Advanc. Limnol. **65**, p. 343–357
Freshwater Phytoplankton of Argentina

Photosynthetic picoplankton in Argentina lakes

Irina Izaguirre[1]*, Fernando Unrein[2], Beatriz Modenutti[3] and
Luz Allende[1]

With 6 figures and 1 table

Abstract: This article provides an overview of the studies on photosynthetic picoplankton (PPP) carried out in water bodies from different latitudes of Argentina, including Patagonian lakes and shallow lakes from the Chaco-Pampean Plain Region. The PPP of the different aquatic systems: shallow and deep lakes, turbid and transparent water bodies, and lakes with contrasting trophic state are characterized. We focus our attention on light intensity as the major axes of niche differentiation in Pcy. We present examples regarding the distribution of distinct Pcy ecotypes adapted to high- and low-light intensities at different depths in the water column of deep and shallow transparent lakes. In ultraoligotrophic Patagonian lakes phycoerythrin (PE)-rich picocyanobacteria (Pcy) are dominant, whereas eutrophic and hypertrophic shallow lakes from the Pampa Plain present a wide range of PPP abundances dominated by phycocyanin (PC)-rich Pcy. The relevance of the depth of the euphotic layer and nutrient concentration as the main abiotic features explaining the variability encountered are discussed. The PPP from eutrophic shallow lakes and relict oxbow lakes from wetlands from the Lower Paraná Basin are mainly represented by PC-rich Pcy, and Peuk in a lesser extent. Changes in the free-floating plants coverage were found to play a crucial role in structuring the PPP, and on the other hand, there is evidence of a negative relation between the PPP abundance and the hydrometric level. For different aquatic systems the PPP populations are compared by means of the patterns resulting from the flow cytometry analyses.

Keywords: photosynthetic picoplankton, lakes, picocyanobacteria, picoeukaryotes

---

Introduction

Photosynthetic picoplankton (PPP) includes small prokaryotic picocyanobacteria (Pcy) and picoeukaryotic phototrophs (Peuk), whose cell-size are in the range 0.2 to 2 µm. Another component of PPP, only restricted to anoxic or poorly oxygenated waters, are the anoxygenic

---

Authors' addresses:
[1] Depto. Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, (IEGEBA CONICET-UBA), C1428EHA Buenos Aires, Argentina.
[2] IIB-INTECH (Instituto de Investigaciones Biotecnológicas – Instituto Tecnológico de Chascomús – CONICET)
[3] Laboratorio de Limnología, Instituto de Investigación en Biodiversidad y Medioambiente (INIBIOMA, UNComahue – CONICET), Bariloche, Argentina
*Corresponding author: iri@ege.fcen.uba.ar

DOI: 10.1127/1612-166X/2014/0065-0050 1612-166X/2014/0065-0050 $ 4.25

anaerobic photosynthetic bacteria (AnAnPB), which were also reported as very abundant in anoxic environments (e.g. Casamayor et al. 2007, Izaguirre et al. 2010).

PPP are distributed worldwide and are ubiquitous in all types of lakes and oceans of varying trophic states (Callieri 2008 and cites therein). Their great importance in the pelagic food webs has been largely documented (Stockner & Porter 1988, Weisse 1993, Vörös et al. 1998, Callieri & Stockner 2002, Drakare 2002), and now it is widely recognized that this fraction is the major contributor to the carbon flow in many aquatic systems, particularly in oligotrophic waters (Agawin et al. 2000, Bell & Kalff 2001, Richardson & Jackson 2007). Their contribution to total carbon production has been estimated ranging from 16 to 80% for different freshwater systems (Nagata et al. 1994, Steitz & Velimirov 1999, Greisberger et al. 2007).

The PPP structure in lakes is regulated by different factors, which were discussed by Callieri (2008) in her review on picophytoplankton. Among them, the most important are trophic state, thermal regime, hydrological retention time, nutrients, light conditions, lake morphometry and biotic interactions. In relation to the trophic state, many studies have shown that whereas PPP abundance and biomass increase with rising nutrient content, their contribution to total phytoplankton biomass and production decreases following the same gradient (Søndergaard 1991, Stockner 1991, Weisse 1993, Sommaruga & Robarts 1997, Bell & Kalff 2001). Differences in the trophic state among lakes also determine differences in their light climate conditions, which in turn have been shown to influence the PPP pigment composition. Phycocyanin (PC)-rich Pcy are usually dominant in eutrophic shallow lakes where red light prevails, whereas phycoerythrin (PE)-rich Pcy succeed in oligotrophic deep lakes dominated by green light (Vörös et al. 1998, Camacho et al. 2003, Callieri 2008, Stomp et al. 2007). On the other hand, several studies suggested that Peuk seem to prefer low light levels (Pick & Agbeti 1991, Craig 1987, Vörös et al. 2009).

Despite their great importance in the pelagic food webs of the lakes, the inclusion of the picoplanktonic fraction in the analysis of phytoplankton of freshwaters from Argentina is fairly recent; the first study was published at the beginning of this century (Zunino & Díaz 2000). Later on, studies on PPP were performed in shallow lakes and deep oligotrophic lakes from North Patagonia (Callieri et al. 2007, Bastidas Navarro et al. 2009, Caravati et al. 2010, Callieri et al. 2013). Recently, new data on autotrophic picoplankton were reported for lakes and shallow lakes located in South Argentinean Patagonia and Tierra del Fuego (Schiaffino et al. 2013). For middle latitudes of Argentina there are also few published papers on PPP, and they involve aquatic systems located in the extense Chaco-Pampean Plain region. Particularly, some recent studies were conducted in different types of shallow lakes (clear-vegetated, algal-turbid and inorganic-turbid) from the Pampa Plain (Allende et al. 2009, Silvoso et al. 2011, Diovisalvi et al. 2010, Fermani et al. 2013); these include also experimental studies, where the response of PPP to different light conditions was analysed together with other microbial components (Llames et al. 2009). Another study was carried out in a wetland from the Lower Paraná Basin, in the Otamendi Natural Reserve, evaluating the influence of the free-floating macrophytes on the structure and productivity of PPP (Izaguirre et al. 2010).

Noticeably, there is a lack of information on PPP for the warm region of Argentina, since the phytoplankton studies carried out in the water bodies of this region did not include the autotrophic picoplanktonic fraction.

