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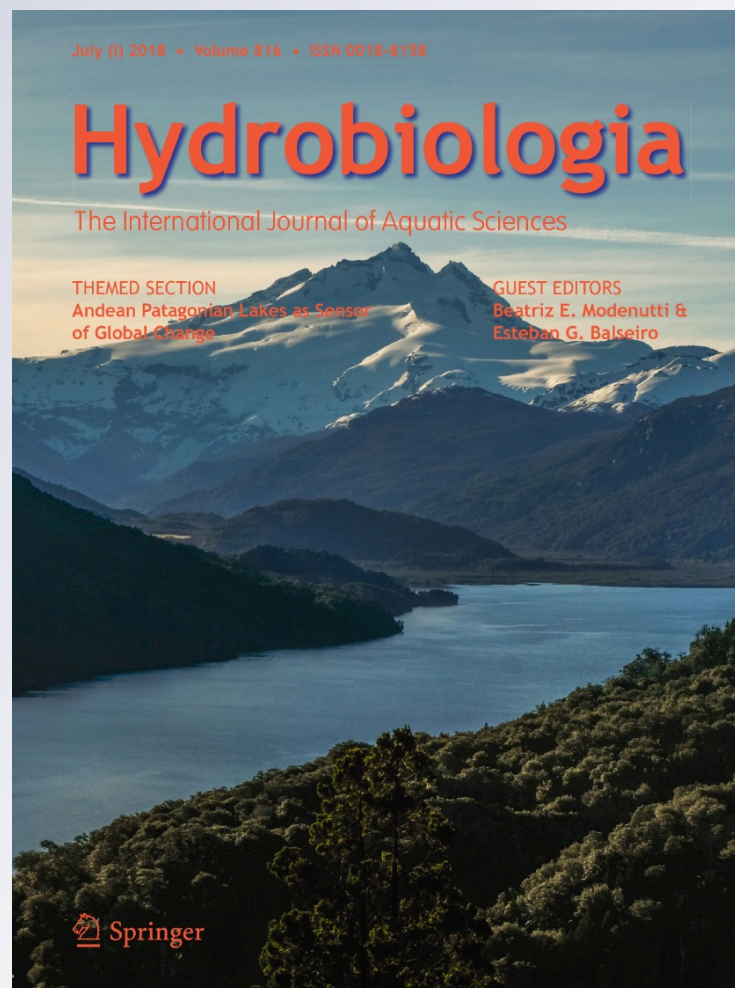
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# Effect of glacial lake outburst floods on the light climate in an Andean Patagonian lake: implications for planktonic phototrophs

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**Abstract** Climate change is altering temperature and precipitation patterns all over the world. In North Patagonia, glaciers of the Tronador mountain (41°S) show a continuous and maintained recession, and these meltwaters are transported to Lake Mascaradi via the Upper Manso River that carries a large amount of glacial clay. These suspended sediment particles cause a very sharp light longitudinal gradient along the western branch of Lake Mascaradi (Tronador arm). Here we analysed changes in the water transparency along the gradient, in particular before and after a glacial lake outburst flood (GLOF) event that occurred in the headwaters that feed Lake Mascaradi. The GLOF caused a significant decrease in turbidity over the years following the event. The depth of the deep chlorophyll maxima (DCM) was directly related to the light penetration, and the decrease in suspended solids load deepened the DCM in the years after the GLOF event. Among photosynthetic organisms, picocyanobacteria and total nanoflagellates abundances increased after the GLOF event when transparency increased due to the decrease in the clay and sediment

inputs into the lake. Our data demonstrated that the DCM and phytoplankton are useful variables to predict changes in the lake light climate.

**Keywords** Glacial lake outburst floods · Glacial clay · Turbidity · Picocyanobacteria · Mixotrophic nanoflagellates

## Introduction

Global warming, including changes in temperatures and the precipitation regime, is expected to have severe consequences in aquatic ecosystems around the world (Adrian et al., 2009; Van De Waal et al., 2010). The worldwide retreat of glaciers is one of the most prominent signs of climate change (Zemp et al., 2009; IPCC, 2013; Sommaruga, 2015). Glaciers are now melting rapidly in many regions, including particularly vulnerable areas such as the Alps, Greenland and the Central and Southern Andes (Masiokas et al., 2008; Casassa et al., 2009). Most glaciers are expected to significantly shrink in the coming decades and many low-elevation glaciers will disappear during this century (Zemp et al., 2009). This phenomenon has given rise to the formation of many moraine-dammed glacier lakes, which are commonly called proglacial lakes (Clague & Evans, 2000). These lakes receive the discharge of glacier meltwaters, which cause a high concentration of mineral suspensoids (Sommaruga, 2015).

