

Factors Triggering Cyanobacteria Dominance and Succession During Blooms in a Hypereutrophic Drinking Water Supply Reservoir

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Abstract As freshwater bodies become enriched in nutrients, there is a shift in the phytoplankton community toward dominance by cyanobacteria. Cyanobacterial blooms are a significant problem in water supply reservoirs worldwide because some species can release toxic compounds and are also associated with the production of bad odor and taste. The aims of this paper were to elucidate the mechanism inducing the development of cyanobacterial blooms and to understand the species succession during the bloom, as well as the influence of abiotic factors on the species composition. Total phosphorus level and parameters related to seasonality, i.e., temperature and solar radiation, were the factors triggering the development of the blooms. Blooms were dominated by *Microcystis natans* and *Anabaena circinalis*. Phosphorus was an important

limiting factor for *Anabaena* development but never limited *Microcystis* growth. Water temperature was optimum until end of February for *Anabaena*, whereas *Microcystis* growth was slightly limited since water temperature never reached the optimal. Solar radiation was more limiting than temperature, and the decrease in light had a strong role in the bloom decline. Four species of cyanobacteria recorded in Paso de las Piedras reservoir are potentially toxic: *Snowella fennica*, *Microcystis aeruginosa*, *Planktothrix agardhii*, and *A. circinalis*, being the last one as the most abundant species during the blooms. Considering the Alert Level Framework for cyanobacteria, alert level 2 was exceeded only during blooms while alert level 1 was exceeded during almost all the year.

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1 Introduction

During their annual development, phytoplankton communities undergo changes in both species quantity and species composition. It is generally assumed that as freshwater bodies become enriched in nutrients, there is a shift in the phytoplankton community toward dominance by cyanobacteria (Smith 1986; Trimbee and Prepas 1987; Watson et al. 1997; Paerl and Huisman 2009). However, cyanobacteria also dominate in oligotrophic and mesotrophic waters (Hecky and Kling 1987;

Canfield et al. 1989; Blomqvist et al. 1994; Huszar and Caraco 1998).

Cyanobacteria dominance has been associated with several factors such as the following: low turbulence (Reynolds 1987), low euphotic to mixing zone ratio (Jensen et al. 1994), high temperature (Shapiro 1990), low CO₂/high pH (Shapiro 1990; Caraco and Miller 1998), high total P (Trimbee and Prepas 1987; Watson et al. 1997), low total N (Smith 1983), low N/P ratio (Smith 1983), low dissolved inorganic nitrogen (Blomqvist et al. 1994), phosphorus storage strategy (Pettersson et al. 1993), ability to minimize grazing (Haney 1987), and buoyancy regulation (Reynolds 1987).

Although different pattern of seasonal succession can be assumed to be a general trend in different types of lakes, phytoplankton dynamics is affected by a more complex scenario of external and internal driving factors, in which different species interact not only with the environment but also with each other, rendering any attempt at prediction or modeling particularly challenging.

Bloom-forming cyanobacteria have become a significant problem in public water supply reservoirs worldwide because some species can release a wide range of toxic compounds into the water. Blooms are also associated with the production of bad odor and taste and the clogging of the water filtration systems at water treatment plants, which have an important economic impact. In addition, cyanobacterial blooms have considerable negative effects on aquatic food webs and ecosystem functioning (Havens 2008; Paerl et al. 2011). In Argentina, there have been registered cyanobacterial blooms since 1950, most of them in water supply reservoirs, being *Anabaena* and *Microcystis* the most conspicuous genera (Pizzolon et al. 1999).

All this make the management of water for human use particularly challenging, and it is important to understand how such blooms can be avoided or at least reduced in size. To predict and prevent nuisance cyanobacterial blooms in freshwater systems, it is necessary to understand the conditions that lead to their dominance as well as the dynamics of the bloom-forming species, since not all bloom-forming cyanobacteria have the same impact on the water quality. Nevertheless, the succession amongst different cyanobacteria species remains understudied and poorly understood, as much of the focus has been on monospecific blooms.

The aims of this paper are as follows: (1) to elucidate the mechanism inducing the development of cyanobacterial bloom, (2) to understand the succession of species during the bloom, and (3) to evaluate the influence of abiotic factors on the cyanobacteria taxa that contribute to the development of the bloom. We describe the composition, abundance, and succession of cyanobacteria populations during two consecutive cyanobacterial blooms (years 2004 and 2005) in the nonstratified highly eutrophic Paso de las Piedras reservoir and evaluate the impact of abiotic parameters on the dominant cyanobacterial taxa applying a process-based dynamic mathematical model.

2 Methods

2.1 Study Area

Paso de las Piedras reservoir (38–39° S, 61–62° W) is located in the south of Buenos Aires Province (Argentina) (Fig. 1). It was built in 1978 to supply drinking water to more than 450,000 residents in Bahía Blanca city and for industrial purposes at a petrochemical complex nearby. The lake has two tributaries: El Divisorio Stream and Sauce Grande River, which run through an important agricultural area. The reservoir has a surface area of 36 km², with a mean depth of 8.2 m. It is a nonstratifying system; the continuous mixing is due to morphometric features along with the wind effect (Intartaglia and Sala 1989).

Paso de las Piedras reservoir is a highly eutrophic system which has experienced recurrent cyanobacterial blooms since 1982 (Gayoso 1993; Pizzolon et al. 1999; Echenique et al. 2001; Fernández et al. 2009). The high nutrient concentration recorded in Paso de las Piedras reservoir has been explained by the concurrence of various diffuse sources, including the intense agricultural and cattle activity throughout the basin, the characteristics of the land area in which the reservoir is located, and the increasing urbanization and use of watercourses as drainage basins (Fernández et al. 2009).