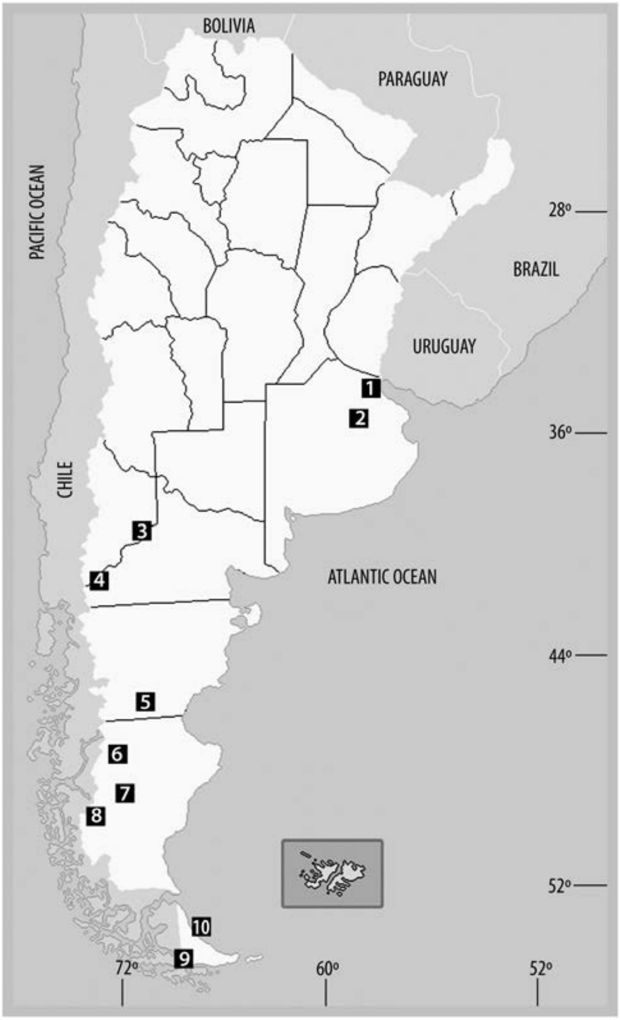

Fig. 1. Geographic position of the water bodies for which there is available information on phytosynthetic picoplankton. 1. floodplain shallow lakes from the Lower Paraná River Basin; 2. Pampean Plain shallow lakes; 3. Reservoirs from Neuquén and Rio Negro Provinces; 4. North Andean Patagonian lakes; 5. Lakes from the south of Chubut Province; 6. Andean lakes from the north of Santa Cruz Province; 7. lakes and shallow lakes from the Strobel Plateau, Santa Cruz Province; 8. Andean lakes from the south of Santa Cruz Province; 9. Lakes and shallow lakes from Tierra del Fuego (near the Andes); 10. Shallow lakes from Tierra del Fuego, Patagonian Plateau near Rio Grande. The divisions in the map of Argentina correspond to the provinces.

All the information obtained until present for Patagonian and Chaco-Pampean Plain regions is described and compared in this article. The geographic position of the regions for which there is available information on PPP is indicated in Fig. 1.

Patagonian lakes

The first report on autotrophic picoplankton for Andean North Patagonian lakes was given by Zunino & Diaz (2000), who sampled 9 natural lakes and 4 reservoirs of this region covering an oligo-eutrophic range, and reported average PPP abundances varying from 2 x 10^3 to 6 x 10^4 cells. ml^{-1}. The highest values were registered in Lake Fonck (2 x 10^5 cells. ml^{-1}), whereas the lowest abundances corresponded to high altitude lakes (2–4 x 10^2 cells. ml^{-1}). For the same lakes the PPP biomass varied between 2 and 12 µg C L^{-1}. This study showed that Pcy were numerically more abundant (up to two orders of magnitude) that Peuk in the studied lakes; PE-rich Pcy dominated in the oligotrophic lakes, whereas PC-rich Pcy dominated in the more eutrophic water bodies.

As it was pointed out by Morris et al. (1995) and Callieri et al. (2007), North Andean Patagonian clear deep lakes generally exhibit extinction coefficients of photosynthetically active radiation (PAR, K_d) as low as 0.09 m^{-1}. In these environments blue light dominates the deep euphotic layers (Pérez et al. 2002), and Chl *a* shows a pronounced deep maximum generally situated below the thermocline around 1% PAR level (Callieri et al. 2007, Pérez et al. 2007). In these lakes, about 30% of total Chl *a* can be attributed to Pcy (Modenutti & Balseiro 2002, Callieri et al. 2007).

In a study describing the light climate at the deep chlorophyll maxima (DCM) from Andean lakes, Pérez et al. (2002) indicated that the maximum abundance of PPP is in coincidence with the DCM. These authors suggested that dim light conditions and the prevalence of green and blue wavelengths favoured the development of PPP populations.

Bastidas Navarro et al. (2009) carried out a summer survey in three shallow North Patagonian lakes (Escondido, Morenito and El Trébol), where the light climate along the water column was related with the photosynthetic production and efficiency of two phytoplankton size fractions: picophytoplankton and phytoplankton > 2 µm. This study showed that PPP abundance varied between 1.05 x 10^4 and 6.7 x 10^5 cells. ml^{-1} and did not differ greatly among lakes. PPP was mainly composed by *Synechococcus* spp. dominated by PE-rich cells, whose abundances increased to the bottom. PC-rich cells were much less abundant and they did not show differences along the water profile in lakes Morenito and El Trébol. Contrarily, in Lake Escondido PC-rich Pcy slightly increased near the bottom, and a significant decrease in the PE:PC ratio with depth was observed; this vertical variation may indicate that the dissolved organic matter (DOM), acting as an absorption filter, changes the underwater light spectrum and consequently the pigment composition of Pcy.