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Glacial melting results in the mobilisation and transport of high amounts of suspended sediment particles that are carried by streams/ivers or by runoff to different freshwater environments (Hylander et al., 2011). The particles, so-called glacial flour or glacial milk, increases water reflectance (Gallegos et al., 2008), with a characteristic grey hue, particularly in young proglacial/ice-contact lakes. On the other hand, when glacial flour enters a clear lake through a river, the lake becomes more turbid and bright turquoise. Depending on the topology of the receiving lake basin, the input of a river loaded with sediments forms a longitudinal gradient in lakes and estuaries from very turbid water close to the discharge to clear water far away from the river inflow (Joint & Pomroy, 1981; Modenutti et al., 2000). Thus, over long-term time-scales, glacial recession and ablation in many regions around the world produce rapid changes in light attenuation and the spectral composition of the underwater light field in these lakes (Williamson et al., 2001; Rose et al., 2014). However, over shorter time-scales, extreme events such as avalanches or intense storms may mobilise glacial flour from the watershed and have the potential to rapidly decrease the transparency of glacially fed lakes.

Light, including the exposure to biologically damaging ultraviolet radiation (UVR), regulates a number of critical physical, chemical and biological ecosystem processes (Kirk, 1994; Williamson & Rose, 2009, 2010). The discharge of turbid glacier meltwaters has an effect on the attenuation of both UVR and photosynthetically active radiation (PAR) (Modenutti et al., 2013a; Rose et al., 2014) and this turbidity-induced attenuation of PAR can reduce phytoplankton primary production and biomass (Joint & Pomroy, 1981; Cloern, 1987). Glacial meltwater significantly reduces the extent of the euphotic zone (Svendsen et al., 2002; Hylander et al., 2011; Rose et al., 2014) and this was associated with the development of the deep chlorophyll *a* maxima (DCM) in oligotrophic lakes (Modenutti et al., 2013a).

Some of the newly created proglacial lakes are not stable and can be emptied through dangerous outburst floods (Worni et al., 2012). Glacial lake outburst floods (GLOFs) are catastrophic events in which mobile mixtures of water and sediment that occur suddenly are capable of travelling kilometres with a large peak of discharges and higher volumes than normal floods (Worni et al., 2014). GLOFs include a

series of different processes: rock slope failures, ice avalanches, or mass movements from moraines that may impact glacial lakes and thus produce displacement waves that overtop and breach the dam, generating extreme floods and debris flows. Therefore, the dimensions of this unexpected outburst flood should be evaluated in order to reduce the risks from GLOFs for humans and land downstream (Worni et al., 2012). In addition, GLOF events may also give an insight into sudden ecological changes that affect the transparency of downstream lakes. These impacts may constitute a threat to lake food webs since different aspects of organism dynamics and stoichiometry were observed to be affected by changes in transparency due to glacial clay input (Laspoumaderes et al., 2013; Slemmons et al., 2013; Sommaruga & Kandolf, 2014). In addition, glacial meltwater can also result in changes in the distribution of autotrophs with a lack of the development of a Deep Chlorophyll Maximum (Slemmons & Saros, 2012).

The end moraine that impounds the proglacial Ventisquero Negro Lake (41°12'S, 71°49'W; 1,000 m above sea level) in the Patagonian Andes, Argentina, breached catastrophically on 21 May 2009 devastating the valley below the dam (Worni et al., 2012). The breach was triggered by an increase in the lake level caused by heavy precipitation and by blockage with ice of the lake outlet, which was washed away suddenly (Worni et al., 2012). A huge mass of debris was mobilised and transported through the Upper Manso River to the deep oligotrophic Mascardi Lake situated 16 km downstream. Since many past moraine breaches and subsequent lake outburst floods often went unrecorded or occurred in remote areas, the effect of this event on Mascardi Lake is crucial and challenging for the analysis of these events on aquatic ecosystems. We hypothesised that the GLOF event in lake Ventisquero Negro during 2009 affected the turbidity of Lake Mascardi, with a subsequent effect on primary producers. In a previous study on many lakes in the region that included Lake Mascardi in the dataset, Modenutti et al. (2013a) showed that the development of a deep chlorophyll maximum was dependent on lake transparency, and the DCM was located at 1% of the surface PAR irradiance level. Although other studies in alpine lakes (depth less than 50 m) have shown that the development of the DCM may also be driven by nutrients or grazing (Pilati & Wurtsbaugh, 2003; Saros et al., 2005) in North



Andean Patagonian Deep Lakes (deeper than 200 m), it was observed that light extinction coefficient of PAR ( $K_{dPAR}$ ) was the primary variable that was associated with variation in phytoplankton biomass (chlorophyll *a*) both, experimentally and in the field (Modenutti et al., 2013a, b). This outcome can be attributed to the extremely high transparency to PAR and UVR that this North-Patagonian Andean Lake District has (Morris et al., 1995). Therefore, the aim of this study was to evaluate the effect of the Ventisquero Negro GLOF on the water transparency of Lake Mascaradi by analysing the phytoplanktonic community, in particular, the variation in the depth of the DCM. For this purpose, we took advantage of previous data of Lake Mascaradi (Modenutti et al., 2000, 2013a) and compared the data before and after the GLOF event.

