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Picoplankton structure in clear and turbid eutrophic shallow lakes: A seasonal study

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ABSTRACT

The relative abundance of the different picoplankton components (eukaryotic picophytoplankton (Peuk), picocyanobacteria (Pcy) and bacterioplankton), and their relationships with the lake conditions were studied in three types of shallow lakes from the Pampa Plain (Argentina) that differ in their optical properties: clear-vegetated, phytoplankton-turbid and inorganic-turbid. All the selected lakes, but one, are characterized by their different *alternative steady state* (clear-vegetated and phytoplankton-turbid water phases) following the model proposed by Scheffer et al. (1993).

Autotrophic and heterotrophic picoplankton abundances were analyzed seasonally in relation to environmental variables. All the lakes presented high concentrations of total nitrogen (TN) (>229 μg L^{-1}), total phosphorus (TP) (>46 μg L^{-1}) and dissolved organic carbon (DOC) (>13.7 mg L^{-1}). Clear-vegetated lakes were characterized by vertical diffuse PAR (photosynthetic active radiation) attenuation coefficient (kd$_{PAR}$) lower than 11 m^{-1}, whereas inorganic-turbid lake always showed values higher than 21.1 m^{-1}. The euphotic zone depth ($Z_{1\%}$) was wider in clear-vegetated lakes (40–140 cm) and thinner in the inorganic-turbid (10–20 cm). The phytoplankton-turbid lakes presented a wide range in the values of these variables (kd$_{PAR}$: 5.2–35.8 m^{-1}; $Z_{1\%}$: 10–90 cm). Phytoplankton chlorophyll-a (Chl-a) strongly differed, ranging from 1.6 to 334.6 μg L^{-1}. Picophytoplankton was mainly represented by phycocianine-rich (PC-rich) Pcy in all cases, dominating over Peuk algae. The total and relative abundances of eukaryotic picophytoplankton, Pcy and bacterioplankton, as well as the size structure of the phytoplankton community differed among the water bodies. In general, clear-vegetated water bodies exhibited similar abiotic characteristics, picophytoplankton/bacterioplankton ratios, and phytoplankton size structure. Contrarily, no clear trend was identified for the group of turbid lakes. The contrasting results obtained for the importance of the picoplankton components in phytoplankton-turbid shallow lakes evidence that the availability of the energetical and nutrient resources cannot be solely considered to predict their relative importance in this type of shallow lake.

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Introduction

Since Lewontin (1969) first proposed that communities can be found in one of several possible alternative stable states, ecologists are increasing the empirical evidence in this respect (Holling, 1973; May, 1977; Laycock, 1991). The theoretical possibility of ecosystems having more than one equilibrium has long been recognized (Noy-Meir, 1975; May, 1977; Sutherland, 1990; Scheffer et al., 1993). In particular, many observations in shallow lakes have led aquatic ecologists to suspect that these ecosystems may indeed possess different stable states (Jeppesen et al., 1990). Based on the model proposed by Scheffer et al. (1993), shallow lakes can alternate between two possible states, one characterized by more transparent waters in which the primary production is dominated by submerged macrophytes (clear-vegetated), and another turbid, dominated by phytoplankton (phytoplankton-turbid). Other shallow lakes owe their turbidity mainly to the suspended unpigmented particles (inorganic-turbid) (Pérez et al., 2010), and are characterized by a weak development of aquatic macrophytes and/or phytoplankton (Padisák and Dokulil, 1994; Allende et al., 2009).

Studies including the picoplankton community, which considers prokaryotic and eukaryotic autotrophs and heterotrophs <2 μm, in shallow lakes with contrasting submerged macrophytes development and optical properties are relatively scarce (Søndergaard and Moss, 1997; Jürgens and Jeppesen, 1998; Mazzeo et al., 2003).

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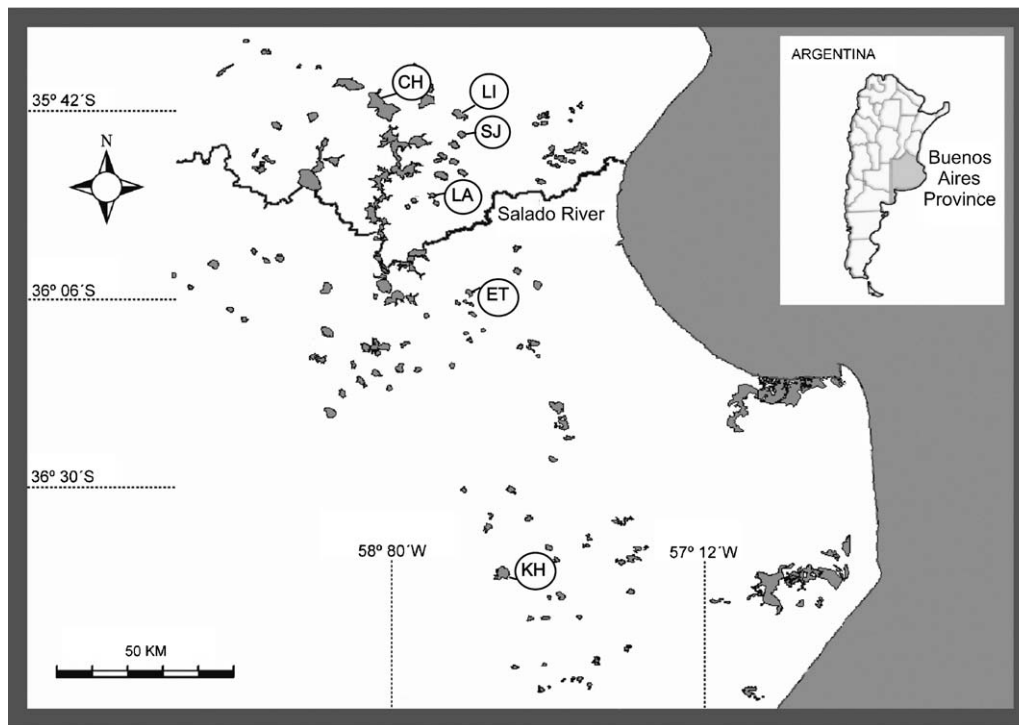E-mail address: lallende@ege.fcen.uba.ar (L. Allende).

Fig. 1. Location of the six studied lakes in the Pampa Plain (Buenos Aires – Argentina) (KH, Kakel Huincul; ET, El Triunfo; LA, Lacombe; SJ, San Jorge; CH, Chascomús; LI, La Limpia).

