

Phytoplankton structure and diversity in the eutrophic-hypereutrophic reservoir Paso de las Piedras, Argentina

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Abstract This study aimed at analyzing the phytoplankton structure and dynamics in Paso de las Piedras Reservoir, Argentina, through the study of dominant species, diversity and similarity in relation with the abiotic environment. Samples were collected weekly or biweekly (January 2004–June 2005) at four sampling stations. The reservoir experienced a seasonal progression in phytoplankton composition that underlines six successional periods, each one characterized by the dominance of one or a few species. Cyanobacteria, green algae and diatoms were the most important constituents of the reservoir's phytoplankton. Cyanobacteria dominated during summer and early autumn, green algae during late autumn and early winter, and diatoms during winter and spring. A high abundance of *R. lacustris* (Cryptophyceae) was observed during late September and early October. The general pattern of species succession is coherent with the general model of plankton seasonal succession described by the PEG model; however, the major discrepancy is the extremely short clear water phase observed. Successional

periods were associated with changes in abiotic variables, and they showed differences in ecological traits. Cyanobacteria-Dictyosphaerium, Cyclotella, Stephanodiscus and Anabaena-diatom periods were characterized by a low number of cells, high diversity, with both dominance and specific richness low. On the contrary, during Cyanobacteria and Cyanobacteria II periods, the highest abundance was observed associated with low diversity and high dominance.

Keywords Phytoplankton succession · SIMI index · Diversity

Introduction

Phytoplankton community structure responds to trophic and seasonal gradients through changes in species composition and quantitative ecological traits such as biomass, species richness and diversity (Watson et al. 1997). These changes tend to be more pronounced in eutrophic lakes and have a number of quite separate drivers (Tschumi et al. 1982). On the one hand, these may be non-biological, i.e., physical forces named allogenic mechanisms that destroy or modify the environment structure in favor of tolerant species. On the other hand, they can be biological, autogenic mechanisms that produce changes in the community structure owing to the action of organisms that alter the environment so that it becomes more amenable to the establishment of individuals of other species (Reynolds 1988).

The structure of the algal communities is determined by the number of species present and by its biomass, by their physiological properties and by the genetic potential of the organisms making up the community (Elbert and Schanz

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1989). Analyzing changes generated by environmental variations, either natural or produced by deliberate management, reveals important aspects of tolerances and susceptibilities of the species that form the community (Kruk et al. 2002).

The phytoplankton of Paso de las Piedras Reservoir has been described already according to other various aspects, such as taxonomical (Sala and Intartaglia 1985; Sala 1990a, b, 1996a, b, c, 1997; Fernández and Parodi 2005), ecological (Intartaglia and Sala 1989), limnological (Fernández et al. 2009) and also with regard to episodes of massive proliferations (Guerrero and Echenique 1997; Echenique et al. 2001).

This article aims at analyzing the phytoplankton seasonal variation in Paso de las Piedras Reservoir, with emphasis on its dynamics and structure in relation with the abiotic environment. Temporal changes in dominant species, diversity and similarity of the phytoplankton community were investigated over an 18-month period. The different approaches pursue an improvement in the understanding of phytoplankton succession and development since phytoplankton closely tracks both short- and long-term environmental changes in lake ecosystems. This study aspires to provide valuable information for the implementation of management and restoration strategies, taking into account the high rates of anthropogenic eutrophication prevailing in the reservoir (Fernández et al. 2009).

Methods

Area of study

Paso de las Piedras Reservoir (38–39°S, 61–62°W) was built in 1978 by damming the Sauce Grande River in its confluence with El Divisorio Stream in the south of the Buenos Aires Province, Argentina. It is the primary source of drinking water for the cities of Bahía Blanca and Punta Alta; it also provides raw water for industrial purposes, and is used for recreation and fishing.

The reservoir has a surface area of 36 km², with a mean depth of 8.2 m. It is a polymictic system; the continuous mixing is due to morphometric features along with the wind effect (Intartaglia and Sala 1989).

The total rainfall recorded during the study period was 862.8 mm; the water level was mostly influenced by the water input (rainfall runoff), ranging from 162.2 to 164.5 m a.s.l. The directions of prevailing winds were N and NW. The air temperature presented a typical seasonal cycle with a maximum of 27.8°C in December 2004 and a minimum of 1.4°C in June 2005. Based on the total phosphorus (TP) data, the reservoir fits within the

hypereutrophic category, whereas it is a eutrophic reservoir considering the concentration of chlorophyll *a* and the Secchi depth (Fernández et al. 2009).

Sampling

Sample collection was carried out between January 2004 and June 2005. Four sampling sites were established: S1 (in the water intake tower of the purifying plant); S2 (near the mouth of the Sauce Grande River); S3 (near the mouth of El Divisorio Creek); and S4 (in a transitional area between the tail and dam of the reservoir) (Fig. 1). Stations S2 and S4 were sampled from the coast, outside the vegetation belt, whereas station S1 was sampled from the tower of the purifying plant and station S3 from a bridge. 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 bi-weekly from January to June 2005. A total of 80, 70, 79 and 67 samples were collected at S1, S2, S3 and S4, respectively; the number varied because sometimes the weather conditions made the access to the sampling stations difficult, principally S2 and S4.

Samples for qualitative analyses were taken with a 30- μ m-mesh plankton net and a Van Dorn bottle; some of

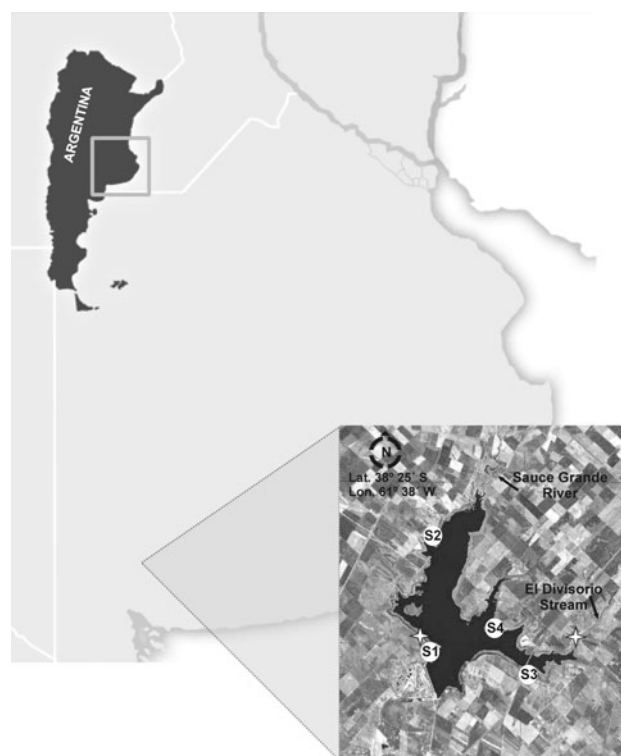


Fig. 1 Location of Paso de las Piedras Reservoir and sampling sites (S1, S2, S3, S4; stars indicate the location of the meteorological stations)

the samples were maintained alive, while others were fixed immediately with 4% formaldehyde. Samples for quantitative analyses were collected with a Van Dorn bottle and fixed immediately with Lugol's solution.

