

Phytoplankton Development in a Highly Eutrophic man-made Lake From the Pampa plain of Argentina – a functional Approach

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Received 11 May 2013;

Revised 27 Sep. 2013;

Accepted 4 Oct. 2013

ABSTRACT: The phytoplankton structure and dynamics were analysed in relation to abiotic variables in Paso de las Piedras Reservoir, Argentina. Phytoplankton driving forces were explored using a functional approach. A total of 15 functional groups were identified among which D, P, H1, F, J and C were the most important. A Canonical variate analysis indicated that the categorization of the species in functional groups and its relationship with the temporal species clustering was not a random result. In the redundancy analysis, temporal ordination dynamics of functional groups was well described by the distribution of samples. Remarkable shifts in composition and biomass of phytoplankton occurred in agreement with changes in temperature, N:P ratio and transparency. The group succession could be summarized as: P/J (early summer)→P/H1 (late summer)→P (early autumn)→P/F (late autumn)→C (early winter)→D (late winter)→Y (early spring)→D (early spring)→P (late spring). The majority of the associations detected were typical of eutrophic-hypertrophic systems. With the exception of H1, the groups that most contribute to biovolume were those characteristics of mixed aquatic environments, i. e., non-stratifying lakes or deep, well-mixed epilimnia of stratifying lakes. The diversity indices, in terms of functional groups, were low, meaning that a small number of traits were present and/or that there was an inequitable distribution.

Key words: Functional groups, Phytoplankton dynamics, Paso de las Piedras Reservoir, Diversity

INTRODUCTION

During their annual development phytoplankton communities undergo changes in both species quantity and species composition. Such changes may be repeated on a more or less regular basis from one year to another (Hutchinson, 1961). Lakes of widely dispersed geographical locations, but sharing similar morphometric, climatological and chemical properties show similar patterns of seasonal changes (Reynolds, 1984).

The number and biological traits of organisms, the relative abundance of species and their functional roles are all parameters that contribute to the observable community structure (Reynolds, 2006). Changes in structure affect key aspects of the ecosystems functioning, such as those related to energetic, homeostasis or nutrients cycling (Odum, 1969; Reynolds, 1997), which in turn may feedback on species number or species composition. To understand the role of phytoplankton communities in the ecosystems, the species composition is of paramount importance since species differ drastically in their potential for nitrogen

fixing and carbon sequestration (Verity *et al.*, 2002) and in their nutritional value for grazers (Sterner and Elser, 2002).

It is now widely appreciated that the functioning of a given ecosystem is dictated to a large extent by biodiversity (Chapin *et al.*, 1998; Hooper *et al.*, 2005; Ptacnik *et al.*, 2008). However, there is a growing consensus that the functional diversity given by the value and range of species traits, rather than the species number *per se* is what strongly determines ecosystem functioning in higher plants (Diaz and Cabido, 2001).

In relation to phytoplankton, species have developed diverse morphological and physiological adaptative strategies for surviving in different environments (Reynolds, 1998). As a consequence, the most frequent species in a particular environment share many common features in morphology, the ability to regulate buoyancy, the requirement for specific resources, or the ability to obtain alternative carbon and nutrient resources (Weithoff, 2003). In spite of

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that, community structure and phytoplankton dynamics have traditionally been studied considering only the biomass variations in the major taxonomic classes disregarding that they do not always reflect the perceived ecological functions. In this sense, Reynolds *et al.* (2002) presented a new insight for the study of phytoplankton communities describing 31 phytoplankton assemblages understood as functional groups, i.e. groups of species with more or less precisely defined demands for several different combinations of physical, chemical and biological properties (Padisák *et al.*, 2006). At present, 38 functional groups have been described, each one having alphanumeric symbols (codons) (Padisák *et al.*, 2009).

Reynolds' classification system has been successfully applied to freshwater and marine phytoplankton (Padisák and Reynolds, 1998; Smayda and Reynolds, 2001; Alves-de-Souza *et al.*, 2008; Fonseca and Bicudo, 2008). It has proved to be more useful in reconstructing community structures and sequences of replacement of dominant species than the traditionally used phylogeny-based systems (Huszar and Caraco, 1998; Kruk *et al.*, 2002; Devercelli, 2006). In fact, several authors have concluded that phytoplankton taxonomical relationships are poor predictors of ecological similarities, whereas a functional classification has many advantages for ecological interpretations and predictions (Litchman *et al.*, 2003; Weithoff, 2003).

The main objective of the present study was to analyse the phytoplankton structure and dynamics and their relationship with abiotic variables in the Paso de las Piedras Reservoir, located in the south of Buenos Aires Province, Argentina. Particular goals were (i) to analyse the phytoplankton structure and dynamics in terms of functional groups and (ii) to identify the driving forces, based on the group autecology related to their adaptations to environmental changes.

Paso de las Piedras Reservoir is a hypereutrophic non-stratifying reservoir experiencing recurrent cyanobacteria blooms during summer and early autumn months since 1982 (Pizzolon *et al.*, 1999; Echenique *et al.*, 2001; Fernández *et al.*, 2012). The blooms are dominated principally by *Microcystis aeruginosa* and *Anabaena circinalis* (Fernández *et al.*, 2012) causing serious inconveniences for the drinking water supply since they give bad odor and taste to the water.

Previous studies of phytoplankton in Paso de las Piedras Reservoir focused on 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; Fernández *et al.*, 2009, 2011, 2012) and also with regard to episodes of massive proliferations (Echenique *et al.*, 2001). A lake

eutrophication model has also been developed for this reservoir, resulting from temporal and spatial dynamic mass balances in the major groups of phytoplankton, key nutrients, and oxygen biochemical demand and dissolved oxygen (Estrada *et al.*, 2009).