The picoplankton plays an important role in the aquatic microbial food web providing important services in nutrient regeneration and energy transfer to higher trophic levels (Cotner and Biddanda, 2002). As regards their interactions with submerged macrophytes, most works separately studied the heterotrophic bacterioplankton or picophytoplankton instead of the whole picoplankton community. Eventhough there is an increasing evidence of the importance of the presence–absence of submerged macrophytes in structuring the bacterioplankton community (Jürgens and Jeppesen, 1998; Huss and Wehr, 2004; Wu et al., 2007) the impact of this interaction has been less explored for the picophytoplankton (Mazzeo et al., 2003; Angeler et al., 2005). It is important to note that the model proposed by Scheffer et al. (1993, 2003) for clear and turbid shallow lakes, is mainly focused on the large phytoplankton and its interaction with submerged macrophytes. Thus, it is a novel approach to include the relative importance of the pico-sized organisms in these ecosystems.

The Pampa Plain (Argentina) is a deeply studied wetland in South America (Izaguirre and Vinocur, 1994a,b; Gabellone et al., 2001; Quirós et al., 2002; Renella and Quirós, 2006; Cano, 2008; Allende et al., 2009; Pérez et al., 2010) very rich in shallow lakes. According to Quirós et al. (2002) three types of permanent shallow lakes are found in this region: clear-vegetated, phytoplankton-turbid and inorganic-turbid. The high annual and interannual variability of the Pampean landscape is reflected in the seasonal behavior of the lake ecosystem and, in some cases, complex ecosystem interactions favor a lake usually turbid to be recolonized by macrophytes and become clear, especially during the growing season (Quirós et al., 2002). However, during the last century Pampean lakes have increased their levels of eutrophication by human action becoming turbid those that are subject to an intense land use in their drainage basins (Quirós and Drago, 1999) with the concomitant modification of their biological communities.

This paper focuses on the abundances and seasonal variations of picoplankton components, eukaryotic picoplankton (Peuk), picocyanobacteria (Pcy) and heterotrophic bacteria, of eutrophic Pampean shallow lakes with contrasting *alternative steady states* (Scheffer et al., 1993) and optical properties. The hypotheses tested were that: (a) picophytoplankton and bacterioplankton should have different absolute and relative abundances under contrasting *alternative steady states* and water optical properties of the shallow lakes, as their energetical resources (light availability and dissolved carbon concentrations) would differ among them; (b) the phytoplankton size structure should differ in clear-vegetated and turbid shallow lakes as it is well known that the presence of macrophytes affects large phytoplankton (Scheffer, 1998; and cites therein). Based on the negative effect of the presence of submerged macrophytes on large algae (e.g. increased zooplankton grazing, nutrient competition) (Scheffer, 1998), and the advantages of being small-size (e.g. increased surface area/volume ratio, lower sinking rate, lower zooplankton predation susceptibility) (Raven, 1986; Chisholm, 1992; Drakare et al., 2003) we predict a higher relative abundance of picophytoplankton over large phytoplankton in clear-vegetated as compared to turbid shallow lakes.

Materials and methods

Study area

The studied lakes are located in the Pampa Plain (35°32′–36°48′S; 57°47′–58°07′W), in the Buenos Aires Province (Argentina), which is encompassed in the Temperate Region (Peel et al., 2007). All Pampean lakes are permanent and relative homogeneous in depth (mean depth ∼2 m), and have high levels of nutrients (Quirós and Drago, 1999).

For this study we have selected six shallow lakes of this region (Fig. 1). Two of them (Kakel Huincul and El Triunfo) are in a vegetated-clear state, profusely colonized by submerged plants (mainly *Myriophyllum* sp. and *Ceratophyllum demersum*) and emergent macrophytes (*Schoenoplectus californicus*) (Allende et al., 2009). Three lakes are characterized by low Secchi depth values and high phytoplankton abundances (Lacombe, San Jorge and

Table 1
Morphometric features of the studied lakes (KH, Kakel Huincul; ET, El Triunfo; LA, Lacombe; SJ, San Jorge; CH, Chascomús; LI, La Limpia).

	KH	ET	LA	SJ	CH	LI
Geographic position	36°48′S; 57°47′W	35°51′S; 57°52′W	35°49′S; 57°49′W	35°40′S; 57°47′W	35°36′S; 58°02′W	35°37′S; 57°48′W
Surface area (km^2)	29.5[b]	1.5[b]	1.6[b]	3.0[b]	28.7[a]	5.6[a]
Max. length (km)	10.7[b]	1.8[b]	1.9[b]	2.2[b]	10.4[d]	4.1[b]
Max. width (km)	4.1[b]	1.5[b]	1.5[b]	2.0[b]	7.9[d]	2.2[b]
Perimeter (km)	32.2[b]	5.1[b]	6.2[b]	7.4[b]	37.8[d]	1.4[b]
Max. depth (m)	4[c]	nd	2[d]	nd	1.9[a]	2.3[a]
Mean depth (m)	1.8[c]	nd	1[d]	nd	1.5[a]	1.9[a]

Data obtained from:

[a] Quirós (2004).
[b] Calculated from Google earth.
[c] http://www.irapescar.com/kakelhuincul/index.html.
[d] Calcagno et al. (1995); nd, no data.

Chascomús) and are defined as phytoplankton-turbid; in the case of Lacombe, previous studies have shown that this shallow lake may alternate between the phytoplankton-turbid and the clear-vegetated states (Cano, 2008). The remaining lake (La Limpia) is turbid mainly due to the suspended inorganic matter and thus it was classified as inorganic-turbid (Allende et al., 2009). The main morphometric features of the studied lakes are shown in Table 1.

Samples were collected seasonally in November 2005 (spring), February 2006 (summer), June 2006 (autumn) and September 2006 (winter). Three sites were established in each water body for the collection of biological samples. Whenever possible, three measurements of environmental variables and three samples for the determination of abiotic variables were obtained at the selected sites. If not, and due to the polimyctic nature of the shallow lakes, integrated samples from the three sites were collected for the measurement of environmental variables. The following parameters were measured *in situ*: temperature, pH, conductivity and concentration of dissolved oxygen (DO) with HI 8314 and HI 9143 Hanna portable instruments. Additionally, a measure of the water transparency was obtained using a Secchi disk. As well, water samples were collected sub-superficially for the determination of total suspended solids (TSS), percentage of organic matter in seston (%OM), nutrients – total phosphorous (TP) and total nitrogen (TN) – and phytoplanktonic chlorophyll-*a* (Chl-*a*) concentrations. TSS were determined by weighing the residue resulting from the filtration of the samples through pre-burned Whatman^{TM} GF/F filters, and the percentage of organic matter in seston was estimated as the difference between dry weight and ash-free dry weight (550 °C for 2 h). TP and TN concentrations were determined after an acid digestion by the molybdate-ascorbic method. All the determinations were performed following APHA (1998). Phytoplankton Chl-*a* concentrations were estimated from samples collected onto glass-fiber filters (GF/F, Whatman^{TM}). Filters were wrapped immediately in aluminum foil and stored at −80 °C until processing (within 2 months of sampling). Chlorophyll was extracted using 90% aqueous acetone (V:V) at 10 °C, in darkness and in a nitrogen saturated atmosphere. The extracts obtained were cleared by centrifugation at 3000 rpm for 10 min. Pigment extracts were measured by ion pairing reverse-phase HPLC. A detailed description of the method employed is given by Allende et al. (2009).

