Precipitation patterns, dissolved organic matter and changes in the plankton assemblage in Lake Escondido (Patagonia, Argentina)

Marcela A. Bastidas Navarro & Beatriz E. Modenutti

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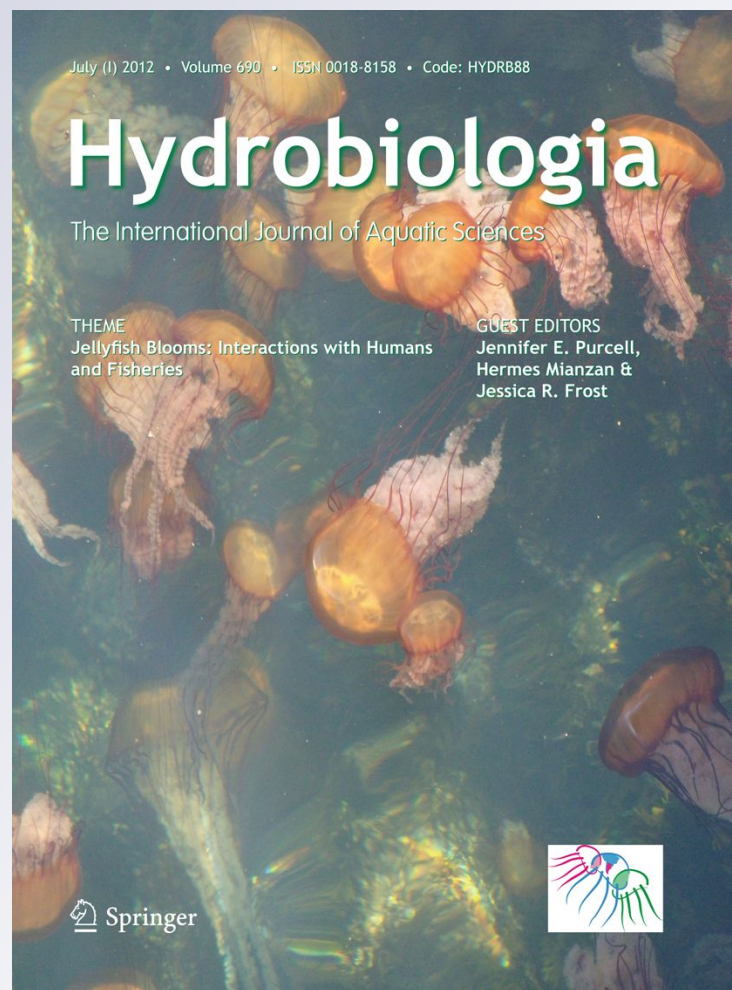
**Marcela A. Bastidas Navarro ·
Beatriz E. Modenutti**

Abstract Global warming affects the hydrological cycle by increasing the frequency and intensity of extreme rainfall events and dry spells. These changes potentially affect the quantity and quality of dissolved organic matter (DOM) input into lakes. In this study, we investigated if changes in precipitation over a 3-year period correspond to changes in DOM and whether these changes affect light attenuation and plankton community composition. We sampled Lake Escondido, a shallow, oligotrophic Andean lake, nine times, analyzing coloured DOM and plankton community composition. During the study period, we observed that variations in the precipitation regime correlated with DOM parameters (water colour and molecular weight), and this, in turn, affected the plankton composition. Chlorophyll *a* concentrations of both phytoplanktonic fractions (less than and greater than 2 μm) were related to water colour and TDP. We observed in the small fraction (<2 μm) an increase in phycocyanin-rich cells during periods of high water colour. Larger phytoplanktonic cells (>2 μm) presented two biomass peaks corresponding to increases of the cyanophyte *Chroococcus* *planctonicus* and of the haptophyte *Chrysochromulina parva*. As precipitation decreased, the lake became more transparent, favouring *C. planctonicus* and mixotrophic oligotrich ciliates with endosymbiotic Chlorella. In the context of global climate change, our results highlight the potential impact of changes in precipitation patterns and, consequently, in DOM quality on the plankton community.

Keywords Precipitation · Dissolved organic matter · Plankton community · Shallow oligotrophic · Andean lake

Introduction

The concentration of dissolved organic matter (DOM) in lakes is strongly influenced by climatic and topographic characteristics and as well as by catchment area and internal lake properties (Sobek et al., 2007). An expected consequence of global warming are changes in the hydrological cycle (Marengo et al., 2009), with expected increases in the frequency and intensity of both extreme rainfall events and dry spells (IPCC, 2007a, b), although significant regional and local variation is also expected (Christensen et al., 2007). These changes will likely affect DOM levels in lakes because droughts reduce the input of DOM and sediments (Schindler et al., 1996; Schindler, 1997), while increased precipitation might favour runoff and DOM input (Rae et al., 2001; Zepp et al., 2011).

M. A. Bastidas Navarro (✉) · B. E. Modenutti
Laboratorio de Limnología, INIBIOMA,
CONICET—Universidad Nacional del Comahue,
8400 Bariloche, Argentina
e-mail: mbastidas@comahue-conicet.gob.ar

In freshwater ecosystems, DOM derived from the surrounding watershed is a major component of the total organic matter. The principal decomposers of DOM are heterotrophic bacteria that are, in turn, the main food source for bacterivorous microorganisms at the base of the trophic food web (Šimek et al., 2001). The chemical composition of DOM differs considerably between humic and clear-water lakes and, accordingly, bacterioplankton assemblages vary in relation to their ability to use different size fractions of organic matter (Kritzberg et al., 2004). In addition, as DOM absorbs light, changes in DOM concentrations alters the depth to which light penetrates the water column (Kirk, 1994). In general, DOM coming from watersheds consists mainly of coloured dissolved organic matter (CDOM), which effectively absorbs solar radiation, particularly ultraviolet radiation (UVR) (Osburn et al., 2001; Brinkman et al., 2003). In addition to protection against UVR, DOM can have other effects on phytoplankton growth (Klug, 2002). In particular, the high absorbance of green and blue wavelengths by DOM compounds benefits green picocyanobacteria which use phycocyanin to capture the predominant red light (Stomp et al., 2007). DOM may also contain substantial levels of nutrients and phytoplankton may be able to access the bound phosphorus if it is released by photolysis (De Haan, 1992). Thus, in CDOM-rich lakes a poor light climate potentially restricts production by photoautotrophic organisms (Carpenter et al., 1999), while DOM as a nutrient source, may drive the outcome of competition between the different fractions of autrophic plankton (picophytoplankton, and larger phytoplankton) and bacteria (Drakare et al., 2002). The magnitude of these effects varies depending on the origin of DOM and the composition of the planktonic assemblages (Klug, 2002). For example, a recent study compared small unproductive lakes along a water colour gradient, showing that coloured terrestrial organic matter controls benthic primary production through its effects on light attenuation (Karlsson et al., 2009).