The functional groups approach has never been used to study the structure and dynamic of phytoplankton in this aquatic ecosystem. If Reynolds' classification system proves more useful than the taxonomical, the incorporation of this schema in the eutrophication model will provide valuable information for making decisions with regard to management strategies.

MATERIALS & METHODS

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 (Fig. 1). 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. The reservoir has a surface area of 36 km², with a mean depth of 8.2 m. It is a non stratifying lake with continuous mixing due to morphometric features along with the wind effect (Intartaglia and Sala, 1989). Based on the total phosphorus 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). 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). 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 and 79 samples were collected at S1 and S3 respectively. All samples were taken at a depth of 0.5 m. Samples for qualitative analyses were taken with 30- μ m-mesh plankton net and van Dorn bottle; some of the samples were maintained alive, while others were fixed immediately with 4% formaldehyde. Samples for quantitative analyses were collected with 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 camera DXM1200F. Phytoplankton were identified using 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 x400. 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). Cells were identified to the species level when possible; cell counts were converted to biovolume according to their size and geometric form (Sun and Liu, 2003). Water samples for nutrient analysis were collected with a Van Dorn bottle. Nitrate (NO₃⁻), nitrite (NO₂⁻), ammonium, total phosphorus (TP), soluble reactive phosphorus (SRP) and silica were analysed in the Water Authority of Buenos Aires Province (ADA) Laboratory, following the methods described by APHA (1992). 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 solids (TSS) concentration was also determined in accordance with APHA (1992) by PROFERTIL S.A. In addition, *in situ* measurements of electrical conductivity, temperature and pH were also conducted using a Horiba U-10 multisensor. The Hydraulic Laboratory at Universidad Nacional del Sur provided data of air temperature, wind speed and direction, precipitations, reservoir water volume and level, and tributary flows obtained from two meteorological stations located in the mouth vicinities of El Divisorio Creek and the reservoir area, respectively (Fig. 1). Taxa were classified into functional groups according to Reynolds et al. (2002), Reynolds (2006) and Padisák et al. (2009). Those species that were not considered in the schemas were assigned to a particular group taking into account their morphological and ecological characteristics and the environmental conditions prevailing during their highest occurrence. Phytoplankton diversity was calculated using the Shannon-Wiener function (Shannon, 1948) on the basis of biovolume. This was done separately for species (H' SP) and functional groups (H' FG):

$$H' = - \sum p_i \log_2 p_i \quad (1)$$

where p_i is the relative amount of biovolume of each species i or each functional group i .

Spearman Rank Correlation was used to test association between functional groups and environmental variables, the nonparametric Kruskal-Wallis test was used to assess differences between sampling stations and linear regression analysis was used to test the relations between diversity (H' SP and H' FG) with total biovolume. Kruskal-Wallis test, linear regression and correlation analyses were performed using the software InfoStat (Student version). A canonical variate analysis (CVA) was carried out according to ter Braak (1995) to test the null hypothesis that *a priori* phytoplankton species classifications in

principal taxonomic groups and in associations and its relationship with the temporal clustering of species are a random result. A multivariate ordination method was used to analyse the relationship between functional groups and environmental variables, using the software CANOCO 4.5. Detrended correspondence analysis (DCA) was employed to decide whether linear or unimodal ordination methods should be applied (ter Braak and Smilauer, 2002). Redundancy analysis (RDA) was applied to examine the relationship between the functional groups and the environmental data. The response variables data set was based on the functional groups biovolume that appeared with a biovolume >5% to the total at any sampling occasion. The functional groups biovolume were root square transformed ("data+0.5) and abiotic data were standardized by error variance. A Monte Carlo test of significance based on 499 permutations under unrestricted model tested the hypothesis (Ho) of no relationship between the functional groups and the environmental data.

RESULTS & DISCUSSION

A total of 162 phytoplankton taxa were identified, including many species not previously recorded in Argentina. Species belonged to nine taxonomical groups: Cyanoprokaryota (35), Chlorophyceae (69), Zygnemaphyceae (12), Bacillariophyceae (34), Cryptophyceae (3), Chrysophyceae (2), Euglenophyceae (2), Xanthophyceae (3) and Dinophyceae (2). Thirty-eight species were registered as having reached a biovolume >5% on any sampling occasion, so they were considered descriptive species. Phytoplankton biovolume was high throughout the study period with a mean value of 9659.7 mm³ m³. Bacillariophyceae and Zygnematophyceae were mainly the groups with the greatest total biovolume (Fig. 2). A peak in the biovolume of Cryptophyceae was observed during the end of September and beginning of October. We found that 15 of the proposed functional groups outlined by Reynolds et al. (2002), Reynolds (2006) and Padisák et al (2009) were represented in the set of selected species (Table 1). The typical traits of the detected functional groups are exhibited in Table 2. These functional groups together accounted for more than 90% of the total biovolume for most of the study period. Groups D, P, H1, F, J and C were the most important (Fig.3). *Lagerheimia citriformis*, *Rhodomonas lacustris* and *Closterium moniliferum* had not previously been assigned to the schema, in this study they were fitted to F, X2 and P group, respectively, by their morphological and ecological characteristics and also by conditions at the time of their higher abundance.