Aliquots of filtered water were stored at 4 °C until analysis of dissolved organic carbon (DOC). DOC was determined in sonicated and acidified water samples using a high temperature Pt-catalyst oxidation method (Shimadzu TOC-5000) following the recommendations of Sharp et al. (1993).

The optical characteristics of the lakes were studied using an underwater turbidimeter (SCUFA, Turner^{TM}) and a spectrum-submersible radiometer (USB2000, Ocean Optics), during the annual period (2005–2006). Data were provided by the Photobiology Laboratory – IIB INTECH (Chascomús – Buenos Aires). The variables considered were: vertical diffuse PAR (photosynthetic active radiation) attenuation coefficient (kd_{PAR}), euphotic zone depth ($Z_{1\%}$) and nephelometric turbidity (T_n). The techniques used were described in Pérez et al. (2010).

Two sets of plankton quantitative samples were obtained at each of the three stations in each lake. The ones for micro- and nanophytoplanktonic (>2 μm phytoplankton) fractions were fixed with 1% acidified Lugol's iodine solution, and those for the quantification of the picoplankton components were preserved with 2% ice-cold glutaraldehyde and maintained in the dark at 4 °C until processed (within 24 h). The counts of micro- and nanoplanktonic fractions were performed using an inverted microscope (Utermöhl, 1958) at 400× magnification. Samples for picoplankton counts were processed for epifluorescence microscopy (Porter and Feig, 1980; MacIsaac and Stockner, 1993). For picophytoplankton, each filter was examined for pigment autofluorescence with a Zeiss^{TM} Axioplan Microscope equipped with an HBO 50 W lamp. A filter set for blue light excitation (BP 450–490 nm, FT 510 nm, LP 520 nm) was used to count Peuk algae, and green light excitation (BP 546 nm, FT 580 nm, LP 590 nm) for Pcy (Wynn-Williams, 1992). Bacterioplankton was DAPI-stained and was observed under UV light (BP 365 nm, FT 395 nm, LP 397 nm). A minimum of 400 cells was counted (corresponding at least 20 fields of view) at 1000× magnification corresponding to an error <15%. Due to involuntary sample loss, there are no data available for picoplankton counts for Chascomús shallow lake in springtime.

Data analysis

Statistical differences among the three types of shallow lakes (clear-vegetated, phytoplankton-turbid and inorganic-turbid) in relation to physical and chemical variables were tested by a one-way ANOVA. Normality was assessed performing the Kolmogorov–Smirnov analysis. To test for significant differences between types of shallow lakes, *post hoc* comparisons were made by using Tukey's test. Correlations (Spearman's Rho) between the abundance of the different picoplankton components and the environmental variables were carried out. All these analyses were performed with SPSS 15.0.1 (StatSoft, USA).

The spatial variation in the composition of picoplankton in relation to the environmental variables was explored performing the multivariate analysis RDA (redundancy analysis). A linear species–environment model was selected based on the length of gradient on a detrended correspondence analysis (DCA). Calculations were performed by the program CANOCO (Ter Braak, 1991). The data set was analyzed based on picoplanktonic counts obtained from each of the six lakes and environmental parameters. Forward selection was used for adding limnological variables to the model. The significance of the ordination axes was assessed by Monte Carlo permutations. The following variables were included in the

Table 2
Physical and chemical parameters measured *in situ* in the six lakes at the different periods of sampling (KH, Kakel Huincul; ET, El Triunfo; LA, Lacombe; SJ, San Jorge; CH, Chascomús; LI, La Limpia; Sp, Spring; S, Summer; A, Autumn; W, Winter; Temp., water temperature; DO, dissolved oxygen; DO Sat., dissolved oxygen saturation).

			Temp. (°C)	pH	Conductivity ($\mu S\,cm^{-1}$)	DO ($mg\,L^{-1}$)	DO Sat. (%)
Clear lakes	KH	Sp	20.0	9.80	2187	10.6	116
		S	24.3	7.31	1673	9.3	110
		A	12.0	8.39	1540	9.9	92
		W	10.7	8.69	1720	8.0	71
	ET	Sp	21.0	9.40	1640	12.0	135
		S	24.4	9.42	1873	8.0	95
		A	12.6	9.38	1660	9.0	83
		W	10.0	8.36	1320	8.3	73
Turbid lakes	LA	Sp	20.6	9.19	2160	9.8	110
		S	25.1	9.21	2500	9.4	114
		A	16.0	8.75	2290	8.8	89
		W	11.0	8.33	2140	7.8	71
	SJ	Sp	18.8	9.00	1430	8.8	95
		S	23.9	9.14	1513	9.4	112
		A	12.1	8.85	1350	9.2	85
		W	9.5	8.40	1337	8.4	74
	CH	Sp	22.0	9.13	1583	9.2	106
		S	23.0	8.93	1760	9.5	111
		A	11.2	8.89	1797	11.0	100
		W	9.0	8.35	1750	8.2	71
	LI	Sp	23.0	9.12	820	8.3	72
		S	23.4	7.85	1133	7.8	91
		A	12.0	8.85	917	8.6	80
		W	10.7	8.66	913	8.4	76

analysis: conductivity dissolved oxygen, total nitrogen, kd_{PAR} and dissolved organic carbon. Total phosphorus concentration was not included in the analysis as it was strongly correlated with kd_{PAR}.

Results

Physical and chemical properties

Table 2 summarizes the average values of the physical and chemical variables measured *in situ*. Water temperature was similar in all shallow lakes at each sampling date, following the seasonal temperature fluctuations. All lakes exhibited high pH values (7.31–9.80), and conductivities (820–2500 $\mu S\,cm^{-1}$). The lowest conductivity figures were systematically registered in the inorganic-turbid shallow lake La Limpia. The concentration of dissolved oxygen showed high levels as well as the dissolved oxygen saturation percentage.