Long-term studies have shown increases in concentrations of dissolved organic carbon (DOC) in the surface waters of northern and central Europe (Monteith et al., 2007) and that increases in temperature result in accelerated DOC accumulation (Weyhenmeyer & Karlsson, 2009). However, in temperate zones of the Southern Hemisphere (i.e. Patagonia) there have been few attempts to measure changes in lake DOM, even though Masiokas et al. (2008) documented significant warming and decreasing precipitation in the region north of 45°S for the last century. Aquatic systems in Patagonia include both deep and shallow oligotrophic lakes (Modenutti et al., 1998). Shallow lakes (maximum depth <15 m) exhibit high relative light attenuation coefficients and high concentrations of CDOM that strongly affect the spectral light quality (Pérez et al., 2002).

During 1950–1999, precipitation series in the North-Patagonian region revealed an increase of precipitation amounts (Castañeda & González, 2008). The precipitation changes that occurred during our 3-year (2006–2008) sampling period allowed us to compare the effect of fluctuating precipitation on a small oligotrophic lake in North Patagonia. In particular, here we investigated Lake Escondido, a small and closed glacial lake, in order to assess whether changes in precipitation correlated with major DOM dynamics affecting both water colour and the plankton community.

Materials and methods

Study area

Lake Escondido is a small shallow lake (maximum depth 8 m) located 764 m above sea level in northwestern Patagonia (Argentina) (41°03′S and 71°34′W). This is a small, closed basin related to a series of large glacier-carved lakes (Gogorza et al., 2002); therefore the primary input into the lake is runoff from precipitation received in the drainage basin. The climate of the region is temperate cool (mean annual temperature 8.7°C) with a dominance of westerly humid winds (Paruelo et al., 1998). The surrounding vegetation is a mixed subantarctic forest of the perennial *Nothofagus dombeyi* (Mirb.) Blume, the deciduous *Nothofagus antarctica* (Forster f.) Oersted and *Austrocedrus chilensis* (D. Don.) Flor. et Boutl. The area is within the Nahuel Huapi National Park and is free of industries and other heavy human impacts, so the observed changes result mainly from natural events.

The lake thermal regime is characterised by continuous mixes with weak summer stratification periods (Balseiro & Modenutti, 1990). The lake is oligotrophic, with summer chlorophyll *a* concentrations of <3 µg l^{-1} and total phosphorus (TP) concentrations under 7 µg l^{-1} (Bastidas Navarro et al., 2009b). The littoral

zone is well developed, and it is colonised by two macrophytes: the emergent *Schoenoplectus californicus* (Meyer) Soják and the submersed *Potamogeton linguatus* Hangström. In comparison with deep lakes and other shallow lakes of the area, Lake Escondido exhibits high DOC content (~ 2.70 mg l^{-1}) (Morris et al., 1995; Bastidas Navarro et al., 2009a).

Data collection

We sampled Lake Escondido nine times over a 3-year period (2006–2008): February (austral summer) 2006–2007–2008, August (austral winter) 2006–2007–2008 and November (austral spring) 2006–2007–2008. Water samples were obtained with a Van Dorn bottle from a central sampling station in the deepest zone of the lake (8 m) at 0, 3 and 6 m depth in two replicates. Concurrently, temperature profiles and dissolved oxygen concentration and conductivity were measured with a multiparameter sensor YSI 85. Lake water was immediately transported to the laboratory in thermally insulated containers and in darkness.

Precipitation data over the sampling period (2006–2008) were obtained from the INTA Meteorological Station (41°07′S and 71°15′W).

Laboratory determinations

Spectrophotometric scans (250–790 nm) were performed on filtered lake water (pre-combusted GF/F filters). Scans were carried out in 10 cm path-length quartz cuvettes in a Shimadzu UV2450 double-beam spectrophotometer. In situ absorption coefficients due to yellow substances [$a_g (\lambda)$; U m^{-1}] were obtained by converting the measured base 10 values to base e logarithms following Kirk (1994):

$$a_g = 2.303A/l$$

where a is the absorption coefficient (m^{-1}), A is the absorbance, and l is the path length (m).

Water colour was estimated following (Pace & Cole, 2002) considering the absorbance at 440 nm [$a_g(440)$] in a 100-mm cuvette. Colour is expressed as a wavelength-specific absorption coefficient in units of inverse meters. The spectral slopes for the intervals 275–295 nm ($S_{275-295}$) and 350–400 nm ($S_{350-400}$) were calculated using linear regression of the log-transformed spectra Ln (a_g). Slopes were calculated based on positive values fit to an exponential decay.

Higher (or steeper) slopes indicate a more rapid decrease in absorption with increasing wavelength (Helms et al., 2008). The ratio of $S_{275-295}$ to $S_{350-400}$ (S_R) was also calculated. S_R is inversely related to CDOM molecular weight (i.e. larger values of S_R indicate lower mean molecular weight of CDOM and also DOM (Helms et al., 2008).

