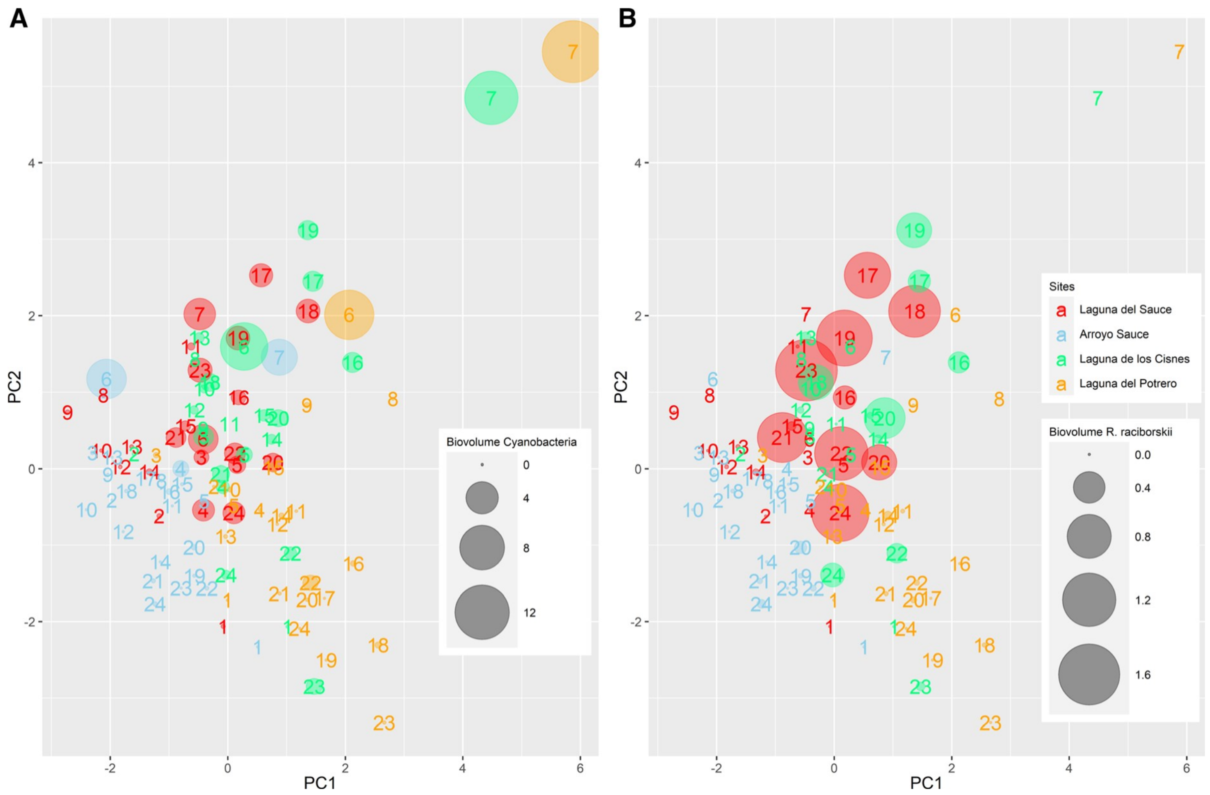

Fig. 6 Bubble plot with total cyanobacteria biovolume ($mm^3 l^{-1}$) (A) and Raphidiopsis raciborskii (B), considering the sites and sampling dates of growing season 2019–2020 and the sampling ordination obtained from Principal Component Analysis. The first sampling date corresponded to November 6, 2020 and the last corresponded to May 28, 2020 (Program D). Numbers indicate sampling dates, within this period a total of 24 samplings were performed

Discussion

The field evidence gathered combining different spatio-temporal approaches (daily throughout 17 years and weekly monitoring across five growing seasons) allowed us to identify that Raphidiopsis raciborskii blooms in Laguna del Sauce depend on infrequent combinations of low water level, high water transparency (low turbidity), and low water color.

Laguna del Sauce has high inorganic turbidity most of the time, limiting light availability in the water column, which is a relevant factor that controls phytoplankton dynamics (Crisci et al., 2017a). The variables of transparency, water color, and water level, in the big and shallow system of Laguna del Sauce, are conditioned by dynamic drivers like rainfall and wind regime (Crisci et al., 2017a, Gonzalez- Madina et al., 2018, Levrini et al., in prep). In this ecosystem, extreme rainfall and wind events determine abrupt shifts of inorganic turbidity (Crisci et al., 2017a) due to sediment resuspension and/or soil erosion. Laguna del Sauce subsystem presents a big size (4400 ha) with a fetch oriented towards the direction of the frequent and/or stronger winds (N-NE, S-SW). This generates a predominance of high inorganic turbidity due to sediment resuspension caused by wind. In this sense, a decline in water level increases, even more, the probability of sediment resuspension. Hence, combinations of periods with low water levels and low inorganic turbidity are very infrequent in the system. The observed pattern reveals the relevance of understanding the relationship between water transparency and the regular wind regime, in addition to the dynamics of extreme wind events previously explored by Crisci et al. (2017a). Moreover, rainfall impacts the concentration of dissolved organic material inputs, which can be washed out from the catchment, as well as its export to associated wetlands, which determines water color and plays a key role in this system by governing light quality in the water column (Levrini et al., in prep).