There were significant differences in the mean biovolume between S1 and S3 (H=4.95; p<0.05), with higher values at S3. There were also significant biomass differences in some functional groups in S3

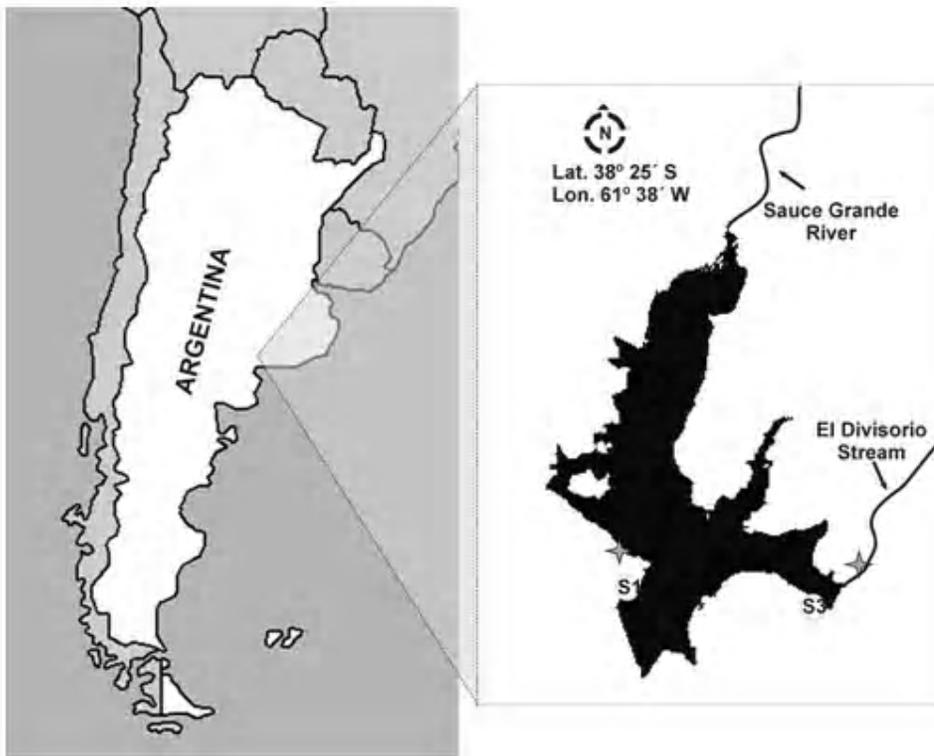


Fig. 1. Location of Paso de las Piedras Reservoir and sampling sites (S1, S3). Stars indicate the location of the meteorological stations

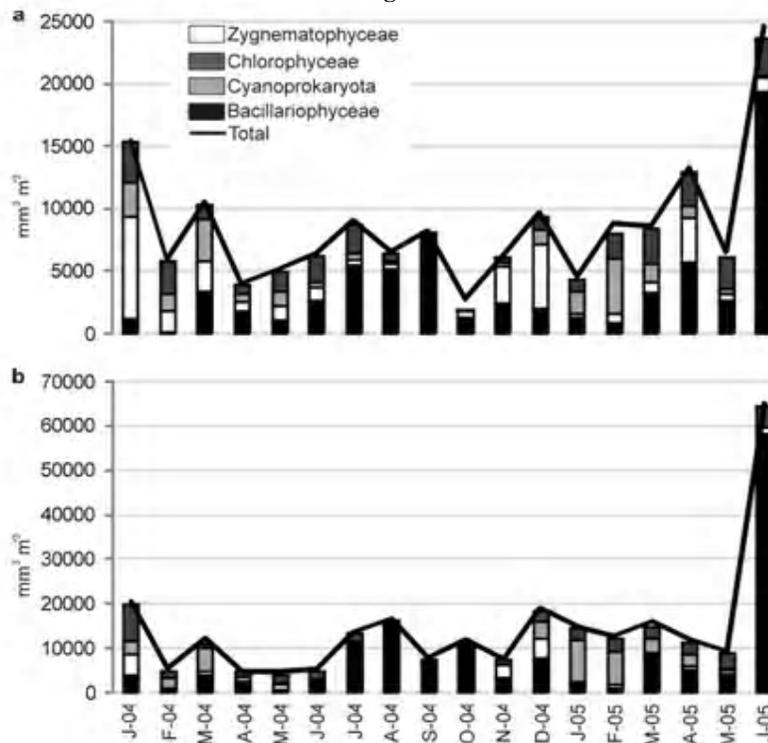


Fig. 2. Variation in total phytoplankton biovolume and biovolume of the most important taxonomical groups at S1 (a) and at S3 (b). The figure shows the monthly average value

Table 1. Descriptor phytoplankton species (>5% to the total biovolume) from Paso de las Piedras Reservoir