Total dissolved phosphorus (TDP) was determined on lake water filtered through GF/F filters. Total phosphorus (TP) was determined directly on unfiltered lake water. The samples for TP and TDP determinations were digested with potassium persulfate at 125°C at 1.5 atm for 1 h. The *P* concentrations were obtained using the ascorbate-reduced molybdenum method (APHA, 2005).

Chlorophyll *a* concentration was determined for two phytoplankton size fractions: picophytoplankton (<2 μm) and phytoplankton (>2 μm). A volume of 100 ml of lake water was filtered through a 2.0-μm polycarbonate filter (Nuclepore) and, then, through a 0.2-μm polycarbonate filter (Nuclepore). Chlorophyll *a* concentrations were measured by extraction with 90% ethanol, according to Nusch (1980) using a fluorometer (Turner Designs, 10-AU). The fluorometer was previously calibrated against spectrophotometric measurements.

Planktonic prokaryotic assemblage

Bacteria abundance determination and identification of the prokaryotic assemblage were carried out on 50-ml lake water samples fixed with filtered formaldehyde at a final concentration of 2% v/v. Bacteria cells were stained with 4′,6-diamidino-2-phenylindole (DAPI) at a final concentration of 0.2% w/v, following Porter & Feig (1980). Bacterial abundances were determined on 0.2-μm black polycarbonate filters (Poretics, Livermore, CA, USA) under an epifluorescence microscope (Olympus BX50) at 1,250× magnification using UV light (U-MWU filter).

The taxonomic composition of prokaryotic assemblage was characterized on four sampling dates (February 2006, August 2006, November 2006 and February 2007). A volume of 10 ml was filtered through 0.2-μm polycarbonate filters (Nuclepore). Catalyzed reporter deposition–fluorescence in situ hybridization (CARD–FISH) was carried out on filter sections embedded in low-melting point agarose (0.2%). Sections were permeabilised with lysozyme and achromopeptidase

according to Sekar et al. (2003). Hybridization with 5′-horseradish peroxidase (HRP)-labelled oligonucleotide probes was carried out according to Pernthaler et al. (2002). Reactions were performed in 0.5-ml vials containing 300 μl of hybridisation buffer and the 5′-HPR-labelled probes at a final concentration of 0.5 ng μl^{-1}. For the prokaryotic assemblage characterization, six different group-specific oligonucleotide probes (Thermo-Hybrid, Germany) were targeted to the *Archaea* domain (ARCH915), the *Bacteria* domain (EUB338), α-Proteobacteria (ALF1b), β-Proteobacteria (BET42a), Cytophaga-like bacteria (CF319a) and the class Actinobacteria (HGC69a). The probe NON338 was used as a control. The proportion of formamide in the hybridisation buffer was 55% except for the ARCH915 (40%) and HGC69a (35%) probes. Cells were hybridized at 35°C for 2–4 h. After hybridization, the filter sections were washed in a pre-warmed buffer at 37°C for 15 min with the appropriate amount of sodium chloride, depending on the proportion of formamide in the hybridization buffer (Sekar et al., 2003). The filters were stained with DAPI (1 mg/100 ml) and inspected with an Olympus BX50 epifluorescence microscope at 1,250× magnification using UV (U-MWU filter) and blue light (U-MWB filter). At least ten randomly selected microscopic fields were used for counting FISH-stained bacteria and total DAPI-stained bacteria, and the percent value of each bacterial taxon was calculated.

Picophytoplankton (<2 μm) and phytoplankton >2 μm

A volume of 80 ml of lake water was fixed with filtered formaldehyde at a final concentration of 2% v/v for picophytoplankton and nanoflagellate abundance determinations. Picophytoplankton were enumerated on 0.2-μm black polycarbonate filters (Poretics, Livermore, CA, USA) under epifluorescence using blue light (U-MWB filter) and green light (U-MWG). Nanoflagellate abundance was also determined by staining with DAPI on 1-μm polycarbonate black membrane filters (Poretics, Livermore, CA, USA), and the phototrophic cells were recognized using the natural autofluorescence of chlorophyll under blue light (Kemp et al., 1993).

In addition, 250 ml of lake water was fixed with acid Lugol's solution for phytoplankton (>2 μm) enumeration and determination. Samples were counted in 50-ml Utermöhl chambers under an inverted Olympus

IX70 microscope. Determinations of nanoflagellate abundance from the Lugol's samples and from formaldehyde-preserved samples were tested to be similar.

Calculations and statistical analysis

For the analysis of the precipitation data, we estimated the expected precipitation for each month as the average of that month for the last 10 years. We then calculated the difference between the expected and the recorded cumulative precipitation in order to characterize precipitation shifts.

Differences in TDP and TP concentrations were estimated through a Two-Way ANOVA with sampling depth and dates as factors. The post hoc comparisons were carried out with the Tukey test with an overall significance level of $P = 0.05$. Normality and homoscedasticity were checked before analysis.

We calculated the regressions (linear and nonlinear) between water colour [$a_g(440)$] and TDP relative to the dominant algae cells (*Chrysochromulina parva* and *Chroococcus planctonicus*) and the ratio Prostomatida:Oligotrichida. The ratio between Prostomatida:Oligotrichida was calculated in order to estimate the importance of mixotrophic ciliates (Oligotrichida). All the analyses were performed with the entire dataset ($n = 27$), otherwise is indicated in the figure legend.

Results

The lake

We were able to distinguish two clearly different precipitation periods within the three study years. During 2006, cumulative precipitation was higher than expected (precipitation shift >0) (Fig. 1) while, from 2007 to June 2008, cumulative precipitation was lower than expected (precipitation shift <0) (Fig. 1). Following this, precipitation increased (Fig. 1).

The lake was completely mixed year-round in each of the three study years. Lake temperature ranged between 6.34 ± 0.27°C in winter and 21.5 ± 1.32°C in summer. Dissolved oxygen concentration was always close to saturation (between 82.1 ± 0.07% and 100.8 ± 0.06%) and conductivity was nearly constant at ~ 50 μS cm^{-1}.