Another study conducted during summer stratification in six deep ultraoligotrophic Andean lakes (Moreno, Gutiérrez, Mascardi, Nahuel Huapi, Correntoso and Espejo) showed that PPP were composed exclusively by *Synechococcus* spp. in five of these lakes, whereas low abundances of Peuk were also observed only in Lake Nahuel Huapi (Callieri et al. 2007). Total PPP abundances in these lakes ranged between 6.5 x 10^4 and 1.4 x 10^5 cells. ml^{-1}, and the biomass of this fraction varied between 2.9 and 8.9 µg C L^{-1}, with maximum abundances always registered at the DCM. Interestingly, this study showed that the inclusion of Andean-Patagonian lakes in the extended database of Vörös et al. (1998) fitted well in the three trends of North Hemisphere lakes: an increase of autotrophic picoplankton cell number and biomass (Chl *a*), and a decrease of its relative contribution to total biomass as the trophic state increases. This study also revealed a strong photoinhibiting effect of high photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) at the surface level, and a high photosynthetic efficiency towards deep layers. At the same ultraoligotrophic lakes, Caravati et al. (2010) performed the first analysis of the Pcy biodiversity for Patagonian lakes, which was based on the ARISA fingerprinting technique. Internal Transcribed Spacer (ITS) fragments generated for ARISA were subsequently cloned, and the ITS sequences retrieved were published in the GenBank. This analysis allowed to retrieve a total of 18 operational taxonomic units (OTUs), of which only one was found in all the lakes at all depths, whereas 50% were unique to one lake or one lake group. A principal component analysis based on the OTUs showed two clear groups of lakes: Nahuel Huapi and Moreno on one hand, and Gutiérrez, Mascardi, Espejo and Correntoso on the other. It has been hypothesized that during lake evolution some Pcy OTUs could result from specific adaptations favoured by even minor differences in irradiance conditions. Recently, the sequences derived from monoclonal Pcy strains isolated from five North Patagonian ultraoligotrophic lakes were included in a phylogenetic analysis, together with sequences of other nonmarine Pcy strains retrieved from lakes of different latitudes and with contrasting limnological features (Callieri et al. 2013), interestingly, this study showed that the sequences of Lake Nahuel Huapi clustered distant from other isolates of Argentinean lakes, and formed a sister clade to the subalpine cluster II and the marine *Synechococcus* subcluster 5.2.

During austral springs 2007 and 2008, 33 water bodies (including deep lakes, shallow lakes and temporary ponds) of Austral Argentinean Patagonia (45.368°S Chubut Province – 54.776°S Tierra del Fuego Province) were surveyed, and samples for PPP analyses were collected in all the environments (Schiafino et al. 2013). This study revealed important differences in the PPP structure among the aquatic systems, which were mainly related to their trophic states and vertical extinction coefficients (K_d). Ranges of PPP abundances varied from 2.11 x 10^4 to 3.65 x 10^5 cells. ml^{-1} in oligotrophic lakes, from 2.94 x 10^4 to 1.44 x 10^6

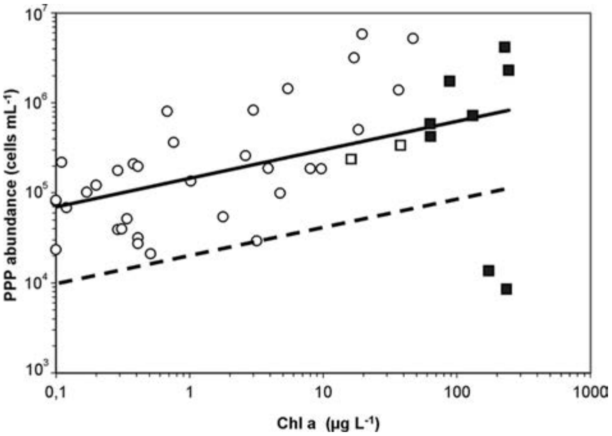

Fig. 2. Relationship between total phytoplankton biomass (µg Chl *a* L^{-1}) and picophytoplankton abundance. Circles: lakes from Austral Argentinean Patagonia (Izaguirre et al., unpubl. data); squares: Pampean shallow lakes, turbid (in black) and clear (in white), data from Allende et al. (2009) and Silvoso et al. (2011). Dotted line: modified from the trend published by Callieri (2008) based on data from a wide range of water bodies (Vörös et al. 2008) and from North Andean Patagonian lakes (Callieri et al. 2007).

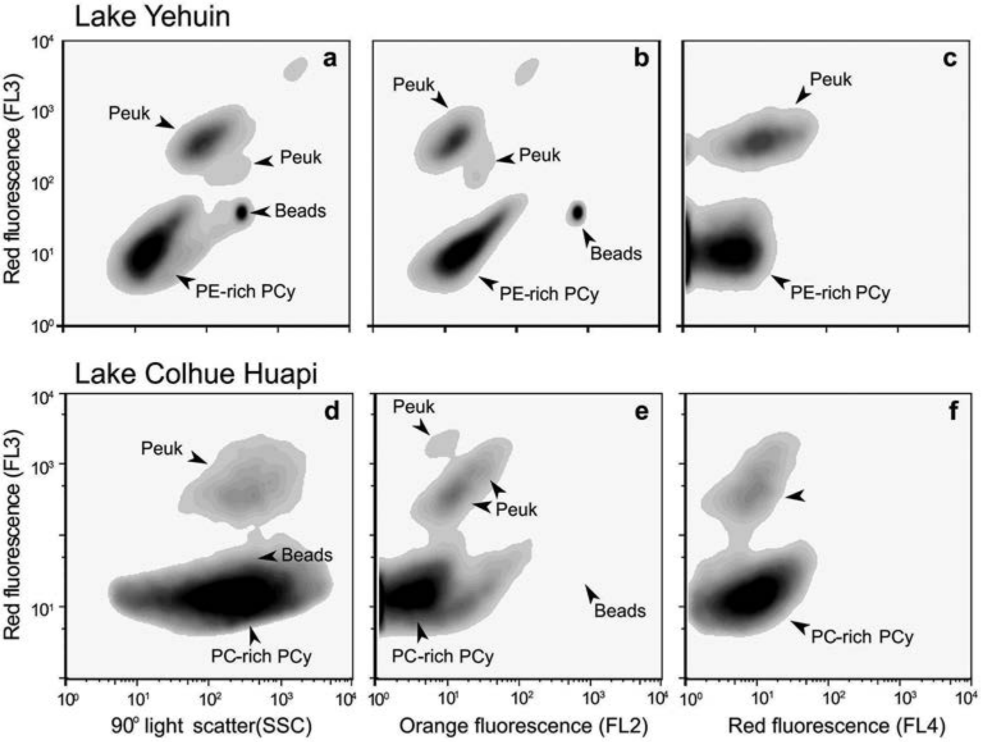

Fig. 3. Examples of cytograms showing the autotrophic picoplankton populations (unstained samples) of the clear Lake Yehuin (October 2008) dominated by PE-rich (phycoerythrin) picocyanobacteria (a, b, c) and the turbid Lake Colhue Huapi (November 2007) dominated by PC-rich (phycocyanin) picocyanobacteria (d, e, f). Different picoeukaryotic (Peuk) populations were also presented in both lakes. Cytograms were obtained using a FASCalibur Flow Cytometer (BD) equipped with a blue (488 nm) and a red (635 nm) laser. SSC: the 90º light scatter is related to the size and internal granularity of the cell; FL3: chlorophyll *a* autofluorescence (red emission after blue light excitation); FL2: phycoerythrin autofluorescence (orange emission after blue light excitation); FL4: phycocyanin autofluorescence (red emission after red light excitation). Fluorescent beads are yellow-green 1 μm in size (Polysciences).