2.2 Sampling

Sample collection was carried out between January 2004 and June 2005. Two sampling sites were established: S1 (in the water intake tower of the purifying plant) and S3 (near the mouth of El Divisorio Creek)

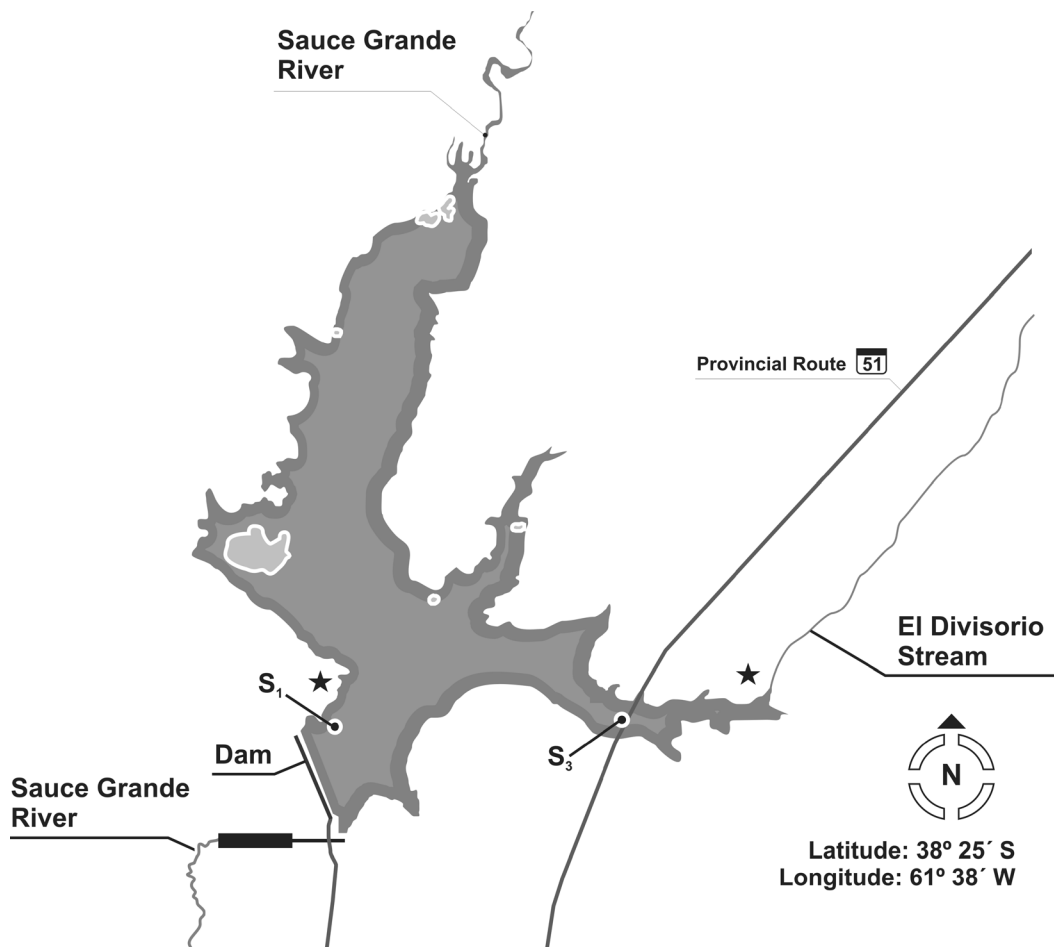


Fig. 1 Location of Paso de las Piedras reservoir and sampling sites (S1, S3). Stars indicate the location of the meteorological stations

(Fig. 1). All the samples were taken at a depth of 0.5 m. The sampling frequency was two times a week from January to April 2004, weekly from May to December 2004 and biweekly from January to June 2005. A total of 80 and 79 samples were collected at S1 and S3, respectively. Samples for qualitative analyses were taken with 30- μ m mesh plankton net and van Dorn bottle and fixed with 4 % formaldehyde. Samples for quantitative analyses were collected with a van Dorn bottle and fixed with Lugol's solution.

For qualitative analysis, samples were observed under an optical microscope Nikon Eclipse 80i with a digital DXM1200F camera. Phytoplankton were identified using the keys of Hindák (1988, 1990), Komárek and Anagnostidis (1989, 1998, 2005), Komárek and Fott (1983), and Krammer and Lange-Bertalot (1986, 1988, 1991a, b). The Utermöhl method (1958) was used to quantify the phytoplankton under an inverted microscope (Wild) with a magnification of $\times 400$.

Sedimentation time was more than 12 h. The number of settling units counted in each individual sample varied according to the species accumulation curve; the same chamber volume (10 ml) was used throughout the study, and at least 40 fields were counted for each chamber (Rott 1981). The cells were discriminated to the species level, wherever possible. The cell number of colonial organisms, such as big colonies of *Microcystis* spp. or big and screwed filaments of *Anabaena circinalis*, was estimate from the size of the colony using the method proposed by Joung et al. (2006). A total of 20 colonies of each species were separated via the micropipette technique (Oh and Rhee 1990). The size of each colony was determined, and the colonies were considered as spheres. The single colonies were then divided into single cells via the boiling method, and the resultant cell were enumerated with a hemocytometer under an optical microscope. Thereafter, the counted cell numbers were assessed via

regression analysis with the volume of the original colony.