For qualitative analysis, samples were observed under an optical microscope Nikon Eclipse 80i with a digital DXM1200F camera. Phytoplankton was identified using the keys of Komárek and Anagnostidis (1989, 1998, 2005), Komárek and Fott (1983), Hindák (1988, 1990), 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, and the results were expressed as cells number per ml. In the case of colonial organisms, cell number was estimated from the size of the colonies. Previously, the average cell number of colonies of different sizes had been calculated.

Cell counts were converted to biovolume according to their size and geometric form (Hillebrand et al. 1999; Sun and Liu 2003).

Water samples for nutrient 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 24–48 h after being collected. Nitrate (NO_3^-), nitrite (NO_2^-), ammonium, 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 American Public Health Association (1992). The mass N:P ratio (i.e., mg l^{-1}) was expressed as the concentration of biologically available nitrogen (nitrate + nitrite + ammonium) divided by the concentration of SRP. Total suspended solids (TSS) concentrations were also determined in accordance with the method outlined by the American Public Health Association (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.

Two meteorological stations located in the vicinities of the mouth of El Divisorio Creek and the reservoir area, respectively, were used to obtain data of air temperature, wind speed and direction and precipitations (Fig. 1). The Laboratory of Hydraulic at the Universidad Nacional del Sur provided these data, along with data on reservoir water volume and level, and tributary flows.

Data analysis

Phytoplankton diversity (H') was calculated using the Shannon-Wiener function (Shannon 1948):

$$H' = - \sum_{i=1}^s p_i \cdot \log_2 p_i$$

where p_i is the proportional abundance of i th species and s is the number of species in the sample.

The evenness (or equitability) was calculated using H' (Pielou 1969) as follows:

$$E = \frac{H'}{H'_{\max}}$$

where H' is the Shannon's index in a sample, and H'_{\max} is the theoretical maximum diversity ($H'_{\max} = \log_2 s$).

Simpson's index (D) was used as the index of dominance (Simpson 1949):

$$D = \sum p_i^2$$

The species richness referred to the number of algal taxa registered in each sample.

All the indices were calculated considering all taxa present at each sample; the value of each successional period represents the average of the relative samples.

The Stander's (1970) similarity index (SIMI) was calculated to compare two successive phytoplankton communities:

$$\text{SIMI} = \sum_{i=1}^s a_i \cdot b_i \cdot \left(\sum_{i=1}^s a_i^2 \cdot \sum_{i=1}^s b_i^2 \right)^{-1/2}$$

where a_i = ratio of the number of individuals of species i to the total number of individuals N in sample A; b_i = ratio of the number of individuals of species i to the total number of individuals N in sample B; and s = total number of species in both samples. The value of the SIMI index can vary from 0 (no similarity) to 1 (identical). The criteria of Rohr (1977) were applied to evaluate the meaning of the SIMI index; they employ a graduated scale in which 0.00–0.199 represents dissimilarity, 0.20–0.499 low similarity, 0.50–0.699 medium similarity, 0.70–0.899 similarity, and 0.90–0.999 high similarity.

Species with >10% of relative abundance at some date or at some sampling station were selected to study the phytoplankton succession. The species with a density higher than 50% of the average density for each period were considered dominant, whereas those with a lower density were considered associated species.

The non-parametric Kruskal-Wallis test was used to assess differences between successional periods since data did not attend criteria of parametric methods. Biotic parameters, such as biovolume, diversity, dominance,

evenness, specific richness and density, and abiotic parameters, such as, air temperature, water temperature, water level, solar radiation, N:P ratio, pH, TSS, conductivity, TP, SRP, NO_3^- , NO_2^- and silica, were taken into consideration. If any statistical differences among values were detected, a pairwise multiple comparison Dunn's test was applied to distinguish differences between pairs of values.

Correlations among biological parameters were calculated using the Spearman coefficient. Significance values were assumed at $p < 0.01$.

To determine which variables were correlated and to summarize characteristics of sampling dates in an ordination diagram, multivariate descriptive analysis was carried out by applying principal component analysis (PCA) to abiotic data. Water level, water temperature, air temperature, precipitations, pH, N:P ratio, NO_3^- , NO_2^- , silica, TP and SRP were taken into account. Data were first centered and standardized, since those variables had different units (software XLSTAT 7.5.2; Addinsoft Inc., Paris, France).

Results

A total of 162 phytoplankton taxa were identified. Only 26 species presented a relative abundance higher than 10% in some samples, and 8 species dominated the phytoplankton (Table 1).

Phytoplankton succession during the study period

Six successional periods were recognized in connection with the seasonal progression in species dominance (Fig. 2). Within the study period each succession step was characterized by the development of different organisms.

I. Cyanobacteria period From January to May: This successional period was associated with the highest phytoplankton density ($>30 \times 10^4$ cells ml^{-1}), a low diversity and the highest dominance index. It was dominated almost exclusively by species of cyanobacteria, in some cases with relative abundances of $>80\%$. *Microcystis natans* was the dominant species during almost all the bloom. *Microcystis aeruginosa* dominated at the very beginning at S1 and S4, *Anabaena circinalis* in the middle at S1, S3 and S4, and, at the end of the period, *Microcystis flos-aquae* and *Synechocystis aquatilis* dominated at S1, S3 and S4 and S1 and S2, respectively. *Microcystis protocystis*, *Woronichinia elorantae*, *Coelastrum microporum*, *Oocystella parva*, *Pediastrum duplex* var. *duplex*, *Sphaerocystis schroeteri*, *Dictyosphaerium ehrenbergianum*, *Aulacoseira granulata* and *Synechococcus epigloicus* were associated species.

