

# Balance between primary and bacterial production in North Patagonian shallow lakes

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**Abstract** The shallow Andean North Patagonian lakes are suitable environments for the evaluation of autotrophic and heterotrophic production under a scenario of high radiation in high dissolved organic matter (DOM) systems. We aimed to study the balance between primary and bacterial production in three shallow Andean lakes, in a summer sampling (high irradiance condition). Our hypothesis is that two factors would interact: high light and high DOM, affecting bacteria and algae. We carried out experiments of bacterial production (BP) by measuring [ $^{14}\text{C}$ ]-L-leucine incorporation and PP by  $^{14}\text{C}$  uptake in two fractions: picophytoplankton and phytoplankton  $>2\ \mu\text{m}$ . Cell abundance, chlorophyll *a*, nutrients, DOM, light, and temperature were also measured. The contribution of picophytoplankton to total primary production (PP) was, in general, very high exceeding 50%. Picophytoplankton was photosynthetically more efficient than the larger autotrophs in all lakes. We observed a decrease in PP at surface levels due the high solar irradiances, while BP was not affected. Changes in the PP:BP ratios were observed

in relation to DOM content and light effect. Our data indicate that the amount of available DOM drives the balance between PP and BP. However, solar radiation should be included as an important factor since PP:BP ratio may decrease because of PP photoinhibition.

**Keywords** Picophytoplankton ·  
Phytoplankton  $>2\ \mu\text{m}$  · Bacterioplankton ·  
Primary and bacterial production ·  
Dissolved organic matter · Shallow Andean lakes

## Introduction

In lake ecosystems the energy flow is maintained mainly by algae, using light as energy source, and by heterotrophic bacteria, using autochthonous and allochthonous organic matter for their metabolic requirements (Moran and Hodson 1990; Jones 1992). High rates of primary production (PP) provide an important carbon source for epilimnetic bacteria (Lovell and Konopka 1985), while in systems with high humic substances bacterioplankton can even dominate the total energy mobilization (Hessen 1998; Jansson et al. 2000). Bacteria compete efficiently for the same inorganic nutrients that limit phytoplankton growth (Currie and Kalff 1984) and, as usually, show that higher affinities for phosphorus than phytoplankton are frequently superior competitors at low

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phosphorus concentrations (Gurung et al. 1999). The higher affinity of bacteria for nutrients has been linked to a greater surface area to volume ratio, promoting efficient uptake of nutrients, which gives them the competitive advantage over larger autotrophs when nutrients are scarce (Hessen et al. 1994; Jansson et al. 1996). Also, within phytoplankton, differences in size have important ecological and physiological significance. Floating, sedimentation, nutrient uptake, and grazing are processes that are influenced by algae size (Uehlinger and Bloesch 1989). For instance, the small-sized phytoplankton fraction (picophytoplankton: 0.2–2  $\mu\text{m}$ ) do best in resource-poor habitats in comparison with the larger size fraction (phytoplankton >2  $\mu\text{m}$ ) (Callieri 2008) for the same reason as bacteria (high surface to volume ratio). Therefore, picophytoplankton often dominates the summer production in oligotrophic clearwater lakes (Stockner 1991; Callieri et al. 2007) and in autumn in the mesotrophic, Alpine lake Mondsee in Austria (Greisberger et al. 2008). In addition, picophytoplankton seems to be pre-adapted to low levels of photosynthetically active radiation (PAR; Callieri et al. 1996; Gervais et al. 1997). Callieri et al. (2007) found that low light and low TDP may interact to create the most favorable conditions for the smaller photosynthetic organisms.

Considering the cell size, bacterioplankton and picophytoplankton would compete for nutrient very efficiently; however, in this case light can also influence the outcome of competition. In highly transparent environments, the water itself becomes a major radiation-absorbing component, but in less transparent freshwaters the amount of colored dissolved organic matter (DOM) is the major factor responsible for the absorption of at least the short wavelength of the spectrum (ultraviolet radiation; Osburn et al. 2001). The absorption of light by these dissolved compounds, mainly humic substances, may cause direct competition with phytoplankton for capture of available light energy (Kirk 1980). Therefore, a high availability of colored DOM becomes important substrate for bacteria but also affects light for photosynthesis (Bergström and Jansson 2000). In that sense, the absorbance of the green and blue wavelengths of this spectrum reduces light quality for autotrophs (Pick and Agbeti 1991; Stomp et al. 2007). Thus, the production by photoautotrophic organisms would be restricted in humic lakes by poor light

climate (Carpenter et al. 1998) and the outcome of competition between the autotrophic picoplankton, heterotrophic picoplankton and larger phytoplankton would be influenced by DOM inputs (Drakare et al. 2002). The ratio between PP and bacterial production (BP) can be used as an estimation of the autotrophy/heterotrophy balance (Jansson et al. 2000). A PP:BP < 1.0 means that BP provides more particulate carbon than phytoplanktonic production; then, the food base for grazers is mainly heterotrophic (Jansson et al. 2000).