Water samples for nutrient and chlorophyll *a* analysis were collected with a van Dorn bottle at the same sites and depth as samples for phytoplankton; they were stored in darkness at 4 °C and processed within 24 h after being collected. Nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+), total phosphorus (TP), soluble reactive phosphorus (SRP), and silica were analyzed in the Autoridad del Agua of Buenos Aires Province (ADA) Laboratory, following the methods described by the APHA (1992). The chlorophyll *a* concentration was measured in accordance with the spectrophotometric technique described by Lorenzen (1967), after being extracted in a 90 % acetone solution. The mass N/P ratio was expressed as the concentration of biologically available nitrogen (nitrate + nitrite + ammonium) divided by the concentration of SRP. Total suspended solid (TSS) concentration was also determined in accordance with the method outlined by the APHA (1992) by Profertil S.A. In addition, in situ measurements of selected chemical and physical characteristics, including electrical conductivity, temperature, and pH using a Horiba U-10 multisensor, were also conducted.

The Laboratory of Hydraulic at the National University of South provided meteorological (air temperature, wind speed and direction, and precipitations) and hydraulic (water volume and level in the reservoir and tributary flows) data from two meteorological stations (Fig. 1). Solar radiation data were provided by CERZOS (CONICET-UNS).

2.3 Mathematical Model and Data Analysis

In previous works, we formulated a process-based dynamic mathematical model of Paso de las Piedras reservoir in order to describe the main biogeochemical processes that take place in the water body (Estrada et al. 2009a, b). The model includes mass balances for the main phytoplankton groups, organic nitrogen and phosphorus (ON, OP), nitrate, ammonium, SRP, dissolved oxygen (DO), and biochemical oxygen demand (BOD) for two horizontal layers.

For accounting of phytoplankton growth limitation, the model includes limiting functions for temperature, solar radiation, and nutrients with specific parameters for each phytoplankton group. These functions (Table 1) can take values between 0 and 1 and modify the maximum growth rate. Values closer to zero indicate

greater growth limitation by the variable. In the model, phytoplankton species were grouped in functional groups following the criteria established by Reynolds et al. (2002) and Padišák et al. (2009) and previously applied to Paso de las Piedras reservoir by Fernández et al. (2013). Cyanobacteria are represented by functional groups H1 and M which include *A. circinalis* and species of the genus *Microcystis*, respectively.

Solar radiation limiting function includes the photoinhibition under high light intensity process. The function is represented by the Steele (1962) function coupled with Beer's law to adjust the extinction of the incoming solar radiation with depth and take into account the light extinction for the background and for phytoplankton biomass accumulation.

Results of a long-term whole-ecosystem study revealed that phosphate is the most important limiting nutrient for phytoplankton growth in lakes (Schindler et al. 2008). Hence, the model includes Monod-type kinetics to account for phosphate limitation (for a more detailed description of model equations, calibration, and validation processes, see Estrada et al. 2009a, b).

Significant differences between sampling stations and periods for the parameters pH, Secchi depth, TSS, N/P ratio, chlorophyll *a*, and cell number were determined with two-way ANOVA and Bonferroni multiple comparison test. The nonparametric Kruskal-Wallis and pairwise multiple comparison Dunn's tests were used to assess differences in the parameters TP, SRP, NO_3^- , NO_2^- , silica, air temperature, water temperature, water level, and solar radiation since data did not attend criteria of parametric methods. The analyses were performed using the software InfoStat (Student version).

3 Results

3.1 Climatic and Physicochemical Conditions

The physicochemical and environmental parameters examined in the study area are given in Table 2.

Both solar radiation and air temperature showed the typical seasonal patterns of the temperate climate prevailing in the study area. The total rainfall recorded during the study period was 862.8 mm, and the water level was mostly influenced by the water input (rainfall runoff).

The pH was alkaline and the values registered during spring-summer period were statistically higher than the

Table 1 Limiting function equations of Paso de las Piedras model

Limiting function	Equation	Nomenclature
Temperature	$f(T)_j = \frac{T}{T_{opt_j}} \exp\left(1 - \frac{T}{T_{opt_j}}\right)$	T : water temperature (°C) T_{opt_j} : optimal growth temperature for j (°C)
Phosphorus	$f(P)_j = \frac{C_{SRP}}{C_{SRP} + K_{P_j}}$	C_{SRP} : SRP concentration (mg/l) K_{P_j} : half saturation constant for SRP uptake (mg/l)
Solar radiation	$f(I)_j = \frac{I_o}{I_{opt_j}} \exp\left(1 - \frac{I_o}{I_{opt_j}}\right)$ $I_o = \frac{I[1 - \exp(-K_e \Delta D)]}{K_e \Delta D}$ $K_e = K_1 + K_2 \sum \frac{C_j}{ccl}$	I : incoming solar radiation (W/m ²) I_o : adjusted solar radiation (W/m ²) I_{opt_j} : optimal growth light intensity for j (W/m ²) K_e : light attenuation (1/m) K_1 : background light attenuation (1/m) K_2 : light attenuation coefficient for chl a (m ² /mg) ccl : phytoplankton to chl a ratio (mg C/mg chl a) C_j : phytoplankton functional group concentration (mg C/l)

j functional groups of phytoplankton

values of autumn-winter ($F=17.93$; $p<0.0001$). The electrical conductivity showed values statistically higher at S3 ($H=31.44$; $p<0.0001$), and also during winter, the values were significantly higher than in the remaining months ($H=93.86$; $p<0.0001$).

