



Research Article

Bloom-forming cyanobacteria and dinoflagellates in five Argentinian reservoirs: Multi-year sampling

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ABSTRACT

Harmful algal blooms are important threats to reservoir condition. Over a 15-year period, we sampled five Argentinian reservoirs to identify the responsible species for harmful algal blooms and determine the water quality factors driving their occurrence. These reservoirs exhibit diverse morphological and hydrological characteristics and are distributed across varying climatic zones. Cyanobacterial blooms included an array of species, including toxin producers such as *Raphidiopsis raciborskii*, *Aphanizomenon gracile*, and *Microcystis aeruginosa*. In contrast, dinoflagellate blooms were predominantly characterized by *Ceratium*. The cyanobacterial blooms primarily occurred in the shallower reservoirs located in warmer regions, whereas dinoflagellate blooms occurred where temperatures were lower. The most intense blooms occurred during the summer, and although cyanobacterial and chlorophyte blooms co-occurred, they never coexisted with dinoflagellate blooms. We identified cyanotoxins in the reservoirs over the past three years, a phenomenon previously unreported in the region. Given that these reservoirs are drinking water sources for human populations, ongoing and systematic monitoring is needed to protect public health. Controlling the proliferation of algae and cyanobacteria in reservoirs requires resource management at the watershed level, and in the case of the Itiyuro and El Limón, requires binational management with Bolivia.

1. Introduction

Blooms of harmful algae and cyanobacteria occur worldwide and are known by their acronym HABs (Harmful Algal Blooms). HAB impacts include the production of toxins that are potentially harmful or lethal to other organisms; hypoxic or anoxic zones; increased water treatment costs; and decreased water body quality and potential uses (O'Farrell et al., 2019). Earlier, HABs were only those blooms that produced or released potentially dangerous toxins, but today HABs include "any event that has a negative impact on human health, socioeconomic interests, or aquatic systems" (Kudela et al., 2017). The U.S. Environmental Protection Agency adopted a similarly broad definition of HABs. It included potentially toxic species and high biomass species that cause hypoxia or anoxia and mortalities after reaching dense concentrations, whether or not toxins are produced (Heisler et al., 2008). Many factors act as promoters of these blooms, including excess nutrients, reduced precipitation, and climate heating (Moore, 2011; Janssen et al., 2019).

The UNESCO Intergovernmental Oceanographic Commission lists 178 toxigenic, microalgae species that occur in marine or freshwaters (Moestrup et al., 2009). The list includes genera and species of diatoms, raphidophytes, haptophytes, and cyanobacteria, although most are dinoflagellates. HABs can be found worldwide and are becoming more frequent and intense, and it is expected that these blooms will spread to areas where the phenomenon has not yet been observed (Cheung et al., 2013). On the other hand, the increase in HAB reports is also associated with more sampling, better species identification, and the use of current technologies. For example, remote sensing has been acknowledged as a valuable tool for investigating algal and cyanobacterial blooms because of its wide-scale applicability, real-time data collection capabilities, and long-term monitoring abilities. To verify that the reported increases are real, historical HABs data series are necessary, including the environmental conditions that promoted them (Reguera, 2002).

The first records of cyanobacterial blooms in Argentina date to 1944 (Mullor, 1945), but in the 1990s the records increased considerably,

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probably related to increased anthropogenic activities (Pizzolon et al., 1999; Quirós and Drago, 1999). Most cyanobacterial blooms have been detected in the central and coastal areas of the country (Aguilera et al., 2017; O'Farrell et al., 2019), whereas most dinoflagellate blooms were reported in the temperate and Patagonian zones of Argentina. *Ceratium*

hirundinella (O.F.Müller) Dujardin was reported in Patagonian lakes in the 1990s (Izaguirre et al., 1990), expanding rapidly towards the central and northern areas of the country, especially in reservoirs, showing a high invasive capability (Boltovskoy, 2004). Blooms of *C. hirundinella* and *Ceratium furcoides* (Levander) Langhans now have been reported in