The North Patagonian Andean lakes of Argentina (41° S) comprise large deep and small shallow lakes of glacial origin (Modenutti et al. 1998). Shallow lakes (maximum depth < 15 m) in comparison with large ones show higher light attenuation coefficients, with higher concentration of dissolved yellow substances that cause substantial differences in the spectral light quality (Pérez et al. 2002). The high content of DOM present in these lakes could be associated with the presence of annual macrophytes in their extended littoral zones (Bastidas Navarro et al. 2008). In addition, these lakes are located in a region under the influence of the Antarctic ozone hole (Díaz et al. 2006). Consequently, these environments are very interesting for the evaluation of autotrophic and heterotrophic production under a scenario of high radiation in high DOM systems. In these lakes, we aimed to study the contribution of bacterioplankton and phytoplankton to lake production in a summer sampling (high irradiance condition, and the highest annual autotrophic biomass), considering that DOM would influence bacterial activity, interacting with light climate, thus affecting the different phytoplanktonic size fractions. As the main hypothesis of this study, we propose that in shallow Andean lakes bacteria and algae would be affected by the interaction of high irradiances and high DOM content. Previous studies in these lakes have shown that bacteria are affected by quantity and quality of DOM (Bastidas Navarro et al. 2008); therefore, our main goal here was to study the balance between primary and bacterial production. We performed an early summer survey in three shallow North Patagonian Andean lakes measuring light climate along the water column and assessing bacterial and photosynthetic production and efficiency of two phytoplankton size fractions: picophytoplankton and phytoplankton >2  $\mu\text{m}$ .

## Materials and methods

### Field study and sampling

Three small lakes included in the Nahuel Huapi National Park, Patagonia, Argentina, around 41° S and 71° W, were studied during summer (January 2006): Escondido, Morenito, and El Trébol. The selected lakes are small (area  $\leq 1 \text{ km}^2$ ) and shallow ( $Z_{\text{max}} \leq 12 \text{ m}$ ) (Table 1; Fig. 1). Their littoral zones are colonized by two aquatic weeds: the emergent *Schoenoplectus californicus* (Meyer) Soják and the submersed *Potamogeton linguatus* Hangstrom. The climate of the region is temperate cool (mean annual temperature 8.7°C) with an annual precipitation of 1,500 mm (Páruelo et al. 1998). The surrounding vegetation is constituted by a mixed forest of *Nothofagus dombeyi* (Mirb.) Blume and *Austrocedrus chilensis* (D. Don) Florin et Boutleje. Planktonic communities of the lakes were previously described by Balseiro and Modenutti (1990), Balseiro et al. (1997), Díaz and Pedrozo (1993), and Modenutti and Pérez (2001).

We carried out field work and in-lake experiments once on each lake (January 2006) in a sampling point located at the deepest part of each lake. The three lakes were studied in three consecutive days in order to minimize variation in phytoplankton and bacterioplankton composition. We performed vertical water column profiles of temperature, ultraviolet (UV) bands (UV-B 305 and UV-A 340 nm) and PAR (400–700 nm) with a PUV 500B submersible radiometer (Biospherical Instruments). Oxygen concentration and conductivity were also measured on each sampling occasion with an oxymeter and conductimeter (YSI Model 85). Water samples were obtained with a Van Dorn bottle at 0, 3, and 6 m depth in Lake Escondido, and at 0, 4, and 8 m in lakes Morenito and El Trébol. The water was distributed in different acid washed (HCl) containers for subsequent analysis.

### Chemical and biological parameters

Water for nutrient determination was immediately carried to laboratory in darkness and thermally insulated. Total dissolved phosphorus (TDP) and

**Table 1** Location, morphometry, light parameters and chemical features of the three shallow Patagonian Andean lakes

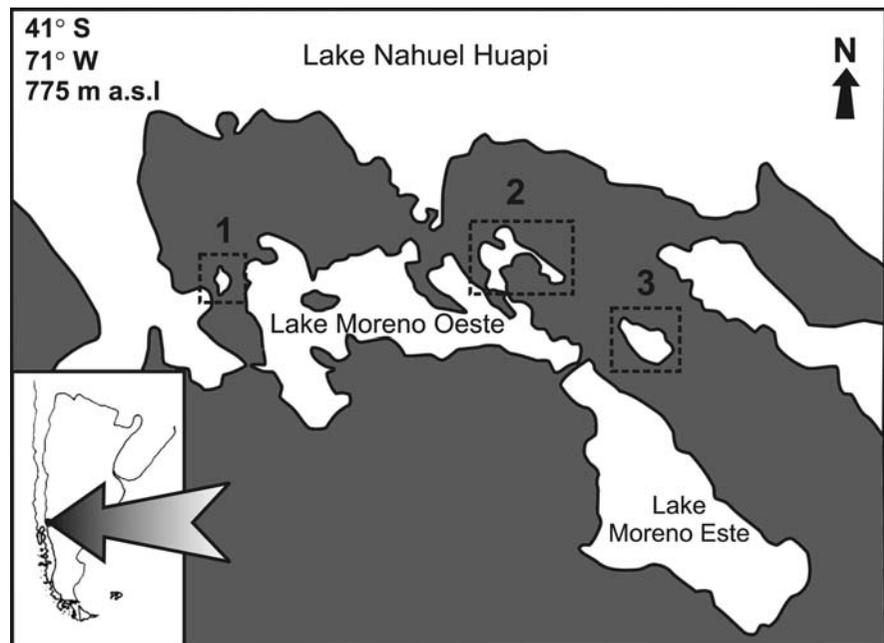
Lake	Escondido	Morenito	El Trébol
Location	41°3' S 71°34' W	41°3' S 71°30' W	41°2' S 71°4' W
Surface (km <sup>2</sup> )	0.08	0.83	0.3
$Z_{\text{max}}$ (m)	8	12	12
$K_d$ (PAR)	0.586	0.430	0.505
$K_d$ (305 nm)	8.85	3.44	3.33
$K_d$ (340 nm)	7.6	2.67	2.9
$Z_{1\%}$ (PAR)	7.8	10.7	9.1
$I_0$ ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ )	2,118	1,768	2,225
PAR% at 3 or 4 m	17.2	13.3	17.9
PAR% at 6 or 8 m	2.9	1.8	3.2
DOC (mg l <sup>-1</sup> )	2.96 $\pm$ 0.09	1.80 $\pm$ 0.003	2.27 $\pm$ 0.09
$a_{250}:a_{365}$	5.17 $\pm$ 0.05	5.95 $\pm$ 0.46	7.31 $\pm$ 0.21
TDP ( $\mu\text{g l}^{-1}$ )	4.05 $\pm$ 0.29	5.70 $\pm$ 0.69	5.26 $\pm$ 0.33
TP ( $\mu\text{g l}^{-1}$ )	6.24 $\pm$ 0.09	11.96 $\pm$ 2.01	11.78 $\pm$ 1.62
DIN ( $\mu\text{g l}^{-1}$ )	55.42 $\pm$ 19.82	20.75 $\pm$ 1.15	32.32 $\pm$ 15.6