## Materials and methods

### Study area

Mount Tronador (41°10'S, 71°52'W; 3,480 m above sea level) is the highest mountain in Nahuel Huapi National Park and is situated on the border between Chile and Argentina in north Patagonia. The upper part of the mountain is covered by a continuous ice cap, with eleven outlet glaciers that occupy an area of about 64 km<sup>2</sup> (Masiokas et al., 2008) and the largest glaciers reach down to 950 m above sea level, well below the local tree line of 1,700 m above sea level (Villalba et al., 1997). The Upper Manso River valley glacier in Argentina flows down the southeastern flanks of Mount Tronador. The glacier is separated from the ice cap by a steep cliff, and produces snow, ice and debris avalanches to form a secondary, lower glacier known as Ventisquero Negro (Black Glacier). The rapid recession of Ventisquero Negro resulted in the formation of a proglacial lake between the end moraine and the glacier fronts. The lake grew rapidly after the 1990s, with a maximum extent of ~47 ha before the moraine breach in May 2009 (Worni et al., 2012).

Meltwater from the Ventisquero Negro and Castaño Overo glaciers (part of the ice cap) is transported by the Upper Manso River to Lake Mascaradi (Fig. 1). Lake Mascaradi is a V-shaped lake with a western arm (Tronador arm) and an eastern arm (Catedral arm).

Lake Mascaradi has an area of 40 km<sup>2</sup> and a maximum depth of 218 m. Because the Upper Manso River enters at the northwestern end of the Tronador arm loaded with suspended glacial clay particles, it produces a longitudinal light gradient along the Tronador arm of Lake Mascaradi that was described previously (Modenutti et al., 2000; Hylander et al., 2011; Laspoumaderes et al., 2013). This situation continues nowadays.

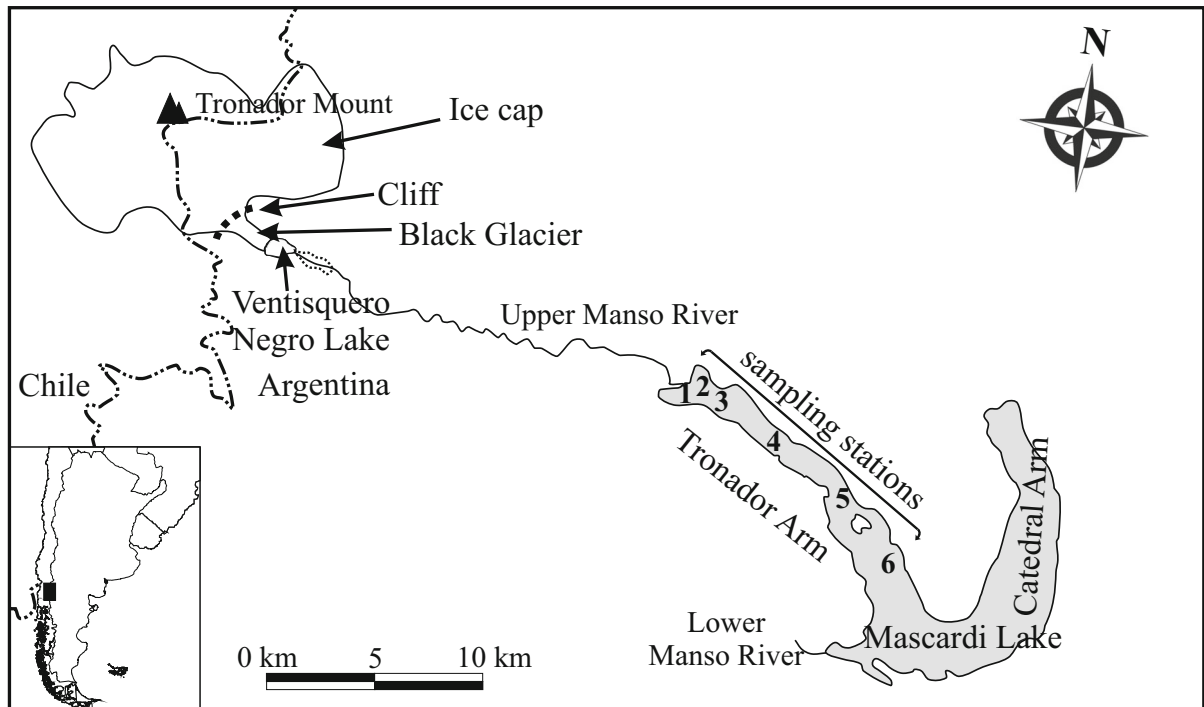
### Sampling

We established six sampling stations in the Tronador arm along the longitudinal gradient (Fig. 1). We compared data from 1998, 2009, 2010, 2011, 2014, 2015 and 2016. On each sampling occasion, we performed vertical profiles (0–50 m) of UVR bands (305, 320, 340 and 380 nm), PAR (400–700 nm), and temperature using a PUV 500B submersible radiometer (Biospherical Instruments). Water samples (2 l) were collected with a Ruttner bottle within the euphotic zone (0, 15, 30 and 45 m depth, which is approximately at 100, 50, 10 and 1% of the surface PAR irradiance, respectively).