Specie	Taxonomic group	Functional group
<i>Synechocystis aquatilis</i> Sauvageau	Cyanoprokaryota	L _O
<i>Synechocystis fuscopigmentosa</i> Kovác.	Cyanoprokaryota	K
<i>Microcystis aeruginosa</i> (Kütz.) Kütz.	Cyanoprokaryota	M
<i>Microcystis flos-aquae</i> (Wittr.) Kirchn.	Cyanoprokaryota	M
<i>Microcystis natans</i> Lemm. ex Skuja	Cyanoprokaryota	M
<i>Microcystis protocystis</i> Crow	Cyanoprokaryota	M
<i>Abaena circinalis</i> Rab.	Cyanoprokaryota	H1
<i>Sphaerocystis schroeteri</i> Chod.	Chlorophyceae	F
<i>Planktosphaeria gelatinosa</i> G.M. Smith	Chlorophyceae	F
<i>Pediastrum duplex</i> var. <i>duplex</i> Meyen	Chlorophyceae	J
<i>Dictyosphaerium ehrenbergianum</i> Näg.	Chlorophyceae	F
<i>Dictyosphaerium pulchellum</i> Wood	Chlorophyceae	F
<i>Lagerheimia citrifomis</i> (Snow) Coll.	Chlorophyceae	F
<i>Oocystella borgei</i> (Snow) Hind.	Chlorophyceae	F
<i>Oocystella lacustris</i> (Chod.) Hind.	Chlorophyceae	F
<i>Oocystella marssonii</i> (Lemm.) Hind.	Chlorophyceae	F
<i>Oocystella parva</i> (W & G.S. West) Hind.	Chlorophyceae	F
<i>Oocystella solitaria</i> (Wittr. in Wittr & Nordst.) Hind.	Chlorophyceae	F
<i>Coelastrum microporum</i> Näg.	Chlorophyceae	J
<i>Coelastrum astroideum</i> De Not.	Chlorophyceae	J
<i>Coelastrum indicum</i> Tur.	Chlorophyceae	J
<i>Closterium aciculare</i> T. West	Zygnemaphyceae	P
<i>Closterium moniliferum</i> (Bory) Ehrenb. ex Ralfs	Zygnemaphyceae	P
<i>Staurodesmus cuspidatus</i> Bréb ex Ralfs	Zygnemaphyceae	N
<i>Staurastrum chaetoceras</i> (W. & G.S. West) G.M.Sm.	Zygnemaphyceae	P
<i>Staurastrum gracile</i> Ralfs ex Ralfs	Zygnemaphyceae	P
<i>Aulacoseira granulata</i> (Ehrenb.) Simonsen	Bacillariophyceae	P
<i>Aulacoseira granulata</i> var. <i>angustissima</i> (Müller) Simonsen	Bacillariophyceae	P
<i>Cyclotella meneghiniana</i> Kütz.	Bacillariophyceae	C
<i>Stephanodiscus</i> sp.	Bacillariophyceae	D
<i>Navicula peregrina</i> (Her.) Kütz.	Bacillariophyceae	P
<i>Tribonema</i> sp.	Xanthophyceae	T
<i>Cryptomonas ovata</i> Her.	Cryptophyceae	Y
<i>Cryptomonas marssonii</i> Skuja	Cryptophyceae	Y
<i>Rhodomonas lacustris</i> Pasch. et Ruttn.	Cryptophyceae	X2
<i>Peridinium</i> sp.	Dinophyceae	L _O
<i>Ceratium hirundinella</i> (Müller) Duj.	Dinophyceae	L _M
<i>Euglena variabilis</i> Klebs	Euglenophyceae	W1

Table 2. Trait of phytoplankton functional groups detected in Paso de las Piedras Reservoir (quoted from Reynolds et al. 2002, Reynolds 2006 and Padisák et al. 2009)

Functional groups	Habitat template	Tolerance	Sensitivity
C	Eutrophic, mixed, small and medium sized lakes	Light and C deficiencies	Si exhaustion, stratification
D	Shallow and enriched turbid waters, including rivers	Flushing	Nutrient depletion
N	Mesotrophic epilimnia	Nutrient deficiency	Stratification and pH rise
P	Eutrophic epilimnia	Mild light and C deficiency	Stratification and silica depletion
T	Deep and well mixed epilimnia	Light deficiency	Nutrient deficiency
X2	Shallow and clear mixed layers in meso-eutrophic lakes	Stratification	Mixing and grazing
Y	The representative species have the ability of living in almost all lentic ecosystems when grazing pressure is low	Low light	Phagotrophs
F	Clear, deeply mixed meso-eutrophic lakes	Low nutrients	CO2 deficiency and high turbidity
J	Shallow, mixed, highly systems (including many low-gradient rivers)		Settling into low light
K	Shallow, nutrient-rich water columns		Deep mixing
H1	Eutrophic, both stratified and shallow lakes with low nitrogen content	Low nitrogen, low C	Mixing, poor light, low phosphorus
LO	Deep and shallow, oligotrophic, medium to large lakes	Segregated nutrients	Prolonged or deep mixing
LM	Eutrophic to hypertrophic, small to medium-sized lakes	Low C, stratification	Mixing, poor light
M	Eutrophic to hypertrophic, small to medium-sized water bodies	High insolation	Flushing, low total light
W1	Small organic ponds	High BOD	Grazing

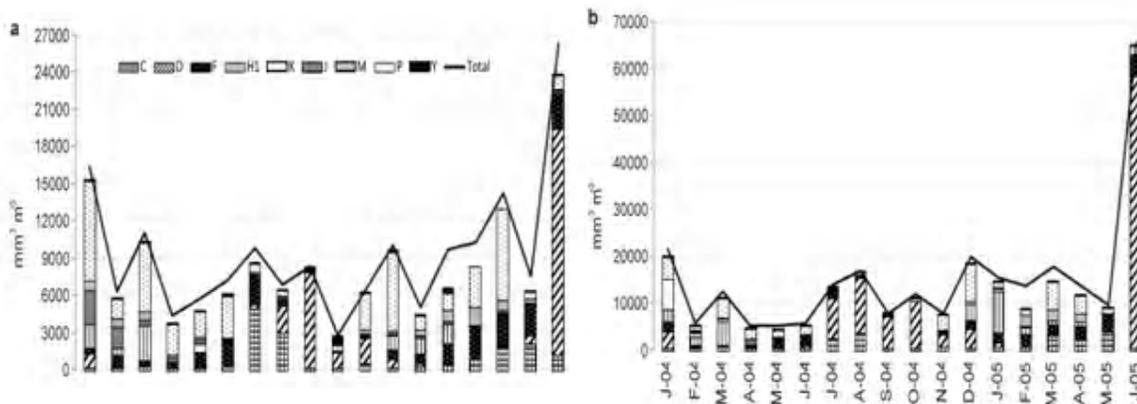


Fig. 3. Variation in total phytoplankton biovolume and the biovolume of the most important functional groups at S1 (a) and at S3 (b). The figure shows the monthly average value

since groups C ($H=11.7$; $p<0.01$), D ($H=7.06$; $p<0.01$), Y ($H=9.15$; $p<0.01$) and X2 ($H=10.63$; $p<0.01$) showed higher biovolume. According to Fernández et al. (2009) differences in community structure between these two sampling stations could be the result of differences in the characteristics of the water inflow since S3 is located near the mouth of El Divisorio Creek, one of the two main tributaries, which brings a significant quantity of particulate matter and dissolved salts.