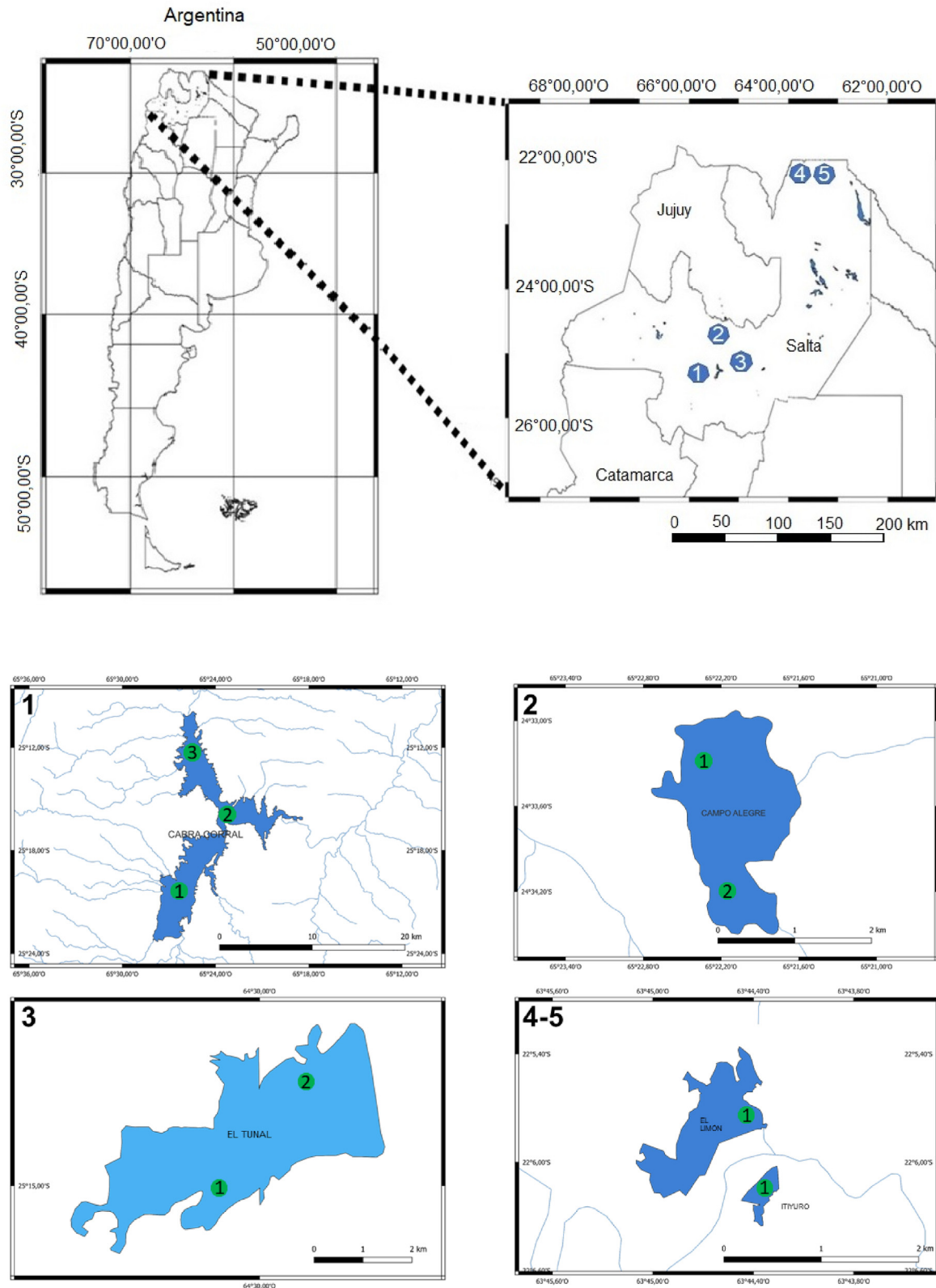


Fig. 1. Reservoir and sampling point locations. The numbers in the reservoirs correspond to sampling stations.

reservoirs throughout Argentina and in northern bordering countries (Fontúrbel et al., 2006).

To test the hypothesis that environmental conditions explain both, kind and intensity of bloom, we compiled limnological data from five reservoirs in the province of Salta between 2007 and 2021.

2. Materials and methods

2.1. Study reservoirs

We built a dataset from five reservoirs sampled by our laboratory in the last 15 years (2007–2022): Cabral Corral (CC), El Tunal (ET), Campo Alegre (CA), El Limón (LIM), and Itiyuro (ITI) (Fig. 1). The reservoirs vary in use, altitude, climate, volume, area, and depth (Table 1). Cabra Corral is one of the largest in Argentina and is used for hydropower, irrigation, and recreational. El Tunal is used to refill Cabra Corral reservoir; sport fishing and recreational activities are also important. Campo Alegre, Itiyuro and El Limón reservoirs provide drinking water and direct contact recreation. El Limón and Itiyuro are in a tropical area, the other reservoirs are in a subtropical mountain region.

2.2. Study design

The number of sampling stations and visits per reservoir varied with reservoir size and complexity and study duration (Table 1, Table 2). In El Tunal and Campo Alegre, the stations were at the entrance of the main tributaries (after the mixing zone) and in the deepest central zone; in Cabra Corral an extra station was added in a reservoir arm. In Itiyuro and El Limón, the stations were in the drinking water intake area.

2.3. Water quality parameters

We took 2-L water samples with a Van Dorn sampler at a depth of one Secchi disk between 10:00 and 12:00. We measured electrical conductivity ($\mu\text{S}/\text{cm}$), pH, temperature ($^{\circ}\text{C}$) and oxygen (mg/L) *in situ* with an Orion multiparameter sensor, turbidity (NTU) with a HACH brand turbidimeter, and transparency (m) with a Secchi disk. True color; soluble reactive phosphorus ($\text{mg SRP}/\text{L}$); nitrates, nitrites, and ammonium ($\text{mg N}/\text{L}$); alkalinity ($\text{mg CaCO}_3/\text{L}$); hardness ($\text{mg CaCO}_3/\text{L}$); chemical oxygen demand (COD) (mgO_2/L); and solids (mg/L) were determined in the laboratory (APHA, 2005). We calculated soluble inorganic nitrogen (SIN) as the sum of nitrites, nitrates and ammonium, and the nitrogen/phosphorus ratio as SIN/SRP (N/P). We determined Chlorophyll-a (CL-a) via the modified Scor-Unesco technique (Supplementary Material 1).

2.4. Phytoplankton counting and identification

All samples were collected at the designated sampling points in each reservoir (Fig. 1). Samples for qualitative phytoplankton analysis were subsurface collected with a 30 μm mesh net and fixed in 4% formaldehyde, whereas samples for quantitative analysis were collected at the Secchi depth, fixed in acidified Lugol, and stored at 4 $^{\circ}\text{C}$ until analysis. Counts were made after 24 h sedimentation in combined chambers using an inverted Zeiss L microscope (Utermöhl, 1958). Each sample was

Table 1
Reservoir characteristics.