Table 2 Values of physicochemical and environmental variables of Paso de las Piedras reservoir during the studied period

Parameters	Promedio	Max	Min	n
Solar radiation (kW m ⁻²)	5.56 ^a	12.44	0.37	332 ^a
Air temperature (°C)	14.2 ^a	27.8	1.4	327 ^a
Water level (m)	162.58	164.46	160.65	908
Water volume (hm ³)	254.24	311.3	200.14	908
Water temperature (°C)	16.6 ^a	25	6.29	121 ^a
pH	8.57	9.75	7.39	152
TSS (mg l ⁻¹)	4.44	18.4	0.4	59
Conductivity (mS cm ⁻¹)	0.39	0.52	0.18	59
Euphotic zone	4.15	6.62	2.93	126
NO ₃ ⁻ (mg l ⁻¹)	1.34	2.10	0.7	117
NO ₂ ⁻ (mg l ⁻¹)	0.02	0.11	0.005	119
NH ₄ ⁺	nd	nd	nd	nd
TP (mg l ⁻¹)	0.43	1.83	0.23	115
SRP (mg l ⁻¹)	0.23	0.83	0.09	115
N/P	6.66	13.49	0.83	113
Silica	1.18	6	0.13	117
Chlorophyll a (mg m ⁻³)	23.55	70.03	3.39	45

nd values under the detection limit of the method (<0.05 mg l⁻¹)

^aMedia value and n of 1 year (2004)

The mean euphotic zone depth, regarded as the depth where the PAR is 1 %, was statistically lower at S3 than at S1 ($F=17.84$; $p<0.0001$); further in summer months, the values registered were lower than in cold months ($F=4.97$; $p<0.0001$).

Nitrate was the most important nitrogen compound whereas ammonium concentrations always exhibited values under the detection limit of the employed method (0.05 mg l⁻¹). Nitrate concentration was higher at S1 than S3 ($H=15.44$; $p<0.01$).

The mean chlorophyll a concentration was statistically higher at S3 than at S1 ($F=3.36$; $p<0.05$).

3.2 Cyanoprokaryote Dominance

Cyanobacteria were one of the most abundant groups of photosynthetic microorganisms during the studied period. Thirty-five cyanobacteria taxa were recorded. The highest species richness was found in Chroococcales, with 22 taxa, followed by 11 Oscillatoriales and 2 Nostocales. *Microcystis* was the genera with the highest number of species (Table 3).

Along the studied period, two cyanobacterial blooms were registered. At S1, the first bloom (bloom 1) began in mid-January 2004 and ended in March 2004, while the second bloom (bloom 2) started in December 2004 and ended in April 2005. At S3, bloom 1 occurred between mid-January 2004 and April 2004, while bloom 2 began in December 2004 and ended in April 2005.

Table 3 Cyanobacteria species found in Paso de las Piedras reservoir showing its occurrence frequency (F%) and the type of species (*R* rare, $F < 10\%$; *C* common, $10\% < F < 50\%$; *CT* constant, $F > 50\%$)

Cyanobacteria species	S1 F%		S3 F%	
<i>Aphanothece smithii</i>	6.3	R	10.1	C
<i>Synechococcus epigloeicus</i>	57.5	CT	60.8	CT
<i>Rhabdogloea scenedesmoides</i>	22.5	C	15.2	C
<i>Synechocystis aquatilis</i>	76.3	CT	55.7	CT
<i>Synechocystis</i> sp.	41.3	C	38.0	C
<i>Synechocystis fuscopigmentosa</i>	10.0	C	11.4	C
<i>Aphanocapsa delicatissima</i>	11.3	C	22.8	C
<i>Merismopedia trolleri</i>	—	—	—	—
<i>Merismopedia tenuissima</i>	—	—	—	—
<i>Merismopedia elegans</i>	7.5	R	8.9	R
<i>Coelosphaerium aeruginum</i>	35.0	C	26.6	C
<i>Coelosphaerium dubium</i>	3.8	R	6.3	R
<i>Coelosphaerium punctiferum</i>	5.0	R	8.9	R
<i>Snowella lacustris</i> ^a	41.3	C	36.7	C
<i>Snowella fennica</i>	—	—	—	—
<i>Woronichinia elorantae</i>	50.0	CT	41.8	C
<i>Microcystis aeruginosa</i> ^a	45.0	C	60.8	CT
<i>Microcystis flos-aquae</i>	58.8	CT	49.4	C
<i>Microcystis natans</i>	77.5	CT	82.3	CT
<i>Microcystis protocystis</i>	30.0	C	31.6	C
<i>Chroococcus limneticus</i>	11.3	C	6.3	R
<i>Chroococcus minutus</i>	8.8	R	10.1	C
<i>Pseudanabaena mucicola</i>	5.0	R	3.8	R
<i>Limnothrix guttulata</i>	—	—	—	—
<i>Jaaginema minimum</i>	3.8	R	2.5	R
<i>Spirulina major</i>	1.3	R	3.8	R
<i>Planktothrix agardhii</i> ^a	2.5	R	8.9	R
<i>Planktothrix</i> sp.	—	—	3.8	R
<i>Phormidium hamelii</i>	—	—	—	—
<i>Phormidium aerugineo-caeruleum</i>	3.8	R	2.5	R
<i>Phormidium tergestinum</i>	3.8	R	2.5	R
<i>Tychonema</i> sp.	1.3	R	1.3	R
<i>Oscillatoria foreau</i>	13.8	C	11.4	C
<i>Anabaena circinalis</i> ^a	86.3	CT	93.7	CT
<i>Anabaena sphaerica</i>	10.0	C	24.1	C

— Only registered during the qualitative analysis

^a Potentially toxic species

These two bloom periods were characterized by a marked increase in the number of cells in the phytoplankton ($>50,000$ cells ml^{-1}) and a dominance of

cyanobacteria (relative abundance $>70\%$), which, in some months, reached relative abundances higher than 95 % (Fig. 2).