Chemical features are expressed as mean of the three depth levels  $\pm$  standard error

$Z_{\text{max}}$ , maximum depth;  $K_d$ , extinction coefficient;  $Z_{1\%}$ , depth of 1% of surface irradiance; 305 nm (UV-B) and 340 nm (UV-A);  $I_0$  is PAR irradiance at the surface

PAR photosynthetically active radiation, DOC dissolved organic carbon, TDP total dissolved phosphorus, TP total phosphorus, DIN dissolved inorganic nitrogen

**Fig. 1** Geographical location of the three studied lakes. 1 Lake Escondido, 2 Lake Morenito, 3 Lake El Trébol



dissolved inorganic nitrogen (DIN = the sum of nitrate and ammonium) were determined on lake water filtered through GF/F filter. Total phosphorus (TP) was determined directly on unfiltered lake water. For TP and TDP determinations, the samples were digested with persulphate at 125°C at 1.5 atm for 1 h. The concentrations were obtained through the ascorbate-reduced molybdenum method (APHA 2005). Ammonium determination was measured with the indophenol blue method and nitrate with the cadmium reduction method (APHA 2005). Dissolved organic carbon (DOC) concentration was measured on 50 ml filtered lake water (GF/F precombusted filters) with a Shimadzu analyzer (TOC 5000A). Additionally, we carried out spectrophotometric scans of the same filtered lake water in a 10 cm quartz cuvette using a double beam spectrophotometer Shimadzu UV2450 in order to obtain DOM absorbance spectrum. Absorbance units were converted to absorption coefficients as follows:

$$a = 2.303A/l$$

where  $a$  is the absorption coefficient ( $\text{m}^{-1}$ ),  $A$  is the absorbance, and  $l$  is the cuvette path length (m). The relative size of DOM was estimated through the ratio  $a_{250}:a_{365}$  (Pérez and Sommaruga 2007).

Autotrophic biomass estimated as chlorophyll  $a$  (Chl  $a$ ) concentration was analyzed discriminating

between the contribution of the picophytoplankton ( $<2 \mu\text{m}$ ) and phytoplankton  $>2 \mu\text{m}$ . For the fraction  $>2 \mu\text{m}$ , 100 ml lake water were filtered through a 2.0  $\mu\text{m}$  pore size polycarbonate filter (Nuclepore). Then, the filtrate was filtered through a 0.2  $\mu\text{m}$  pore size polycarbonate filter (Nuclepore) in order to analyze the smaller fraction. For control, total Chl  $a$  was also determined directly filtering 100 ml whole sample on 0.2  $\mu\text{m}$  pore size polycarbonate filter (Nuclepore). Chl  $a$  concentration was measured by extraction with 90% ethanol following Nusch (1980) and measured with a 10-AU fluorometer (Turner Design). The fluorometer was previously calibrated against direct spectrophotometric measurements.

Samples for bacteria and autotrophic picophytoplankton counting were fixed with filtered formaldehyde (0.2  $\mu\text{m}$ , final concentration 2% v/v). Bacteria were stained with 4',6-diamidino-2-phenylindole (DAPI, final concentration 0.2% w/v) according to Porter and Feig (1980). Both bacteria and picophytoplankton were enumerated on 0.2  $\mu\text{m}$  pore size black membrane filters (Poretics) at 1,250 $\times$  magnification with an Olympus BX50 epifluorescence microscope, using UV light (U-MWU filter) for bacteria and blue light (U-MWB filter) and green light (U-MWG filter) for picophytoplankton. Phycoerythrin and phycocyanin rich picocyanobacteria cells were distinguished based on their different

fluorescence signals (MacIssac and Stockner 1993). Cells were measured with an image analysis system (Image ProPlus).

A volume of 250 ml lake water was immediately fixed with acid Lugol solution for phytoplankton quantification. Samples were counted with an inverted microscope using 50-ml Utermöhl chambers.