	Reservoir	Altitude (m.a.s.l)	Area (km^2)	Volume (Hm^3)	Average Depth (m)	Annual Rainfall (mm)	Average Annual Temp. ($^{\circ}\text{C}$)
1	Cabra Corral	945	113.6	3100	27.5	450	21
2	El Tunal	470	38	310	4.5	550	17.5
3	Campo Alegre	1398	3.15	44	14.4	684	14.6
4	El Limón	540	0.74	2	5	970	21
5	Itiyuro	540	0.11	2	4	970	21

Table 2
Sampling visits per reservoir.

	Reservoir	Sampling years	Visits
1	Cabra Corral	2007–2009	18
2	El Tunal	2007–2009	10
3	Campo Alegre	2007-08-17-19-21	22
4	El Limón	2013–2020	45
5	Itiyuro	2013–2020	37

counted to obtain <20% error of the most frequent taxa (Venrick, 1978); most counts were <5%, and results were expressed in cells/mL. Organisms without cellular content were not considered in the count. Taxa were identified by capturing images with an Axio Cam1Cc3 digital camera and by using taxonomic keys (Komárek and Anagnostidis, 1999, 2005; Komárková-Legnerová, 1969; Komárek et al., 2014). Biovolumes were calculated from their measurements using the models of geometric composition for each taxon (Hillebrand et al., 1999).

We considered a Cyanobacteria or Chlorophyta bloom as those samples that exceed 10,000 cells/mL. In the case of dinoflagellates, we deemed 1000 cells/mL for *Ceratium* a bloom (Kawabata and Kagawa, 1988; Guerrero and Echenique, 1997; Mac Donagh et al., 2005; Hart and Wragg, 2009; Silverio et al., 2009). We used a Venn diagram to visualize the unique species of each reservoir and the species shared between the reservoirs.

2.5. Cyanotoxin equivalents determination

Microcystin equivalents (MCYST-LR equivalents L-1) were determined using the ELISA immunoassay technique or phosphatase inhibition assay. Once the samples were collected, the collected samples were refrigerated during their transfer to the laboratory. Upon arrival at the laboratory, the samples were stored at a temperature of -20°C until the analysis was conducted. We quantified toxins by using an ELISA Quantiplate™ kit for microcystin (Envirologix™ brand), using the Elx800 reader model (Biotek) for reading the plates and MicroCystest (ZEULAB SL). Results equal to or greater than 1 $\mu\text{g}/\text{L}$ were considered positive. The tests were carried out regardless of the presence or absence of cyanobacterial cells to detect toxins in dissolved form (Ruibal Conti et al., 2005).

2.6. Statistical analysis

We used InfoStat 2018 for descriptive analysis of the limnological variables and Spearman correlations between physical, chemical, and biological variables. To contrast differences between the means of two independent samples, a T-test (Student's *t*) was used, after verifying the assumptions of normality and homoscedasticity were met. In those cases where the data did not meet those assumptions, we used the Mann-Whitney *U* test. When multiple comparisons were made, we used ANOVA if the data met normality and homoscedasticity assumptions. When the data did not meet those assumptions, we used the non-parametric Kruskal-Wallis *H* test.

We used RDA (Redundancy Analysis) in R using the Vegan and GGplot packages to analyze the bloom data. Before the analysis, the abundances of each group were standardized using the Hellinger

transformation and the environmental variables by using “standardize” to ensure comparability and remove any scaling effects (Oksanen et al., 2007).

3. Results

3.1. General information of the reservoirs

Water quality in the five reservoirs differed to varying degrees (Fig. 2). The reservoirs located in the central area of the province (CA, CC) displayed average electrical conductivity, N/P, COD, and hardness values lower than those in the northern reservoirs. Turbidity was lowest in CC and LIM, but alkalinity varied similarly across all five reservoirs.

Phytoplankton abundance and richness differed markedly among reservoirs. The average phytoplankton abundance was much higher in the northern reservoirs (El Limón and Itiyuro). El Limón ($7.3 \times 10^4 \pm 1.1 \times 10^5$ cells/mL), Itiyuro ($1.1 \times 10^4 \pm 2.1 \times 10^4$ cells/mL), Cabra Corral ($5 \times 10^3 \pm 1.1 \times 10^4$ cells/mL), Campo Alegre ($2 \times 10^3 \pm 1.5 \times 10^3$ cells/mL), and El Tunal ($9 \times 10^2 \pm 4 \times 10^2$ cells/mL). The number of taxa also varied amongst reservoirs, ranging from 183 (73 unique) in El Limon to 39 (7 unique) in Campo Alegre (Fig. 3; Supplementary Material 3). Probably because of their proximity and greater taxa richness, Limón and Itiyuro shared the most taxa (76); only five taxa occurred in all five reservoirs.

Cyanobacteria and dinoflagellate abundances were both significantly

correlated with N/P (positively for the former, negatively for the latter), but only explained 18% and 11% of their variability, respectively (Table 3). Cyanobacteria abundance was also weakly, positively correlated with TC and SIN, whereas dinoflagellate abundance was weakly, negatively correlated with conductivity and hardness.

Cyanobacteria were more successful when the N/P ratio was >15 , but dinoflagellates were more successful when the N/P ratio was <4 . When cyanobacteria were dominant, hardness was >300 mgCaCO₃/L, but when dinoflagellates dominated, it was always <200 mgCaCO₃/L.