The most frequent species were *M. natans* and *A. circinalis*, which were present in more than 75 % of the samples. At both sampling stations, around 85 % of the samples contained a cyanobacteria cell number higher than alert level 1 for raw waters (Bartram et al. 1999) (≥ 2000 cells ml^{-1}) whereas alert level 2 ($\geq 100,000$ cells ml^{-1}) was exceeded in around 20 % of the samples. Alert level 2 was exceeded only during the blooms while alert level 1 was exceeded during all the year, except in September and October (Fig. 2).

There was no significant difference in cyanobacteria abundance between sampling stations ($F=0.1$; $p=0.75$).

3.3 Pattern of Species Succession

The most abundant species during the blooms were as follows: *A. circinalis*, *M. natans*, *M. aeruginosa*, and *M. flos-aquae* (Fig. 3).

At the beginning of the bloom 1, in mid-January, there was a high density of *M. aeruginosa* at S1 (relative abundance higher than 70 %), but it quickly decreased, and thereafter, *A. circinalis* (20–40 %) and *M. natans* (40–50 %) dominated the phytoplankton until the end of January. At S3 instead, it was not observed the peak of *M. aeruginosa*. In February, *M. natans* dominated the community, representing more than 70 % of the total phytoplankton density in both sampling stations. During March, the phytoplankton community was again dominated by *A. circinalis* (relative abundance higher than 50 and 70 % at S1 and S3, respectively) and *M. natans* (relative abundance higher than 35 and 40 % at S1 and S3, respectively). During March at S1, there was also a peak in *M. flos-aquae* abundance (about 60 %) whereas at S3, the peak was registered in April (70 %).

During bloom 2, *M. natans* dominated almost throughout the bloom at S1 (relative abundance of 45–65 %). At S3 however, the abundance of *M. natans* at the beginning of the bloom was lower, reaching a value of relative abundance higher than 70 % at the end whereas the relative abundance of *A. circinalis* was high during the first part of the bloom, with values higher than 80 % in January.

The most obvious difference in the community structure between blooms 1 and 2 was the lower contribution

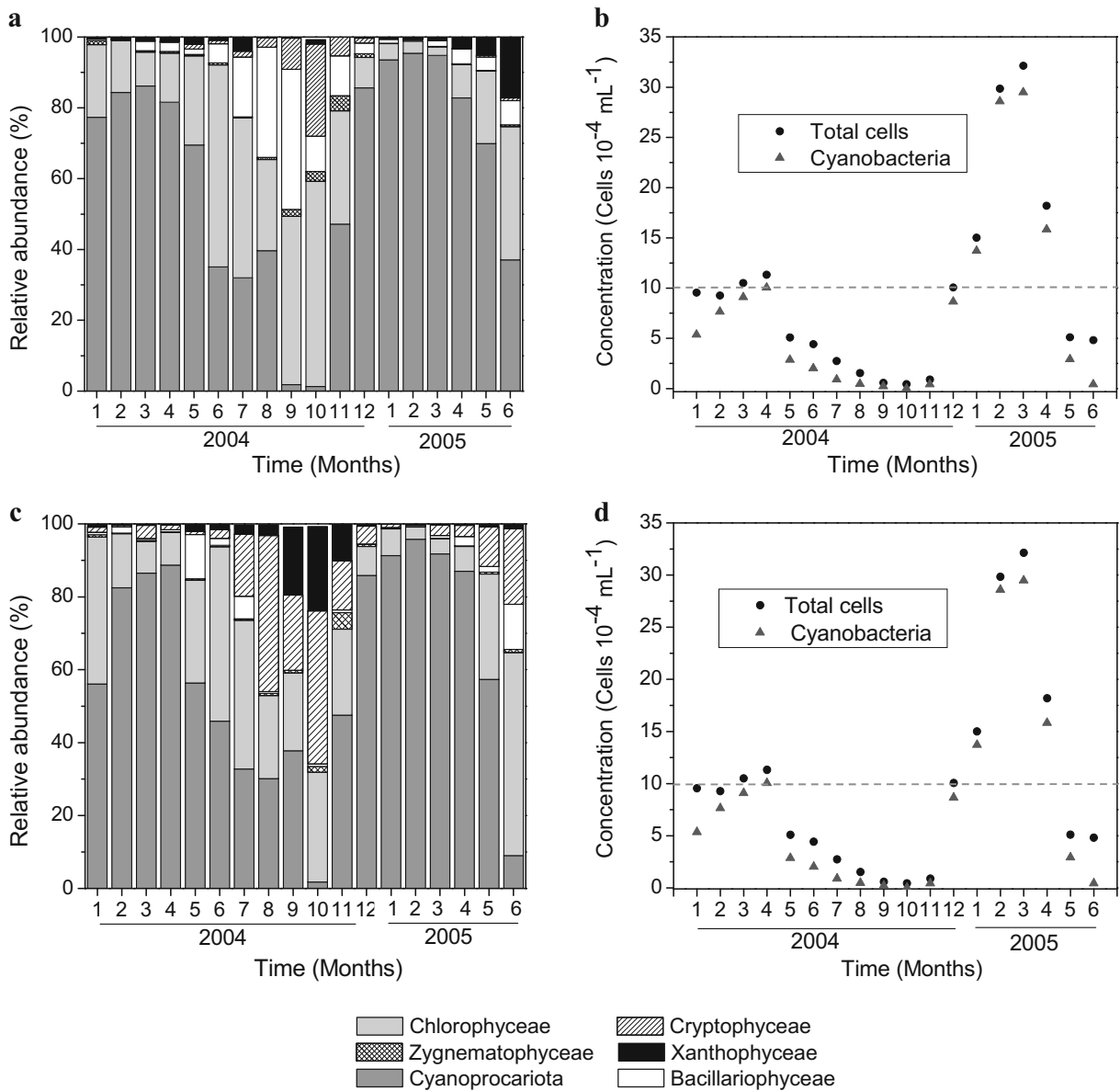


Fig. 2 Relative abundance of each phytoplankton group at S1 (a) and S3 (c) and cyanobacteria abundance in relation to total phytoplankton abundance at S1 (b) and S3 (d). The dashed line indicated alert level 2

of *M. flos-aquae* (11–18 %) and *M. aeruginosa* (15–28 %) during bloom 2 in both sampling stations.