#### Net primary production (NPP) and bacterial production determinations

Net primary production of the two autotrophic fractions was measured in each lake as  $\text{H}^{14}\text{CO}_3^-$  in situ uptake (Steeman-Nielsen 1951, 1952). Dark bottle measurements were substituted by the “time 0” organic  $^{14}\text{C}$  measurement by adding the isotope to the dark bottle and immediately filtering and analyzing it (Fahnenstiel et al. 1994). Water samples were taken from the different sampling depths (0, 3, and 6 m in Lake Escondido and 0, 4, and 8 m in lakes Morenito and El Trébol) with a Van Dorn bottle. The incubation was carried out in quartz tubes (14 ml each) added with a sodium bicarbonate solution containing  $^{14}\text{C}$  (Amersham,  $2.22 \text{ KBq NaH}^{14}\text{CO}_3 \text{ ml}^{-1}$ ). Tubes were held in a frame at the three different depths, in three replicates. Incubations were performed around noon, for 4 h. After incubation, 500  $\mu\text{l}$  aliquots were taken to check total activity. In order to discriminate between the PP of picophytoplankton and  $>2 \mu\text{m}$  fractions, the samples were filtered using plastic disposable syringes and plastic 25 mm filter holders. The autotrophic fraction  $>2 \mu\text{m}$  was obtained filtering through polycarbonate filters (Osmonics<sup>TM</sup>) of 2  $\mu\text{m}$ . The filtrate was concentrated on 0.22  $\mu\text{m}$  pore size nitrocellulose membranes (Millipore<sup>TM</sup>). Filters were transferred into 20-ml scintillation vials and acidified with 200  $\mu\text{l}$  1 N HCl for 60 min. After adding 10 ml scintillation liquid, the vials were counted in a Beckman LS3801 scintillation counter. Photosynthetic carbon assimilation was calculated based on the proportion between  $^{14}\text{C}$  uptake and total inorganic carbon (TIC) availability (Steeman-Nielsen 1951, 1952). The TIC availability was determined from pH and alkalinity measurements on lake water.

Bacteria production was determined immediately after sampling by measuring [ $^{14}\text{C}$ ]-L-leucine incorporation (Simon and Azam 1989) in the dark at the in situ lake temperature for 2 h. We incubated 1.4 ml lake water (three replicates) and one control with

15  $\mu\text{l}$  of  $^{14}\text{C}$ -leucine (specific activity: leucine  $11.3 \text{ GBq mmol}^{-1}$ , Amersham, UK) at 90 nM final concentration. Control was fixed with 75  $\mu\text{l}$  of 100% trichloroacetic acid (TCA). After incubation, the samples were also fixed with TCA as control. The samples were then maintained for 30 min at the incubation temperature, after which they were centrifuged (10 min, 12,000 rpm). After removing the supernatant, 1.4 ml 5% TCA were added to each microtube and then centrifuged again. This procedure was carried out twice and then rinsed with ethanol and centrifuged again. The supernatant was removed and 1 ml scintillation liquid was added. Then, microtubes were placed in scintillation vials and counted in a Beckman LS 3801 TA scintillation counter.

The ratio between PP and BP was calculated for each lake and depth, in order to analyze interaction between trophic levels and to estimate the autotrophy/heterotrophy balance.

#### Data analysis

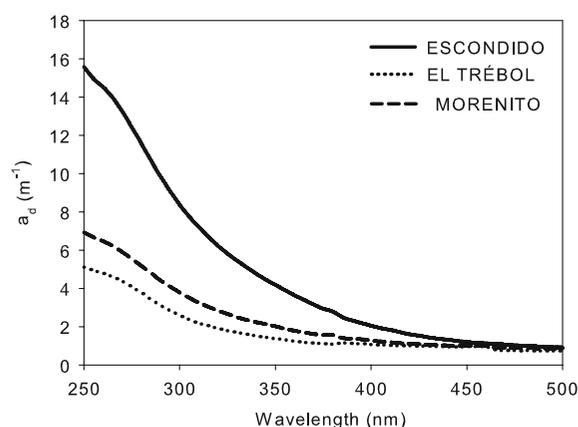
Differences in DOC, nutrient concentrations and the  $a_{250}:a_{365}$  ratio among lakes were tested with one-way ANOVA. Also a one-way ANOVA was performed to test the differences in the PE:PC ratio among depth within each lake. For the analysis of phytoplankton biomass, primary and bacterial production and the PP:BP ratio, a  $3 \times 3$  factorial analysis of variance was applied (two-way ANOVA), with lakes and depth as factor. Normality and homoscedasticity were checked before analysis, and transformation were applied when needed. The post-hoc comparisons were carried out with the Tukey test with an overall significance level of  $P = 0.05$ .

## Results

In Lake El Trébol the whole water column was at 16°C while lakes Escondido and Morenito exhibited a thermal gradient from 18°C at surface to 11°C (Escondido) and to 14°C (Morenito). Dissolved oxygen concentration remained always at 100% saturation and conductivity was fairly constant within and between lakes with values of 60  $\mu\text{S cm}^{-1}$ . The euphotic zone of the three lakes extended approximately up to the maximum depth of each lake

(Table 1). The irradiance received at the surface level of lakes during the studied period was high for both PAR ( $\sim 2,000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ) and UV radiation ( $\sim 1.8 \mu\text{W cm}^{-2} \text{nm}^{-1}$  in the 305 nm band). Considering the ultraviolet radiation, Lake Escondido was less transparent than Morenito and El Trébol, showing almost threefold  $K_d$  values (at 305 and 340 nm; Table 1; Fig. 2). The DOC concentration varied among lakes (one-way ANOVA,  $P < 0.001$ ) with Lake Escondido exhibiting the highest values (Table 1). DOC showed a direct relationship with  $K_d$  of each wavelength; our data lie within the 95% confident limits of the models of Morris et al. (1995).

The spectrophotometric absorbance spectrum of DOM lake water was observed to develop a similar



**Fig. 2** Spectrophotometric absorbance spectrum of the three studied lakes

trend in the three lakes, with maximum absorbance values in the UV band. Nevertheless, Lake Escondido exhibited a much higher absorbance at the UV-B and UV-A range (Fig. 2). The ratio  $a_{250}:a_{365}$  was considered as a measure of the relative size of DOM and resulted in differences among lakes (post-hoc Tukey test all pairs,  $P < 0.02$ ). Lake Escondido exhibited the lowest ratio values, suggesting a comparatively higher mean molecular size of DOM.