3.2. Blooms

Out of the 132 site visits, 61 were bloom events, 46 from Cyanobacteria, 10 from dinoflagellates, and 5 mixed (Cyanobacteria + Chlorophyta). Chlorophyta blooms alone were not recorded. Most cyanobacterial blooms were in El Limón and Itiyuro, although four occurred in Cabra Corral. Blooms in El Limón and Itiyuro were always multi-taxa, but those in Cabra Corral were *Microcystis* sp. (Fig. 4). Dinoflagellate blooms in Campo Alegre and Cabra Corral were monospecific (*Ceratium*), dominated by *C. hirundinella*, or a mix of *C. hirundinella* and *C. furcoides*. No blooms were observed in El Tunal.

Dinoflagellate blooms were predominantly observed in years with higher rainfall compared to historical records. For instance, 126% higher in Cabra Corral and 46% higher in Campo Alegre. *Ceratium* blooms occurred in both wet and dry seasons in Cabra Corral and Campo Alegre.

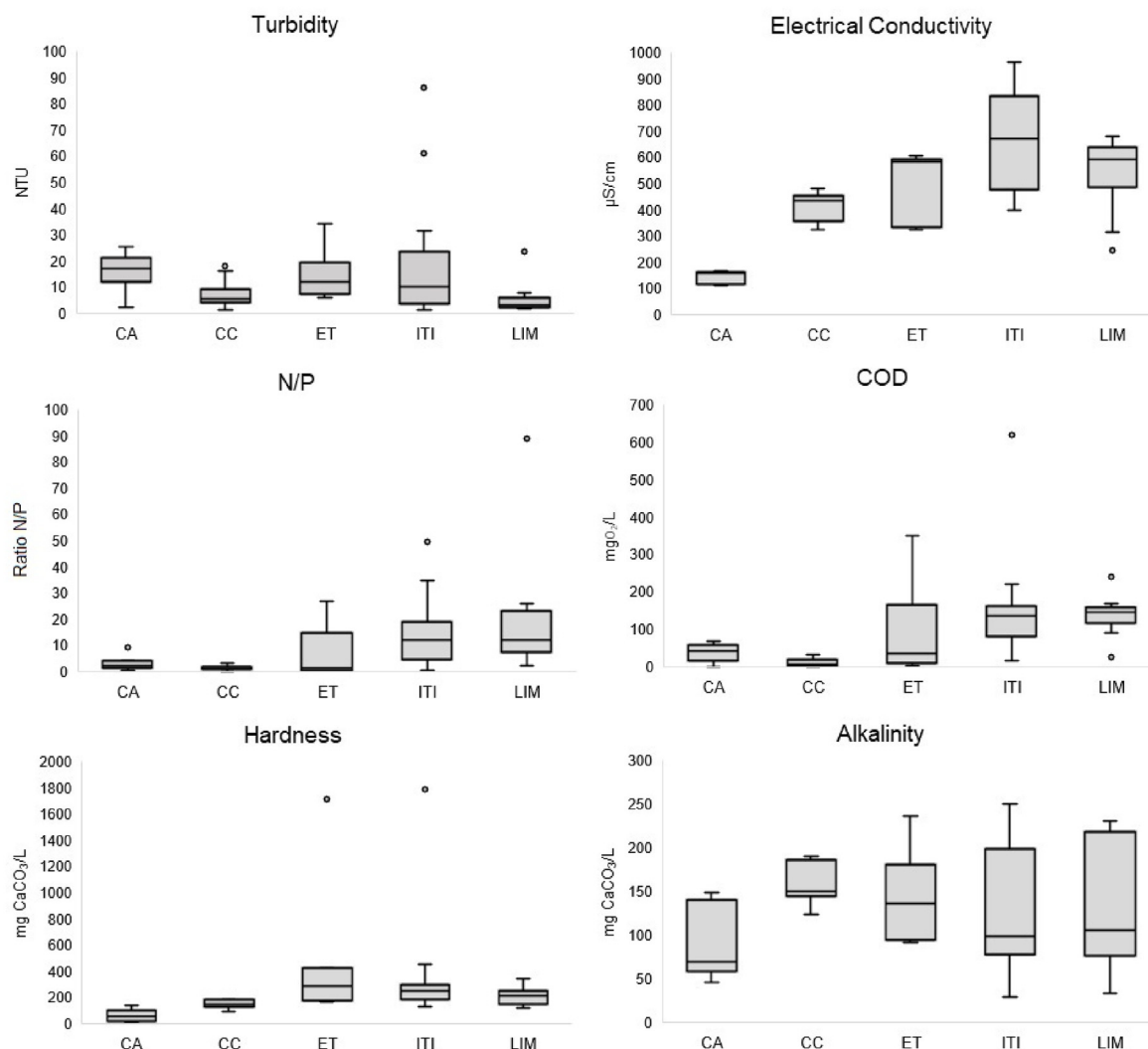


Fig. 2. Water quality in the reservoirs, considering all the sampled years and seasons. CA: Campo Alegre; CC: Cabra Corral; ET: EL Tunal; ITI: Itiyuro; LIM: Limón.