We observed that TDP and TP concentrations did not vary among the three sampling depths (Two-way

Fig. 1 Variation in monthly and cumulative precipitation (expected-recorded cumulative precipitation) for the period of 2006–2008 in Bariloche
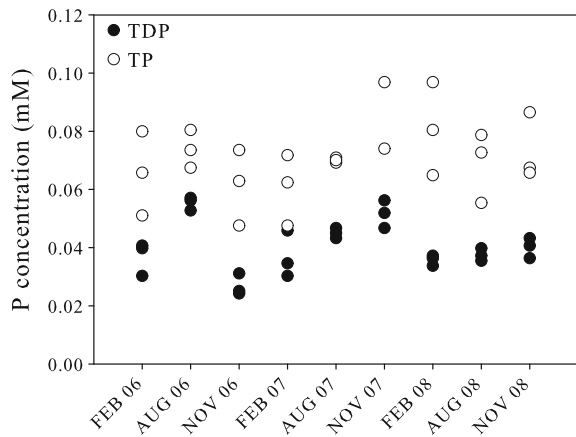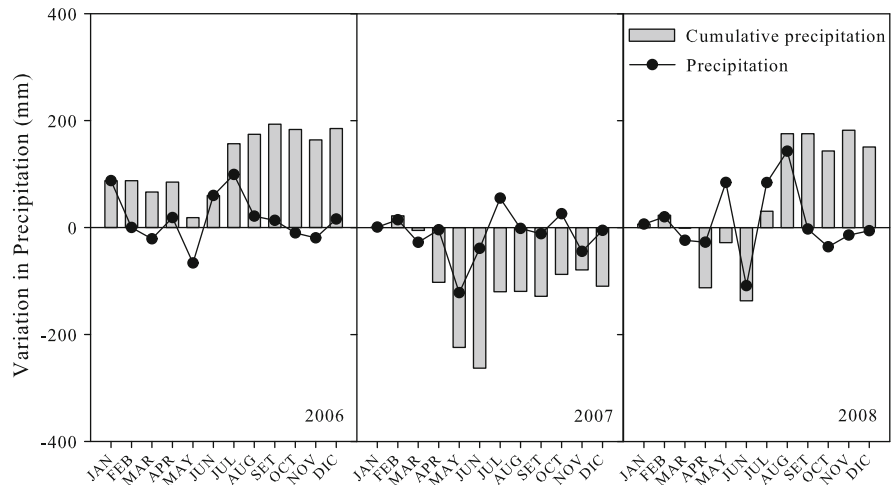

Fig. 2 TP and TDP concentrations ($n = 27$) over the study period in Lake Escondido

Fig. 3 Ln-transformed absorption spectra obtained from the different sampling times, with best-fit regression lines (S) for two regions (275–295 and 350–400 nm). Data are presented as an average of the three sampling levels of the water column

ANOVA, TDP $P = 0.928$ and TP $P = 0.189$) but did vary across the nine sampling occasion (Two-way ANOVA, TDP $P = 0.001$ and TP $P = 0.004$) (Fig. 2). No relationship was observed between precipitation and TDP and TP concentration (TDP vs precipitation, $R^2 = 0.02$, $P = 0.704$ and TP vs precipitation $R^2 = 0.06$, $P = 0.614$), suggesting that factors other than precipitation affect P concentration.

Lake water light absorption in the UV-B band was generally higher than in the other wavelengths (Fig. 3). We observed a decrease in overall spectral absorbance from February (summer) 2006 to February (summer) 2008 and an increase in August (winter) and November (spring) 2008. Changes in $a_g(440)$ values were closely consistent with shifts in the overall absorption spectra
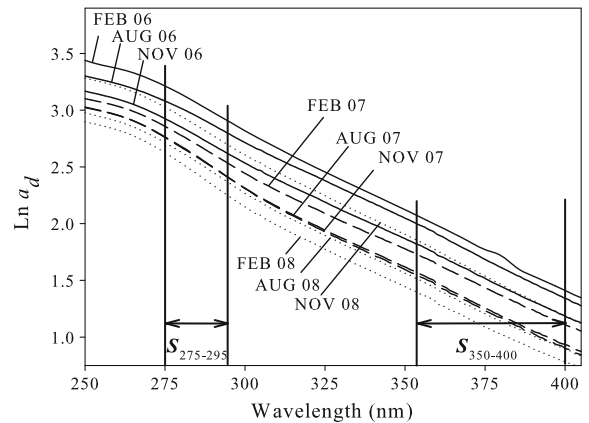
and showed a continuous decrease in water colour from February (summer) 2006 to February (summer) 2008 and a subsequent increase in August and November 2008 (Fig. 4). This pattern was inversely correlated with S_R, indicating that high water colour values were associated with higher molecular weight DOM ($R^2 = 0.55$, $P < 0.001$) (Fig. 4).

The spectrophotometric variable $a_g(440)$ was positively correlated with variation in cumulative precipitation (Fig. 5) ($R^2 = 0.53$, $P < 0.001$), whereas DOM size (S_R) was negatively correlated ($R^2 = 0.45$, $P < 0.001$) (Fig. 5). In addition, no relationship was observed between $a_g(440)$ or S_R and phosphorus concentrations [$a_g(440)$ vs TDP/TP, $P > 0.10$, and S_R vs TDP/TP, $P > 0.27$].
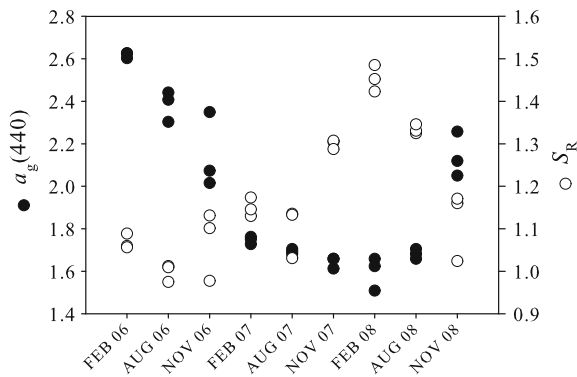
Fig. 4 Water colour [$a_g(440)$] and S_R ratio ($n = 27$) for the studied period in Lake Escondido

The planktonic assemblage

Total chlorophyll a concentration was low, ranging from 0.4 to 2.7 µg l^{-1} with no significant differences in the three sampling levels (Two-Way ANOVA $P = 0.230$). However, the contributions of both phytoplankton size fractions to total chlorophyll a concentration varied over time (Fig. 6). During 2006, picophytoplankton (<2 µm) reached its highest relative contribution, representing up to 69% of total chlorophyll a (Fig. 6). Picophytoplankton was dominated by phycoerythrin-rich picocyanobacteria (*Synechococcus*-like cells of 0.91-µm diameter). However, phycocyanin-rich cells were also observed particularly in samples with high water colour (February and August 2006 and November 2008) when their proportion increased causing a decrease in the PE:PC ratio (Fig. 6).