Table 1 Phytoplankton species composition of Paso de las Piedras Reservoir

Cyanoprokaryota	<i>Korshikoviella limnetica</i>
<i>Aphanothece smithii</i>	<i>Schroederia setigera</i>
<i>Synechococcus epigloicus</i> ^a	<i>Golenkinia radiata</i>
<i>Rhabdogloea scenedesmoides</i>	<i>Pediastrum boryanum</i> var. <i>cornutum</i>
<i>Synechocystis aquatilis</i> ^b	<i>Pediastrum duplex</i> var. <i>duplex</i> ^a
<i>Synechocystis</i> sp.	<i>Pediastrum tetras</i>
<i>Synechocystis fuscopigmentosa</i>	<i>Micractinium pusillum</i>
<i>Aphanocapsa delicatissima</i>	<i>Quadricoccus ellipticus</i>
<i>Merismopedia trolleri</i>	<i>Dictyosphaerium ehrenbergianum</i> ^b
<i>Merismopedia tenuissima</i>	<i>Dictyosphaerium pulchellum</i> ^a
<i>Merismopedia elegans</i>	<i>Botryococcus braunii</i> ^a
<i>Coelosphaerium aerugineum</i> ^a	<i>Coenocystis planctonica</i> var. <i>planctonica</i>
<i>Coelosphaerium dubium</i>	<i>Coenocystis planconvexa</i>
<i>Coelosphaerium punctiferum</i>	<i>Thorakochloris nygaardii</i>
<i>Snowella lacustris</i> ^a	<i>Lagerheimia citriformis</i>
<i>Snowella fennica</i>	<i>Lagerheimia subsalsa</i>
<i>Woronichinia elorantae</i> ^a	<i>Lagerheimia balatonica</i>
<i>Microcystis aeruginosa</i> ^b	<i>Lagerheimia ciliata</i>
<i>Microcystis flos-aquae</i> ^b	<i>Oocystis naegeli</i>
<i>Microcystis natans</i> ^b	<i>Oocystella rhomboidea</i>
<i>Microcystis protocystis</i> ^a	<i>Oocystella marssonii</i>
<i>Chroococcus limneticus</i>	<i>Oocystella borgei</i>
<i>Chroococcus minutus</i>	<i>Oocystella lacustris</i>
<i>Pseudanabaena mucicola</i>	<i>Oocystella parva</i> ^a
<i>Limnithrix guttulata</i>	<i>Oocystella solitaria</i>
<i>Jaaginema minimum</i>	<i>Oocystella submarina</i>
<i>Spirulina major</i>	<i>Oocystella ecbalocystiformis</i> var. <i>americana</i>
<i>Planktothrix agardhii</i>	<i>Chlorella homosphaera</i>
<i>Planktothrix</i> sp.	<i>Chlorella oocystoides</i>
<i>Phormidium hamelii</i>	<i>Monoraphidium circinale</i>
<i>Phormidium aerugineo-caeruleum</i>	<i>Monoraphidium dybowskii</i> ^a
<i>Phormidium tergestinum</i>	<i>Monoraphidium tortile</i>
<i>Tychonema</i> sp.	<i>Monoraphidium contortum</i>
<i>Oscillatoria foreau</i>	<i>Monoraphidium komarkovae</i>
<i>Anabaena circinalis</i> ^b	<i>Kirchneriella irregularis</i> var. <i>irregularis</i>
<i>Anabaena sphaerica</i>	<i>Kirchneriella irregularis</i> var. <i>spiralis</i>
Chlorophyceae	<i>Kirchneriella</i> sp.
<i>Sphaerocystis schroeteri</i> ^a	<i>Kirchneriella subcapitata</i>
<i>Planktosphaeria gelatinosa</i>	<i>Kirchneriella contorta</i> var. <i>contorta</i>
<i>Ankyra judayi</i>	<i>Kirchneriella contorta</i> var. <i>elegans</i>

Table 1 continued

<i>Pseudoquadrigula lacustris</i>	<i>Lagynion</i> sp.
<i>Tetraedron minimum</i>	Xanthophyceae
<i>Tetraedron hemisphaericum</i>	<i>Tetraplektron torsum</i>
<i>Coelastrum microporum</i> ^a	<i>Isthmochloron lobulatum</i>
<i>Coelastrum astroideum</i>	<i>Tribonema</i> sp. ^a
<i>Coelastrum indicum</i> ^a	Bacillariophyceae
<i>Tetrastrum komarekii</i>	<i>Aulacoseira granulata</i> ^a
<i>Tetrastrum staurogeniaeforme</i>	<i>Aulacoseira granulata</i> var. <i>angustissima</i>
<i>Rayssiella hemisphaerica</i>	<i>Cyclotella meneghiniana</i> ^b
<i>Scenedesmus arcuatus</i> var. <i>arcuatus</i>	<i>Stephanodiscus</i> sp. ^b
<i>Scenedesmus arcuatus</i> var. <i>platydiscus</i>	<i>Melosira varians</i>
<i>Scenedesmus ellipticus</i>	<i>Diatoma vulgare</i> var. <i>vulgare</i>
<i>Scenedesmus obliquus</i>	<i>Fragilaria vaucheriae</i> var. <i>vaucheriae</i>
<i>Scenedesmus acuminatus</i> var. <i>acuminatus</i>	<i>Tabularia fasciculata</i>
<i>Scenedesmus semipulcher</i> ^a	<i>Cocconeis placentula</i> var. <i>lineata</i>
<i>Scenedesmus bicaudatus</i>	<i>Amphora ovalis</i> var. <i>pediculus</i>
<i>Scenedesmus aldavei</i>	<i>Gomphonema olivaceum</i>
<i>Scenedesmus lefevrii</i> var. <i>manguinii</i>	<i>Gyrosigma spencerii</i>
<i>Scenedesmus intermedius</i> var. <i>intermedius</i>	<i>Navicula cryptocephala</i> var. <i>cryptocephala</i>
<i>Scenedesmus quadricauda</i>	<i>Navicula cryptocephala</i> var. <i>veneta</i>
<i>Scenedesmus raciborski</i>	<i>Navicula peregrina</i>
<i>Chlamydomonas</i> sp. 1	<i>Navicula recens</i>
<i>Chlamydomonas</i> sp. 2	<i>Navicula exigua</i> var. <i>capitata</i>
<i>Chlamydomonas</i> sp. 3	<i>Navicula radiosa</i> var. <i>radiosa</i>
<i>Chlamydomonas peterfii</i>	<i>Navicula radiosa</i> var. <i>tenella</i>
<i>Phacotus lenticularis</i>	<i>Navicula menisculus</i>
Zygnematophyceae	<i>Diploneis puella</i>
<i>Closterium aciculare</i>	<i>Rhoicosphenia abbreviata</i>
<i>Closterium acutum</i> var. <i>variabile</i>	<i>Epithemia sorex</i>
<i>Closterium moniliferum</i>	<i>Epithemia adnata</i> var. <i>proboscidea</i>
<i>Cosmarium botrytis</i>	<i>Rhopalodia operculata</i>
<i>Staurodesmus cuspidatus</i>	<i>Hantzschia amphioxys</i>
<i>Staurastrum chaetoceras</i>	<i>Nitzschia acicularis</i>
<i>Staurastrum gracile</i>	<i>Nitzschia dissipata</i>
<i>Staurastrum hexacerum</i>	<i>Nitzschia palea</i>
<i>Staurastrum</i> sp.	<i>Nitzschia hungarica</i>
<i>Spirogyra</i> sp. 1	<i>Nitzschia constricta</i>
<i>Spirogyra</i> sp. 2	<i>Nitzschia sigmoidea</i>
<i>Zygnema</i> sp.	<i>Surirella caspia</i>
Chrysophyceae	<i>Cymatopleura solea</i>
<i>Salpingoeca</i> sp.	