3.4 Relationship Between Cyanobacteria Succession and Abiotic Variable

The mathematical model allowed the study of the effects of the environmental variable on the dominant cyanobacteria in Paso de las Piedras reservoir at a genus level. Numerical results for the phosphorus limitation

function $f(P)$ (Fig. 4a) show that SRP never limited *Microcystis* growth, maintaining a value close to 1 during the entire considered bloom periods. However, it was for *Anabaena*, exhibiting mean inhibition values of 0.634 and 0.573 for 2004 and 2005 blooms, respectively. The maximum values (i.e., the lowest limitation to the maximum growth rate by SRP) for $f(P)$ were 0.672 (5 May 2004) and 0.617 (30 April 2005) while the minimum values were 0.562 (15 June 2004) and 0.415 (1 January 2005). Mean values for the temperature

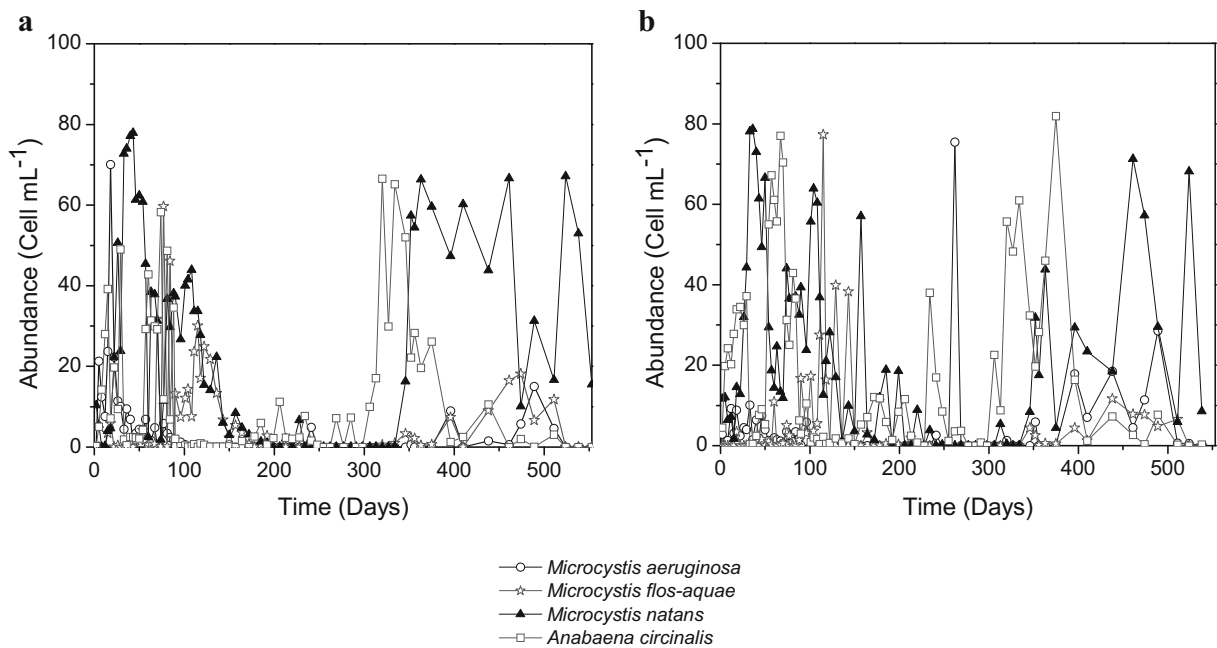


Fig. 3 Temporal variation in the cell number of the dominant cyanobacteria in S1 (a) and S3 (b)

limitation function $f(T)$ (Fig. 4b) for bloom 1 were 0.933 and 0.865 and for the bloom 2 were 0.906 and 0.832 for *Microcystis* and *Anabaena*, respectively. As expected, the $f(T)$ maximum values match with the maximum water temperature record. $f(T)$ *Anabaena* maximum values were 0.998 (23 January 2004) and 0.995 (10 January 2005), respectively, indicating no temperature limitation for around these periods. Minimum values obtained at the end of the considered periods (14 June 2004 and 14 June 2005) were 0.724 and 0.704 for 2004 and 2005, respectively. Figure 4c shows solar radiation limitation function $f(I)$ profiles for both blooms. $f(I)$ for *Anabaena* never reaches values as close to 1 as those reached by $f(T)$ being the maximum values 0.949 (8 January 2004) and 0.855 (1 January 2005) and the mean values 0.740 and 0.629 for 2004 and 2005, respectively. Minimum values for *Anabaena* were 0.392 (15 June 2004) and 0.342 (8 June 2005) indicating a high inhibition by light intensity at the ends of the bloom periods. On the other hands, $f(I)$ daily values for *Microcystis* indicates higher light limitations even in the periods of high solar irradiance with mean values of 0.485 and 0.389 for 2004 and 2005, respectively. Maximum values were reached at 26 January 2004 (0.668) and 1 January 2005 (0.569). At the ends of the considered periods, light was the major growth rate constraint with values of 0.219 and 0.188 for 2004 and 2005, respectively.