The nutrient concentration (TP, TDP, and DIN) and the phytoplanktonic biomass (Chl *a*) showed low values (Tables 1, 2), typical of oligotrophic lakes. Nutrient concentration did not show much variation among lakes (one-way ANOVA, among lakes  $P > 0.05$  for TP, TDP, and DIN). The biomass of the picophytoplankton was different among lakes but not in the vertical distribution along the water column (two-way ANOVA among lakes,  $P = 0.010$  and among depths,  $P = 0.356$ ); nevertheless only Lake El Trébol differed (post-hoc Tukey test: Escondido vs. El Trébol,  $P = 0.024$ ; El Trébol vs. Morenito,  $P = 0.011$ ). The phytoplankton  $> 2 \mu\text{m}$  differed both among lakes and depths (two-way ANOVA, among lakes  $P = 0.004$  and among depth  $P = 0.019$ ). In particular, the biomass of Lake El Trébol differed significantly from the other lakes (post-hoc Tukey test: El Trébol vs. Escondido,  $P = 0.004$ ; El Trébol vs. Morenito,  $P = 0.024$ ). In all lakes, the surface layers had significant lower biomass values (post-hoc Tukey test: 0 vs. 6–8 m,  $P = 0.020$ ; 0 vs. 3–4 m,  $P = 0.038$ ).

Lakes Escondido and Morenito presented similar algae ( $> 2 \mu\text{m}$ ) composition with Chrysophyceae,

**Table 2** Chlorophyll *a* concentration (Chl *a*), primary production (PP) and percentage of contribution of PP  $< 2 \mu\text{m}$  to total PP, in the three shallow Patagonian Andean lakes

Lake	Depth (m)	Chl <i>a</i> $< 2 \mu\text{m}$ ( $\mu\text{g l}^{-1}$ )	Chl <i>a</i> $> 2 \mu\text{m}$ ( $\mu\text{g l}^{-1}$ )	PP $< 2 \mu\text{m}$ ( $\mu\text{g C l}^{-1} \text{h}^{-1}$ )	PP $> 2 \mu\text{m}$ ( $\mu\text{g C l}^{-1} \text{h}^{-1}$ )	PP $< 2 \mu\text{m}$ (% on total PP)
Escondido	0	0.72	0.42	$0.43 \pm 0.043$	$0.14 \pm 0.005$	75.4
	3	1.23	1.15	$0.54 \pm 0.043$	$0.40 \pm 0.029$	57.4
	6	1.28	1.59	$0.25 \pm 0.013$	$0.16 \pm 0.009$	61.0
Morenito	0	0.36	0.64	$0.96 \pm 0.053$	$0.41 \pm 0.029$	70.1
	4	0.22	2.87	$3.16 \pm 0.073$	$2.83 \pm 0.096$	52.8
	8	0.13	3.48	$0.84 \pm 0.116$	$0.50 \pm 0.104$	62.7
El Trébol	0	2.61	3.01	$0.32 \pm 0.029$	$1.23 \pm 0.183$	20.6
	4	5.78	4.73	$0.24 \pm 0.002$	$3.87 \pm 0.087$	5.8
	8	4.65	4.66	$0.28 \pm 0.009$	$0.43 \pm 0.029$	39.4

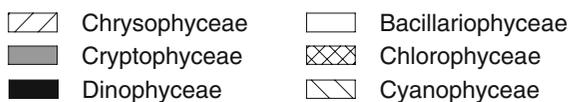
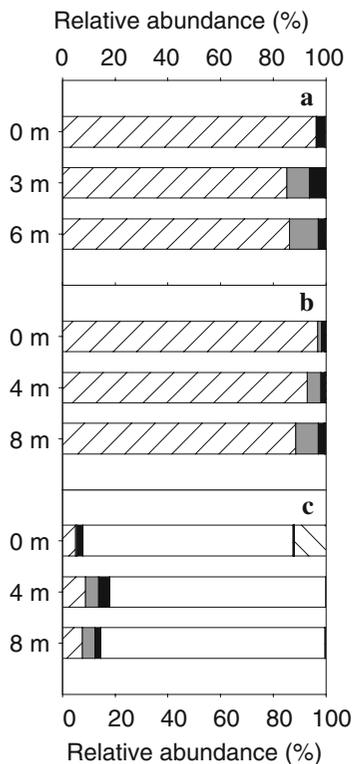
PP is expressed as mean  $\pm$  standard error

Cryptophyceae, and Dinophyceae as dominant groups. In particular, *Chrysochromulina parva* Lackey, *Rhodomonas lacustris* (Pascher & Ruttner) Javornicky, *Ochromonas* sp., *Cryptomonas* sp. and *Gymnodinium varians* Maskell were the dominant species. On the other hand, phytoplankton of Lake El Trébol was dominated by Bacillariophyceae (Fig. 3) with *Cyclotella meneghiniana* Kütz., *Rhizosolenia longiseta* Zach., and *Aulacoseira granulata* (Ehr) Simonsen as dominant. Additionally, at the surface layer, we observed the presence of the cyanobacteria *Chroococcus* sp. The larger phytoplanktonic fraction was observed to be more abundant (up to 6,474 cell ml<sup>-1</sup>) in Lake El Trébol, whereas Lake Escondido presented the lowest ones (~1,500 cell ml<sup>-1</sup>).