Table 1 continued

Dinophyceae	<i>Cryptomonas marssonii</i>
<i>Peridinium</i> sp.	<i>Rhodomonas lacustris</i> ^a
<i>Ceratium hirundinella</i>	Euglenophyceae
Cryptophyceae	<i>Euglena variabilis</i>
<i>Cryptomonas ovata</i> ^a	<i>Trachelomonas rotunda</i>

^a Species with >10% of relative abundance at some date or at some sampling station

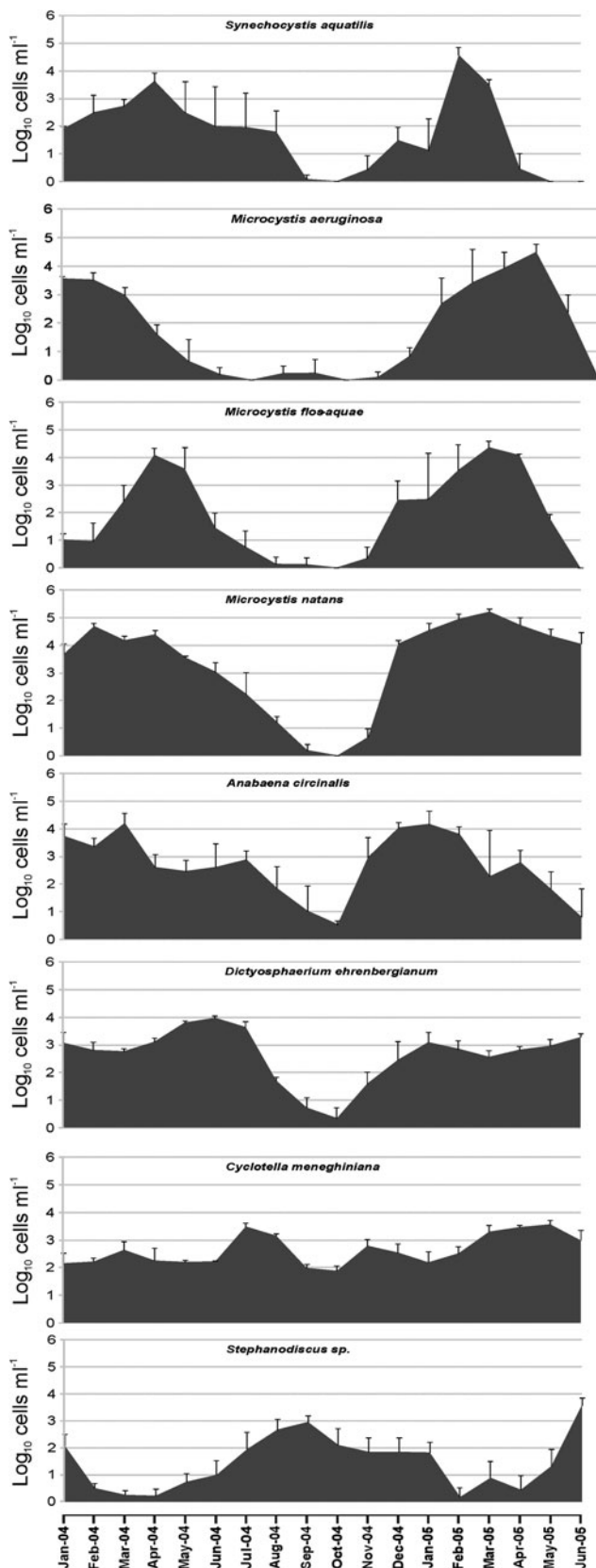
^b Dominant species

II. Cyanobacteria-Dictyosphaerium period From June to July: This period was characterized by a density of phytoplankton of $<7 \times 10^4$ cells ml⁻¹. During this period an increase in the relative abundance of green algae was also observed. Phytoplankton was characterized by a mixture of green algae and cyanobacteria plus diatoms to a lesser extent. Dominant species were: *Dictyosphaerium ehrenbergianum* at all sampling stations, *Synechocystis aquatilis* at S1 and S4, and *Microcystis natans* at S2, S3 and S4. Associated species were: *Anabaena circinalis*, *Microcystis flos-aquae*, *Snowella lacustris*, *Woronichinia elorantae*, *Tribonema* sp., *Dictyosphaerium pulchellum* and *Aulacoseira granulata*.

III. Cyclotella period From July to August: This period was characterized by a decrease in the density of phytoplankton, with values of $<4.5 \times 10^4$ cells ml⁻¹, and by an increase of the relative abundance of diatoms. Dominant species were: *Cyclotella meneghiniana* at all stations and *Synechocystis aquatilis* at S1. Associated species were: *Dictyosphaerium pulchellum*, *Snowella lacustris*, *Anabaena circinalis* and *Microcystis natans*.

IV. Stephanodiscus period From September to October: This period was characterized by a dramatic diminution in phytoplankton density ($<1.1 \times 10^4$ cells ml⁻¹), a high relative abundance of diatoms and the almost total disappearance of cyanobacteria, except in S3. During this period an increase in the relative abundance of Cryptophyceae could also be observed. The dominant species was: *Stephanodiscus* sp. at all stations. Associated species were: *Rhodomonas lacustris*, *Cryptomonas ovata*, *Monoraphidium dybowskii*, *Dictyosphaerium pulchellum*, *Botryococcus braunii*, *Coelastrum indicum* and *Scenedesmus semipulcher*.

V. Anabaena-diatom period During November 2005: This period also showed a low density of phytoplankton similar to the previous period ($<1.6 \times 10^4$ cells ml⁻¹) and with the main taxonomic groups similar to those in the Cyclotella period, but with different dominant species. Dominant species were: *Anabaena circinalis* at S1, S3 and S4, and *Stephanodiscus* sp. and *Cyclotella meneghiniana* at S2. Associated species were: *Monoraphidium dybowskii*, *Botryococcus braunii* and *Rhodomonas lacustris*.



◀ **Fig. 2** Absolute density of the dominant species in Paso de las Piedras Reservoir. The figure shows the average value (data transformed to decimal logarithm) for the four sampling stations; the bars represent the standard deviation

*I**: *Cyanobacteria II* period From December 2004 until May 2005: This period, although similar to the Cyanobacteria period, was different because of a high relative abundance of *Coelosphaerium aeruginum* at S2 and S4 during April, and a smaller abundance of Chlorophyceae.

Analysis of the abiotic factors associated with the successional periods

Cyanobacteria, Anabaena-diatom and Cyanobacteria II periods represented the summer-early autumn and spring periods, and they were characterized by high air and water temperatures and by high solar radiation, in contrast with the Cyanobacteria-Dictyosphaerium and Cyclotella periods, late autumn and winter periods, in which temperatures and solar radiation were lower ($p < 0.01$) (Table 2).

Cyanobacteria, Cyanobacteria II and Cyanobacteria-Dictyosphaerium periods showed a low N:P ratio, in contrast with Stephanodiscus and Anabaena-diatom periods, which showed a higher average N:P ratio (>8) principally because of a fall in phosphorus concentration ($p < 0.01$).