Phytoplankton >2 µm comprised 82 species from 10 different algal classes (Table 1). The dominant species was *C. parva* (Haptophyte) followed by other mixotrophic species, such as *Dinobryon divergens* (Chrysophyte), *Rhodomonas lacustris* (Cryptophyte)

and *Gymnodinium varians* (Dinophyte). In addition, we observed a substantial increase of the cyanophyte *C. planctonicus* in summer 2008.

We observed that the chlorophyll a concentrations of both phytoplankton fractions are related to water colour and TDP (Fig. 7). However, both fractions responded differently to these factors: while the small fraction (<2 µm) appeared to react positively to an increase in colour and P, the large fraction displayed a sinusoidal pattern (Fig. 7). The pattern of increase in picophytoplankton may be related to the observed increase in phycocyanin-rich cells in the periods of high water colour. The larger cells (>2 µm) presented two biomass peaks. The first was present under low TDP and low water colour and corresponded with an increase of the cyanobacterium *C. planctonicus* and the haptophyte *C. parva*. The second peak was observed under low TDP and high water colour and coincided with the increase of *C. parva* and other phytoplankton groups.

Bacteria domain dominated over *Archaea* in the sampling dates (February 2006, August 2006, November 2006 and February 2007) for which we characterized the prokaryotic assemblage (Fig. 8). Bacteria consisted mainly of small cocci (~0.76 µm) and bacilli (<1 µm). Of the *Bacteria* groups, *β-Proteobacteria* dominated and we did not observe significant changes among the different dates in the proportions of α-*Proteobacteria*, *Cytophaga-Flavobacterium* and *Actinobacteria* (Fig. 8). The highest proportion of *Archaea* was observed in August (winter) 2006, reaching up to 28.1 ± 2.1% of the DAPI-stained cells.

A total of 13 ciliate taxa were recorded during the sampling period. Oligotrichida and Prostomatida were the most abundant groups (95% of total) and were present during the entire study period. Oligotrichida included mainly mixotrophic species such as *Limnostrombidium viride* and *Pelagohalteria viridis*

Fig. 5 Relationship between spectrophotometric [$a_g(440)$ and S_R] variables and variation in precipitation (expected-recorded) ($n = 27$)
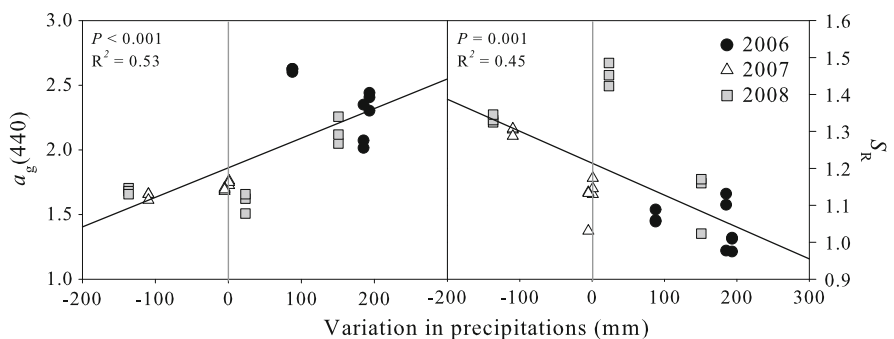
Fig. 6 Contribution to total chlorophyll *a* concentration of phytoplanktonic fractions <2 and >2 μm and the ratio phycoerythrin-rich cells:phycocyanin-rich cells (PE:PC). Data are presented as an average of the three sampling levels of the water column
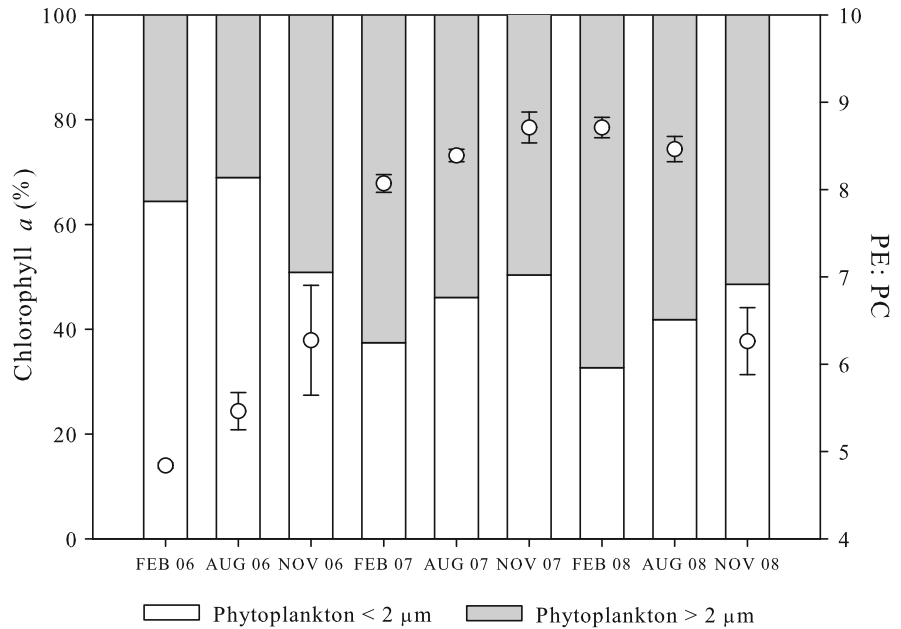