In the field, a volume of 150 mL of water from each depth was preserved with acid Lugol solution for phytoplankton enumeration. A volume of 300 mL was filtered through a GF/F filter for chlorophyll *a* (Chl*a*) determination, and the filters were stored in the dark at 4°C until reaching the laboratory. Finally, a volume of 50 mL of lake water was collected for enumeration of autotrophic picoplankton in sterile tubes and fixed with 0.2- $\mu$ m filtered formaldehyde buffered with 0.1 mol L<sup>-1</sup> sodium cacodylate (final concentration 2% vol:vol), stored in darkness at 4°C, and processed within 2 weeks (Callieri & Stockner, 2002). All sampling was performed in triplicate at midday, within 1 h of astronomical noon.

### Laboratory determinations

Total dissolved phosphorus (TDP) was determined on GF/F-filtered lake water. The samples were digested with potassium persulfate at 125°C at 1.5 atm for 1 h, and the concentrations were analysed according to the ascorbate reduced molybdenum method (APHA 2005). DOC concentration was measured in 50 mL



**Fig. 1** Map of the Tronador Mount area showing the area affected by the 2009 GLOF event and Lake Mascardi with the sampling stations (1–6)

of filtered lake water (GF/F precombusted filters) using a Shimadzu analyser (TOC VCSH).

Chla was extracted in hot ethanol following Nusch (1980) and was measured with a 10-AU fluorometer (Turner design) with previous calibration against spectrophotometric measurements. Autotrophic picoplankton, mainly picocyanobacteria, were counted on black polycarbonate filters (Poretics, 0.2- $\mu\text{m}$  pore size) by autofluorescence of phycoerythrin using an Olympus BH 50 epifluorescence microscope fitted with blue excitation cube (U-MWB) and green excitation cube (U-MWG) light filters. Cells were counted using an image analysis system (Image ProPlus; Media Cybernetics).

Enumeration of phytoplankton ( $>2 \mu\text{m}$ ) and mixotrophic ciliates was performed only for the DCM from one turbid station (station 3, Fig. 1) and one clear station (station 6, Fig. 1) following the Utermöhl technique with an inverted microscope (Olympus IX70) using 50-mL Utermöhl chambers. Autotrophic picoplankton and phytoplankton ( $>2 \mu\text{m}$ ) enumerations were performed for the years 2009, 2010, 2011, 2014, 2015 and 2016.

#### Data analysis

The diffuse attenuation coefficients ( $K_d$ ) were estimated as regression coefficients from the light profiles obtained with the radiometer in the field. The thermocline depth was considered as the depth of the mixing layer (i.e. the top of the discontinuity layer) according to the vertical temperature profiles obtained with the PUV radiometer. The specific temperature difference was  $1^\circ\text{C}$ . The slopes of the regression lines of the  $K_{d(\text{PAR})}$  along the gradient ( $K_d$ —square root of distance from inlet) were compared with an analysis of covariance (ANCOVA).

A forward stepwise regression analysis was performed with the  $K_{d(\text{PAR})}$  slope in the different years as the dependent variable, and the mean flow of the Upper Manto River (5 months prior to sampling, i.e. September to January), number of months since maximum flow, the percentage of ice loss during the previous 5 months to sampling and the surface covered by the glacier at the time of sampling as the independent variables. The first two variables were estimated from a meteorological and hydrological

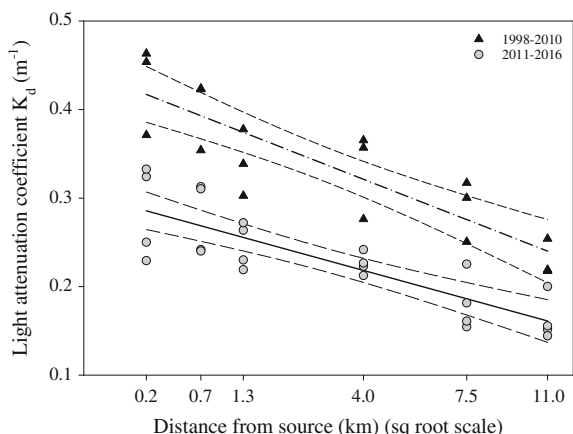
station and the last two variables were estimated from satellite images.

A forward stepwise regression analysis was performed with the depth of the DCM (m) as the dependent variable and the diffuse attenuation coefficients of the different UVR wavelengths (305, 320, 340 and 380 nm) and PAR irradiances.