Raphidiopsis raciborskii traits

Our results showed that three R. raciborskii blooms occurred in 17 years, and when they occurred reached high magnitude. In the 2015 and 2020 blooms, R. raciborskii dominated the phytoplankton assemblage, persisted for 3–4 months, and produced saxitoxin. Nevertheless, as mentioned above, it can be argued that blooms of R. raciborskii were constrained to a particular set of environmental variables (low water level, low turbidity, low color) that coincided only a few times in the 17 years analyzed in Laguna del Sauce. Hence in this ecosystem, blooms of R. raciborskii would be expected in situations of persistent low water levels and high transparence (given by low turbidity and low water color). Like our findings, the studies of Brasil et al. (2016) and Costa et al. (2016) found that drought conditions favored the development of R. raciborskii, but the relationship between turbidity and biomass was a negative one.

Burford et al. (2016) compiled from the literature R. raciborskii (Cylindrospermopsis) traits related to light, nutrients and temperature. Remarkably, our results show trends that seem not to respond to the traits determined for this species. For example, the temperature optima of this species are 29–32 C (Briand et al., 2004; Chonudomkul et al., 2004) with a growth threshold of 25.5 C (Recknagel et al., 2014). Our findings, however, show that growth occurred at a lower temperature range (from 21 to 23 C at the onset of the blooms in autumn down to 10–14 C by the end of the season). Indeed, in other studies performed in Uruguay showed that R. raciborskii developed blooms at low temperatures (Vidal & Kruk, 2008; Fabre et al., 2010; Somma, 2014), growing over a wide range of temperatures possibly due to its phenotypic plasticity (Bonilla et al., 2012). Remarkably, the persistence of cyanobacteria blooms in autumn or even winter was also reported for other shallow lakes located in similar climates in South America (Pacheco et al., 2010; Izaguirre et al., 2015; OFarrell et al., 2021).

Moreover, R. raciborskii is recognized as a species that tolerates significant levels of shading (Padisak, 1997). However, our results showed that the occurrence of this species took place in periods of clear water in conditions with low turbidity and low water color. This agrees with Mehnert et al. (2010) who found that R. raciborskii has maximum growth rates at high light intensities. Blooms of R. raciborskii were generally preceded by blooms of other N-fixing cyanobacteria, such as Aphanizomenon spp or Dolichospermum spp., and its subsequent collapse, which contributed to high transparency conditions. Also, the fact that the euphotic zone can comprise the entire water column, due to its scarce depth, suggests that light availability at the water–sediment interface can play a major role in the emergence of resistance structures of R. raciborskii located at the sediment.

Raphidiopsis raciborskii filaments in the 2020 bloom showed a wide morphological plasticity and were mostly long and lacked heterocytes (or had only one of the two possible heterocytes). Yema et al. (2016) suggested that when filament length in R. raciborskii was large this trait could be used as a proxy of an absence of nitrogen fixation behavior. This seems to coincide with our findings where filaments were long (high number of vegetative cells) and heterocytes were scarce (mostly absent or only up to one per filament). Indeed, our previous studies in Laguna del Sauce showed that most blooms of high magnitude of N-fixing cyanobacteria (Cuspidiotrix, Aphanizomenon and Dolichospermum) lacked heterocytes at high TN concentrations (800–1000 1g l^{-1}), hence bloomed behaving as non-fixers (González-Madina et al., 2018). We observed a high number of filaments with akinetes towards the end of the bloom, which may imply a high pool of dormant cells to the sediments which can germinate when the next favorable conditions arise in the future. A high number of akinetes in a population may be indicative of unfavorable conditions and preclude the ending of the bloom (Litchman et al. 2010).