The significant relationships between the main functional groups biovolume and abiotic variables are shown in Table 3.

The CVA indicated that functional groups were significantly more probable than random groups ($F=8.3$, $p<0.05$). On the contrary, taxonomical associations were not significantly more probable than random groups ($F=4.2$, $p=0.136$).

The results of DCA based on species data showed the relatively short lengths gradient in the first two axes (1.666 and 1.181 standard deviation units, respectively), so the linear ordination method RDA was chosen for analyzing the relationships between the biotic data and environmental variables. The phytoplankton functional groups temporal dynamics in Paso de las Piedras Reservoir was well described by the distribution of samples in the RDA ordination diagram. The first two axes accounted for 45.3% of the variability in phytoplankton data (axis 1= 37.6%; axis 2= 7.7%) and accounted for 82.3% of the variability in the species-environment relation (axis 1= 68.3%; axis 2= 14%). The first axis showing the strongest relationship between species and environmental variables (0.836) was mainly negatively correlated with water temperature (-0.63) and positively correlated with N:P ratio (0.69). The second axis was mainly negatively correlated with Secchi depth (-0.49). Thus, temperature, N:P ratio and transparency appear to be the driving forces affecting phytoplankton growth and assembly. The significance test of all canonical axes by Monte Carlo simulation showed that all canonical axes were significant ($F=3.061$, $p<0.01$, 499 permutations under reduced model). According to axis 1, H1, J, P, N, M, L_M and L_O groups showed the best performance during warm periods associated to diminution in N:P ratio. On the contrary, D, C and X2 groups contributed high biomass during the cold period. Groups F, T, Y and K showed the high biovolume mostly during the transition period. On axis 2, group K was associated to high Secchi depths whereas groups H1, J, P and W1 were associated to low Secchi depths (Fig. 4). Differences in the position of sampling stations in the RDA graph were mostly due to differences in the Secchi depths and N:P ratios. Samples from August 2004 displayed higher Secchi depths at S3 than at S1, whereas samples from October 2004, March 2005 and May 2005 displayed higher

Secchi depth at S1 than at S3. Samples from February 2005 showed higher N:P ratio at S1 than at S3, whereas samples from June 2005 showed higher N:P ratio at S3 than at S1.

The temporal variations in biomass in the main phytoplankton functional groups are shown in fig. 3.

During January 2004, the dominant groups were P and J, together with a relative biovolume of more than 80%. These two groups were represented by *Staurastrum gracile* and *Pediastrum duplex* var. *duplex*, respectively. During the beginning of February 2004, groups P and J also dominated, but now accompanied by groups F and M, with not a clear dominance of any of the species in any of the groups. During mid February and March 2004, groups H1 and P dominated, represented mostly by *Anabaena circinalis* and *Aulacoseira granulata* respectively, which together accounted for 60% to 70% of the total biovolume. The relative contribution of H1 was higher in S3 than in S1. In April 2004, group P was dominant, represented mostly by *Aulacoseira granulata*, with a smaller contribution of groups F, J, L_O and M. Group M had a high biovolume during the last April samplings at S3 due to a high biomass of *Microcystis flos-aquae*. During May and June 2004, there was a dominance of groups P and F, mostly due to the high biomass of *Oocystella solitaria*, *Dictyosphaerium ehrenbergianum*, *Aulacoseira granulata*, *Closterium aciculare* and *Closterium moniliferum*. The relative contribution of group P during this period was higher at S1, and this sampling station also registered a high relative biovolume of group K during the first May sampling, due to a high biomass of *Synechocystis fuscopigmentosa*.

The group P has been associated either with low latitudes or with summer periods in temperate lakes (Reynolds et al., 2002). Species of this group require a continuous or semi-continuous mixed layer of 2-3 m in thickness and has been found in shallow eutrophic lakes with a mean or greater depth of this order, as well as in stratified lakes during the mixing period (Padišák et al., 2009). In Paso de las Piedras Reservoir the group P dominated during summer, autumn and late spring and its dominance was associated with high water temperature, low N:P ratio and low transparency. Groups J and H1 dominated, along with group P, during early and late summer respectively. They were also associated to high temperatures and low N:P relations. Group H1 included the nitrogen-fixing species *Anabaena circinalis*. Although nutrient concentrations -both nitrogen and phosphorous- were always high in the Paso de las Piedras reservoir, the N:P ratio during summer was low. This condition supports Horne and Commins assertion (1987) that ratios of biologically available nitrogen and phosphorus, i.e. N:P ratios, are the major cause for the presence or absence of N₂-fixing cyanobacteria.

Table 3. Spearman correlation between abiotic variables and the main functional groups. Row 2 is sampling stations.