In order to test if phytoplankton (>2 μm) composition and number of years before and after the GLOF (turbid vs. clear years; for more details, see Fig. 2) were significantly different, two PERMANOVA tests were carried out using a Bray–Curtis distance matrix, one with species ranking and the other with species abundances. Prior to the PERMANOVA test, the homogeneity of multivariate variance was checked. Analyses were carried out with Vegan package in R 3.0.3 (R Core development Team, 2014).

**Results**

Lake Mascardi showed a gradient of increasing transparency and a consequent decrease in the diffuse attenuation coefficients of PAR ( $K_{d(PAR)}$ ) from the meltwater inflow (Station 1) to the end of the Tronador Arm (Station 6) in all sampled years (Fig. 2). On the contrary, nutrients (TDP and DOC) did not show any increase along the gradient, though a slight increase ( $\sim 1 \mu\text{g L}^{-1}$  for TDP) after the GLOF event was observed (Table 1). Regarding DOC concentration,



**Fig. 2** Diffuse attenuation coefficients of PAR ( $K_{d(PAR)}$ ) at different distances from the meltwater inflow. Linear fit and slope values are presented for years before and after the GLOF. Distance axis in square-root scale. *Triangles*: 1998–2010, *Circles*: 2011–2016

**Table 1** Total dissolved phosphorus (TDP in  $\mu\text{g L}^{-1}$ ) and dissolved organic carbon (DOC in  $\text{mg L}^{-1}$ ) in the six sampling stations from Lake Mascardi (E1–E6); years before (1998–2010) and after the GLOF (2011–2016)

	Pre-GLOF		Post-GLOF	
	TDP $\pm$ SD	DOC*	TDP $\pm$ SD	DOC $\pm$ SD
<b>E1</b>				
Above	2.2 $\pm$ 0.15	0.44	2.7 $\pm$ 0.57	0.56 $\pm$ 0.08
Below	1.6 $\pm$ 0.63		2.9 $\pm$ 0.38	0.57 $\pm$ 0.10
<b>E2</b>				
Above	2.0 $\pm$ 0.99		1.9 $\pm$ 0.17	0.47 $\pm$ 0.12
Below	1.5 $\pm$ 0.99		3.3 $\pm$ 0.62	0.58 $\pm$ 0.14
<b>E3</b>				
Above	1.9 $\pm$ 0.06		3.1 $\pm$ 0.77	0.65 $\pm$ 0.27
Below	1.1 $\pm$ 1.05		3.0 $\pm$ 0.20	0.56 $\pm$ 0.07
<b>E4</b>				
Above	2.6 $\pm$ 0.72		3.0 $\pm$ 0.51	0.54 $\pm$ 0.35
Below	2.0 $\pm$ 0.29		3.1 $\pm$ 0.06	0.65 $\pm$ 0.17
<b>E5</b>				
Above	2.9 $\pm$ 1.61	0.36	3.0 $\pm$ 0.30	0.53 $\pm$ 0.36
Below	0.9 $\pm$ 0.76		3.5 $\pm$ 0.09	0.51 $\pm$ 0.11
<b>E6</b>				
Above	2.0 $\pm$ 0.54	0.38	3.5 $\pm$ 0.84	0.55 $\pm$ 0.10
Below	0.9 $\pm$ 0.87		2.6 $\pm$ 0.10	0.56 $\pm$ 0.08

Above: Data above the thermocline. Below: Data below the thermocline. Data are expressed as average  $\pm$  SD

\* Indicates DOC data from Morris et al. (1995)

the only reference before the GLOF is the data from Morris et al. (1995) (samples of 1994) that were analysed in the US and are difficult to compare to recent data, nevertheless we only observed an increase of  $0.1 \text{ mg L}^{-1}$  that may be within the error of the method (Table 1).

The different years of the light gradient ( $K_d$  vs. distance from the inlet) can be pooled into two different groups: turbid before and immediately after the GLOF (1998, 2009 and 2010) and clear years after the GLOF (2011–2016). For each station, the first group was always less transparent than the second group and the fitted regression lines were significantly different (ANCOVA  $P < 0.0001$ ; Fig. 2). Of note, the highest  $K_d$  values (highest turbidity) were observed in 2010, i.e. after the GLOF occurred in Ventisquero Negro Lake (Fig. 2).

A forward stepwise multiple regression analysis showed that the  $K_{d(PAR)}$  slope in the different years can

be explained by a model with the following variables: number of months since maximum flow ( $R^2 = 0.364$ ,  $P = 0.04$ ) and the mean flow of the Manso River during the 5 months prior to sampling (cumulative,  $R^2 = 0.784$ ,  $P = 0.049$ ).