3.5 Differences Between Bloom and No-Bloom Periods

The most obvious differences in environmental and physicochemical parameters between bloom and no-bloom periods were registered for the variables air and water temperature, solar radiation, water transparency, and TP. Air and water temperature, solar radiation, and TP concentration were higher during both bloom periods than during the no-bloom period ($p < 0.001$), whereas water transparency was higher during the no-bloom period ($p < 0.001$) (Table 4).

Regarding the biological parameters, cyanobacterial and phytoplankton density as well as chlorophyll *a* concentration showed significantly higher values during bloom periods than no-bloom period ($p < 0.05$); also, there were differences between the two bloom periods, with higher cyanobacterial and phytoplankton density during bloom 2.

4 Discussion

The purposes of the present study were to elucidate the mechanism inducing the development of cyanobacterial blooms and to understand the species succession during the blooms, as well as the influence of abiotic factors on the species composition.

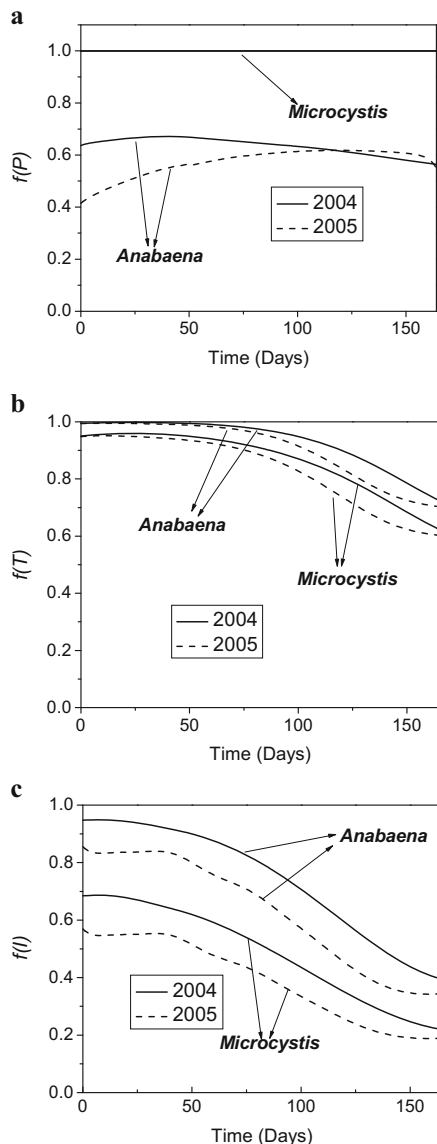


Fig. 4 Simulation profiles for *Microcystis* and *Anabaena* nutrient (a), water temperature (b), and solar radiation (c) limiting functions

The main differences observed between bloom and no-bloom periods regarding abiotic parameters were higher water temperature, air temperature, solar radiation, and TP concentration and lower water transparency during both bloom periods. The differences in the water transparency between bloom and no-bloom periods reflect the differences in phytoplankton biomass between such periods, since the TSS showed no differences. Thereby, the TP level and the parameters related to seasonality, including temperature and solar radiation, would be the factors triggering the development of

cyanobacterial blooms during summer months in Paso de las Piedras reservoir.

A pattern explaining how trophic state controls the relative importance of nutrients, temperature, and their interaction was found by Rigosi et al. (2014), who stated that in eutrophic and hyper-eutrophic lakes, nutrients are important mostly through their interaction with temperature and not individually. It is in accordance with Brookes and Carey (2011) hypothesis which state that cyanobacteria will only respond to increased temperature at high nutrient levels. In this sense, the predominant influence of climatic parameters on the development of cyanobacterial bloom observed in this study is consistent since Paso de las Piedras reservoir is a eutrophic-hypereutrophic lake, with phytoplankton species and associations typical of highly enriched systems (Fernández et al. 2009).

In the present study, both blooms were dominated by *M. natans* and *A. circinalis*, and *M. aeruginosa* and *M. flos-aquae* were also present and sometimes with high relative abundance. *A. circinalis* dominated at the beginning and at the end of the bloom 1 and at the beginning of bloom 2, whereas *M. natans* was important during the whole bloom. Temperature, solar radiation, and phosphate concentration have been pointed as the most important driving forces in the development of *Microcystis* and *Anabaena* blooms (Rajaniemi-Wacklin et al. 2008; Imai et al. 2009; Cai and Kong 2013). It is known that *Microcystis* grow better than *Anabaena* in nonlimited phosphorus conditions (Nalewajko and Murphy 2001). In agreement, numerical results show that phosphorus concentration never limited *Microcystis* growth. On the other hand, the model suggests that phosphorus was an important limiting factor for *Anabaena* development over the entire study periods, being prominent the effect at the beginning of 2005. This fact indicates that although SRP concentration in Paso de las Piedras reservoir was high, an increment in concentrations of this nutrient could encourage even more the growth of this potentially toxic cyanobacterium. This agrees with findings by other authors for eutrophic water bodies (Tezuka and Nakano 1993) and with numerical experiment results obtained with the mathematical model under different nutrient download scenarios (unpublished data).