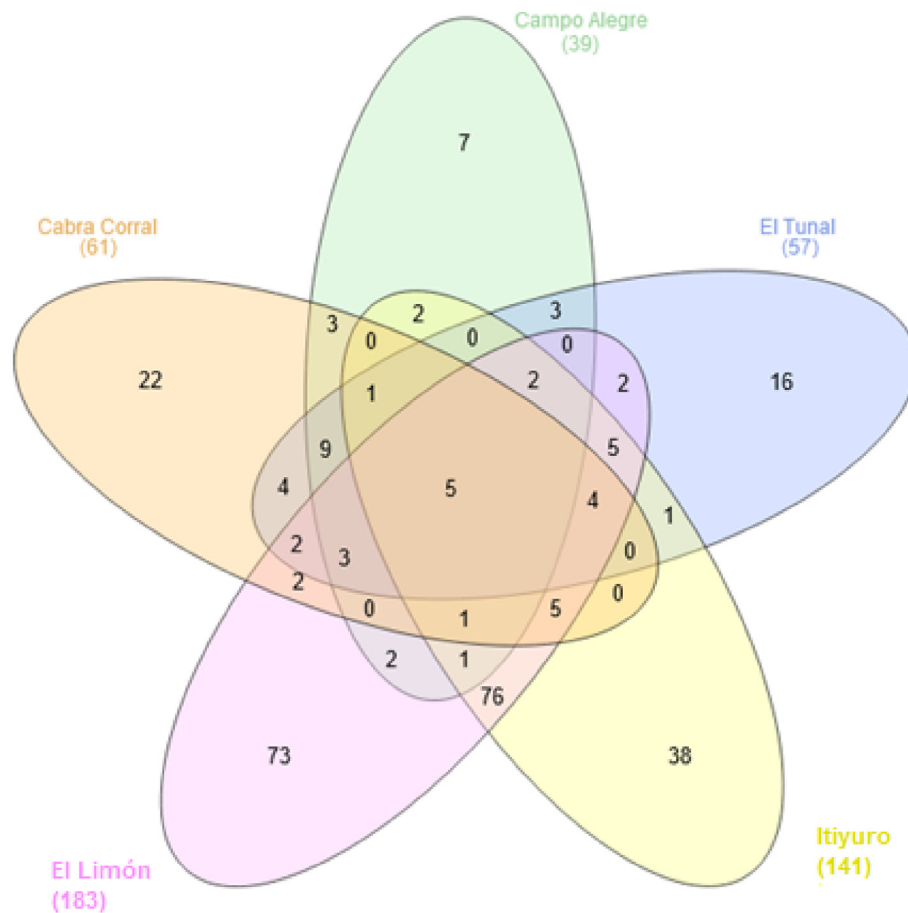


Fig. 3. Number of taxa recorded in each reservoir and shared among reservoirs.

Table 3

Pearson correlations between water quality and the abundances of cyanobacteria and dinoflagellates. All correlations were $p < 0.005$, those highlighted in bold were $p < 0.0001$.

Variable	Cyanobacteria	Dinoflagellata
Electrical Conductivity ($\mu\text{S}/\text{cm}$)	0.36	-0.45
Water Temperature ($^{\circ}\text{C}$)	0.47	-0.28
Turbidity (NTU)	-0.34	0.25
Hardness (mg CaCO_3/L)	0.35	-0.51
N- NO_3 (mg/L)	0.41	
SIN (mg/L)	0.52	-0.28
N/P	0.43	-0.33

Temperatures recorded during these years remained within historical norms.

Cyanobacterial blooms were observed in years with temperatures exceeding historical averages. For Limón and Itiyuro, temperatures during the blooms were 1.2°C higher. Blooms in Limón and Itiyuro were registered equally in high and low water periods, but in Cabra Corral, the four blooms occurred during the wet season.

The sizes of Cyanobacterial blooms have increased. Between 2009 and 2018 blooms did not exceed 200,000 cells of Cyanobacteria/mL, but blooms in 2020 and 2022 were $>350,000$ cells/mL, reaching $>700,000$ cells/mL in Limón (2020).

From the 54 potentially toxic taxa identified in the reservoirs, eight were Nostocales (42.6% of total records), five were Chroococcales (14.7%), and nine were Synechococcales (29.4%). Together with *Ceratium* sp. These accounted for 97.0% of the total records (Fig. 5). The full list of Cyanobacteria morphospecies responsible for blooms in Salta is in Supplementary Material 2.

3.3. Redundancy analysis (RDA)

The first axis of the RDA explained 72.94% of the bloom variability (Fig. 6). Along this axis, blooms from the northern reservoirs (Limón and Itiyuro) were separated from those in the central zone (Campo Alegre and Cabra Corral). The biological variables associated with this separation were cyanobacteria and dinoflagellate abundances, and temperature, electrical conductivity, and pH were the most important environmental explanatory variables. During blooms dominated by Cyanobacteria in the northern region, higher values of electrical conductivity and temperature occurred, whereas Campo Alegre and Cabra Corral blooms exhibited higher pH values.

Microcystins (MCYST-LR equivalents L-1) were assessed in 67 samples from 2007, 2008, 2009, 2018, 2019, 2020 and 2021 in all five reservoirs. Cabra Corral and El Tunal toxin concentrations were lower than the quantification limit of the test ($0.175 \mu\text{g}/\text{L}$), despite the presence of potentially toxic Cyanobacteria. In Campo Alegre, the results from 2007, 2008 and 2009 were below the detection limit, but in 2021, a positive value ($2.23 \mu\text{g}/\text{L}$) was recorded (Table 4). El Limón and Itiyuro had levels above those recommended by the WHO on several occasions (Table 4).