cells. ml^{-1} in mesotrophic lakes and from 5.05 x 10^5 to 5.8 x 10^6 cells. ml^{-1} in eutrophic lakes. A significant regression ($R^2 = 0.566$; $p < 0.000001$; $n = 33$) was observed between Chl *a* (as an indicator of trophic state) and PPP abundance. This pattern is in agreement with that shown by Callieri (2008) based on data from a wide range of water bodies and trophic conditions (Vörös et al. 1998), and on data obtained in North Patagonian lakes (Callieri et al. 2007). Fig. 2 illustrates the relationship between PPP abundance and Chl *a* from the lakes of the Austral Patagonia and the Pampa Plain ($R^2 = 0.23$; $p < 0.05$; $n = 43$); this figure also includes the trend published by Callieri (2008). Another interesting finding of this regional study was that a significant direct correlation was found between the abundance of Peuk and the K_d values of the lakes ($r = 0.75$; $p < 0.05$; $n = 33$). The highest Peuk densities were registered in the most turbid water bodies. This pattern agrees with other observations in that

Peuk seem to be favoured under severe light limitation conditions (Stockner & Antia 1986, Craig 1987, Søndergaard 1991, Vörös et al. 2009). The flow cytometry analyses allowed recognizing the more representative PPP populations at the different lake types (Schiaffino et al. 2013). A well-defined PE-rich Pcy population commonly dominated PPP in large transparent oligotrophic lakes (e.g. Lake Yehuin), whereas PC-rich Pcy became more important in turbid environments like Lake Colhue Huapi (Fig. 3). In addition, a higher number of Peuk populations were recognised by flow cytometry in eutrophic systems (from 3 to 6 populations, e.g., ponds from the Strobel plateau) compared to oligotrophic ones, which were usually characterized by at most two or three different Peuk populations.

The most important grazers on PPP in the Patagonian lakes are mixotrophic ciliates (Modenutti & Balseiro 2002) and nanoflagellates (Balseiro et al. 2004). These protists can exert a strong top-down effect on PPP populations; however the presence of the cladoceran *Daphnia* (mainly *D. commutata*) may contribute significantly to PPP grazing. In an experimental study carried out in the oligotrophic Lake Rivadavia, (Modenutti et al. 2003), it was observed that PPP was affected by different zooplankton structures. *Daphnia* spp. (2.5 mm in body length) showed a strong selection towards PPP, causing a direct significant decrease of this fraction. In addition, indirect effect on this fraction can occur through nutrient supply provided by *Daphnia* spp. that causes positive effect on bacterioplankton. Finally, when zooplankton was dominated by small *Boeckella* (*B. michaelseni* and *B. gracilipes*) – copepods which feed upon nanoflagellates (Balseiro et al. 2001) – an indirect positive effect on PPP can be also observed because of the decrease of bacterivores.

Chaco-Pampean Plain Region

Shallow lakes from the Pampa Plain

Three types of shallow lakes can be recognized in the Pampa Plain (Fig.1) according Quirós et al. (2002): clear-vegetated lakes with high development of submersed macrophytes and low phytoplankton biomass; algal-turbid lakes dominated by phytoplankton, and turbid lakes resulting from suspended inorganic material (inorganic-turbid). The first comparative studies on the autotrophic picoplankton of shallow lakes of this region performed in environments with contrasting features (Allende et al. 2009, Silvoso et al. 2011) showed that the highest densities and biovolumes of PPP were registered in two algal-turbid lakes (Chascomús and Vitel) with mean densities varying from 2.3 x 10^6 to 6.5 x 10^6 cells. ml^{-1}. The lowest values were observed in algal-turbid lake (San Jorge) where Cyanobacteria > 20 µm dominated; PPP ranged 8.3 x 10^3 to 3.5 x 10^4 cells. ml^{-1}. In all the studied shallow lakes PPP were dominated by PC-rich Pcy cells, representing almost always more than 98% of the total picophytoplankton. The contribution of Peuk to total PPP was generally low, and the highest value (9.4%) was observed in one inorganic-turbid shallow lake (La Limpia). Interestingly, Silvoso et al. (2011) observed that among six Pampean shallow lakes, only one (Lacombe) exhibited seasonal variability in the relative proportion of phytoplankton size fractions (picoplankton and algae > 2 µm), which was attributed to the fact that this lake can present two alternative steady states: one clear with submersed plants and another turbid with phytoplankton dominance (Cano 2008). Another finding of this study was that PPP structure differed

Table 1. Characteristic of autrotrophic picoplankton for shallow lakes of the Pampa Plain. *Allende et al. (2009), **Silvoso et al. (2011), ***Diovisalvi et al. (2010).

	Phytoplankton-turbid shallow lakes	Inorganic-turbid shallow lakes	Clear-vegetated shallow lakes
Ranges of picoplankton densities (cells. ml^{-1})	$8.60 \times 10^3 – 4.17 \times 10^6$ * $8.30 \times 10^3 – 6.25 \times 10^6$ ** $2.00 \times 10^6 – 2.00 \times 10^7$ ***	$7.18 \times 10^5 – 1.75 \times 10^6$ * $2.94 \times 10^5 – 1.21 \times 10^6$ **	$2.37 \times 10^5 – 3.38 \times 10^5$ * $3.40 \times 10^4 – 1.98 \times 10^6$ **
Ranges of PCy/ total picoplankton	0.89 – 0.99 * 0.83 – 1.00 **	0.86 – 0.96 * 0.86 – 0.93 **	0.97 – 0.99 * 0.96 – 1.00 **

between turbid and clear lakes, and also within the turbid systems. This analysis in eutrophic and hypertrophic shallow lakes provides further evidence of the lack of a linear relationship between the trophic status and the abundance of Pcy, both at high Chl-*a* concentrations and in the hypertrophic end of the trophic spectrum, as previously reported by Sommaruga & Robarts (1997) and Vörös et al. (1998). In general, the clear-vegetated lakes exhibited similar picophytoplankton/bacterioplankton ratios, and phytoplankton size structure. Contrarily, no clear trend was identified for the group of eutrophic turbid lakes, and a great dispersion in the relationship between PPP abundance and Chl *a* was observed at this trophic extreme (Fig. 2). The information on picophytoplankton obtained in the three types of shallow lakes of the Pampa Region is summarized in Table 1.