	C			D			F			HI			J			P		
	SI	S3	SI	SI	S3	SI	SI	S3	SI	S3	SI	SI	S3	SI	S3	SI	S3	
pH	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	-0.47*	ns	ns	
WT	-0.47*	ns	-0.44*	ns	ns	ns	0.6**	0.81**	ns	ns	ns	ns	ns	0.48*	ns	ns	ns	
NO₃	ns	ns	0.4*	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
NO₂	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	
TP	ns	ns	-0.46*	ns	ns	ns	ns	0.58**	0.67**	ns	ns	ns	ns	ns	ns	ns	ns	
SRP	-0.44*	ns	-0.55**	ns	ns	ns	0.48*	0.57**	0.78**	ns	ns	ns	ns	ns	ns	ns	ns	
Silica	ns	ns	ns	ns	ns	ns	ns	ns	0.5*	ns	ns	ns	ns	ns	ns	ns	ns	
Air T	-0.47*	ns	-0.44*	ns	ns	ns	0.68**	0.82**	ns	ns	ns	ns	0.52*	ns	ns	ns	ns	
Rain	ns	ns	ns	ns	ns	ns	0.45*	0.53*	ns	ns	ns	ns	ns	ns	ns	ns	ns	
WL	ns	ns	ns	0.43*	ns	ns	ns	ns	-0.42*	-0.51	ns	ns	ns	ns	ns	ns	ns	
N:P	ns	ns	0.47*	0.62**	ns	ns	-0.48*	-0.58**	-0.69**	ns	ns	ns	ns	ns	ns	ns	ns	
SD	ns	ns	ns	ns	ns	ns	-0.44*	-0.53*	ns	0.47*	ns	ns	ns	ns	ns	ns	ns	

WT= water temperature; NO₃⁻= nitrate; NO₂⁻= nitrite; TP= total phosphorus; SRP= soluble reactive phosphorus;

Air T= air temperature; WL= water level; N:P= N:P ratio; SD= Secchi depth

* p<0.05

** p<0.01

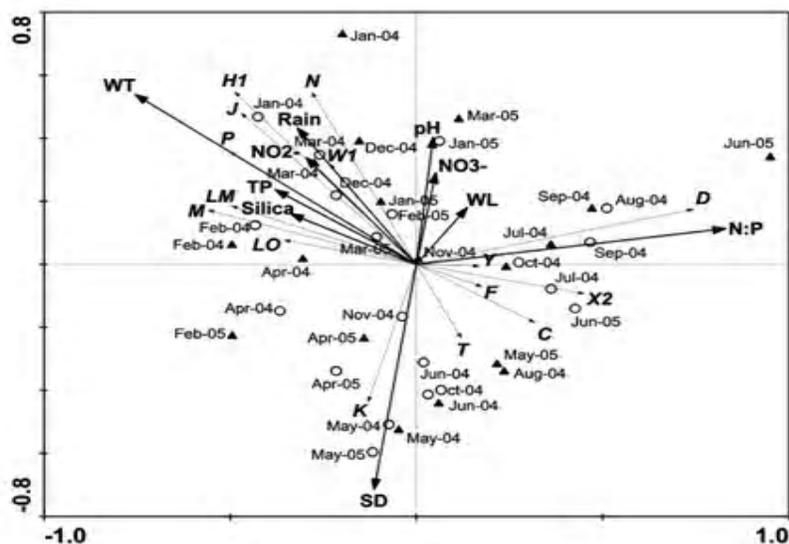


Fig. 4. Redundancy analysis (RDA) ordination diagram of the main functional groups and abiotic variables (WT= water temperature; NO₃⁻= nitrate; NO₂⁻= nitrite; TP= total phosphorus; WL= water level; SD= Secchi depth; N:P= N:P ratio) in Paso de las Piedras Reservoir. Circle indicates sampling station S1, up-triangle indicates sampling stations S3

During July and October, diatoms from groups C and D dominated, represented by *Cyclotella meneghiniana* and *Stephanodiscus* sp., respectively. At the beginning of this period, there was a high biomass in groups C and F, but they were quickly replaced by group D, which dominated until mid November. The monthly average relative biovolume of group C during July and mid August was higher at S1 than at S3 ($H=4.44$; $p<0.05$).

Although it is well known that the development of diatoms populations depends on silica availability (Ragueneau, 2000), this assertion has not been validated in the present study, neither by the RDA, nor by the correlation analysis, since neither group C nor group D were significantly correlated to the levels of this nutrient. Silica concentration in Paso de las Piedras was uniformly moderate to low, as in most eutrophic lakes, but it never fell below 0.1 mg/l, i.e. the value of limitation for the development of diatoms (Reynolds, 2006). Instead, the start in the dominance of diatoms groups C and D during the end of June was strongly associated with temperature decrease. Groups D and C were plotted in the RDA graph in relation to conditions of low temperature and high N:P ratio. Several authors have also correlated diatoms increases to temperature decreases (Harris and Trimbee, 1986; Zhang and Prepas, 1996; Huszar and Caraco, 1998; Calijuri *et al.*, 2002) and da Silva *et al.* (2005) found them preferentially in temperatures below 18°C.

Water temperature is an important factor regulating phytoplankton physiological rates (Rhee and Gotham, 1981). Empirical and experimental results suggest that water temperature is also directly linked to changes in

phytoplankton species composition (Zhang and Prepas, 1996; De Senerpont Domis *et al.*, 2007).

Besides, increases in air temperature and changes in climatic conditions have also been linked to variations in plankton population in both marine (Edwards and Richardson, 2004) and freshwater (George and Taylor, 1995; Straile, 2000; Winder and Schindler, 2004) ecosystems. In fact, lakes with small volume/surface area ratios like the Paso de las Piedras reservoir efficiently transfer heat across the atmosphere–water interface leading to water temperatures closely matching ambient air temperatures; therefore, phytoplankton structure is more strongly influenced by air temperature in shallow lakes than in deeper ones (Carpenter *et al.*, 1992).

The increase of diatoms during late winter and early spring is a typical feature of several lakes, e.g. Lake Garda (Salmaso, 1996), Lake Como (Buzzi, 2002), Lake Iseo (Garibaldi *et al.*, 2003).