Average values of chemical and biological variables measured in the laboratory, from triplicate or integrated samples are summarized in Table 3. The values of TSS in clear-vegetated lakes were low in all the seasons while the phytoplankton-turbid Chascomús and the inorganic-turbid lake La Limpia always evidenced the highest values. The concentration of suspended organic matter was also low in clear-vegetated lakes in all seasons and it represented almost

Table 3
Chemical and biological parameters of the six lakes at the different periods of sampling (KH, Kakel Huincul; ET, El Triunfo; LA, Lacombe; SJ, San Jorge; CH, Chascomús; LI, La Limpia; Sp, Spring; S, Summer; A, Autumn; W, Winter; TSS, total suspended solids concentration; %OM, percentage of organic matter in the seston, nutrients (TP, total phosphorus; TN, total nitrogen); DOC, dissolved organic carbon; Chl-*a*, phytoplankton chlorophyll-*a* concentration).

			TSS ($mg\,L^{-1}$)	%OM	TP ($\mu g\,L^{-1}$)	TN ($\mu g\,L^{-1}$)	DOC ($mg\,L^{-1}$)	Chl-*a* ($\mu g\,L^{-1}$)	>2 μm phytoplankton density (cell mL^{-1})
Clear lakes	KH	Sp	6	83	135	302	82.40	1.6	2204
		S	12	100	276	721	58.95	7.7	58,513
		A	2	100	50	1140	54.10	4.1	44,706
		W	2	100	46	721	38.70	2.1	926
	ET	Sp	5	100	179	229	38.31	2.7	4743
		S	4	100	250	688	49.79	3.0	9365
		A	1	100	70	268	37.30	5.5	2453
		W	2	100	202	395	38.20	4.0	4630
Turbid lakes	LA	Sp	69	97	261	922	36.26	63.2	222,876
		S	69	97	294	256	67.42	56.4	138,721
		A	25	96	110	1052	31.00	24.6	126,887
		W	29	72	170	743	31.70	20.6	118,038
	SJ	Sp	98	39	229	1628	42.14	36.0	113,248
		S	78	90	336	947	60.00	334.6	881,817
		A	64	100	290	1724	51.20	207.6	425,858
		W	55	82	340	1433	42.10	252.5	114,218
	CH	Sp	265	32	662	1676	17.63	124.7	75,607
		S	224	33	639	301	21.47	93.9	93,357
		A	101	44	410	654	47.20	50.2	121,463
		W	337	26	698	1818	26.40	135.4	94,508
	LI	Sp	351	15	811	774	15.34	18.3	2524
		S	221	16	866	722	16.06	35.4	2023
		A	129	15	620	974	40.30	31.4	1730
		W	325	12	720	823	13.70	28.8	1793

Table 4
Secchi disk depth and optical characteristics of the lakes during the sampling period (KH, Kakel Huincul; ET, El Triunfo; LA, Lacombe; SJ, San Jorge; CH, Chascomús; LI, La Limpia; Sp, Spring; S, Summer; A, Autumn; W, Winter; kd_{PAR}, attenuation coefficient of photosynthetic active radiation; $Z_{1\%}$, euphotic zone depth; T_n, nephelometric turbidity).

			Secchi (cm)	kd_{PAR}[a] (m^{-1})	$Z_{1\%}$[a] (cm)	T_n[a] (NTU)
Clear lakes	KH	Sp	102	3.4	140	4
		S	78	3.6	130	2
		A	>120	3.6	130	3
		W	>120	3.7	120	2
	ET	Sp	>45	6.2	70	5
		S	>44	3.4	140	3
		A	>45	6.9	80	1
		W	84	11.0	40	1
Turbid lakes	LA	Sp	17	5.2	90	13
		S	30	9.0	50	11
		A	46	9.2	60	5
		W	43	13.5	30	15
	SJ	Sp	12	23.4	20	49
		S	13	17.2	30	31
		A	15	11.5	40	42
		W	16	16.6	30	41
	CH	Sp	8	31.5	10	72
		S	10	35.8	10	75
		A	12	16.6	30	41
		W	10	33.0	10	112
	LI	Sp	8	44.8	10	111
		S	10	49.8	10	106
		A	14	21.1	20	89
		W	9	32.1	10	109

[a] Data provided by the Photobiology Laboratory – IIB INTECH.

100% of TSS. Phytoplankton-turbid ones showed the highest concentrations but the contribution to TSS differed within this group of lakes. In the inorganic-turbid lake the organic matter always accounted for a very low contribution to TSS (<16%) (Table 3).

The lowest concentrations of TP were found in clear-vegetated lakes ranging between 46 and 276 $\mu g\,L^{-1}$. For the phytoplankton-turbid shallow lakes the concentrations varied between 110 and 698 $\mu g\,L^{-1}$, while the inorganic-turbid lake presented the highest values (620–866 $\mu g\,L^{-1}$). Regarding the TN, the phytoplankton-turbid shallow lakes showed a wide range of variation (256–1818 $\mu g\,L^{-1}$).

Values of DOC also differed among the lakes. Highest mean annual concentration was found in the vegetated shallow lake Kakel Huincul (59 $mg\,L^{-1}$) reaching its maximum figure in the spring sample. El Triunfo, San Jorge and Lacombe showed a similar annual average (41, 42 and 49 $mg\,L^{-1}$ respectively), with highest values in summer. The lowest annual average of DOC concentrations were found in the phytoplankton-turbid lake Chascomús and in the inorganic-turbid La Limpia (28 and 21 $mg\,L^{-1}$ respectively), reaching the maximum value in autumn with concentrations of ~47 $mg\,L^{-1}$ for Chascomús and ~40 $mg\,L^{-1}$ for La Limpia.

Table 4 shows the Secchi depth values and some optical variables of the lakes during the sampling period. Strong differences in transparency are evident, being higher in the clear-vegetated lakes (El Triunfo and Kakel Huincul), where Secchi ranged from 44 cm to more than 120 cm (always down to the upper limit of the submerged macrophyte bed). Both types of turbid lakes showed low transparencies (8–16 cm) with the exception of Lacombe that presented a wider range of seasonal variation (17–46 cm). kd_{PAR} values showed a wide range (3.4–49.8 m^{-1}). The clear-vegetated lakes and Lacombe evidenced in general the lowest kd_{PAR} values (less than 13.5 m^{-1}); while the rest of the turbid lakes presented higher values (between 11.5 and 49.8 m^{-1}). The $Z_{1\%}$ was higher in clear-vegetated lakes ranging between 40 and 140 cm and lowest in the inorganic-turbid one with values between 10 and 20 cm. The phytoplankton-turbid lakes San Jorge and Chascomús also showed low values ranging between 10 and 40 cm. It should be noted that within the group of phytoplankton-turbid lakes Lacombe showed

the highest values of $Z_{1\%}$ (30–90 cm). The T_n was also lowest in clear-vegetated lakes, followed by phytoplankton-turbid Lacombe. The highest values were observed in the inorganic-turbid lake La Limpia.