4. Discussion

HABs in South America have received limited research attention, with most studies focusing on Brazil and Argentina. In Argentina, research has primarily concentrated on the largest reservoirs, possibly because of greater investment, easier access, and the need for controls in water used for agriculture (Pierotto et al., 2003; Rodríguez et al., 2005; Daga et al., 2011; O' Farrell et al., 2019; Mancini et al., 2011; Bordet et al., 2017;

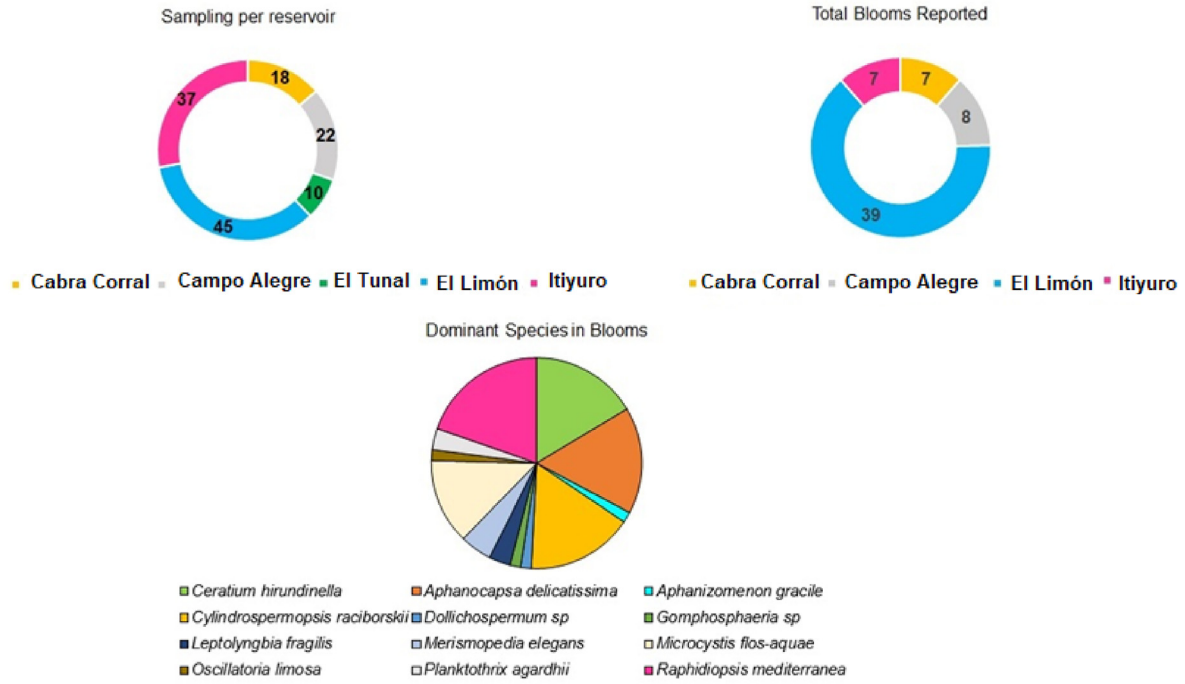


Fig. 4. Total blooms per reservoir and dominant taxa in blooms.

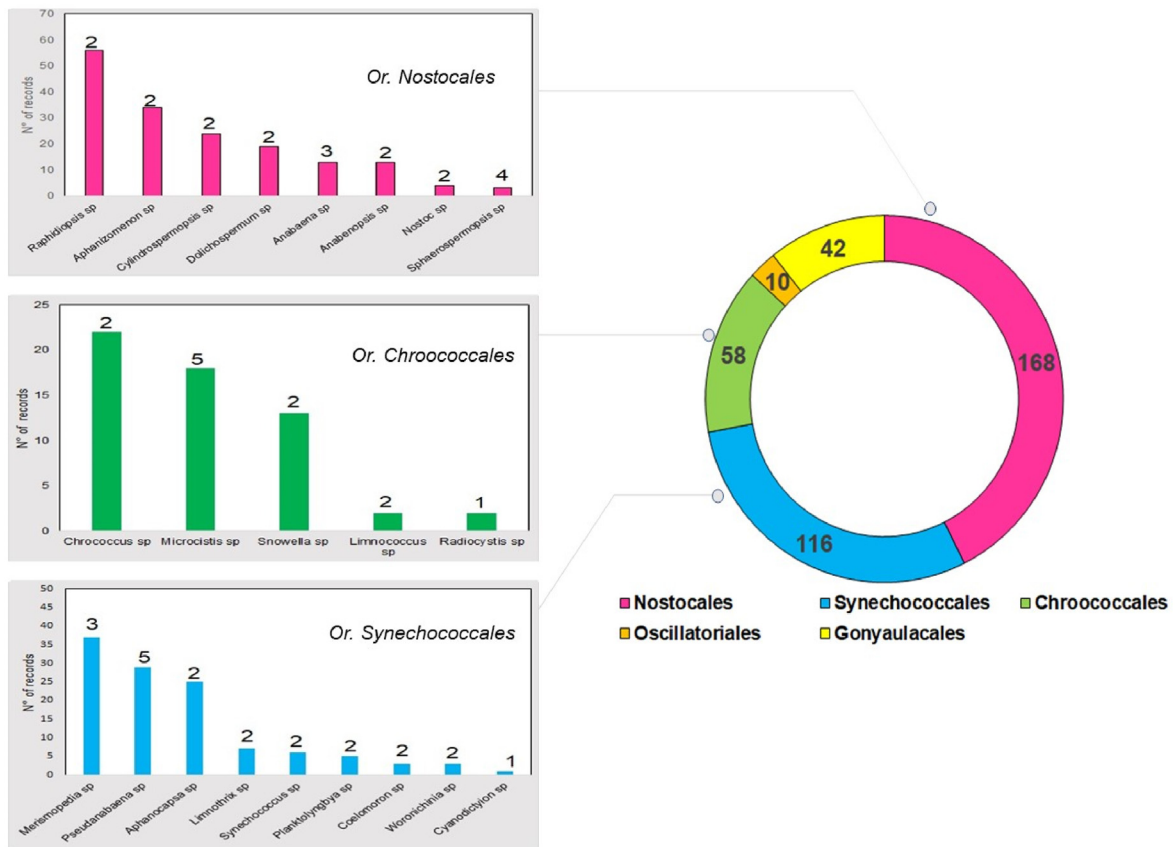


Fig. 5. Number of records of potentially toxic phytoplankton taxa over 2007–2021. Above each bar, the number of reservoirs in which each taxon appeared is indicated.