In spite of the fact that the habitat was similar for both groups, in the present study they dominated differently in both samples sites: group C dominated during July and the first half of August at S1 and then was replaced by group D, whereas group D dominated during the entire period at S3. Such differences may be accounted for by different competitive capabilities among species. In the present case, differences in size must be considered, since *Stephanodiscus* sp. has a biovolume more than eight times greater of that of *C. meneghiniana*, so that even if the latter would have reached the same growth rate, the first quickly would have overcome it in terms of biomass.

The increase in biomass of functional groups C and D during spring had important consequences for the ecosystem functioning since diatoms have been suggested to enhance the transfer of energy to higher trophic levels (Doering *et al.*, 1989), either through fewer trophic links or higher food quality (Ryther, 1969). Also, when increasing temperature conditions become unsuitable for the development of diatoms, their sinking rates can increase dramatically (Tilman and Kilham, 1976; Bienfang *et al.*, 1982) leading to a rapid settling of fresh organic matter and biogenic silica to the sediments (Smetacek, 1985), which in turn leads to reductions in water column silica concentration that may have a significant impact on the structure and functioning of the entire food web (Conley *et al.*, 1993). At both sampling stations a replacement of group D for group Y was observed during the two first samplings of October. Group Y includes large cryptomonads living in almost all lentic ecosystems, regardless of their trophic state. They are typically present in low numbers most of the year, but commonly demonstrate intermittent increases in abundance following the demise of the previously-dominant species (Stewart and Wetzel, 1986). Such opportunistic behaviour is favoured by their *r*-selected behaviour, i.e., the ability to respond quickly to the availability of environmental resources, taking advantage from potential high growth rates (Salmaso and Tolotti, 2010). In the present study, the species involved in group Y included *Cryptomonas ovata* and *Cryptomonas marssonii*. This group displayed a small biomass throughout the year and dominated only simultaneously with the biomass fall of group D. However, in other eutrophic lakes and rivers, group Y has been recorded with high biomass around the year, e.g. Xiangxi Bay (Wang *et al.*, 2011) and Paraná River (Devercelli, 2006). The position of group Y close to the origin in the RDA diagram confirms the independence of this group from nutrients and environmental parameters evaluated. That could be due to the fact that this group enhances its competitiveness by the possession of flagella, which allow vertical migration to water layers with both optimal light conditions and nutrient concentrations (Bovo-Scamparin and Train, 2008). Furthermore, they have abilities to improve their nutrient uptake by mixotrophy, which allows them to increase in light-limited conditions (Jones, 2000). Their high nutritional quality, short turnover times, ability to grow and reproduce at low intensities of light, and effective pulse timing, make group Y as an ecologically-significant internal stabilizing component of planktonic communities (Stewart and Wetzel, 1986). In December 2004, as the water temperature increased, the relative biovolume of the diatoms groups decreased and group P became dominant again. Between January and May 2005 there was not a clear dominance of any

of the functional groups, but the general pattern showed that the functional groups that more contributed to the total biomass were similar to those observed during 2004. The most obvious differences were: 1) a higher biovolume of group H1 in January 2005 and a smaller one in March 2005 in comparison with the same months of 2004, and 2) the dominance of group D in June 2005 with a total biovolume between 2 and 5 times higher than in 2004 with a relative biovolume higher than 85%.

Diversity indices, both in terms of species and functional groups, varied rather irregularly throughout the whole study period (Fig. 5). There were negative relations between total biovolume and diversity, both H'SP and H'FG, although the fraction of the variance explained by diversity in the entire community biovolume was low (Fig. 6). Such a relationship could be due to the paradoxical fact that during periods of low biomass, many species contributed to the community, while in periods of high biomass it was associated to low diversity.

In August and October 2004 and June 2005, the lowest values of H'SP and H'GF occurred but the differences between both indices were smaller than those occurring during most of the sampling period (Fig. 5). The higher values of H'SP compared with H'GF registered suggest that a large number of species share similar functional behaviour, as was indicated by Chapin *et al.* (1996) for terrestrial communities, increasing the probability that at least some of them survive changes in the environment maintaining the properties of the ecosystem. Even though H'SP values were relatively high, considering the reservoir trophic status,

H'GF values were low, so that a small number of traits were present and/or that there was an inequitable distribution of traits among the species in the lake.

As Paso de las Piedras Reservoir has been classified into the eutrophic-hypereutrophic category (Fernández *et al.*, 2009) phytoplankton biomass and dominant species were as expected: i.e. typical of highly enriched systems and with functional associations characteristic of eutrophic to hypereutrophic systems. Only four groups, namely F, L₀, N and X2, were more closely related to mesotrophic and meso-eutrophic systems, being F the only dominant group. The transitional position of this group was well corroborated for its position in the RDA diagram. Group F has an elevated light threshold; its species function better in clear waters but otherwise they are tolerant to deep mixing waters. Besides, they are sensitive to the additional demands on carbon and light fluxes that high biomass may place. For this reasons, this group normally co-dominated in a transitional period characterized by a high Secchi depth and a low total biovolume.