The one-way ANOVAs performed for each of the measured environmental variables and the different types of shallow lakes (clear-vegetated, phytoplankton-turbid and inorganic turbid) showed significant differences for the following variables: Secchi depth, kd_{PAR}, $Z_{1\%}$, T_n (all of them with $p < 0.0001$); conductivity ($p = 0.001$), TP, TSS and %OM (all of them with $p < 0.0001$), and DOC ($p = 0.023$). Chl-a also differed among the different lake types ($p = 0.006$). *Post hoc* contrasts showed that the three types of shallow lakes differed regarding the measured optical variables, TP, TSS and %OM. Differences in Secchi depth were evident between the clear-vegetated water bodies and both turbid types. Conductivity values and DOC presented significant differences between clear-vegetated and inorganic-turbid shallow lakes, whereas Chl-a only differed between clear-vegetated and phytoplankton-turbid water bodies.

>2 μm phytoplankton and chlorophyll a

Chl-a concentration displayed strong differences among the three types of water bodies. Differences were significant between the clear-vegetated and both types of turbid lakes ($p < 0.005$). Clear-vegetated lakes presented the lowest values in all samples (1.6–7.7 $mg\,L^{-1}$), whereas the phytoplankton-turbid lakes always showed the highest ones (20.6–334.6 $mg\,L^{-1}$). However, in Lacombe autumn and winter samples the concentration was reduced to more than a half. The inorganic-turbid lake showed high and intermediate Chl-a concentrations (18.3–35.4 $mg\,L^{-1}$) (Table 3).

Micro- and nanophytoplankton densities were low both in clear-vegetated lakes, Kakel Huincul and El Triunfo, and in the inorganic-turbid La Limpia (Table 3). The lowest density was found in winter in Kakel Huincul (926 cells mL^{-1}). Phytoplankton from clear-vegetated shallow lakes was mainly represented by Cryptophyceae and Crysophyceae, while that from inorganic-turbid by
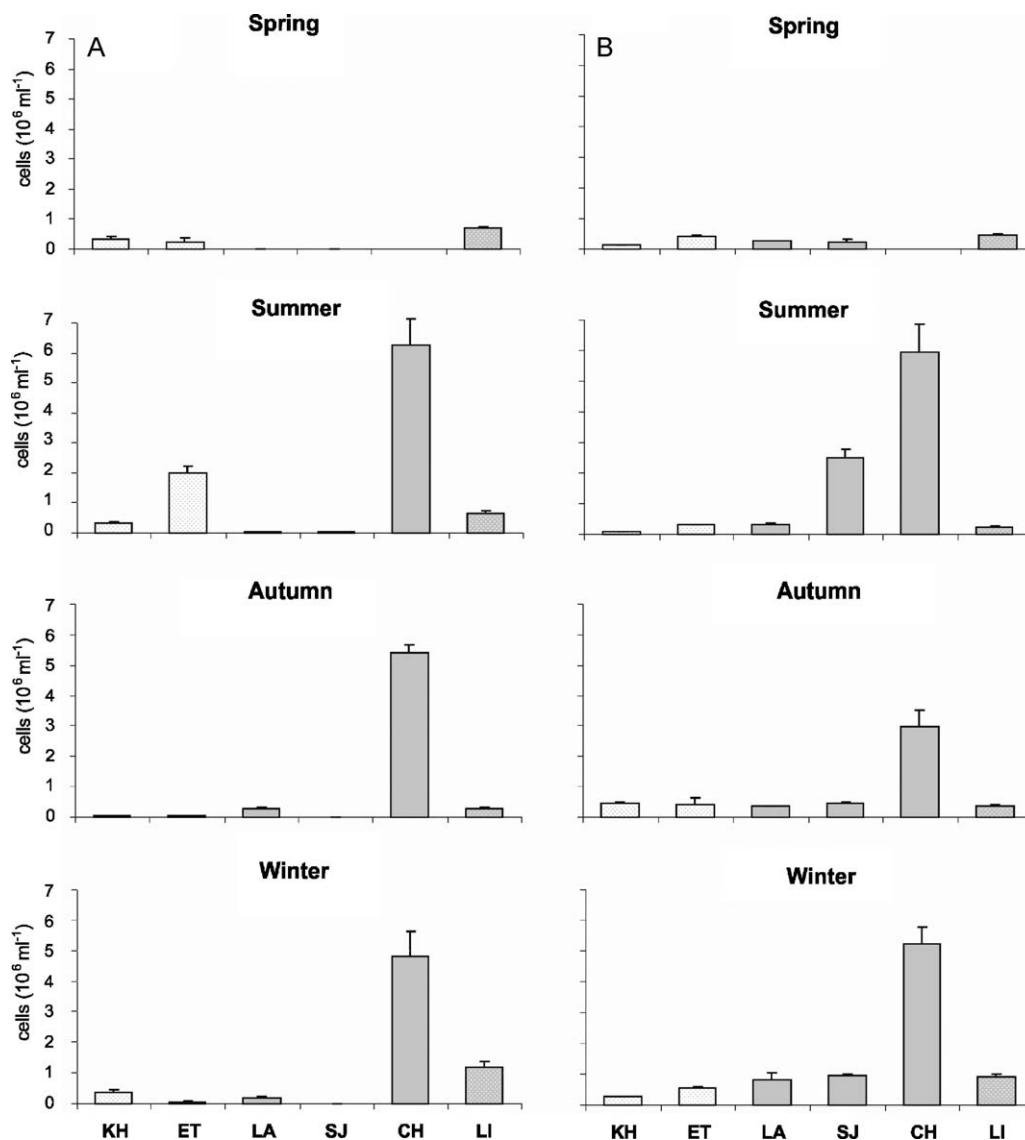
Fig. 2. Seasonal variation of the picoplankton abundance. (A) Picophytoplankton and (B) bacterioplankton (KH, Kakel Huincul; ET, El Triunfo; LA, Lacombe; SJ, San Jorge; CH, Chascomús; LI, La Limpia) (no data available for Chascomús spring sampling). Bars represent ± standard deviation.

Bacillariophyceae and Desmidiaceae. Higher densities of this algal fraction were found in the phytoplankton-turbid lakes (Lacombe, San Jorge and Chascomús), with the highest value in summer in San Jorge (8.82×10^5 cells mL^{-1}). The phytoplankton-turbid shallow lakes differed in their algal compositions. Lacombe was clearly dominated by Chlorophyta followed by colonial Cyanobacteria. San Jorge was almost exclusively dominated by filamentous Cyanobacteria, and Chascomús was mainly represented by Bacillariophyceae and Chlorophyta species. Aggregated forms represented the Cyanobacteria from Chascomús.