During Cyanobacteria and Cyanobacteria-Dictyosphaerium periods, the reservoir's water level remained low ($p < 0.01$). By the end of July it suffered an increase, probably more as a consequence of a smaller consumption or a diminution of the evaporation rate than because of an increase in precipitations, which in fact were higher during the Cyanobacteria II period.

The TSS was significantly lower in the Cyanobacteria period ($p < 0.01$) than in the Cyclotella and Stephanodiscus periods. The pH presented lower values during the Cyanobacteria-Dictyosphaerium and Cyclotella periods, higher values during Stephanodiscus, Anabaena-diatom and Cyanobacteria II periods, and intermediate values at the Cyanobacteria period ($p < 0.01$). Conductivity showed higher values during Cyanobacteria-Dictyosphaerium and Cyclotella periods than during Cyanobacteria and Stephanodiscus periods ($p < 0.01$).

With regard to nutrients, the concentration of phosphorus (both TP and SRP) was higher in both Cyanobacteria and Cyanobacteria II periods than in the Anabaena-diatom period ($p < 0.01$); nitrogen concentration (both NO_3^- and NO_2^-) was higher in the Stephanodiscus period and lower in the Cyanobacteria, Cyanobacteria-Dictyosphaerium, Anabaena-diatom and Cyanobacteria II periods. Silica concentration was higher in Cyanobacteria, Cyanobacteria

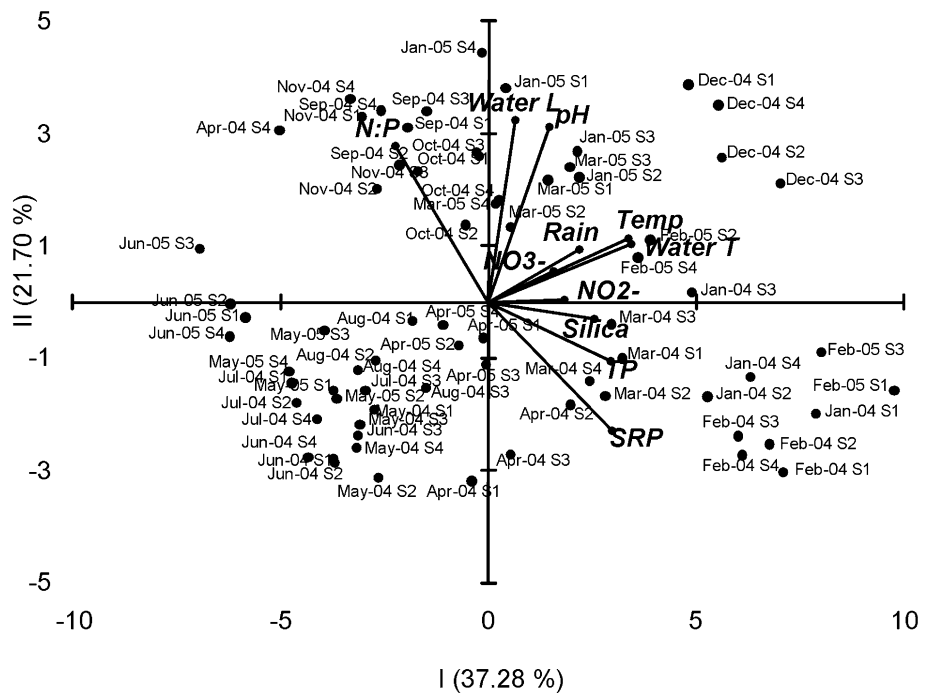
Table 2 Summary of the abiotic and biotic variables at each successional stage in Paso de las Piedras Reservoir

Variable	I	II	III	IV	V	I*
pH, \bar{x}	8.45a	8.14b	7.88b	9.10c	8.79c	8.74c
Water temperature (°C), \bar{x}	20.29a	9.36b	8.54b	12.03bc	17.42cd	18.75da
Temperature (°C), \bar{x}	18.11a	9.43b	8.47b	12.69c	16.93a	18.43a
Conductivity (mS cm ⁻¹), \bar{x}	0.36a	0.47b	0.50b	0.35a	0.38ab	0.37ab
TSS (mg l ⁻¹), \bar{x}	2.73a	3.46ab	7.21b	8.02b	4.90ab	3.80ab
TP (mg l ⁻¹), \bar{x}	0.487a	0.378b	0.418ab	0.384b	0.291c	0.504a
SRP (mg l ⁻¹), \bar{x}	0.304a	0.220b	0.213b	0.193bc	0.136c	0.237b
NO ₂ ⁻ (mg l ⁻¹), \bar{x}	0.023bc	0.018c	0.022ab	0.022a	0.016bc	0.017bc
NO ₃ ⁻ (mg l ⁻¹), \bar{x}	1.311bc	1.296bc	1.419ab	1.544a	1.181c	1.339bc
Silica (mg l ⁻¹), \bar{x}	1.427a	0.794bc	1.357ab	0.773bc	0.401c	1.309ab
N:P, \bar{x}	5.19a	6.15b	7.02bc	8.38c	9.24c	6.40b
Water level (m a.s.l.), \bar{x}	162.55a	162.43a	163.16b	163.67c	163.72c	163.47c
Solar radiation (kW m ⁻²), \bar{x}	6.86ab	2.69c	2.53c	6.36b	8.09a	nad
Specific richness, \bar{x}	53.91a	60.56b	47.43ac	30.91d	39.95cd	61.75b
Density (cells 10 ³ ml ⁻¹), \bar{x}	84.26a	38.79b	21.76bc	4.21c	8.12c	133.10a
Diversity, \bar{x}	2.69a	3.33b	3.43b	3.14b	3.26b	2.64a
Dominance, \bar{x}	0.31a	0.19b	0.18b	0.20b	0.22ab	0.31a
Evenness, \bar{x}	0.47a	0.56b	0.62b	0.64b	0.61b	0.45a
Dominant species	<i>A. circinalis</i> <i>M. aeruginosa</i> <i>M. flos-aquae</i> <i>M. natans</i> <i>S. aquatilis</i>	<i>D. ehrenbergianum</i> <i>M. natans</i> <i>S. aquatilis</i>	<i>C. meneghiniana</i> <i>S. aquatilis</i>	<i>Stephanodiscus</i> sp.	<i>A. circinalis</i> <i>Stephanodiscus</i> sp. <i>C. meneghiniana</i>	<i>A. circinalis</i> <i>M. aeruginosa</i> <i>M. flos-aquae</i> <i>M. natans</i> <i>S. aquatilis</i>

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

\bar{x} arithmetic median, *nad* not available data

Fig. 3 Biplot of PCA performed on abiotic parameters. Sampling site codes: first abbreviation corresponds to month and year, and the subsequent one to sampling site. Environmental variables: N:P (nitrogen to phosphorus ratio), Water L (water level), pH, NO₃⁻ (nitrate concentration), NO₂⁻ (nitrite concentration), Silica (silica concentration), TP (total phosphorus concentration), SRP (soluble reactive phosphorus concentration), Temp (air temperature), Water T (water temperature) and Rain (cumulative rainfall in the days previous to sampling)



II and Cyclotella periods and lower in the Anabaena-diatom period.