Table 1 Abundance (average ± standard deviation) of different algal classes in Lake Escondido during the studied period

	Chrysophyceae	Haptophyceae	Cryptophyceae	Dinophyceae	Cyanophyceae	Other classes
Feb 06	20.1 ± 6.1	1381.1 ± 101.4	92.1 ± 13.2	188.2 ± 18.4	2.8 ± 0.2	2.21 ± 0.9
Aug 06	39.9 ± 1.83	523.9 ± 87.8	240.5 ± 54.8	63.6 ± 13.6	2.8 ± 0.6	3.95 ± 0.3
Nov 06	4.4 ± 0.8	1329.6 ± 171.6	123.1 ± 16.5	72.0 ± 13.9	4.3 ± 0.7	5.61 ± 1.3
Feb 07	10.6 ± 1.05	719.8 ± 78.2	225.5 ± 32.9	150.6 ± 29.1	7.9 ± 1.0	0.49 ± 0.1
Aug 07	10.6 ± 1.05	719.8 ± 78.2	225.5 ± 32.9	150.6 ± 29.1	50.9 ± 1.2	0.49 ± 0.1
Nov 07	4.6 ± 1.8	700.4 ± 63.38	125.8 ± 18.6	157.2 ± 18.2	64.0 ± 3.2	0.35 ± 0.07
Feb 08	45.5 ± 5.2	486.9 ± 55.1	196.7 ± 44.2	176.7 ± 22.2	189.3 ± 11.3	4.38 ± 0.4
Aug 08	3.2 ± 0.24	1759.2 ± 138.6	212.0 ± 46.5	43.6 ± 8.4	21.2 ± 3.1	0.32 ± 0.05
Nov 08	15.0 ± 1.22	417.6 ± 1.96	235.7 ± 33.2	196.4 ± 21.0	2.3 ± 0.2	1.10 ± 0.4

Data are presented as an average of the three sampling levels of the water column

Fig. 7 Relationship between chlorophyll *a* concentration (Chl*a*) from picophytoplankton (**a**) and phytoplankton >2 μm (**b**), water colour and TDP concentration ($n = 27$)
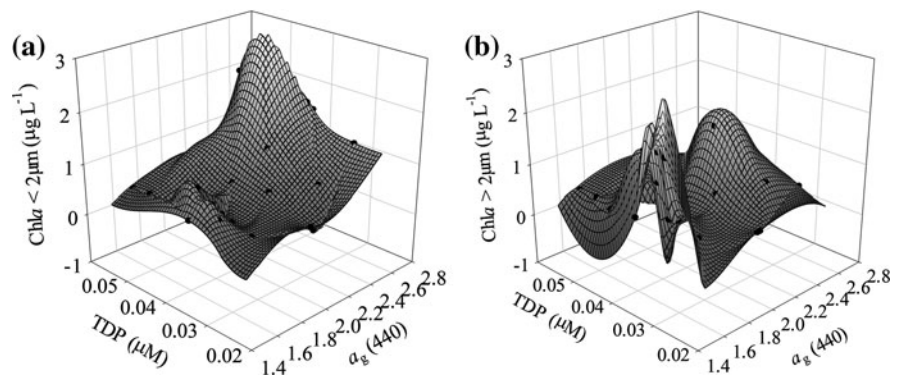
Fig. 8 Changes in prokaryotic total abundance and taxonomic composition of the *Bacteria* and *Archaea* domains. Data are presented as an average of the three sampling levels of the water column
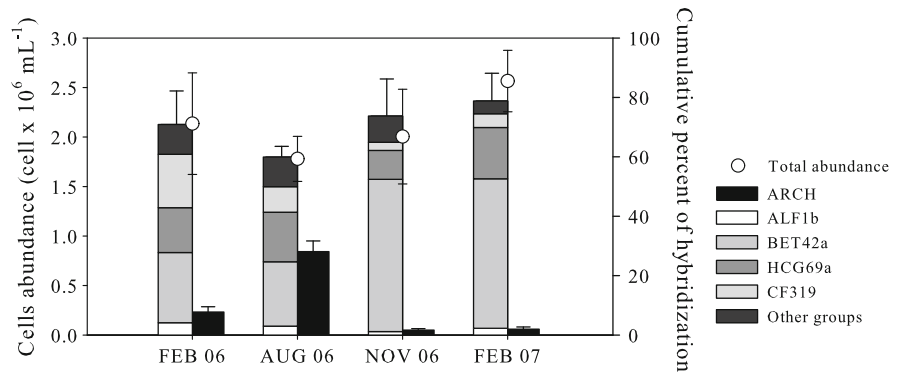