Aguilera et al., 2017; O'Farrel et al., 2019). However, studies in northern Argentina are scarce leading to an undervaluation of the problem (Salusso and Moraña, 2000; 2014a, b, 2015, 2018; Vidaurre et al., 2018;

Borja et al., 2021; Alvarez Dalinger et al., 2022). Intense monitoring in certain areas suggests an increased bloom frequency, but these biased records are not representative of all HABs in Argentina. We found HABs

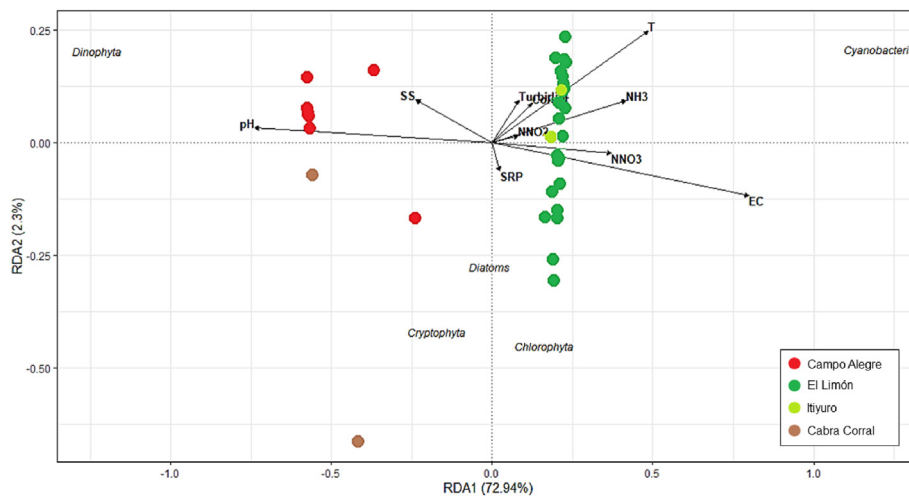


Fig. 6. RDA results in reservoirs with blooms. Variables: pH, SS (suspended solids), SRP (soluble reactive phosphorus), NNO₂ (nitrite), NNO₃ (nitrate), NH₃ (ammonia), EC (electric conductivity), Turbidity, T[°]C, Cyanobacteria, Diatoms, Dinophyta, Chlorophyta, and Cryptophyta.

Table 4
MCYST-LR equivalents L-1 positive results ($\geq 1 \mu\text{g/L}$) in three reservoirs.

Reservoir	Year	Date/Month	MCYST-LR ($\mu\text{g/L}$)	Dominant taxa
Campo Alegre	2021	November	2.23	<i>Leptolyngbia</i> sp.
Itiyuro	2019	December	2.56	<i>Raphidiopsis mediterranea</i>
Itiyuro	2020	15-January	3.69	<i>Aphanocapsa delicatissima</i>
Itiyuro	2020	30-January	2.58	<i>Aphanocapsa delicatissima</i>
El Limón	2019	15-December	1.14	<i>Raphidiopsis mediterranea</i>
El Limón	2019	30-December	3.16	<i>Raphidiopsis mediterranea</i>
El Limón	2020	15-January	2.39	<i>Merismopedia elegans</i>
El Limón	2020	30-January	2.78	<i>Merismopedia elegans</i>

since at least the 2000s in northern Argentina, aligning with reports from other reservoirs. Disparate sampling programs highlight the importance of establishing a unified national monitoring program and database, particularly for drinking-water bodies (Ramírez et al., 2022).

Our five-reservoir sampling was not temporally uniform, which hinders detecting HAB trends and their attribution to environmental factors. However, despite the inconsistent sampling, we observed that the most intense cyanobacteria blooms occurred in recent years (2018–2020), which is associated with increased human activity and temperature in the area. The main cyanobacterial blooms in Salta province, specifically in El Limón and Itiyuro near the Bolivian border, have remained relatively constant over the past decade but have intensified in recent years (2018–2020). Dinoflagellate blooms, primarily *Ceratium hirundinella*, occurred mainly in Campo Alegre. Chlorophyta blooms, although less abundant, occurred with cyanobacterial blooms.

Microcystis sp. (Chroococcales) is the prevalent bloom-causing cyanobacteria in Argentinean water bodies, particularly in subtropical reservoirs (Aguilera et al., 2017). However, our results reveal the dominance of filamentous and nitrogen-fixing taxa in temperate reservoirs. As for the Nostocales, *Raphidiopsis* was the most-observed genus in Argentina and Brazil, which aligns with our observations in the Salta reservoirs. Contrary to the coexistence of *Microcystis* and *Raphidiopsis* reported in other tropical American studies (Mowe et al., 2015), we did not observe that such coexistence. Instead, *Raphidiopsis* was generally accompanied by *Merismopedia* sp. or *Pseudanabaena* sp.