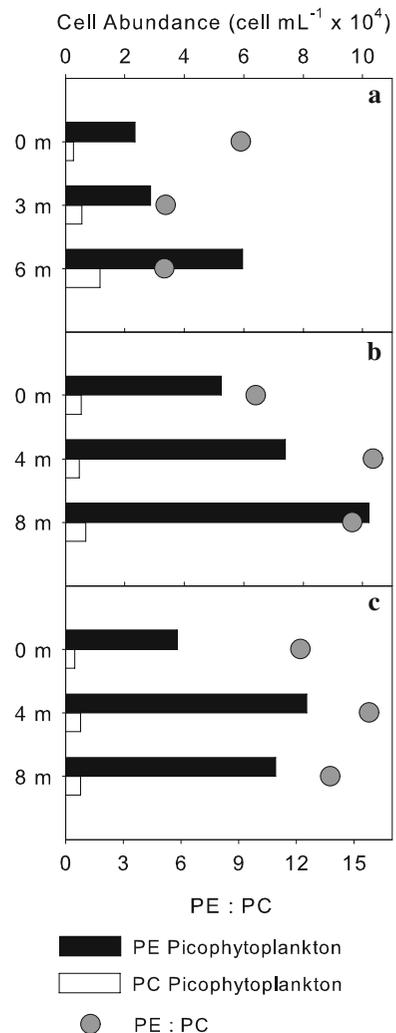
Picophytoplankton cell abundance did not differ greatly among lakes, and it was composed by

prokaryotic cocci (*Synechococcus* spp.) dominated by phycoerythrin-rich (PE) cells. PE cells increased their abundance towards the bottom in lakes Escondido and Morenito (Fig. 4). On the other hand, phycocyanin-rich (PC) cells were quite constant along the water column in lakes Morenito and El Trébol and increased slightly near the bottom in Lake Escondido. In this lake we observed a decrease in the PE:PC ratio with depth (one-way ANOVA,  $P < 0.05$ ) (Fig. 4).

Primary production of the two autotrophic fractions varied between lakes (two-way ANOVA,  $P < 0.0001$ ; Table 2). In lakes Escondido and Morenito,

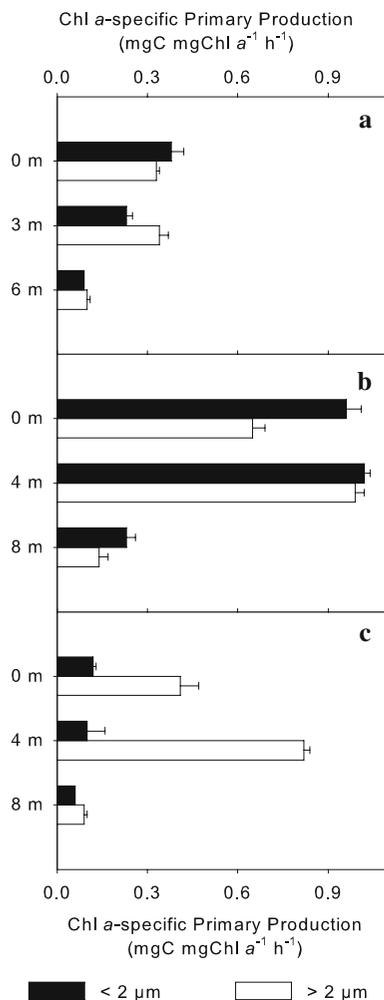


**Fig. 3** Phytoplankton taxonomic composition of the three studied lakes. **a** Lake Escondido, **b** Lake Morenito, **c** Lake El Trébol



**Fig. 4** Picophytoplankton abundances and ratio of phycoerythrin (PE) and phycocyanin (PC)-rich cells at the different depth. **a** Lake Escondido, **b** Lake Morenito, **c** Lake El Trébol

the picophytoplankton showed a high relative contribution to total PP. On the other hand, in lake El Trébol, the PP was dominated by phytoplankton  $>2\ \mu\text{m}$  (post-hoc Tukey test: El Trébol vs. Escondido or Morenito  $P < 0.0001$ ; Table 2). In all three lakes, at intermediate depth, the relative importance of the  $>2\ \mu\text{m}$  fraction increased (post-hoc Tukey test: 3–4 vs. 0 or 6–8 m,  $P < 0.002$ ). However, in lakes Escondido and Morenito the contribution of picophytoplankton to total PP remained always  $>50\%$ . Chlorophyll-specific PP was clearly dominated by the larger fraction in lake El Trébol, and in lakes Escondido and Morenito, both fractions

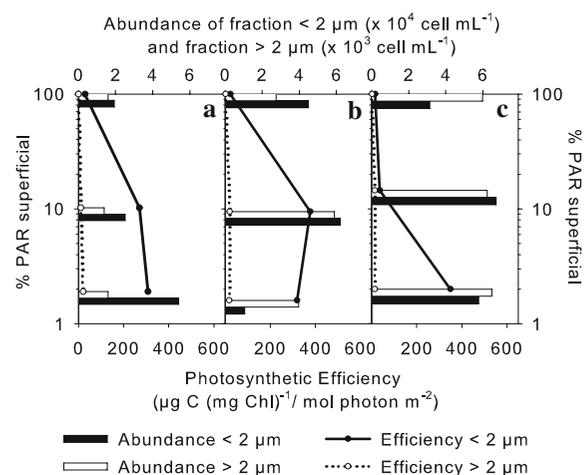


**Fig. 5** Chlorophyll-specific primary production corresponding to picophytoplankton and phytoplankton  $>2\ \mu\text{m}$  at the different depth in the studied lakes. **a** Lake Escondido, **b** Lake Morenito, **c** Lake El Trébol

showed more similar values (Fig. 5). Picophytoplankton resulted much more efficient than the larger autotrophs, and both fractions decreased its efficiency at surface layer (Fig. 6).