More recent studies based on epifluorescence (Fermani et al. 2013) and flow cytometry on different planktonic components of the turbid Lake Chascomús, revealed one of the highest picophytoplanktonic abundance ever estimated for natural environments reflected in the cytograms depicted in Figure 4, at times exceeding 10^7 cells. ml^{-1}. Pcy presented the maximum abundances at the beginning of spring and the minimum values at the end of summer, while Peuk showed always the maximum abundances on middle summer. At least two populations of PC-rich Pcy and two of Peuk have been identified by flow cytometry (Fig. 4). Cells sorted from Pcy-A and -B populations were indistinguishable when viewed by epifluorescence microscopy, and consisted mostly of solitary coccoid to ovoid forms. Peuk-1 was represented by unicellular ovoid chlorophytes, whereas Peuk-2 was conformed by a "mix" of different species (Unrein, unpubl. data).

The application of flow cytometry in the studies of PPP allows also to detect imperceptible changes in the mean cell size or in the internal granularity of the particle (by analysing the side angle scatter = SSC signal) and in the mean relative per-cell chlorophyll content of a given population (by analysing the red fluorescence, FL3). The analysis of the SSC of Pcy and Peuk-1 along an intensive study (sampling every 8 hours during 5 consecutive days) revealed that both populations exhibited a clear daily pattern, with lower SSC values always recorded in the morning and higher values that were recurrently measured in the afternoon (Kranewitter 2010). These results clearly showed that cell cycle of these two populations are synchronized with the daily light cycle, as it was already observed for marine picoplanktonic algae (Jaquet et al. 1998).

Another interesting finding was the positive significant correlation observed for both Pcy and Peuk-1, between the turbidity and the relative red fluorescence (FL3) of each population (Kranewitter 2010). Considering that phytoplankton growth in this shallow lake is permanently limited by the low underwater light intensity (Torremorell et al. 2009), this result

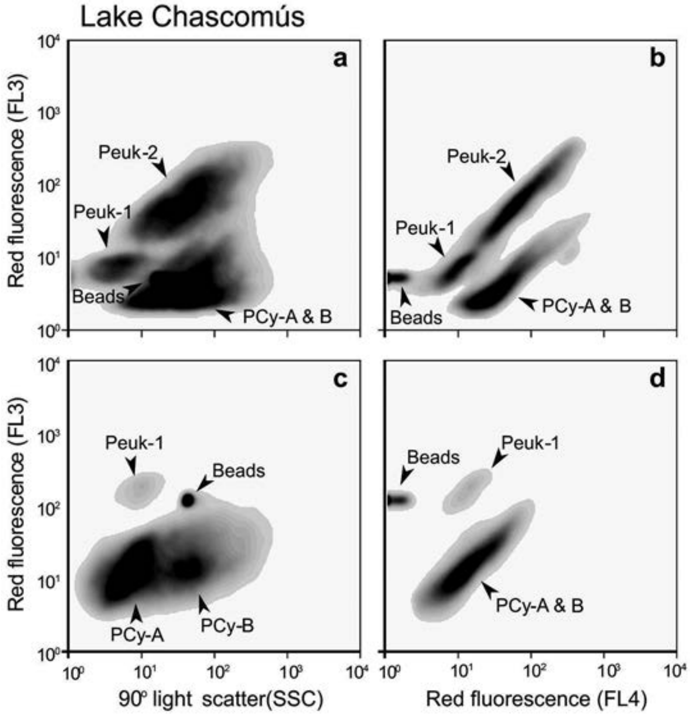

Fig. 4. Typical cytograms of a Lake Chascomús sample showing the autotrophic populations (unstained samples). (a, b) Upper panels show two picoeukaryotic populations (Peuk-1 and Peuk-2). See the text for detailed description. In the lower panels (c, d) settings in the flow cytometer were changes in the same sample in order to visualize picoplanktonic populations with lower red fluorescence, i.e., picocyanobacterial populations (Pcy-A and Pcy-B). The information on the cytometer and the laser used are the same indicated in Figure 3.

suggests that both PPP populations seem to be able to change the per-cell chlorophyll content in response to small variations in water turbidity, increasing in a few hours, the amount of pigment when mean underwater light intensity is being reduced (Fig. 5).

Wetland of the Lower Paraná Basin (Otamendi Natural Reserve)

In South America the higher proportion of surface occupied by wetlands corresponds to the large rivers floodplains, most of them (80%) occurring in warm climates (Neiff & Malvárez 2004). In spite of their regional importance, there are few references on PPP for these ecosystems (e.g., Rahaingomanana et al. 2002, Angeler et al. 2005). In Argentina, the studies are restricted to the Otamendi wetland, included in the region called ¨Bajo Delta del Paraná¨ (Malvárez 1999), located in the Lower Paraná Basin (Fig. 1). Experimental studies conducted in the main shallow lake of this system showed that PPP were dominated by Pcy (Sinistro et al. 2006, de Tezanos Pinto et al. 2007). The first experiment was carried out in microcosms,

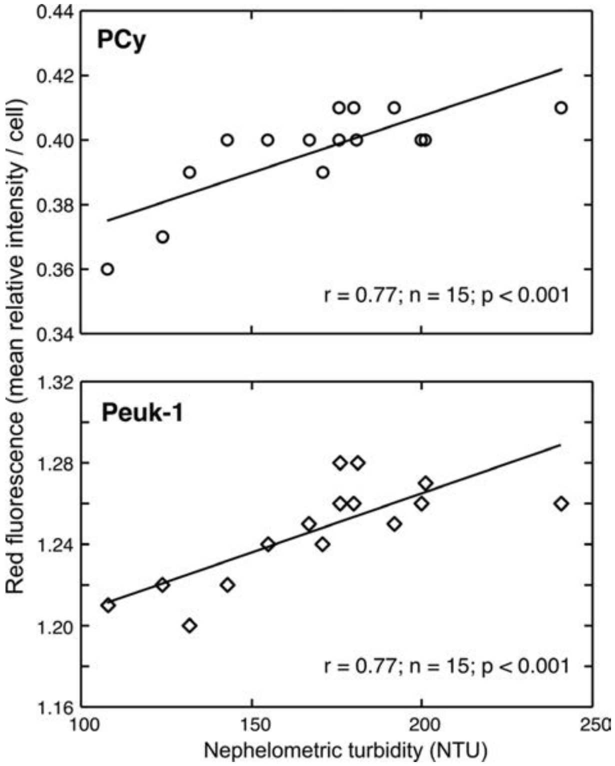

Fig. 5. Relationship between the red fluorescence intensity of each population (PCy and Peuk-1) in Lake Chascomús and the nephelometric turbidity. Relative red fluorescence intensity corresponds to the mean relative per-cell chlorophyll content, and it was estimated by dividing the log transformed mean value of FL3 of each population by the log mean value of FL3 of the fluorescent beads (1 µm, YG Fluoresbrite carboxylate microspheres, Polysciences Inc.). The Pearson correlation coefficient (r), number of samples (n) and significance (p) are included in each graph