Noteworthy, R. raciborskii can produce either cylindrospermopsin or saxitoxin, yet in Laguna del Sauce, only saxitoxin was produced, as observed in other water bodies in Uruguay (Bonilla, 2009; Piccini et al., 2011). The high concentration of saxitoxin recorded in the 2015 bloom (up to 9.8 1g l^{-1}) posed a great challenge for the drinking water supply facilities, as its concentration in drinking water cannot surpass 3 1g l^{-1} (reviewed in Chorus and Welker, 2021). In the 2020 bloom, however, saxitoxin concentrations (up to 0.9 1g l^{-1}) were always below levels considered of risk for drinking water. The concentration of saxitoxin, either followed the biovolume of R.

raciborskii, or was low in relation to the biomass. Moreover, after the blooms collapsed low saxitoxin concentrations (below risk levels for drinking water) persisted in the environment for up to 4–5 months. Noteworthy, blooms containing high concentrations of saxitoxin (such as the one recorded in 2015) are rare, as evidenced by the study run by Dolman et al. (2012) across 102 German lakes, where only 13 lakes had saxitoxin presence, and at low concentrations (lower than 2 lg l^{-1}). Beamund et al. (2016) found that the production of saxitoxin could be a response to the stress for exposure to UV-B irradiation. Hence, it is possible that the exposure of R. raciborskii to high light intensities could have influenced the production of saxitoxin observed in Laguna del Sauce blooms. Moreover, several authors argue that high concentrations of cyanobacteria toxins are related to the excess availability of nitrogen (Gobler et al., 2016; Brandenburg et al., 2020), probably because toxin molecules are rich in nitrogen. In Laguna del Sauce the total nitrogen concentrations are within eutrophic values and hence could favor the synthesis of saxitoxin. In this system N-fixing cyanobacteria blooms mostly occur at absolute nutrient values within 800–900 lg l^{-1} TN and 80–90 lg l^{-1} TP and blooms at higher TN reached more biomass than those at low TN (González-Madina et al., 2018). Our results show a higher coefficient of variation in TN compared to TP through the 5 growing seasons. Higher TN could boost higher bloom magnitude (with non-N-fixing behavior) and could favor the synthesis of toxins.

Impacts of R. raciborskii, adaptation and anticipatory capacities

Raphidiopsis raciborskii presence interferes with the provision of drinking water as well as with recreation activities. In the first case, the challenge is associated with physical (mechanical) interferences due to its small cell diameter (ca. 3 lm width), difficulties in the flocculation process related to daily pH variability, and presence of saxitoxin levels above the ones allowed in drinking water supply. In this sense, the 2015 bloom triggered multiple actions in the infrastructure level of the OSE (water treatment facilities), and the establishment of new monitoring programs.

The experience of Laguna del Sauce demonstrated the relevance of creating and strengthening capacities from a polycentric perspective (Biggs et al., 2015), that is, having a real capacity for analysis in the time periods and places where key decision-making processes occur (i.e., drinking water supply company). This is a key message in a country like Uruguay that is excessively centralist. The defragmentation in the analysis and decision-making processes observed in Laguna del Sauce (based in scientific evidence supported by robust monitoring programs) is one of the classic patterns in the transition between command-control paradigms towards integrated management (Pahl-Wostl, 2015; Trimble & Mazzeo, 2020). However, in other key areas such control and implementation of action plans (i.e., reduction of diffuse external nutrient inputs), as well as in communication programs, the classical fragmentation persists.

The capacity for adaptation and resilience depends on a set of factors related to individual and social learning, innovation and anticipation (Chapin et al., 2009; Biggs et al., 2015). The advances observed and analyzed here indicate that the system continues in a fundamentally reactive, not proactive format. Cyanobacterial blooms and their consequences continue to be analyzed mainly from an adaptation perspective, especially in the absence of effective control of the main causes (i.e., external nutrient inputs). Building a different future from the present (sensu Miller et al., 2018) presents great difficulties in the example analyzed. Current key challenges include the limitation in the understanding of the multicausality and dynamics of the eutrophication (and the sudden regime changes that can occur) and the weak intra and inter-institutional cooperation in terms of implementation and control of the strategies and actions designed by the basin committee (Mazzeo et al., 2018).

Water level management is a key factor determining multiple ecosystems processes (Bakker & Hilt, 2015). After the 2015 bloom, the dam management was modified, trying to store water during spring and avoiding severe drops during the summer season, where a major consumption (due to tourism) occurs. Since 2015 phases of major water transparency had been observed, which had been most of times interrupted with sediment resuspension during periods with low water level. In Laguna del Sauce maintaining a high-water level has its positive aspects (dilution of nutrients in the water, e.g. the TP decrease between 2015 and 2020) but also a negative one (less sediment resuspension caused by wind action and hence higher light availability in the water column). These aspects must be explored in detail in order to decrease risks associated with cyanobacteria blooms, particularly those which can reach high toxicity levels, as observed for R. raciborskii.

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