Bacterial abundances varied between  $1.6 \times 10^6$  and  $4.6 \times 10^6\ \text{cell ml}^{-1}$ . The highest values were observed at 4 m in Lake Morenito and the minimum ones in Lake Escondido at 3 m (Table 3). BP and cell specific BP were lower in Lake El Trébol, while in lakes Escondido and Morenito similar activities were observed (Table 3). At surface level, the differences among lakes were significant (two-way ANOVA,  $P < 0.05$ ), with the highest specific BP in Lake Morenito (post-hoc Tukey test, all pairs  $P < 0.001$ ).

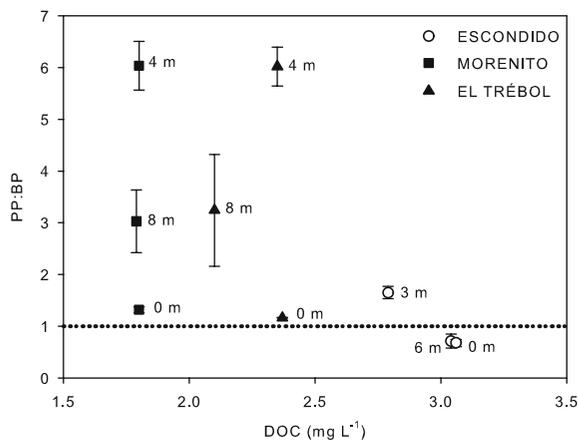
The PP:PB ratio was observed to be significantly different in the three lakes (two-way ANOVA,  $P < 0.05$ ). In lakes Morenito and El Trébol, the PP:BP ratio was higher than 1.0 in all depths, with maximum values corresponding to 4 m and minimum ones at surface level (Fig. 7). Within each of these lakes, there were significant differences among all the depth (post-hoc Tukey test: 0 vs. 4 m,  $P < 0.001$ ; 0 vs. 8 m,  $P = 0.004$  and 4 vs. 8 m,  $P = 0.008$ ). Thus, in these lakes, PP seemed to provide the particulate carbon. On the contrary, Lake Escondido showed ratios lower than 1.0 at surface and 6 m and there were no significant differences among depth (post-hoc Tukey test,  $P > 0.05$ ). This result indicated that lake production could be based mainly on bacterial mobilization of chemical bound energy.



**Fig. 6** Vertical profiles of photosynthetic efficiency and cell abundances of  $<2\ \mu\text{m}$  and  $>2\ \mu\text{m}$  fractions in the three lakes. **a** Lake Escondido, **b** Lake Morenito, **c** Lake El Trébol

**Table 3** Bacterial production ( $^{14}\text{C}$ -leucine incorporation), cell-specific bacterial production, and cell abundance in the three shallow Patagonian Andean lakes (January 2006)

Lake	Depth (m)	Bacterial production ( $\mu\text{g C l}^{-1} \text{h}^{-1}$ )	Cell-specific bacterial production ( $\text{fg C cell}^{-1} \text{h}^{-1}$ )	Bacterial abundance ( $10^6 \text{ cell ml}^{-1}$ )
Escondido	0	$0.78 \pm 0.089$	$0.308 \pm 0.034$	2.54
	3	$0.57 \pm 0.052$	$0.365 \pm 0.033$	1.56
	6	$0.63 \pm 0.068$	$0.272 \pm 0.030$	2.30
Morenito	0	$0.97 \pm 0.059$	$0.423 \pm 0.026$	2.30
	4	$0.93 \pm 0.061$	$0.201 \pm 0.013$	4.63
	8	$0.42 \pm 0.017$	$0.205 \pm 0.009$	2.03
El Trébol	0	$0.54 \pm 0.089$	$0.174 \pm 0.029$	3.08
	4	$0.69 \pm 0.043$	$0.285 \pm 0.018$	2.41
	8	$0.61 \pm 0.025$	$0.200 \pm 0.008$	3.08



**Fig. 7** Total primary production/bacterial production (PP/BP) ratio in relation to lake water DOC concentration at the different depth in the three studied lakes

## Discussion

In shallow lakes, the light penetrates up to the bottom sediments, thus supporting the photosynthesis all along the water column (Wetzel 2001). At the same time, shallow lakes may receive high amounts of autochthonous and allochthonous DOM from phytoplankton, macrophytes, and the drainage of terrestrial detritus present in their catchments. The relationship between attenuation of UV and DOM is strong (Morris et al. 1995; Morris and Hargreaves 1997); therefore, within a shallow lake, the spectral composition and intensity of the light can significantly change along the water column. Our data on the DOC- $K_d$  relationship fitted well general models published for lakes from Alaska to Patagonia (Morris et al. 1995), indicating that these shallow lakes are

well described by this general trend. In shallow Andean lakes, the radiation absorption is high in the violet-blue edge of the spectrum (Pérez et al. 2002). Underwater light intensity and spectral characteristics have been considered as important factors for niche differentiation in phytoplankton communities (Huisman et al. 2004). In particular, for picocyanobacteria, the importance of underwater light climate has been exposed in early studies (Pick 1991) and recently emphasized (Stomp et al. 2007). These photosynthetic prokaryotes are well adapted to 1% PAR irradiance (Gervais et al. 1997; Callieri et al. 2007) and a clear relationship between picocyanobacterial types and the extinction coefficient of red, green and blue light has been demonstrated (Callieri et al. 1996). In this sense, PE cells are present in the very clear oligotrophic lakes, whereas in shallow eutrophic lakes with high attenuation coefficients PC cells dominate (Voros et al. 1998; Katano et al. 2005; Stomp et al. 2007). The decrease in the PE:PC ratio observed in Lake Escondido may indicate that the DOM, acting as an absorption filter, changes the underwater light spectrum and consequently the pigment composition of picocyanobacteria.