PCA using 11 abiotic variables explained the 59% of data variability in the first two ordination axes (Fig. 3). The following variables were the most important ($r > 0.7$) for axis 1: water temperature, TP, SRP and air temperature. For axis 2, however, pH, water level and N:P ratio were the most contributing variables ($r > 0.7$). Samples from the Cyanobacteria and Cyanobacteria II periods were placed on the positive side of axis 1, associated with higher temperature and phosphorus, except the samples from April and May, located close to the origin, which registered lower temperatures and lower concentration of phosphorus. These two blue-green periods were separated according to axis 2 because the Cyanobacteria period was associated with a lower water level, pH and N:P ratio than Cyanobacteria II period.

Samples from periods Cyanobacteria-Dictyosphaerium, Cyclotella, Stephanodiscus and Anabaena-diatoms were placed on the negative side from axis 1, associated with lower temperatures and phosphorus. These periods were ordered according to axis 2, with samples from Cyanobacteria-Dictyosphaerium and Cyclotella periods on the negative side since they showed values of pH and water level lower than Stephanodiscus and Anabaena-diatom periods; the Cyanobacteria-Dictyosphaerium period also showed a lower N:P ratio than the Stephanodiscus and Anabaena-diatom periods, whereas the Cyclotella period did not have differences either with the Cyanobacteria-Dictyosphaerium period or the Stephanodiscus and Anabaena-diatom periods; thus, it was placed in a position closer to the origin in the PCA.

Phytoplankton density, specific richness, diversity, dominance and evenness during successional periods

Diversity indices, as well as the dominance index, varied rather irregularly throughout the whole study period (Fig. 4). The highest diversity ($H' = 4.19$) was observed at the beginning of January 2004 in concurrence with one of the lowest dominance values ($D = 0.08$); the lowest diversity ($H' = 0.93$) was registered in February 2004 simultaneously with the maximum dominance value ($D = 0.78$).

In spite of the high diversity registered at the beginning of the Cyanobacteria and Cyanobacteria II periods, the values quickly fell and remained low, with values statistically lower than in the remaining periods ($p < 0.01$). Evenness had a similar behavior, with values statistically higher in the Cyanobacteria-Dictyosphaerium, Cyclotella, Stephanodiscus and Anabaena-diatom periods ($p < 0.01$). The Cyanobacteria-Dictyosphaerium, Cyclotella and Stephanodiscus periods showed a dominance index statistically lower than the Cyanobacteria and Cyanobacteria II

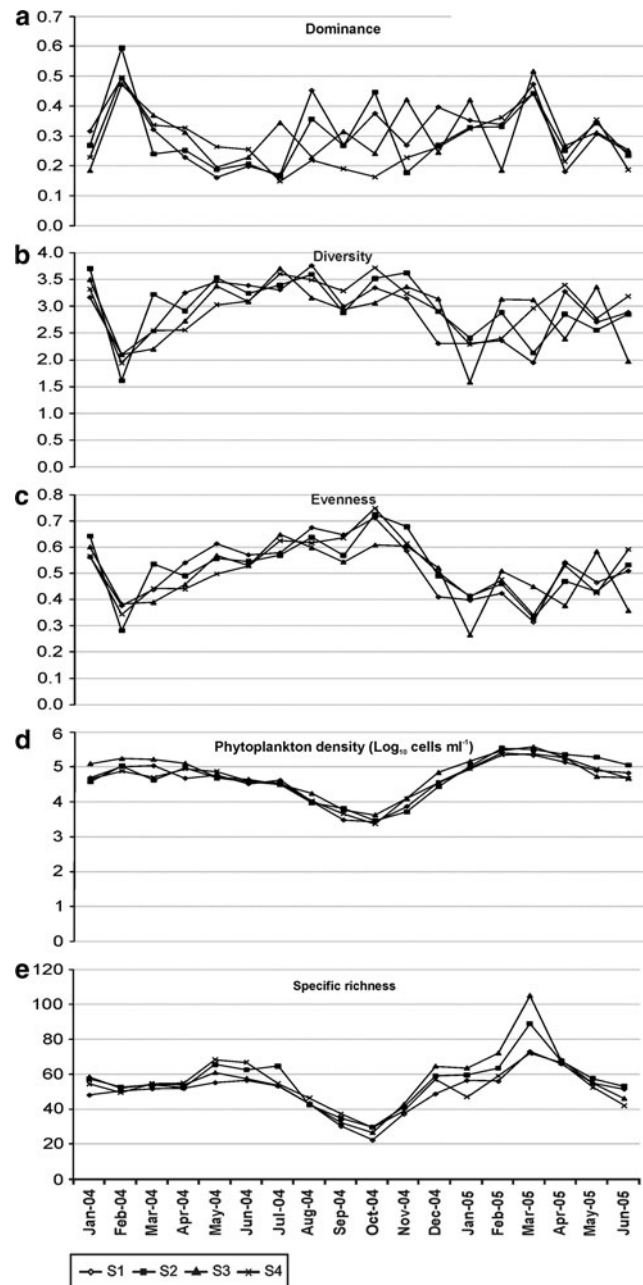


Fig. 4 Variations of **a** Simpson's dominance index; **b** Shannon diversity index; **c** evenness; **d** total phytoplankton density and **e** specific richness

periods ($p < 0.01$), whereas the Anabaena-diatom period showed no differences either with the Cyanobacteria and Cyanobacteria II periods or with the Cyanobacteria-Dictyosphaerium, Cyclotella and Stephanodiscus periods (Table 2). Phytoplankton density was statistically higher in the Cyanobacteria and Cyanobacteria II periods than in the remaining periods ($p < 0.01$) (Table 2).

Diversity had a significant negative correlation with both dominance ($r_s = -0.95$; $p < 0.0001$; $n = 296$) and phytoplankton density ($r_s = -0.56$; $p < 0.0001$; $n = 296$),

and a positive correlation with evenness ($r_s = 0.94$; $p < 0.0001$; $n = 296$). On the contrary, it did not have a significant correlation with the specific richness.

With regard to specific richness, it exhibited the statistically highest values during the Cyanobacteria-Dictyosphaerium and Cyanobacteria II periods, and the lowest ones during the Stephanodiscus period ($p < 0.01$). It showed a significant correlation with phytoplankton density ($r_s = 0.55$; $p < 0.0001$; $n = 296$) (Table 2).

In summary, considering biological features, the Cyanobacteria and Cyanobacteria II periods were characterized by very high phytoplankton density, low diversity and high dominance. In contrast, the Cyanobacteria-Dictyosphaerium, Cyclotella, Stephanodiscus and Anabaena-diatom periods were characterized by low phytoplankton density, high diversity and low dominance.