Fig. 9 Relationship between water colour [$a_g(440)$], TDP, and the total abundance of *C. planctonicus* (**a**) and *C. parva* (**b**), and the Prostomatida:Oligotrichida ratio (**c**) ($n = 27$)
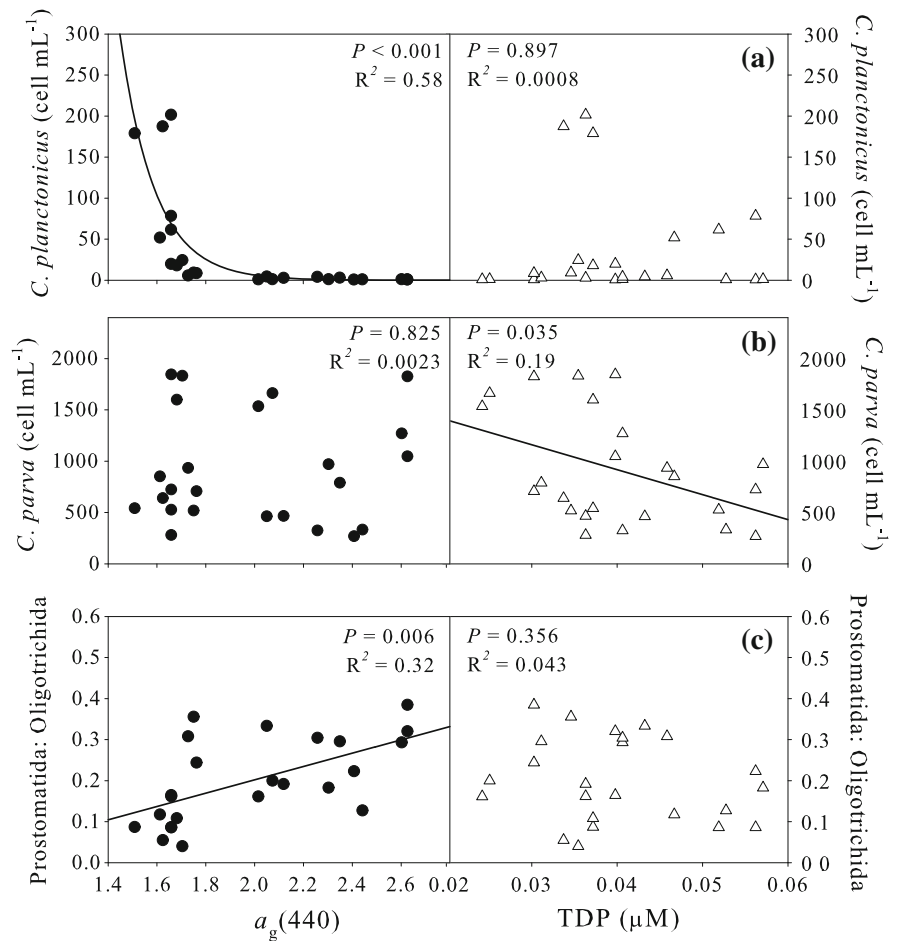
whereas Prostomatida included heterotrophic taxa (*Balanion planctonicum*, *Urotricha planctonicum* and *U. furcata*).

Water colour and TDP were analyzed for correlation with planktonic assemblage composition (Fig. 9). *C. planctonicus* exhibited an exponential population decrease when water colour increased ($P < 0.001$) (Fig. 9a) but no significant relationship with P was observed. Conversely, no significant relationship was observed between water colour and abundance of *C. parva*, but this species was found to be significantly influenced by P concentrations ($P = 0.035$) (Fig. 9b).

Finally, the relative abundance of the two ciliate classes (i.e. Prostomatida:Oligotrichida ratio) was positively correlated with water colour ($P = 0.006$) (Fig. 9c), indicating that mixotrophic oligotrichs were favoured when water colour decreased.

Discussion

Climatic factors such as precipitation and temperature are central factors regulating DOM dynamics (Gjessing, 2003). In lakes with forested watersheds, a strong relationship has been observed between intensity of precipitation and DOC due to increased organic matter discharge from the upper parts of the soil profile during periods of increased runoff (Bishop et al., 2003). Altered precipitation patterns attributed to global climate change is thought to be a main reason for changes in lake surface water colour and DOM concentration (Evans & Monteith, 2001; Skjelkvåle et al., 2001). Our results for this small Andean lake surrounded by *Nothofagus* forest also indicate that water colour [$a_g(440)$] and DOM features (S_R, as an index of DOM molecular size) are influenced by changes in the precipitation regime (Fig. 5). Even during our short time frame (3 years), we were able to observe how substantial changes in precipitation affected water colour and DOM characteristics. In Lake Escondido, we observed a continuous decrease in water colour from February (summer) 2006 to February (summer) 2008 followed by an increase during August (winter) and November (spring) 2008 (Fig. 4). During these periods, the mean molecular size of DOM showed an inverse trend (Fig. 4). The covariation observed between these two parameters and the precipitation regime suggests that the make-up of Lake Escondido DOM was strongly dependent on allochthonous inputs from the *Nothofagus* forest drainage area. Similar results have been obtained in lakes surrounded by coniferous forest in Sweden, in which discharge also had a strong correlation with water colour (Johansson et al., 2010). Even if we did not perform a study on DOM origin (autochthonous vs allochthonous) i.e. stable isotope monitoring (Tank et al., 2011), the allochthonous origin of Lake Escondido DOM is supported by the facts that DOM have a comparatively larger molecular size than other lakes in the area (Bastidas Navarro et al., 2009b), and that the lake is a close basin (Gogorza et al., 2002) with

very low nephelometric turbidity (0.50 NTU) (Pérez et al., 2010). Macrophytes also generate DOM, either through extracellular release or following ageing and subsequent release of dissolved and particulate constituents to the surrounding water (Bertilsson & Tranvik, 2000). In Lake Escondido, the contribution of DOM originating from macrophytes (*P. linguatus* and *S. californicus*) can be an important carbon source for bacteria production (Bastidas Navarro et al., 2009a). Precipitation can also affect macrophyte leaching through the increase or decrease in lake water levels (Amado et al., 2005; Suhett et al., 2007) therefore, future studies in Lake Escondido should discriminate between DOM of macrophyte origin interacting with changes in precipitations as compared to that from the surrounding forest.

Native *Nothofagus* forests have soils that are predominantly derived from volcanic ash (Andisols) and are characterized by a high capacity to retain P (Diehl et al., 2003). This may account for our finding no relationship between precipitation and TDP and TP. Other factors may play a larger role than runoff in Lake Escondido P concentrations. For instance, UVR causes photoreduction of Fe(III) associated with DOM and this mechanism is involved in PO_4 reduction (Maranger & Pullin, 2003). Previous studies from Lake Escondido have shown that UVR produces an increase of P in both lake water and from macrophyte lecheates (Bastidas Navarro & Modenutti, 2010).