Ultraoligotrophic, transparent and deep Andean lakes are highly suitable for growth and development of picophytoplankton (Callieri et al. 2007). Also in lakes Escondido and Morenito, we observed a higher contribution of picophytoplankton both in abundance and production in comparison with the  $>2 \mu\text{m}$  phytoplanktonic fraction. Our in-lake experiments indicated that PAR was adequate to support photosynthesis at any depth, almost up to the bottom of the lakes. However, we observed a decrease in photosynthetic efficiency at surface layers, probably as a

consequence of the high irradiances (PAR and UVR). The inhibitory effect of solar radiation on PP in a wide range of freshwater planktonic organisms has been largely documented (Karentz et al. 1994; Neale et al. 2001) and, in particular, on picophytoplankton (Callieri et al. 2001, 2007). In our data of PP, the inhibitory effect seems to affect both phytoplanktonic fractions, being more affected picophytoplankton in Lake Escondido and the larger fraction in lakes El Trébol and Morenito.

Autochthonous and allochthonous DOM provides a source of carbon and energy for bacterial growth (Jones 1992), and a coupling of bacteria and PP has been well documented (e.g., Lovell and Konopka 1985). Additionally, macromolecules from allochthonous DOM has been also documented as source of carbon for pelagic bacteria (Hessen 1992). In relation with this, one of the most important findings has been the recognition that DOM with high molecular weight can be photodegraded to more biologically labile molecules and then directly assimilated by bacterioplankton (Moran and Covert 2003; Bastidas Navarro et al. 2008). Therefore, in lake Escondido, where DOM of high molecular weight is the prevailing carbon source, the action of UV radiation over these substances could stimulate bacterioplankton activity. The different sources of DOM can be analyzed based on the ratio  $a_{250} : a_{365}$  since it indicates the relative size of DOM. In our case, Lake El Trébol exhibited the highest ratio indicating that DOM is of relative smaller size; thus, the main origin of DOM in this environment would be PP. Accordingly, we observed the highest phytoplanktonic biomass being Bacillariophyceae the most abundant group. The lower importance of diatoms in the other two lakes cannot be attributed to silica limitation, as Andean lake waters are dominated by dissolved silica (Pedrozo et al. 1993), and our data on nutrient (N and P) concentration were very similar in all three lakes. On the contrary, Lake Escondido exhibited a DOM of comparatively larger molecular size. The high abundance and BP recorded in this lake may be related to this DOM feature. Previous experimental studies performed with the bacterial assemblage from Lake Escondido showed that the addition of macrophyte leachates, DOM with high molecular weight, caused an increase in the DOM mean molecular size and in cell abundance (Bastidas Navarro et al. 2008). In Lake Örträsket, a large humic lake in Sweden, the BP

showed to be almost entirely dependent on the utilization of allochthonous DOM during summer (Jansson et al. 1999; Jonsson et al. 2001). Also, our shallow lakes, although with less DOM content, exhibited a comparatively similar bacteria production as Swedish lakes (Jansson et al. 1996).

In ecosystems where the plankton community is dominated by bacteria, mixotrophic organisms are favoured relative to the obligate autotrophs (Jansson et al. 1999; Bergström et al. 2003). The dominance of mixotrophic organisms (Chrysophyceae and Cryptophyceae) in Lake Escondido is related with the high-specific BP recorded here. In fact, bacteria can dominate in environments with a high allochthonous DOC input due to the availability of this energy and carbon source and to their ability to outcompete obligate autotrophs for inorganic nutrients (Jansson et al. 2000; Karlsson et al. 2001).

The relationship between planktonic PP and BP in unproductive lakes seems to be related to the DOC concentration, with a change from PP:BP > 1.0 to PP:BP < 1.0 when the allochthonous DOC input increases above  $10 \text{ mg l}^{-1}$  (Jansson et al. 2000). The PP:BP ratios (>1.0) obtained in this study showed that autotrophic production in lakes Morenito and El Trébol (4 and 8 m depth) would be enough to support bacterial growth. On the other hand, in Lake Escondido, the ratio <1.0 would indicate that, although DOC concentration is well below  $10 \text{ mg l}^{-1}$ , the production switches from autotrophic to heterotrophic. Lake Escondido has higher concentration of DOM constituted by larger molecules, suggesting a prevalence of allochthonous origin. Besides, the surface PP:BP ratios of the three lakes are near 1, suggesting that BP may be less negatively affected than PP by surface solar irradiance as shown in Tables 2 and 3. In these Andean shallow lakes, changes in the PP:BP ratio would occur at low DOC concentration because of the low nutrient availability, thus even minor changes in DOC supply could be particularly important, modifying the community structure and the productivity of these environments.

In conclusion, our data support the initial hypothesis that high light and high DOM interact affecting bacteria and algae and thus the amount of available DOM drives the balance between PP and BP. However, solar radiation should be included as an important factor since PP:BP ratio may decrease because of PP photoinhibition independently of DOM concentration.

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