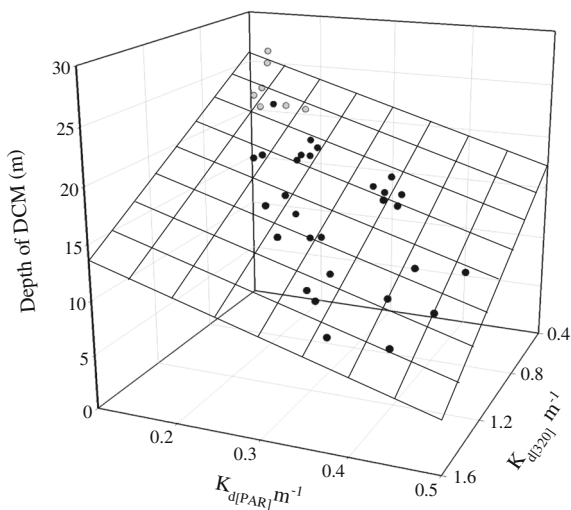
The deep chlorophyll maxima (DCM) depth was related to  $K_{d(\text{PAR})}$  ( $R^2 = 0.54$ ,  $P = 0.002$ ) and  $K_{d320}$  (cumulative  $R^2 = 0.713$ ,  $P = 0.007$ ; Fig. 3). The DCM developed at higher depths (>20 m) in the clearest years (2014, 2015 and 2016; see grey symbols in Fig. 3). The chlorophyll *a* concentration at the DCM was significantly correlated to the picocyanobacteria (Picy) abundance ( $\rho = 0.693$ ;  $P < 0.001$ ). The Picy was dominated by phycoerythrin-rich cells and Picy abundance was positively affected by an increase in transparency ( $K_{d(\text{PAR})}$  vs. Picy abundance  $\rho = -0.612$ ;  $P = 0.001$ ). When analysing turbid versus clear years (2010 with the highest  $K_d$  and 2015 with the lowest  $K_d$ , see Fig. 2), we observed that the abundance of Picy increased towards the clearer stations (station 6) and the clearer year 2015 (Fig. 4).

Phytoplankton was composed mainly by nanoflagellates belonging to the classes Haptophyceae, Cryptophyceae and Dinophyceae (Fig. 5). Haptophyceae was always dominant and entirely represented by *Chrysochromulina parva* Lackey while *Plagioselmis*

*lacustris* (Pascher & Ruttner) Javornicky was the most abundant Cryptophyceae and was always subdominant. Dinophyceae was mainly represented by *Gymnodinium varians* Maskell. Finally, the classes Bacillariophyceae, Chlorophyceae and Cyanophyceae never exceeded 1% of the total algal abundance. The PERMANOVA analysis that considered species ranking showed no significant differences between turbid years (2009–2010) and clear years (2011–2016;  $P > 0.05$ ). However, phytoplankton species abundances showed significant differences ( $F_{1,8} = 9.92$ ,  $P = 0.001$ ). In fact, phytoplankton abundances increased after the GLOF event when the lake turned more transparent (Fig. 5), but with no change in species composition and relative abundances.