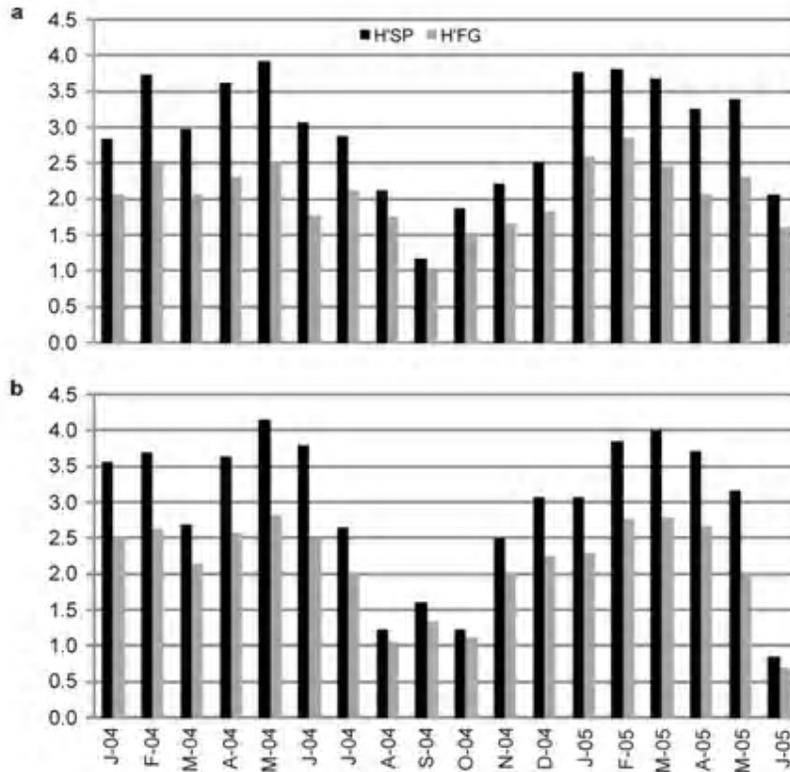


Fig. 5. Variation in diversity indices H'SP and H'FG at S1 (a) and at S3 (b). The figure shows the monthly average value

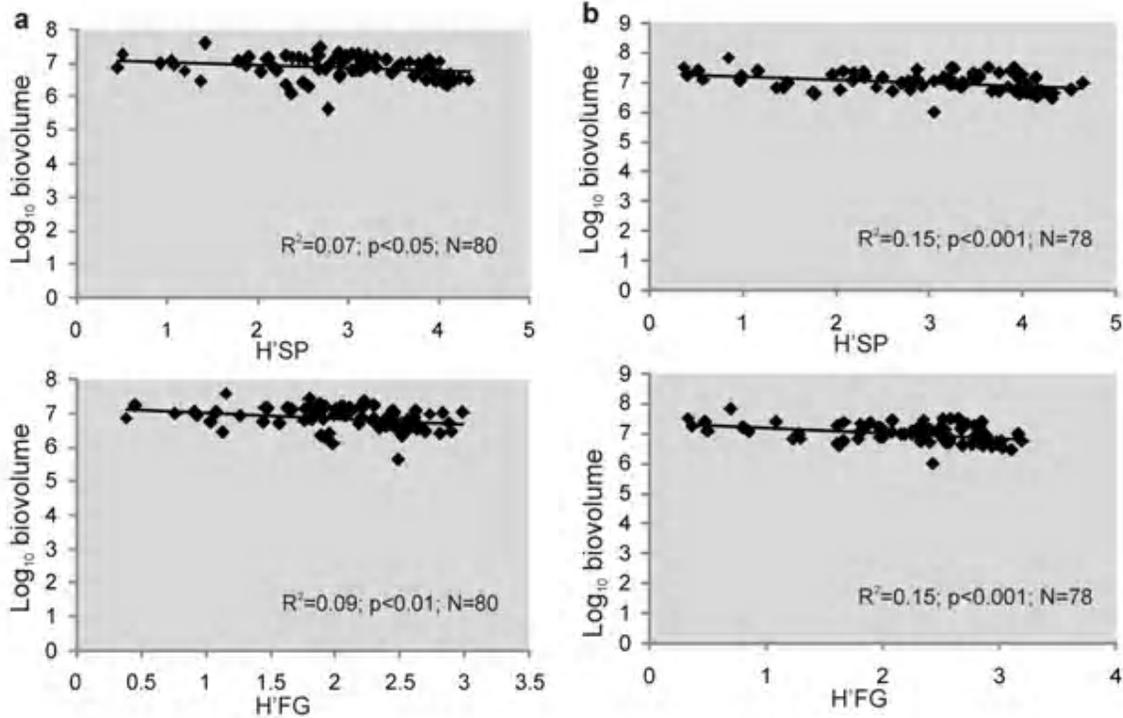


Fig. 6. Regression model relating the total biovolume to the diversity indices H'SP and H'FG at S1 (a) and at S3 (b). Biovolume data were log10 transformed

CONCLUSION

The tendencies revealed in this study indicated that the temperature, N:P ratio and transparency are the main factors affecting the variety of phytoplankton species in Paso de las Piedras Reservoir. Along the year two periods could be clearly distinguished: a warm period with turbid water mostly dominated by organisms grouped in the functional group P, and a cold period with clear water mostly dominated by organisms belonging to groups C and D. From the perspective of the most important species, the phytoplankton succession process in Paso de las Piedras Reservoir could be summarized as:

P/J (early summer) → P/H1 (late summer) → P (early autumn) → P/F (late autumn) → C (early winter) → D (late winter) → Y (early spring) → D (early spring) → P (late spring)

The continuous mixing and high nutrient concentration seems likely to have favoured the dominance of these functional associations since, with the exception of H1, all groups that contributed to biovolume in the study were characteristics of mixed aquatic environments. For a deeper comprehension of the significance of functional groups in this ecosystem further research is necessary to address the effect of another important factor, such as grazing,

ACKNOWLEDGEMENTS

This work was supported by the Secretary of Science and Technology of the Universidad Nacional del Sur [PGI CSU-24 B/145] to [E.R.P.]. [E.R.P.] is a Researcher Member of the National Research Council (CONICET) and [E.J.C.] is a Research Member of the Comisión de Investigaciones Científicas de la Provincia de Buenos Aires, República Argentina (CIC). The authors appreciate the valuable collaborations of the staff of the Laboratorio de Hidráulica at the Universidad Nacional del Sur, Autoridad del Agua (ADA) from Buenos Aires Province and PROFERTIL S.A. that ceded hydrological and physicochemical data.

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