and revealed a great grazing pressure on this fraction by their predators (heterotrophic flagellates, ciliates and mixotrophic algae). In a second experiment, samples for PPP analyses by flow cytometry were obtained from mesocosms that reproduced two contrasting scenarios in the wetland: open waters and with profuse free-floating plants coverage. These data were combined with a seasonal field survey to further analyse the PPP structure and production in different aquatic systems of this wetland, including two permanent shallow lakes (Laguna Grande and El Pescado), and relict oxbow lakes = ROLs (Izaguirre et al. 2010). Periods of contrasting temperatures and water levels were compared at sites differing in their underwater light climate conditions, mostly due to humic content and to free-floating plants coverage. PC-rich Pcy constituted more than 80% in almost all sites and dates, whereas Peuk were only dominant in one occasion at the ROLs. PPP abundances estimated by epifluorescence ranged from 5.7 x 10^3 to 4.6 x 10^5 cells. ml^{-1}, registering the highest values in the permanent shallow lakes and the lowest in the ROLs. These differences were attributed to the higher dissolved organic carbon concentrations present in the ROLs due to the abundant rooted and floating

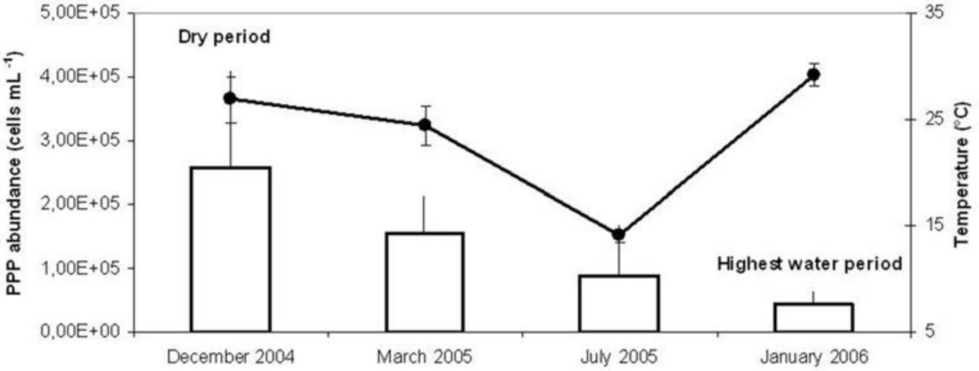

Fig. 6. Bars: mean total picophytoplankton abundance (with standard deviations) over an annual cycle at the main shallow lakes of the Otamendi Natural Reserve (Lower Paraná Basin). Line: mean water temperature. Modified from Izaguirre et al. (2010).

vegetation, which may favour heterotrophic bacteria over autotrophic picoplankton. The seasonal analysis revealed that both temperature and hydrometric level influenced PPP structure in the permanent shallow lakes: the highest densities were observed during the warm dry period, whereas the lowest ones occurred during a summer period of high water phase (Fig. 6). A similar behaviour was described by Camacho et al. (2003), who found scarce Pcy in lakes with low retention time during periods of high surface runoff. Moreover, the overflow triggered a high connectivity among the water bodies, which accounted by for a relatively more homogeneous PPP structure among systems. The different approaches combined in the study carried out by Izaguirre et al. (2010) demonstrated that the free-floating plants play an important role in shaping PPP structure. Changes in the vegetation-cover influence the light availability in the water column and the redox conditions, affecting the PPP composition. The flow cytometry analyses showed that under a thick macrophyte cover (both in natural environments as well as in the experimental conditions) anaerobic anoxygenic photosynthetic bacteria (AnAnPB) were dominant. The identified population would correspond to purple sulphur bacteria, since the signal in the cytogram coincides with that observed by Casamayor et al. (2007), who outlined that these bacteria are typical of a variety of anoxic environments or with episodic oxygen depletion. Contrarily, in enclosures without macrophyte-cover, as well as in natural open waters, AnAnPB were scarce or absent, whereas three different oxygenic picoplanktonic populations were detected: one PC-rich Pcy and two Peuk. On the other hand, this study also showed that PPP production was influenced by temperature and light, registering the highest values of production in summer in better illuminated environments. The photosynthetic rates per unit area of PPP were lower than those of the algae > 3 µm, varying from 1.5 to 100 mg C m^{-2} h^{-1}. Under dense free-floating plants coverage the production was limited by the low light intensities.

General remarks

The light quality and the nutrient contents are relevant abiotic factors in determining the photosynthetic picoplankton composition in the surveyed aquatic ecosystems from different Argentinean limnological regions. High light intensities characteristic of transparent and oligotrophic water bodies led to the dominance of PE-rich Pcy, whereas more turbid conditions in the aquatic environment typically resulted in a greater development of PC-rich Pcy, in agreement with the pattern described by different authors for other aquatic systems around the world. On the other hand, Peuk seem to be more abundant in some shallow turbid environments, whereas in environments with extreme light attenuation due to floating plants, AnAnPB become the dominant PPP component. The PPP abundances encountered in Argentinean water bodies fit in the trend observed by Vörös et al. (1998). The lowest PPP abundances are encountered in deep oligotrophic lakes from the Andean Patagonian region. The abundance of PPP increases together with the trophic status of the aquatic ecosystem, both in Patagonian and Chaco-Pampean limnological regions. However, in the hypertrophic end of the trophic spectrum this trend might either be continued or disrupted, registering a wide range of photosynthetic picoplankton numbers.

Acknowledgments

This work was supported by UBACYT X838-UBA, UBACYT X815-UBA PIP 5354 CONICET, FONCyT PICT 12332, FONCyT PICT 32732, FONCyT PICT 1168, PICT 2240, PICT 1029, PICT 25325, PIPo1301, UNSAM SA 06/017 and PAMPA Project.