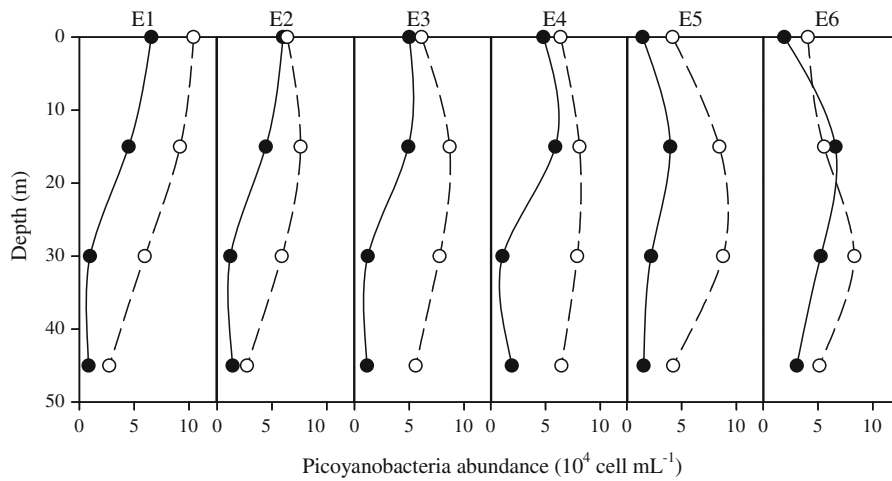
## Discussion

The analysis of transparency ( $K_{d(\text{PAR})}$ ) along the sampling transect in the different years allowed us to distinguish between the turbid years (2010 and before) and the period after with clearer years. The GLOF event, which occurred on 21 May 2009, can be related to the highest turbidity observed in 2010, particularly in the first 4 km away from the meltwater inflow (Stations 1–4; Fig. 2). The breach of the end moraine that impounded the proglacial Ventisquero Negro Lake was produced by an increase in the lake level caused by heavy precipitation and by blockage with ice of the lake outlet (Worni et al., 2012). Analysis of satellite images (SoPI software (CONAE, 2016)) revealed that in the period prior to the GLOF, i.e. between 1998 and 2009, the lake area increased on average by 2.5 ha year<sup>-1</sup>, whereas in the period after the event (2010–2016), the lake area increased at a rate of 3.5 ha year<sup>-1</sup>. The increase in lake size increased the glacial clay sinking, and thus, decreased the amount of suspended solids that were transported by the Upper Manso River downstream and into the Tronador arm of Lake Mascardi. In fact, we observed a higher transparency in the years after the GLOF (2014–2016). However, the slope of the turbidity gradient in the Tronador arm was also observed to be directly related to the flow of the Upper Manso River, particularly the mean value during the 5 months prior to sampling and the number of months from the maximum flow. This finding is of particular interest considering the predictions in precipitation and



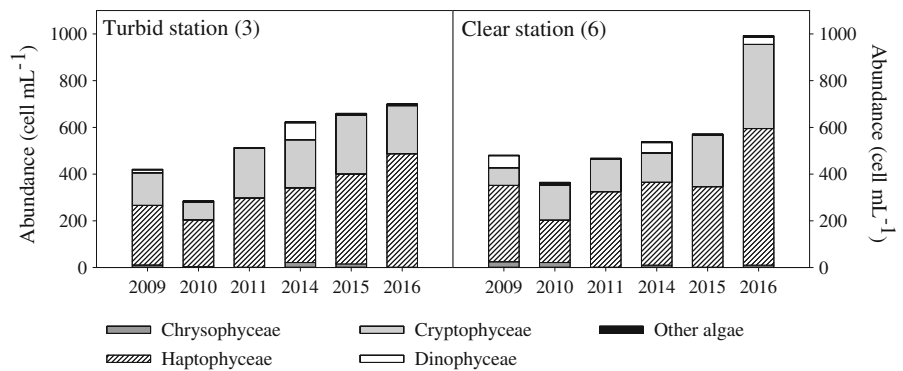
**Fig. 3** DCM depth in relation to the extinction coefficient of 320 nm and PAR ( $K_{d320}$  and  $K_{d(\text{PAR})}$ ) in the Lake Mascardi intralacustrine gradient. Modified from Modenutti et al. (2013a, b) with the addition of years 2014, 2015 and 2016. Grey symbols indicate the DCM at >20 m (Station 4, 5 and 6 for 2014, and 5 and 6 for 2015 and 2016), black symbols indicate DCM at <20 m





**Fig. 4** Picocyanobacteria vertical profile abundances comparing years 2010 (solid lines: turbid year, immediately after the GLOF) and 2015 (dashed lines: clear year, after the GLOF)

**Fig. 5** Phytoplankton abundances comparing stations 3 and 6 (turbid and clear stations, see Fig. 1) in the different years



temperature trends for North Patagonia: Andean mountain rivers (between 30° and 42°S) are predicted to have strong negative trends in flows, mainly caused by a reduction in precipitation, which is expected to decrease by up to 50% (Barros et al., 2013). Thus, the flow of the Upper Manso River, which results largely from precipitation, will determine a decrease in the slope of the turbidity gradient in the Mascardi Lake, i.e. the lake will have a more homogeneous spatial light distribution and become a transparent lake.

Glacial flour is an important factor of light attenuation in isolated glacially fed systems (Gallegos et al., 2008; Sommaruga, 2015) as it is a primary regulator of variation in both UVR and PAR attenuation (Modenutti et al., 2013a; Rose et al., 2014) and it influences the distribution of primary producers (Hylander et al., 2011). Our results indicate an increase in the depth of the DCM in the stations away from the meltwater

inflow to the lake and in the clear years (2014–2016) with a concomitant increase in algal cell abundances (Figs. 3, 4, 5). The pattern of deepening likely resulted from a strong algal photosynthetic inhibition since in Lake Mascardi previous studies found a strong photoinhibiting effect of high PAR and UV-A at surface levels (Callieri et al., 2007a). The results of a study in different North Andean Patagonian lakes and incubation experiments identified light extinction coefficient of PAR ( $K_{PAR}$ ) as the primary variable that was associated with variation in phytoplankton biomass (chlorophyll *a*) and growth (Modenutti et al., 2013b). In Lake Mascardi the diffuse attenuation coefficient ( $K_d$ ) for PAR ranged from 0.46 to 0.16  $m^{-1}$  (Fig. 2) and for UVA from 0.7 to 0.5  $m^{-1}$  (Hylander et al., 2011), close to the meltwater inflow and in the transparent part, respectively. However, we did not find substantial changes in nutrient concentration along

the gradient (Table 1 and Laspoumaderes et al., 2013). The fact that Patagonia is affected by the Antarctic polar vortex (Villafañe et al., 2013) and the low DOC concentration (Morris et al., 1995 and Table 1) probably also contributes to elucidate the importance of light in the location and development of the DCM. However, at the same time, the increase in transparency along the gradient of Lake Mascaradi would favour the development of autotrophs.