Regarding temperature, it is well known that *Microcystis* species dominated when it is above 25 °C, since they have an optimal growth temperature between 30 and 35 °C (Chu et al. 2007; Imai et al. 2009) whereas

Table 4 Physicochemical, climatic, and biological characteristics during bloom and no-bloom periods in Paso de las Piedras reservoir (mean±standard error)

Variable	Bloom 1	No bloom	Bloom 2
Biological			
Cyanobacteria (cells ml ⁻¹)	87435.4±7220.7 a	23335.6±3658 c	170445.4±19936.8 b
Phytoplankton (cells ml ⁻¹)	106822.1±7663 a	36509.9±3958.1 c	186071.1±20029.7 b
Environmental			
Air temperature (°C)	20.61±0.37 a	12.74±0.29 b	20.11±0.35 a
Precipitation (mm)	111	448.6	260.2
Solar radiation (kW m ⁻²)	8.22±0.26 a	4.47±0.17 b	nad
Water level (m)	162.56±0.02 a	163.12±0.04 b	163.62±0.04 c
Volume of water (hm ³)	252.62±0.73 a	269.83±1.23 b	285.5±1.13 c
Physicochemical			
Water temperature (°C)	20.5±0.29 a	12.3±0.49 b	20.13±0.56 a
pH	8.69±0.06 a	8.48±0.07 a	8.78±0.08 a
TSS (mg l ⁻¹)	3.39±0.32 a	4.7±0.53 a	nad
Water transparency (m)	1.39±0.03 a	1.67±0.04 b	1.42±0.07 a
Conductivity (mS cm ⁻¹)	0.36±0.02 a	0.4±0.01 a	0.37±0.01 a
NO ₃ ⁻ (mg l ⁻¹)	1.4±0.06 a	1.39±0.03 a	1.44±0.06 a
NO ₂ ⁻ (mg l ⁻¹)	0.03±0.01 a	0.02±0.00091 a	0.02±0.0012 a
TP (mg l ⁻¹)	0.51±0.02 a	0.39±0.01 b	0.58±0.09 a
SRP (mg l ⁻¹)	0.33±0.02 a	0.21±0.01 b	0.27±0.05 b
N/P	4.5±0.26 a	7.25±0.25 b	6.49±0.82 b
Chlorophyll <i>a</i> (mg m ⁻³)	nad	20.5±2.75 a	30.33±3.49 b

Same letters indicate no difference among means ($P<0.05$)

nad not available data

A. circinalis prefers temperatures below 25 °C (Bormans et al. 2005). This behavior is well represented by the mathematical model which shows that water temperature was optimum until end of February for *Anabaena* in both blooms, whereas *Microcystis* growth was slightly limited during the bloom periods because water temperature in Paso de las Piedras never reached the optimal value.

With regard to solar radiation, numerical results show that it was a more limiting factor than temperature and that the decrease in light availability had a stronger role in the bloom decline during both bloom periods. The effect of light limitation was more pronounced during bloom 2. Also, the limitation was stronger for *Microcystis* than for *Anabaena* during the entire studied period. According to Robarts and Zohary (1992), *Microcystis* species are adapted to high light intensity conditions and their light requirements are greater than those for *Anabaena*.

Coincidentally, in a recent study, Rigosi et al. (2014) found that the sensitivity to nutrients and temperature

was taxon-specific among cyanobacteria, since *Anabaena* was more sensitive to nutrients while *Microcystis* was more sensitive to temperature. Cyanobacteria are a highly diverse group, ranging in size from unicellular picoplankton to multicellular macroscopic colonies; consequently, the different taxa that compose the group have different traits and physiological characteristics. The precise response of individual cyanobacterial taxa to physicochemical variable will be diverse and has not been reviewed in detail to date since most of the studies consider the cyanobacterial blooms as a whole. In this sense, our findings are also in agreement with those of Carey et al. (2012), who suggested that differences in the ecophysiology among cyanobacterial taxa will result in different responses to climate change.

Global warming scenarios predict increased temperatures in freshwater environments potentially favoring cyanobacteria dominance over other phytoplankton groups (Carey et al. 2012; Paerl and Paul 2012).

Taking into account the main environmental forcing drivers for cyanobacteria growth, the two that could experiment a change in time as a consequence of global warming are nutrient concentration by increased down-loads into the lake and temperature due to climate change. It is important to note that based on the numerical results, an increase in the phosphorus download into the lake could favor an increase in *Anabaena* dominance while an increase of water temperature in the long term could lead to an increased development of *Microcystis* biomass and longer blooms in time.

During the bloom, there was a change not only in the species (phylogeny) but also in the life forms since there was a shift between a filamentous, nitrogen-fixing species (*A. circinalis*) and several colonial species (*Microcystis* species). According to Smayda and Reynolds (2001), during a bloom is life form selection and not species selection the norm; it means that there is a set of conditions that favored a particular set of traits, and then, the species which fill the bloom niches should be viewed as being essentially stochastic selections.

Four species of cyanobacteria recorded in Paso de las Piedras reservoir have been reported as potentially toxic, namely *Snowella fennica*, *M. aeruginosa*, *Planktothrix agardhii*, and *A. circinalis*, being the last one as the most abundant species during the blooms. Considering the Alert Level Framework (ALF) for cyanobacteria proposed by Bartram et al. (1999), alert level 2 was exceeded during both blooms while alert level 1 was exceeded during almost all the year. This should be of concern of public authorities since at such high algal biomass, events like generation of bad odor and taste occur with the resulting impact on water quality, even more considering that Paso de las Piedras reservoir is a drinking water source.

An improved understanding of the impact and interactions amongst the environmental and physicochemical factors triggering the development of cyanobacterial blooms along with an understanding of the cyanobacterial taxa present and its physiological and ecological characteristic is crucial for developing management strategies to mitigate the development of blooms and to predict and avoid the potential of more frequent and extending blooms under future climate scenarios.

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