Similarity

The SIMI varied rather irregularly among sampling stations. Comparisons between pairs of sampling dates showed similarity or high similarity (56.25–68.8%), whereas few exhibited a SIMI index indicating low similarity or dissimilarity (10.9–23.4%). At S1 only one value of SIMI, registered in March 2004, was lower than 0.199, thus indicating dissimilarity among phytoplankton communities. It accounted for a fall in the relative abundance of *A. circinalis* and a rise in *M. flos-aquae*. At S2, values lower than 0.199 were never registered. At S3, five values lower than 0.199 were registered, the first one in August as a consequence of a fall in the relative abundance of *C. meneghiniana* and the increase of *Stephanodiscus* sp. It appeared in concordance with the limit between the Cyclotella and Stephanodiscus periods. The next three values lower than 0.199 registered in September and October accounted for a peak in the abundance of *M. aeruginosa*, followed by a replacement of *Stephanodiscus* sp. for *R. lacustris* and *C. ovata* (the latter in a lesser amount) and at the end by a rise in the relative abundance

of *Stephanodiscus* sp. The last value lower than 0.199 was registered during December 2004 and January 2005 as a consequence of the replacement of *M. natans* for *A. circinalis*.

At S4, two values of SIMI indicating dissimilarity were registered: the first one in February 2004 because of a replacement of *M. natans* for *M. aeruginosa*, and the second one between May and June 2004 as a consequence of an increase of *M. natans* and a fall in the relative abundance of *D. ehrenbergianum* and *Synechocystis* sp.

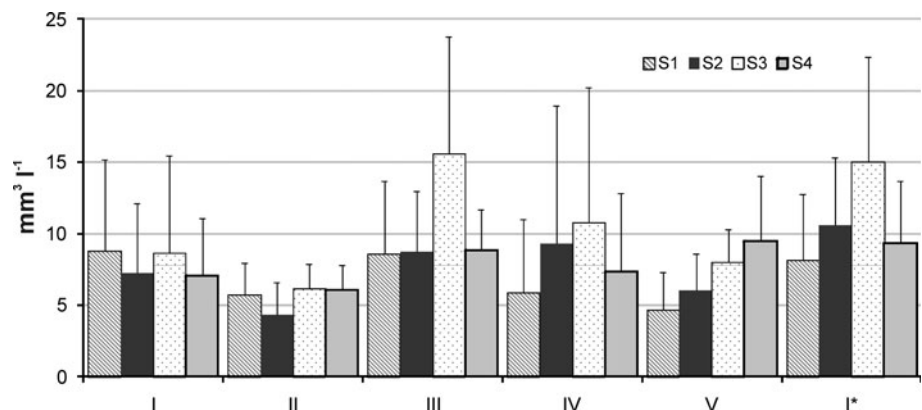
Biovolume during successional periods

Figure 5 shows the average biovolume for each sampling station through all successional periods. The Cyanobacteria II period registered the highest biovolume ($p < 0.01$); however, it did not show significant differences with the Cyclotella period, which was the second period with highest average biovolume. The biovolume showed marked variations along the study period, and the highest values were registered at S3 during the Cyclotella, Stephanodiscus and Cyanobacteria II periods.

Discussion

Cyanobacteria, chlorophytes and diatoms were the most important phytoplankton constituents of Paso de las Piedras Reservoir. During the study period, the taxonomical structure of the phytoplankton community was correlated with environmental and physicochemical parameters, displaying changes in the dominant taxa. From January to May, cyanobacteria dominated with relative abundances up to >95%. They became dominant very quickly and remained so through the whole summer and early autumn. Such dominance of cyanobacteria in eutrophic lakes is a phenomenon already pointed out by several authors (Oliver and Ganf 2000; Calijuri et al. 2002; Mischke 2003; Rahman et al. 2005; Havens 2008).

Fig. 5 Average biovolume ($\text{mm}^3 \text{ l}^{-1}$) for each sampling station at each successional period; the bars represent the standard deviation



In most of the reservoirs of La Plata River Basin and in other lakes of Argentina, cyanobacteria dominance is mainly accounted for by *Microcystis aeruginosa* (Pizzolon et al. 1999; Calijuri et al. 2002; Chalar 2009). In Paso de las Piedras Reservoir, however, this species was dominant only at the very beginning of Cyanobacteria period in only two sampling stations, whereas *Microcystis natans* prevailed on *Microcystis aeruginosa* extensively during almost all the bloom presumably because *Microcystis natans* has lower optimum temperatures. The optimum temperature for the growth of *Microcystis aeruginosa* is 30°C (Chu et al. 2007), a temperature that was never reached in the reservoir during the study. As *Microcystis natans* is not a ubiquitous species, it has never been quoted causing water blooms anywhere, so there is no information about optimal growth conditions, but almost certainly it does not require such high temperatures since it showed high abundances until May.

Among the causal factors involved in a cyanobacterial bloom, the following have been mentioned: (1) high nutrient concentration, (2) high water temperature, (3) high pH, (4) low N:P ratios and (5) stability of the water column (Paerl 1988; Havens et al. 1998; Huisman and Hulot 2005; Havens 2008). Most of these conditions were detected in Paso de las Piedras Reservoir during the Cyanobacteria and Cyanobacteria II periods, but not water column stability since it is a polymictic reservoir.

Our results show that the most important parameters associated with the development of the blooms were water temperature and phosphorus concentration. Likewise, Calijuri et al. (2002) also found that TP was the environmental factor better correlated with the blue-green biomass, and Huszar et al. (2000), studying eight Brazilian lakes, also found that the relative abundance of cyanobacteria was related to high temperature, but not to the pH, TP, TN or TN:TP ratio.

Surprisingly, contrary to what is almost consensus in the literature, the N:P ratio and pH were not correlated with the development of the bloom since the Cyanobacteria and Cyanobacteria II periods were placed both on the positive and negative sides of axis 2 in the PCA. This condition supports the finding of Dowing et al. (2001) who noted that the TP concentration is a better predictor of cyanobacteria dominance than TN:TP ratios. In the case of pH, nonetheless, this does not mean that the cyanobacterial blooms took place under low pH conditions, since the reservoir always presented values higher than 7, but rather that the high pH was not a condition for the initiation of the bloom, as was previously pointed out by Shapiro (1990).

The PEG model (Sommer et al. 1986) describes two phytoplankton maxima, the first one in spring and the second one in summer, both separated by a “clear water phase” during which a change in phytoplankton species

composition occurs from small, edible spring species, e.g., diatoms, cryptophytes, to grazing resistant summer species, e.g., colonial green algae, filamentous cyanobacteria and dinoflagellates.