Picophytoplankton and bacterioplankton

Clear differences in absolute picophytoplankton abundances were observed among the shallow lakes, and both extremes of the picophytoplankton abundance range were observed within the phytoplankton-turbid water bodies (8.30×10^3–6.25×10^6 cells mL^{-1}) (Fig. 2A). The highest values were registered in Chascomús, while the lowest were found in San Jorge in all seasons. Inorganic-turbid and clear-vegetated lakes presented relatively high values and for the latter, their

greater abundances were encountered in the warmest seasons. In all water bodies and seasons, PC-rich Pcy dominated over the Peuk algae, representing almost always more than 98% of the total picophytoplankton. The inorganic-turbid La Limpia evidenced the highest relative abundance of Peuk, contributing 9.4% to the total abundance.

Clear-vegetated lakes always showed low absolute abundances of bacterioplankton (8.66×10^4–5.33×10^5 cells mL^{-1}), whereas no evident pattern was found for turbid lakes. Chascomús had the highest bacterioplankton abundances in all the seasons, peaking in summer (5.94×10^6 cells mL^{-1}) (Fig. 2B). The relative importance of picophytoplankton to bacterioplankton abundances revealed a dominance of picoplanktonic algae in the clear-vegetated lakes in summer and a dominance of bacterioplankton in autumn. No single trend was found for the group of turbid lakes in any season, and Lacombe and San Jorge were always dominated by bacterioplankton (Fig. 3).

The correlation analysis between each of the picoplankton components abundances and individual environmental variables showed that Peuk and Pcy abundances were positively correlated with TP phosphate ($r = 0.674$, $p < 0.001$; $r = 0.430$, $p = 0.036$ respec-
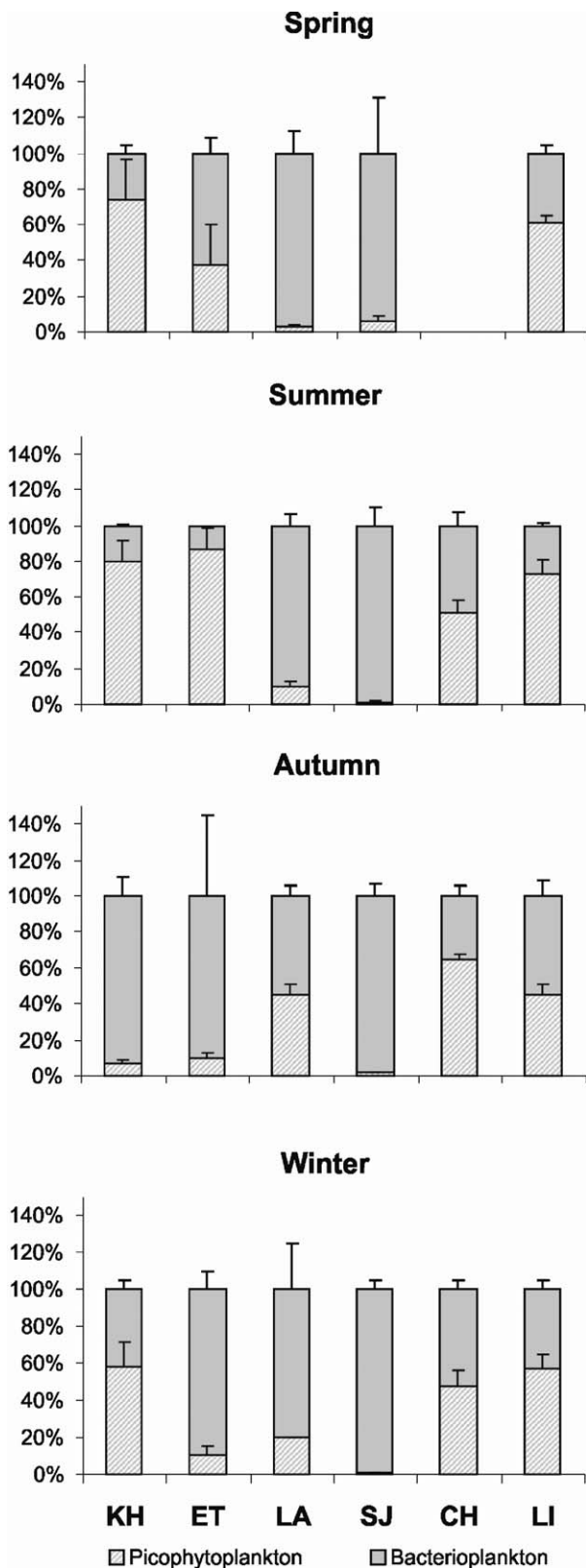
Fig. 3. Relative importance of picophytoplankton and bacterioplankton abundance in the studied lakes and seasons (no data available for Chascomús spring sampling date). Bars represent ± standard deviation.
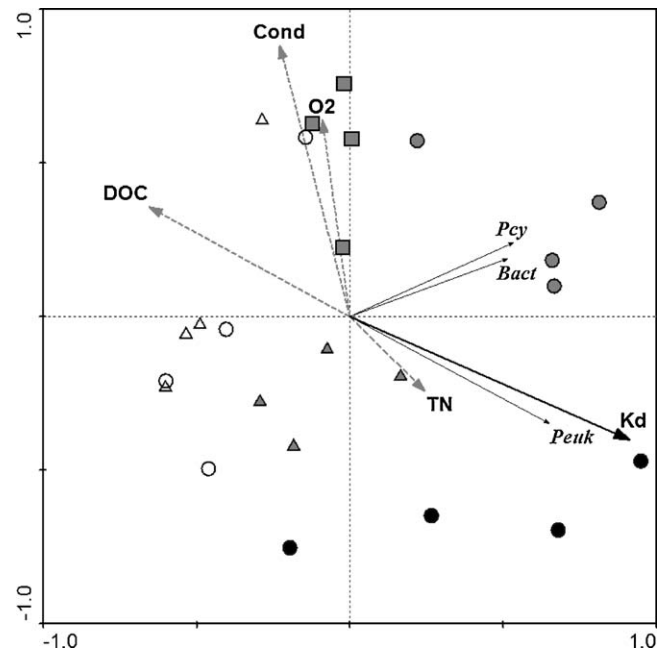

Fig. 4. Three-dimensional representation of the redundance analysis (RDA) based on the abundances of the different picoplankton components (picocyanobacteria, –Pcy–; picoeukaryotic algae, –Peuk–; bacterioplankton, –Bact–) and environmental variables (Cond, conductivity; Kd, diffuse attenuation coefficient; TN, total nitrogen concentration; O_2, dissolved oxygen concentration; DOC, dissolved organic carbon). Clear-vegetated lakes, Kakel Huincul – open triangle, El Triunfo – open circle; phytoplankton-turbid lakes, San Jorge – grey triangle, Chascomús – grey circle, Lacombe – grey square; Inorganic-turbid lake, La Limpia – black circle. Significant environmental variable ($p < 0.05$) is indicated with solid arrow; dotted ones are not significant.

tively), and negatively correlated with DOC ($r = -0.420$, $p = 0.041$; $r = -0.424$, $p = 0.039$ respectively). Peuk was positively correlated with kd_{PAR} ($r = 0.437$, $p = 0.033$), whereas Pcy showed no correlation with this environmental variable. On the other hand, bacterioplankton abundance did not show significant correlation with any of the measured nutrients but did so in a positive manner with kd_{PAR} and Chl-a ($r = 0.504$, $p = 0.012$; $r = 0.480$, $p = 0.018$ respectively).