In Argentinian reservoirs, microcystins were the toxins found with the

highest frequency and concentration (Aguilera et al., 2017). Over 40 toxin-producing Cyanobacteria genera have been identified worldwide (Sivonen and Jones, 1999; Bernard et al., 2011), and additional toxic species may be discovered (WHO, 2003). Globally, 60% of Cyanobacteria samples have tested positive for toxins, highlighting the significance of the issue (WHO, 2003). In Salta, no positive toxin results had been reported in reservoirs or rivers before our study. However, we identified toxins in the two reservoirs with the most intense blooms (Itiyuro and El Limón), and one instance in Campo Alegre. Identifying toxin-producing species in multi-specific blooms poses a significant challenge. Understanding the specific species responsible for toxin production can aid in effective management strategies.

The widespread occurrence of *C. hirundinella* demonstrates the rapid invasion of this species in different environments. Historically it was described in the northern hemisphere, in boreal and temperate lakes, being the most common dinophytes in those regions (Margalef and Gutierrez, 1983). In the 1990s, it was reported in oligotrophic and temperate waters in southern Argentina (Izaguirre et al., 1990). But in recent years it has expanded to central and northern Argentina, including blooms in eutrophic environments (Boltovskoy, 2004). Thus, in 30 years, *Ceratium* has successfully established throughout Argentina (Parodi et al., 2004; Prosseri, 2002; Silverio and Grosman, 2001; 2004; Mac Donagh, 2003).

In warm climates and shallow water bodies like El Limón and Itiyuro, Cyanobacteria dominate over other phytoplankton, with their proportion increasing with temperature (Kosten et al., 2012). Other studies also have shown that higher temperatures promote the growth of Cyanobacteria because of their higher optimum growth temperatures and the increased stability of the water column (Reynolds, 2006; Jeppesen et al., 2009). In Limón, blooms were observed throughout the year, but were particularly intense during the warmest months (November to January).

The combination of temperature increases and eutrophication has been reported to increase cyanobacterial abundances (Jeppesen et al., 2009, 2011). The success of nitrogen-fixing Cyanobacteria under nutrient-limited conditions is still under debate (Reynolds, 1999; Schindler et al., 2008). Our results are similar to other studies (Kosten et al., 2012) and indicate that nitrogen concentration may serve as a useful predictor of cyanobacterial abundances. However, inferring causality from correlational field data remains a significant challenge (Kosten et al., 2012). The relationship between Cyanobacteria, dinoflagellates, and nutrients can be complex, especially in shallow water bodies with significant sediment-water column exchange.

The parameters influencing cyanobacteria and dinoflagellates abundances differed widely. We observed that cyanobacteria positively

correlated with water temperature, whereas dinoflagellates were negatively correlated. Given that cyanobacterial blooms develop at elevated temperatures, blooms will be exacerbated with climate heating. Neither cyanobacteria nor dinoflagellates correlated with P-SRP, but they did with the N/P ratio. Higher N/P ratios were associated with cyanobacteria dominance, but lower ratios were consistently associated with dinoflagellate dominance.

The most intense cyanobacterial blooms were observed during years with the lowest rainfall. This contrasts with the common belief that rainfall would promote greater phytoplankton biomass through nutrient runoff. In this case, rainfall seems to have had the opposite effect, causing mixing and destabilization of the water column. El Limón and Itiyuro are shallow and usually did not stratify, meaning that rainfalls helped maintain destratification, limiting the intensity of cyanobacterial blooms in the rainiest years. Also, the precipitation effect may be related to increased water turbidity because cyanobacteria were correlated negatively with turbidity.

Conversely, the most intense dinoflagellate blooms were recorded in three years with exceptionally high rainfall while temperatures remained within the average range. Although dinoflagellates in tropical reservoirs (El Limón and Itiyuro) did not reach bloom abundances, their highest abundances were observed during years with the highest rainfall and lowest average temperatures in the area. The reservoirs dominated by dinoflagellates are larger and deeper than those dominated by cyanobacteria, and in all the samples with *Ceratium* blooms, the reservoirs were stratified, despite the intense rains.

Taxa richness was much higher in cyanobacterial blooms than dinoflagellate blooms. Cyanobacterial blooms were dominated by several filamentous, non-colonial, low-biovolume taxa. But dinoflagellate blooms were dominated by *Ceratium*. *Ceratium* is one of the largest phytoplankton genera, which could competitively affect the development of the rest of the phytoplankton assemblage. Dinoflagellates are K-strategists, which are strong competitors, and can overshadow the development of other phytoplankton during an intense dinoflagellate bloom.

5. Conclusion

In Salta reservoirs we observed different patterns for cyanobacteria and dinoflagellate blooms. Our hypothesis that environmental conditions explain kind and intensity of blooms was not rejected because we found that higher temperatures were associated with cyanobacteria blooms, and they were more intense during years with temperatures exceeding historical records. Also, dinoflagellate blooms were the most intense during years with precipitation levels surpassing historical records. Cyanobacterial blooms correlated positively with the available nitrogen load and were observed at higher N/P ratios (no limitation by nitrogen or phosphorus) but dinoflagellate blooms occurred when nitrogen was limited. Controlling the proliferation of algae and cyanobacteria in reservoirs requires resource management at the watershed level, and in the case of the Itiyuro and El Limón, requires binational management with Bolivia.

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CRedit authorship contribution statement

Florencia Soledad Alvarez Dalinger: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Claudia Nidia Borja:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft. **Verónica Laura Lozano:** Conceptualization, Data curation, Methodology, Resources, Validation, Visualization, Writing –

original draft, Writing – review & editing. **Liliana Beatriz Moraña:** Formal analysis, Investigation, Project administration, Resources, Supervision, Validation. **María Mónica Salusso:** Data curation, Formal analysis, Funding acquisition, Investigation, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.watbs.2023.100232>.

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