The DCM was largely determined by prokaryotes, in particular, by phycoerythrin-rich picocyanobacteria (PE-rich Picy). We observed a negative relationship between Picy abundance and  $K_{d(PAR)}$  and also a deepening of the maximum of abundance along the gradient similar to the DCM. Therefore, our dataset clearly shows that the Picy became more abundant with increasing transparency along the different sampling years. Underwater light intensity and spectral characteristics have been considered important for niche differentiation in Picy (Stomp et al., 2007; Callieri et al., 2012). In particular, competition experiments have shown that red and green picocyanobacteria can coexist by absorbing different parts of the light spectrum (Stomp et al., 2004). Red picocyanobacteria dominate in relatively clear waters, where green light penetrates the deepest (Stomp et al., 2007). In Lake Mascaradi at the DCM, the green and blue wavelengths prevail (Pérez et al., 2002), and this would explain the dominance of phycoerythrin-rich picocyanobacteria. Phylogenetic studies carried out in Lake Mascaradi revealed that Picy strains belong to isolates grouped within the *Cyanobium gracile* group (group A) (Callieri et al., 2013). Laboratory experiments with different freshwater strains show that photosynthetic responses are strain-specific and sensitive to photo-acclimation (Moser et al., 2009). In this sense, PE-rich Picy seem to be more sensitive to photo-acclimation than PC-rich cells (Crosbie et al., 2003a, b) and tend to saturate photosynthesis and their growth rate at very low irradiances (Stockner & Antia, 1986). Noticeably, at the DCM level in Lake Mascaradi under changing light conditions due to changes in the input of glacial clay (before and after the GLOF), PE-rich Picy would increase their abundance when the transparency increased (both along the gradient and before vs. after the GLOF). Additionally, Picy may also have a competitive advantage over larger phytoplanktonic algae because—due to their smaller size—Picy can utilise nutrients more efficiently under low

nutrient conditions (Gervais et al., 1997). In addition, Picy can grow at low inorganic P concentrations by utilising organic sources of phosphate (Jansson et al., 1988; Whitton et al., 2005) and during periods of N limitation, they can use nitrogen reserves that exist in phycobiliproteins as amino acid storage molecules (Grossman et al., 1993). Along the horizontal gradient in Lake Mascaradi, we observed very low nutrient concentrations and no changes along the gradient (Table 1) (Laspoumaderes et al., 2013; Modenutti et al., 2013a); thus, this limiting nutrient condition would also contribute to the dominance of Picy in the DCM over larger phototrophs. In addition, we also observed only a slight increase in TDP and DOC concentrations (remaining both very low) in years before and after GLOF event. Melting glacial water does not directly enter to Lake Mascaradi since the Upper Manso River carried all sediment for 16 km before entering the lake. During this spatial stretch, there is consumption and recycling of nutrients by the periphyton that cover the river bottom (Martyniuk et al., 2014). Thus, the final input does not represent the nutrient concentration of a direct input of melting ice.

The DCM also comprises eukaryotic cells, of which almost all (more than 92% in all samples) were mixotrophic nanoflagellates, such as *Chrysochromulina parva*, *Plagioselmis lacustris* and *Gymnodinium varians*. Motile phytoflagellates are able to move to lower depths, thus also developing a DCM in Alpine lakes (Sommaruga & Psenner, 1997). Similarly, in Andean lakes, motile mixotrophic nanoflagellates exploit the upper hypolimnetic levels by increasing their photosynthetic efficiency while sheltered from photoinhibition (Callieri et al., 2007b). This pattern was observed before and after the GLOF event, thus highlighting that motile cells can react rapidly to changes in water turbidity. However, we observed an increment in the total nanoflagellate abundances after the GLOF event when the transparency increased due to the decrease in the clay and sediment inputs into the lake. Glacial flour was observed to interfere with the uptake of bacteria in phagotrophic heterotrophic nanoflagellates, thus affecting their growth and survival (Sommaruga & Kandolf, 2014). Similarly, it could be expected that mixotrophic nanoflagellates in Lake Mascaradi immediately after the GLOF (2010) attained low abundances because of the increase of glacial sediments in the lake water column.

We conclude that the glacial recession and the GLOF that occurred in Ventisquero Negro Lake in 2009 influenced Lake Mascardi transparency and thus the distribution of autotrophs in the water column. Our results also highlight the important role of the Upper Manso River flow that enters the lake, which could be affected by climate change, in particular, the negative trend in precipitation that is projected for northwest Patagonia. Finally, we predict that the consequences of changes in water transparency will affect the autotroph distribution in the water column, which seems to be modified more than phytoplanktonic composition.

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