In lakes, water colour has important effects on light transmission in the water column. This, in turn, affects photosynthetic processes (Jones, 1992), the behaviour and interactions among organisms (Williamson, 1995; Thingstad, 2003), and the carbon cycle (Dillon & Molot, 1997; del Giorgio & Duarte, 2002; del Giorgio & Davis, 2003). Previous study has shown that the spectral quality of underwater light in north Andean Patagonian shallow lakes is significantly affected by high concentrations of dissolved yellow substances (that is, absorption is high on the violet-blue edge of the spectrum) (Pérez et al., 2002). The absorption of light by these dissolved compounds can interfere with capture of different wavelengths of light by different phytoplankton taxa (Kirk, 1994), potentially altering community structure due to spectral niche differentiation in phytoplankton communities (Huisman et al., 2004). In particular, changes in the extinction coefficients for red, green and blue light are key variables controlling the relative abundances of various

picocyanobacteria with different accessory pigments (Pick, 1991; Callieri et al., 1996; Vörös et al., 1998; Stomp et al., 2007). Phycoerythrin-rich cells are successful in clear lakes, whereas phycocyanin-rich cells dominate in lakes with light dominated by the red end of the spectrum (Callieri et al., 1996; Stomp et al., 2007). Consistent with these mechanisms, in Lake Escondido, we observed an increase in the abundance of phycoerythrin-rich cells during the period of decreasing water colour (Fig. 6).

Light conditions can also influence the dynamics of other cyanobacteria taxa, as was observed for *C. planctonicus* in Lake Escondido. Changes in the abundance of this species were strongly associated with changes in water colour but not with changes in TDP concentrations (Fig. 9a). Cyanobacteria species are adapted to specific light levels (Havens et al., 1998); in particular, fast-growing cyanobacterial chroococcal species are negatively affected by increased turbidity (Nõges & Nõges, 1999; Steinberg et al., 2006). Our results show that the relative importance of *C. planctonicus* increased during periods with decreased precipitation that cause, in turn, a decrease in water colour. Light-driven changes in *C. planctonicus* abundance may have important ecological implications for the food web of Andean lakes because it is a food item of low nutritional value for cladocerans (Matveev & Balseiro, 1990). Thus, patterns of decrease or increase in precipitation, and subsequent changes in the light field due to associated changes in the impacts of coloured DOM, would not only affect phytoplankton but would also have indirect consequences for the food web.

Mixotrophic nanoflagellates can outcompete strict autotrophs under nutrient or light limitation (Palsson & Graneli, 2004). In Lake Escondido, mixotrophic nanoflagellates were observed to dominate the phytoplankton throughout this 3-year study. In particular, *C. parva* was the dominant nanoflagellate species, as is the case in many other Andean North Patagonian lakes (Díaz & Lorenzo, 1990; Callieri et al., 2007; Bastidas Navarro et al., 2009b). We found that this species' population dynamics were not related to water colour (Fig. 9b), as indicated by its presence across a wide range of DOM concentrations (DOC < 0.6 up to 2.7 mg l^{-1}) (Callieri et al., 2007). Nevertheless, consistent with previous study indicating a competitive superiority of mixotrophic nanoflagellates (Palsson & Graneli, 2004), we observed that the

abundance of *C. parva* was inversely related to TDP concentration. This result differed from studies in Norwegian and Swedish lakes where *C. parva* populations increased after fertilization (Reinertsen & Langeland, 1982; Holmgren, 1984). However, in incubation experiments manipulating zooplankton biomass, it was observed that the abundance of *C. parva* decreased with increased zooplankton biomass despite increased concentrations of P due to nutrient recycling (Balseiro et al., 1997). Thus, the most important factor regulating *C. parva* could be grazing by herbivorous zooplankton (Balseiro et al., 1997; Queimaliños et al., 1998), so the apparent negative relation with P may result from the interaction of nutrient recycling and losses by grazing.

Mixotrophic ciliate species are also affected by changes in light availability (Amblard et al., 1995; Modenutti & Balseiro, 2002; Modenutti et al., 2008). We observed an increase in the relative contribution of Oligotrichida due to the increase of *Chlorella*-bearing species (*P. viridis* and *L. viride*) when the water column reached the lowest water colour [February (summer) 2008] (Fig. 9c). Relative to other strict autotrophs, *Chlorella* is a good competitor for light (Huisman et al., 2004). Therefore, it appears that when light requirements of the endosymbiotic algae were fulfilled [i.e. February (summer) 2008], the abundance of mixotrophic ciliates increased.

Finally, changes in the quantity and quality of DOM can also affect prokaryotic plankton because bacteria are the principal decomposers of DOM. The drainage basin should also be considered as a possible source of allochthonous prokaryotic populations that can affect the in-lake prokaryotic composition as was observed in other glacial Andean lakes by Chaia et al. (2005). In Lake Escondido, the contribution of *Bacteria* (dominated by β-Proteobacteria) to prokaryotic plankton abundance was relatively constant in the four sampling occasions [February (summer) 2006–February (summer) 2007] (Fig. 8). Our limited data suggested that *Archaea* were favoured under high DOM molecular weight, water colour and TDP. Although *Archaea* have been found in a variety of freshwater ecosystems (Keough et al., 2003; Casamayor & Borrego, 2009), little is known about the effects of different DOM levels on their dynamics. In deep lakes, *Archaea* have always been observed in deeper strata, suggesting that these planktonic *Archaea* are actively growing in the dark lake levels (Callieri et al., 2007;

Urbach et al., 2007), as in the ocean (Herndl et al., 2005).

In conclusion, our data for this small, unproductive Andean lake indicate that annual-scale changes in precipitation were correlated with DOM parameters (water colour and molecular size) indicating shifts in the relative contribution of DOM input of allochthonous origin. These shifts strongly affected water colour that, in turn, appeared to influence the abundance and community structure of the planktonic community. As our results are restricted to Lake Escondido, future research will indicate whether this pattern holds true in other lake ecosystems. Our results suggest that future variation in precipitation under various scenarios for global climate change would affect the plankton by shifting DOM inputs from runoff and thereby affecting the lake light regime.

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