The three developing periods of the end of winter and spring (Cyclotella, Stephanodiscus and Anabaena-diatom periods) showed high relative abundance of diatoms, along with an increase in the relative abundance of Cryptophyceae during the Stephanodiscus period. Even though the Cyclotella and Stephanodiscus periods showed a decrease in phytoplankton density, they showed a high biovolume because of the diatom dominance. This situation fits with the PEG model (Sommer et al. 1986), which predicts that Cryptophyceae and small centric diatoms were the first abundant phytoplankton groups during this period of the year because of the greater nutrient availability and increased light. The high abundance of Cryptophyceae observed during the Stephanodiscus period accounted principally for *Rhodomonas lacustris*. Gavrieli (1984), studying the autoecology of this species at Greifensee (Switzerland), also found a spring bloom of *R. lacustris* and explained it as a consequence of the high light intensity and the still low water temperature that avoided the activity of the zooplankton.

There were many aspects of the general pattern of succession that were coherent with the general model of plankton seasonal succession described in the PEG model; however, the major discrepancy is the extremely short clear water phase observed. There was an indication of a short clear water phase in October at the end of Stephanodiscus period only at S1, S2 and S4. During this period, an increase in the depth of the Secchi disc of 0.7 m (more than 40% over the mean range) and a decrease of the chlorophyll *a* concentration of 80–95% were observed, as well as a change in the specific composition, i.e., an increase in the relative abundance of Cryptophyceae and Chlorophyceae during the first days of October. The phytoplankton density also decreased until values lower than 4,000 cells ml⁻¹. At S3, in contrast, there was no increase in depth of the Secchi disc, and the decrease of chlorophyll *a* concentration was very short to quickly return to high values, reaching the annual maximum during this period.

Following the clear water phase, a quick growth of grazing-resistant cyanobacteria was observed, accounted for by *A. circinalis*, which replaced the diatoms because of the silica depletion at the end of the *Anabaena*-diatom period.

The clear water phase usually coincides with a spring peak of the filter-feeding zooplankton, and the increase in water clarity has sometimes been attributed to grazing activity (Lampert and Schober 1978); however, according to Deneke and Nixdorf (1999), in highly eutrophic lakes, the main bottom-up mechanism compensating for algal

losses seems not to be a limitation of grazer biomass because of low food quality, but rather it fosters an early and fast growth of grazing resistant algae, mainly cyanobacteria, before the development of cladocerans. This phenomenon is more pronounced in shallow, hypertrophic lakes since the predation pressure and biomass of cyanobacteria tend to be higher in shallow than in stratified lakes (Jeppesen et al. 1997; Nixdorf and Deneke 1997). In spite of the fact that the dynamic of the zooplankton community was not evaluated during this research, as Paso de las Piedras Reservoir is a polymictic shallow-eutrophic lake, this mechanism could be the factor that determines the short extent of this phase and its irregular occurrence along the reservoir. In this sense, Trifonova (1993) also pointed out that a true clear water phase is not characteristic of shallow eutrophic lakes with rapid nutrient turnover. Another reason could be that Paso de las Piedras Reservoir experiences less seasonal variation than is found in lakes at higher latitudes—on which the PEG model was based. This situation has also been observed in lakes from tropical regions where the cyanobacteria are dominating all year round without any clear water phase at all, as for example in Lake Victoria (Africa) (Haande et al. 2011) and in Funil Reservoir (southeastern Brazil) (Soares et al. 2009).

Sampling station S3 was different from the remaining stations not only because of the lack of a clear water phase, but also because of a greater density of diatoms and a high relative abundance of *M. aeruginosa* during the Stephanodiscus period. In concordance with the higher density of diatoms, the product of a higher concentration of silica (Fernández 2010), this station displayed a higher biovolume. According to Fernández et al. (2009), the differences between S3 and the rest of the reservoir were the result of the different characteristics of water inflows from the two main tributaries since S3 is located near the mouth of El Divisorio Creek, which brings more turbid waters to the lake as it carries a significant quantity of particulate matter and dissolved salts.

Although Paso de las Piedras Reservoir is a eutrophic lake, it showed high diversity indices, with values higher than 4 bits. Several authors have indicated a trend to lower diversity indices in oligotrophic or eutrophic lakes in comparison with mesotrophic lakes because the coexistence of more species is possible in the latter (Harris 1986; Holzmann 1993; Reynolds 1993). Similar to Paso de las Piedras, many other eutrophic lakes exhibit high diversity, for example, Barra Bonita Reservoir (Brazil) (Calijuri et al. 2002) and Salto Grande Reservoir (Argentina-Uruguay) (Chalar 2009). This contradicts the competitive exclusion principle (Hardin 1960). This dilemma, known as the “paradox of the plankton” (Hutchinson 1961), has been explained by non-equilibrium fluctuations of the environment. The intermediate disturbance hypothesis (Connell

1978), adapted to phytoplankton ecology by Reynolds (1988), has suggested interpreting seasonal succession as the interaction between true successional development and intermediate disturbance. In this regard, Trifonova (1993) and Holzmann (1993) explained the higher diversity found in non-stratified lakes in comparison with stratified ones as a consequence of unstable environmental conditions, determined first by the persistent wind mixing and constant circulation of nutrients. The high values of the diversity indices observed in Paso de las Piedras could be explained in the same manner since such conditions of instability also take place in the reservoir.

Diversity was more influenced by the evenness (sensu Pielou 1966) than either by the richness or by the density as shown by the Spearman correlation analysis. These results are similar to those obtained by Moustaka-Gouni (1993) at Lake Volvi, Greece.

Similar to other temperate polymictic lakes (Calijuri et al. 2002; De León and Chalar 2003), the lower diversity occurred during summer-early autumn periods (Cyanobacteria and Cyanobacteria II periods) when the phytoplankton density was higher. This result is inconsistent with Wetzel (2001), who pointed out that in eutrophic temperate waters, diversity tends mainly to increase significantly in summer and to fall in winter in relation to the availability of nutrients. However, in polymictic reservoirs there are no periods of stratification and circulation of nutrients, which remains high in the euphotic layer across the entire annual cycle, so the conditions of light and temperature and low grazing favor the increase of cyanobacteria in summer, thus developing huge populations, and outcompete other species causing the fall in diversity.

According to Sommer et al. (1983), in natural phytoplankton communities, it is often difficult to determine whether a given “phase” in a seasonal sequence can be considered to be in an equilibrium state or not. In our research, only some short periods within Cyanobacteria and Cyanobacteria II periods match Sommer’s criteria for steady state. In this regard, Padisák et al. (2003) found that equilibrium phases in phytoplankton assemblages were relatively rare and that stressed ecosystems are quite likely to support equilibrated phytoplankton communities.

With regard to the SIMI index, changes in composition of the community were also obvious when comparing the phytoplankton communities in pairs. Nevertheless, there was no clear relationship between the successional periods we described based on phytoplankton composition and the SIMI index. This fact is due to the fact that SIMI takes into account alterations in the individual species, whereas the successional periods were defined based on groups of species.

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