References

Agawin, N. S. R., Duarte, C. M., Agustí, S., & Vaqué, D. (2004): Effect of N:P ratios on response of Mediterranean picophytoplankton to experimental nutrient inputs. – Aquat. Microb. Ecol. **34**: 54–67.

Allende, L., Tell, G., Zagarese, H. E., Torremorell, A., Pérez, G., Bustingorry, J., Escaray, R. & Izaguirre, I. (2009): Phytoplankton and primary production in clear-vegetated, inorganic-turbid and algal-turbid shallow lakes from Pampa Plain (Argentina). – Hydrobiologia **624**: 45–60.

Angeler, D. G., Sánchez Castillo, P., Rodrigo, M. A., Viedma, O. & Alvarez-Cobelas, M. (2005): On the Importance of Water Depth, Macrophytes and Fish in Wetland Picocyanobacteria Regulation. – Hydrobiologia **549**: 23–32.

Balseiro, E. G., Modenutti, B. E. & Queimaliños, C. P. (2001): Feeding of *Boeckella gracilipes* (Copepoda, Calanoidea) on ciliates and phytoflagellates in an ultraoligotrophic Andean lake. – J. Plankton Res. **23**: 849–857.

Balseiro, E. G., Queimaliños, C. P. & Modenutti, B. E. (2004): Grazing impact on autotrophic picoplankton in two south Andean lakes (Patagonia, Argentina) with different light:nutrient ratios. – Rev. Chil. Hist. Nat. **77**: 73–85.

Bastidas Navarro, M., Modenutti, B. E., Callieri, C., Bertoni, R. & Balseiro, E. G. (2009): Balance between primary and bacterial production in North Patagonian shallow lakes. – Aquat. Ecol. **43**: 867–878.

Bell, T. & Kalff, J. (2001): The contribution of picophytoplankton in marine and freshwater systems of different trophic status and depth. – Limnol. Oceanogr. **46**: 1243–1248.

Callieri, C. (2008): Picophytoplanton in freshwater ecosystems: the importance of small-sized phototrophs. – Freshw. Rev. **1**: 1–28.

Callieri, C., Modenutti, B. E., Queimaliños, C. P., Bertoni, R. & Balseiro, E. G. (2007): Production and biomass of picophytoplankton and larger autotrophs in Andean ultraoligotrophic lakes: differences in light harvesting efficiency in deep layers. –Aquat. Ecol. **41**: 511–523.

Callieri, C. & Stockner, J. G. (2002): Freshwater autotrophic picoplankton: a review. – J. Limnol. **61**: 1–14.

Callieri, C., Coci, M., Corno, G., Macek, M., Modenutti, B., Balseiro, E. & Bertoni, R. (2013): Phylogenetic diversity of nonmarine picocyanobacteria. – FEMS Microbiol. Ecol. **85**: 293–301

Camacho, A., Miracle, M. R. & Vicente, E. (2003): Which factors determine the abundance and distribution of picocyanobacteria in inland waters? A comparison among different types of lakes and ponds. – Arch. Hydrobiol. **157**: 321–338.

Cano, M. G. (2008): Fitoperifiton de un lago somero y su relación con los estados de biequilibrio. – Tesis Doctoral, Univ. Nacional de La Plata, Argentina.

Caravati, E., Callieri, C., Modenutti, B. E., Corno, G., Balseiro, E. G., Bertoni, R. & Michaud, L. (2010): Picocyanobacterial assemblages in ultraoligotrophic Andean lakes reveal high regional microdiversity. – J. Plankton Res. **32**: 357–366.

Casamayor, E. O., Ferrera, I., Cristina, X., Borrego, C. M. & Gasol, J. M. (2007): Flow cytometric identification and enumeration of photosynthetic sulphur bacteria and potential for ecophysiological studies at the single-cell level. – Environm. Microbiol. **9**: 1969–1985.

Craig, S. R. (1987): The distribution and contribution of picoplankton to deep photosynthetic layers in some meromictic lakes. – Acta Acad. Aboensis **47**: 55–81.

de Tezanos Pinto, P., Allende, L. & O´Farrell, I. (2007): Influence of free-floating plants on the structure of a natural phytoplankton assemblage: an experimental approach. – J. Plankton Res. **29**: 47–56.

Diovisalvi, N., Berasain, G., Unrein, F., Colautti, D., Fermani, P., Llames, M. E., Torremorell, A., Lagomarsino, L., Pérez, G., Escaray, R., Bustingorry, J., Ferraro, M. & H.E. Zagarese, H. E. (2010): Chascomús: estructura y funcionamiento de una laguna pampeana turbia. – Ecología Austral **20**: 115–127.

Drakare, S. (2002): The role of picophytoplankton in lake food webs. – PhD Thesis, Uppsala University.

Fermani, P., Diovisalvi, N., Torremorell, A., Lagomarsino, L., Zagarese, H. E. & Unrein, F. (2013): The microbial food web structure of a hypertrophic warm temperate shallow lake, as affected by contrasting zooplankton assemblages. – Hydrobiologia **714**: 115–130.

Greisberger, S., Dokulil, M. T. & Teubner, K. (2007): A comparison of phytoplankton size-fractions in Mondsee, an alpine lake in Austria: distribution, pigment composition and primary production. – Aquat. Ecol. **42**: 379–389.

Izaguirre, I., Pizarro, H., de Tezanos Pinto, P., Rodriguez, P., O´Farrel, I., Unrein, F. & Gasol, J. M. (2010): Macrophyte influence on the structure and productivity of photosynthetic picoplankton in wetlands. – J. Plankton Res. **32**: 221–238.

Jacquet, S., Lennon, J.-F., Marie, D. & Vaulot, D. (1998): Picoplankton population dynamics in coastal waters of the northwestern Mediterranean Sea. – Limnol. Oceanogr. **43**: 1916–1931.

Kranewitter, V. (2010): Estudio intensivo de la dinámica temporal del picoplancton de la laguna Chascomús. – Tesis de Grado, Univ. de Buenos Aires, Argentina.

Llames, M. E., Lagomarsino, L., Diovisalvi, N., Fermani, P., Torremorell, A., Pérez, G., Unrein, F., Bustingorry, J., Escaray, R., Ferraro, M. & Zagarese, H. E. (2009): The effects of light availability in shallow, turbid waters: a mesocosm study. – J. Plankton Res. **12**: 1517–1529.