The results of the redundance analysis considering the abundances of the different picoplankton components and the environmental variables are shown in Fig. 4. The first two axes accounted for 99.4% of the variance (axis 1: 81.5% and axis 2: 17.9%). The environmental parameters were significantly correlated with the first axis as evidenced by the Monte Carlo test ($p = 0.050$), and the test of significance of all canonical axes was also significant ($p = 0.042$). The first axis was mainly defined by kd_{PAR} (intra-set correlation coefficient: 0.65) and the second one was mainly correlated with conductivity (intra-set correlation coefficient: −0.43). The results of this analysis show that most of the samples of La Limpia (inorganic-turbid) are plotted together at the lower-right side of the graph, and Chascomús (phytoplankton-turbid) at the upper-right side, mainly due to high kd_{PAR} values. However, the rest of the samples are ordinated together in two main groups, in which we can find a mixture of samples coming from both clear-vegetated and phytoplankton-turbid shallow lakes, independently of their kd_{PAR}. A group of samples is situated at the middle-upper side of the graph towards higher conductivity values, and other samples are plotted together with higher levels of DOC (lower-left side of the graph). The most important and significant environmental variable was kd_{PAR} ($p = 0.004$). As regards the relationship of the different picoplankton components and the studied environmental variables, the most outstanding result is that highest Peuk abundances were associated with higher kd_{PAR} values.

Discussion

Our results evidenced that the *alternative steady state* (Scheffer et al., 1993) and/or the optical properties characterizing each of the studied systems were not enough to separate them in well defined groups. As well, our study highlighted that the absolute and relative importance of different picoplankton components (Peuk, Pcy, and bacterioplankton) in these water bodies, cannot be solely determined by their water phase and underwater light characteristics.

As regards the abiotic characteristics, the relative high pH values and water conductivities of most of the shallow lakes (La Limpia, Chascomús, San Jorge, Lacombe, El Triunfo) can be explained by the properties of its catchment, located in the Salado River Basin, which is characterized by a rock rich in carbonates and sulfates (OEA, 1971; CODESA, 1984). The ranges encountered and the differences observed in conductivity values among the different water bodies were already reported by Quirós et al. (2002) for the different types of Pampean shallow lakes (clear-vegetated, phytoplankton-turbid and inorganic-turbid). These authors pointed out that extremely dry conditions or intense precipitations result in drastic changes in the structure and functioning of a typical Pampean shallow lake, leading to strong concentration–dilution effects of their dissolved components. These systems suffer profound changes in their surface, depth and salinity associated to the dry–wet cycles (seasonal or interannual) characteristic of the Pampean landscape (Quirós et al., 2006, and cites therein), which can explain the variability encountered in the conductivity values in our study. It is well known for this region, that during years of low precipitations (as the year of our study) the influence of river Salado on the shallow lakes located in its catchment is diminished and thus, the intrinsic factors of each water body exert more influence on its dynamic (Renella, 2007). Gabellone et al. (2001) also reported important changes in conductivity in a pond belonging to the Salado River Basin, which were strongly determined by dry–wet cycles.

The lakes generally showed saturation levels of DO as they are strongly influenced by wind, mostly those that are not vegetated. The negative effect of vegetation on turbulence is well known (Scheffer, 1998; and cites therein) and as a result the presence of submerged plant beds helps to reduce the resuspension from the sediments and favors the sinking of particles. This fact can explain the low TSS encountered in clear-vegetated lakes which was mostly composed of organic matter, contrasting with what was found in the non-vegetated inorganic-turbid La Limpia. In this sense, it has been already shown that both sediment resuspension and external loading can increase the inorganic turbidity in shallow lakes (Padisák and Dokulil, 1994; Reynolds, 1994; Roland and Esteves, 1998; Quirós et al., 2002). Phytoplankton-turbid lakes (Chascomús, San Jorge and Lacombe) showed a great variability in the %OM. As it was already mentioned, Lacombe can present both *alternative steady states* and hence, the resuspension of sediments would be diminished when submerged macrophytes develop, resulting in a greater importance of the organic fraction.

According to Quirós et al. (2002) Pampean lakes are distributed along a gradient, from eutrophic clear-lakes colonized by macrophytes, to a defined state of hypertrophic turbid-lakes dominated by phytoplankton, and our survey represented a sample of this gradient. TN and TP values were high and within the ranges reported for eutrophic and hypertrophic lakes (Kalff, 2002), and for other lakes of the region (Izaguirre and Vinocur, 1994a; Gabellone et al., 2001; Renella and Quirós, 2006). Comparing the phytoplankton Chl-*a* concentrations, clear-vegetated lakes presented low values, whereas phytoplankton-turbid lakes showed the highest ones, fulfilling the requirements of the model proposed by Scheffer et al. (1993, 2003) for the existence of clear and turbid states. The existence of alternative periods of high organic turbidity and periods

of greater transparency and development of submerged macrophytes in Lacombe (Cano, 2008) can account for its relatively low Chl-*a* concentrations and higher transparency, if compared with the other phytoplankton-turbid systems. As stated by Pérez et al. (2010), the light availability plays a fundamental role in lakes directly affecting the competition outcome between primary producers. The measurement of light attenuation when describing the underwater light availability can provide a good understanding of the conditions for the dominance of phytoplankton or macrophytes (Lowe et al., 2001). The light attenuation in clear-vegetated lakes is related to the concentration of dissolved organic matter, as in Kakel Huincul and El Triunfo. In more turbid systems this attenuation is determined by the progressive absorption and dispersion generated by particulate matter such as non-pigmented particles (heterotrophic microorganisms and inorganic particles) in La Limpia, or algae in Chascomús, San Jorge and Lacombe lakes (Pérez et al., 2010).