Malvárez, A. I. (1999): El delta del río Paraná como mosaico de humedales. – In: Malvárez, A. I. (ed.): Tópicos sobre humedales subtropicales y templados de Sudamérica. UNESCO, Montevideo, pp. 35–53.

Modenutti, B. E. & Balseiro, E. G. (2002): Mixotrophic ciliates in an Andean lake: dependence on light and prey of an *Ophrydium naumanni* population. – Freshw. Biol. **47**: 121–128.

Modenutti, B. E., Queimaliños, C. P., Balseiro, E. G. & Reissig, M. (2003): Impact of different zooplankton structures on the microbial food web of a South Andean oligotrophic lake. – Acta Oecologica **24**: S289–S298.

Morris, D. P., Zagarese, H. E., Williamson, C. E., Balseiro, E. G., Hargreaves, B. R., Modenutti, B. E., Moeller, R. & Queimaliños, C. P. (1995): The Attenuation of Solar UV Radiation in Lakes and the Role of Dissolved Organic Carbon. – Limnol. Oceanogr. **40**: 1381–1391.

Nagata, T., Takai, K., Kawanobe, K., Kim, D.-S., Nakazato, R., Guselnikova, N., Bondarenko, N., Mologawaya, O., Kostrnova, T., Drucker, V., Satoh, Y. & Watanabe, Y. (1994): Autotrophic picoplankton in southern Lake Baikal: abundance, growth and grazing mortality during summer. – J. Plankton Res. **16**: 945–959.

Neiff, J. J. & Malvárez, A. I. (2004): Grandes humedales fluviales. – In*:* Malvárez, A. I. & Bó, R. F. (eds.): Bases ecológicas para la clasificación e inventario de humedales en Argentina. – FCEyN-UBA, RAMSAR, USFWS, USDS, Buenos Aires, pp. 77–85

Pérez, G., Queimaliños, C. P. & Modenutti, B. E. (2002): Light climate and plankton in the deep chlorophyll maxima in North Patagonian Andean lakes. – J. Plankton Res. **24**: 591–599.

Pérez, G., Queimaliños, C. P., Balseiro E. G. & Modenutti, B. E. (2007): Phytoplankton absorption spectra along the water column in deep North Patagonian Andean lakes (Argentina). – Limnologica **37**: 3–16.

Pick, F. R. & Agbeti, M. (1991): The Seasonal Dynamics and Composition of Photosynthetic Picoplankton Communities in Temperate Lakes in Ontario, Canada. – Int. Rev. Hydrobiol. **76**: 565–580.

Quirós, R., Renella, A. M., Boveri, M. B., Rosso, J. J. & Sosnovsky, A. (2002): Factores que afectan la estructura y funcionamiento de las lagunas pampeanas. – Ecología Austral **12**: 175–185.

Rahaingomanana, N., Barbosa, F. A. R. & Petrucio, M. M. (2002): Fractioned primary production of phytoplankton in lakes of the Rio Doce Valley (Southeastern Brazil). – Verh. Int. Ver. Limnol. **28**: 695–699.

Richardson, T. L. & Jackson, G. A. (2007): Small Phytoplankton and Carbon Export from the Surface Ocean. – Science **315**: 838–840.

Schiaffino, M. R., Gasol, J. M., Izaguirre, I. & Unrein, F. (2013): Picoplankton abundance and cytometric group diversity along a trophic and latitudinal lake gradient. – Aquat. Microb. Ecol. **68**: 231–250.

Silvoso, J., Izaguirre, I. & Allende, L. (2011): Picoplankton structure in clear and turbid eutrophic shallow lakes: A seasonal study. – Limnologica **41**: 181–190.

Sinistro, R., Izaguirre, I. & Asikian, V. (2006): Experimental study on the microbial plankton community in a South American wetland (Lower Paraná River Basin) and the effect of the light deficiency due to the floating macrophytes. – J. Plankton Res. **28**: 753–768.

Sommaruga, M. & Robarts, R. D. (1997): The significance of autotrophic and heterotrophic picoplankton in hypereutrophic ecosystems. – FEMS Microbiol. Ecol. **24**: 187–200.

Søndergaard, M. (1991): Phototrophic picoplankton in temperate lakes: seasonal abundance and importance along a trophic gradient. – Int. Rev. Hydrobiol. **76**: 505–522.

Steitz, A. & Velimirov, B. (1999): Contribution of Picocyanobacteria to total primary production and community respiratory losses in a backwater system. – J. Plankton Res. **21**: 2341–2360.

Stockner, J. G. (1991): Autotrophic picoplankton in freshwater ecosystems: the view from the summit. – Int. Rev. Hydrobiol. **76**: 483–492.

Stockner, J. G. & Antia, N. J. (1986): Algal picoplankton from marine and freshwater: a multidisciplinary perspective. – Can. J. Fish. Aquat. Sci. **43**: 2472–2503.

Stockner, J. G. & Porter, K. G. (1988): Microbial foodwebs in freshwater planktonic ecosystems. – In: Carpenter, S. R. (ed.): Complex Interactions in Lake Communities. – Springer-Verlag, New York, pp. 69–84.

Stomp, M., Huisman, J., Vörös, L., Pick, F. R., Laamanen, M., Haverkamp, T. & Stal, L. J. (2007): Colourful coexistence of red and green picocyanobacteria in lakes and seas. – Ecology Letters **10**: 290–298.

Torremorell, A., Llames, M. E., Pérez, G., Escaray, R., Bustingorry, J. & Zagarese, H. E. (2009): Annual patterns of phytoplankton density and primary production in a large, shallow lake: the central role of light. – Freshw. Biol. **54**: 437–449.

Vörös, L., Callieri, C., Balogh, K. V. & Bertoni, R. (1998): Freshwater picocyanobacteria along a trophic gradient and light quality range. – Hydrobiologia **369/370**: 117–125.

Vörös, L., Mózes, A. & Somogyi, B. (2009): A five-year study of autotrophic winter picoplankton in Lake Balaton, Hungary. – Aquat. Ecol. **43**: 722–734.

Weisse, T. (1993): Dynamics of autotrophic picoplankton in marine and freshwater ecosystems. – Adv. Microb. Ecol. **13**: 327–370.

Zunino, L. & Diaz, M. (2000): Autotrophic picoplankton along a trophic gradient in Andean-Patagonian lakes. – Verh. Int. Ver. Limnol. **27**: 1895–1899.