The analysis of the picophytoplankton abundances in relation to the *alternative steady state* and optical properties of the shallow lakes showed that under the clear-vegetated conditions the values were intermediate, whereas in the turbid lakes they were either too high or too low. Our observations agree with the results of a study by Vörös et al. (1998) in 32 lakes representing a gradient from oligotrophy to hypertrophy and Chl-*a* concentrations ranging from 0.2 to 390.0 μg L^{-1}. These authors encountered that at high Chl-*a* values the Pcy abundance cannot be predicted and also stated the absence of a linear relationship between the abundance of Pcy and trophic state. In this respect, Sommaruga and Robarts (1997) also claimed that the abundance of picophytoplankton increases with the trophic level of the lake, but that this trend does not continue in the hypertrophic end of the spectrum, which can present both high and low values of this fraction. Burns and Stockner (1991) determined that Peuk algae usually present an order of magnitude less in terms of density than Pcy. The Peuk algae constitutes an important component in eutrophic shallow lakes (Mózes et al., 2006), and their contribution to the total picoplanktonic biomass increases with the light extinction coefficient (Pick and Agbeti, 1991; Callieri, 2008; Vörös et al., 2009). Our study provides further evidence in this respect as we find a positive correlation between Peuk algae and kd_{PAR} with its greatest contribution in the inorganic-turbid lake La Limpia, which presented the poorest underwater optical characteristics. This was the fraction less represented in all six lakes and seasons, although the difference with respect to Pcy was greater than in the previously reported studies. Weisse (1993) stated that the factors controlling the distribution of Peuk algae differ from those that regulate the Pcy variation in space and time. The interaction of nutrients and light availability in the aquatic ecosystem can favor the development of the pico-sized algae, but as these organisms can adapt quickly to local conditions, their behavior in a long-term basis is difficult to predict.

The concentrations of DOC found in the studied shallow lakes are within the range reported for eutrophic waters (Kalff, 2002), and not limiting for bacterial development (del Giorgio and Peters, 1993). Labile organic matter produced by phytoplankton is considered the most important carbon source for bacterial growth (Tien et al., 2002 and cites therein) and thus, commensalistic interactions can be stated between the heterotrophic bacteria and planktonic algae (Cole, 1982). The positive correlation encountered between the bacterioplankton abundance and Chl-*a* concentration might be considered as further evidence in this respect. Other biotic interactions are reported between the bacterioplankton and the phytoplankton as they might compete for phosphorus when it is limiting (Currie and Kalff, 1984; Jansson et al., 1996). However, since in our study TP showed high levels and DOC was not limiting, we expected to find a lower picophytoplank-

ton abundance relative to bacterioplankton in the turbid lakes as the former would be light-limited. This situation was observed in phytoplankton-turbid lakes Lacombe and San Jorge at all sampling dates. However, Chascomús (phytoplankton-turbid) and La Limpia (inorganic-turbid), showed similar proportions of picophytoplankton/bacterioplankton throughout the sampling period. Thus, the relative proportion of these two picoplankton components cannot be predicted regarding only the availability of nutrient and energy resources. Drakare et al. (2003) proposed that picophytoplankton would only be favoured relative to heterotrophic bacteria under conditions where the latter are dependant on phytoplankton-derived carbon as an energy source, which seems difficult to evaluate in our studied shallow lakes with such high DOC concentrations. We suspect that another biotic interaction that potentially influences the variation in the relative importance of the picoplankton components in these eutrophic and hypertrophic systems is selective grazing (top-down effect). Hirose et al. (2003) also suggested that the abundance of autotrophic picophytoplankton in a hypertrophic pond was substantially associated to the top-down effect exerted by microzooplankton.

Søndergaard and Moss (1997) found that macrophytes may have a structuring effect on phytoplankton size distribution proposing that several mechanisms may be involved in determining the species composition. In this sense, they mentioned (and cites therein) that changes in nutrient regime, differential tolerance to shading, susceptibility to sedimentation in the quiescent and darker waters within the macrophyte beds, allelopathic effects, and increased supply of dissolved organic carbon deriving from the macrophyte–epiphyte complex, alter the planktonic food web and thus, the phytoplankton structure. In our study, as expected, we found a higher proportion of picophytoplankton relative to large phytoplankton in the clear-vegetated lakes. This might be the result of the relationship of large phytoplankton with the submerged macrophytes as it was already demonstrated that the latter can increase the sedimentation of large non-buoyant cells and provide refuge for grazers (Scheffer, 1998). Small algae are then favored in highly vegetated lakes (Søndergaard and Moss, 1997) and large phytoplankton development is limited (Goldsborough and Robinson, 1996; Søndergaard and Moss, 1997) in coincidence with our observations. Regarding phytoplankton-turbid lakes marked differences were encountered in this respect. San Jorge presented blooms of large filamentous Cyanobacteria throughout this study. There is evidence of competition between Pcy and this type of blue-green algae (Stockner and Shortreed, 1988; Callieri and Stockner, 1997). Hence, we may attribute the low development of picophytoplankton in San Jorge to a strong competition with bloom-forming microplanktonic cyanobacteria. Although we expected a higher proportion of >2 μm algae in the phytoplankton-turbid lake Chascomús, picophytoplankton numbers were extremely high. It is noteworthy that the absolute abundance of large phytoplankton was also high, and in terms of biomass its contribution should be much more important. Lacombe was the only turbid shallow lake which presented seasonal variability regarding the relative proportions of the phytoplankton size fractions, and this can again be explained by the fact that this is a shallow lake which can present *alternative steady states*. The large picophytoplankton proportion found in inorganic-turbid Lake La Limpia might be partially explained by the presence of high inorganic turbidity as it causes light limitation and so can modify the composition of the phytoplankton community. The success of picophytoplankton and its greater contribution to total phytoplankton has also been reported for other inorganic-turbid shallow lake (Padisák and Dokulil, 1994). In light limited situations small organisms have a higher specific growth rate as compared with large phytoplankton because of a minimal package effect of the light harvesting machinery (Raven, 1998).

Conclusions

An interesting finding of our study is that picoplankton structure differed between turbid and clear lakes, and also within the turbid systems. The present work highlights that the abundances of the different picoplankton components and the relative importance of the phytoplankton size classes are not only associated with the state of the shallow lakes. It is concluded that the development of the picoplankton is difficult to predict in them only considering the phytoplankton Chl-*a* concentration, the nutrient content or the water column light conditions.

We consider that more picoplankton studies are particularly needed at the hypertrophic end of the trophic spectrum to elucidate their success under these extreme conditions. Moreover, the molecular approaches that are currently increasing, will contribute to open the black box of this plankton size fraction to clarify the ecological requirements of different picoplankton strains.

Acknowledgements

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