

# Environmental changes affecting light climate in oligotrophic mountain lakes: the deep chlorophyll maxima as a sensitive variable

Beatriz Modenutti · Esteban Balseiro · Marcela Bastidas Navarro · Cecilia Laspoumaderes · María Sol Souza · Florencia Cuassolo

Received: 21 August 2012 / Accepted: 1 November 2012 / Published online: 10 November 2012  
© Springer Basel 2012

**Abstract** The North-Patagonian Andean lakes of Argentina are high light, low nutrient environments that exhibit development of deep chlorophyll maxima (DCM) at the metalimnetic layer during summer stratification, at approximately 1 % of surface PAR irradiance. We examined whether the position of DCM changes as a consequence of long-time (global warming: glacial clay input) and short-time (eruption: volcanic ashes) events. We performed different field studies: (1) an interlacustrine analysis of six lakes from different basins, including data of the 2011 volcanic eruption, which caused an unexpected variation in water transparency; and (2) an intralacustrine analysis in which we compared different stations along a transparency gradient in Lake Mascardi caused by glacial clay input at one end of the gradient. In these analyses, we documented changes in DCM depth and its relationship with different parameters. DCM development was not related with thermocline depth or nutrient distribution. In all cases, the only significant variables were  $K_d$  320 nm and  $K_d$  PAR. Our study showed that suspended particles (glacial clay and volcanic ashes) can play a crucial role in transparent lakes, affecting lake features such as the phototrophic biomass distribution along the water column. Suspended solid inputs from either glacial clay or volcanic ashes produce a comparable effect, provoking a decrease in light and, consequently, an upper location of the DCM. Thus, the DCM position is highly sensitive to global changes, such as increased temperatures causing glacier

recession or to regional changes caused by volcanic eruptions.

**Keywords** Light climate · Lakes · Chlorophyll distribution · Transparent lakes · Climate change · Total suspended solids

## Introduction

Water resources are one of the most highly sensitive environmental components, and they can be affected by changes in temperature and precipitation and by the amount of suspended particles and dissolved substances. Lakes and reservoirs have recently been suggested as effective sentinels, integrators, and regulators of climate change (Williamson et al. 2009). Lakes and reservoirs can provide valuable information on the patterns and mechanisms of how global climate change is altering ecosystems (Williamson et al. 2008).

In alpine regions, changes in glacier length are widely recognized as the most reliable and easily observed indicator of climate change (Paul et al. 2007). Because warming affects glacial melting and meltwater carries high amounts of suspended sediments, changes in this input influence water transparency through the attenuation of all wavelengths, including UVR (Hessen 2002; Helbling and Zagarese 2003). However, climate change has also been suggested to influence factors such as the dissolved organic matter (DOM) input to lakes (Schindler and Curtis 1997; Zhang et al. 2010; Couture et al. 2012). Differences in DOM concentrations and, more important, in the optical features of chromophoric dissolved organic matter (CDOM) can cause wide variations in UV attenuation (Williamson and Rose 2010). In addition, geological events

B. Modenutti (✉) · E. Balseiro · M. Bastidas Navarro · C. Laspoumaderes · M. S. Souza · F. Cuassolo  
Laboratorio de Limnología, INIBIOMA,  
UNComahue-CONICET, Quintral 1250,  
8400 Bariloche, Argentina  
e-mail: bmodenutti@comahue-conicet.gob.ar

such as volcanic eruptions can produce catastrophic effects by the ejection and emission of gases, ashes, pumice and lava (Self 2006). The input of these pyroclastic materials to aquatic environments can increase the amount of suspended solids, thus affecting water transparency.

In many aquatic systems, pelagic autotrophs are distributed unevenly along the euphotic zone, and they develop deep chlorophyll maxima (DCM), which are subsurface peaks of chlorophyll often found in large oligotrophic lakes (Brooks and Torke 1977; Moll and Stoermer 1982; Fahnenstiel and Scavia 1987), small lakes (Fee 1976; Pick et al. 1984; Gervais et al. 1997) and marine environments (Cullen 1982). A variety of interacting physical (Sommaruga and Psenner 1997), chemical (Saros et al. 2005), and biological (Falkowski and Raven 2007; Pilati and Wurtsbaugh 2003) hypotheses have been proposed to explain the formation of DCM. Ultraviolet radiation (UVR) avoidance has been suggested as an important factor in the development of DCM in alpine lakes (Sommaruga and Psenner 1997; Sommaruga 2001). Similarly, in the North-Patagonian Andean deep lakes, a strong UVR inhibitory effect in the upper levels of the water column has been observed (Modenutti et al. 2004). Because water transparency is affected, among other factors, by global change via ozone depletion and precipitation (Williamson et al. 2009), the development and position of the DCM may be considered a key feature in deep transparent lakes. However, if the DCM is only determined by UVR avoidance in the epilimnion (Sommaruga and Psenner 1997; Modenutti et al. 2004), then the depth of the mixing layer should provide a good prediction of DCM depth. In addition, in many transparent lakes, the thermocline depth has not been observed to coincide with the DCM (Modenutti et al. 2010; Callieri et al. 2007); thus other factors affecting water transparency should play an important role in the vertical position of the DCM. Here, we analyze the DCM position in the water column, which constitutes another valuable biological testing variable in lakes where water transparency is affected.

The Patagonian Andes, containing more than 20,000 km<sup>2</sup> of glaciers, are the largest glaciated area in South America (Masiokas et al. 2008). From the north to 45°S, and all along the high Andes mountains, there are numerous relatively small glaciers that are currently in drastic recession in coincidence with significant warming and decreasing precipitation from 1912–2002 (Masiokas et al. 2008). The area around 41°S contains important lakes of the Pacific and Atlantic watersheds (Modenutti et al. 1998; Modenutti et al. 2010) with little influence from human activities, making this lake district an appropriate place to establish a baseline in global studies. These lakes have very low dissolved organic carbon (DOC) and high transparency to different wavelengths, which would imply

high exposure to UVR and PAR (Morris et al. 1995). The lakes are very poor in nutrient concentrations; thus they have been referred to as high light, low nutrient environments (Balseiro et al. 2004, 2007). More recently (June 2011), the area has been affected by the Puyehue-Cordon Caulle volcano eruption, and some lakes were affected by the input of ashes.

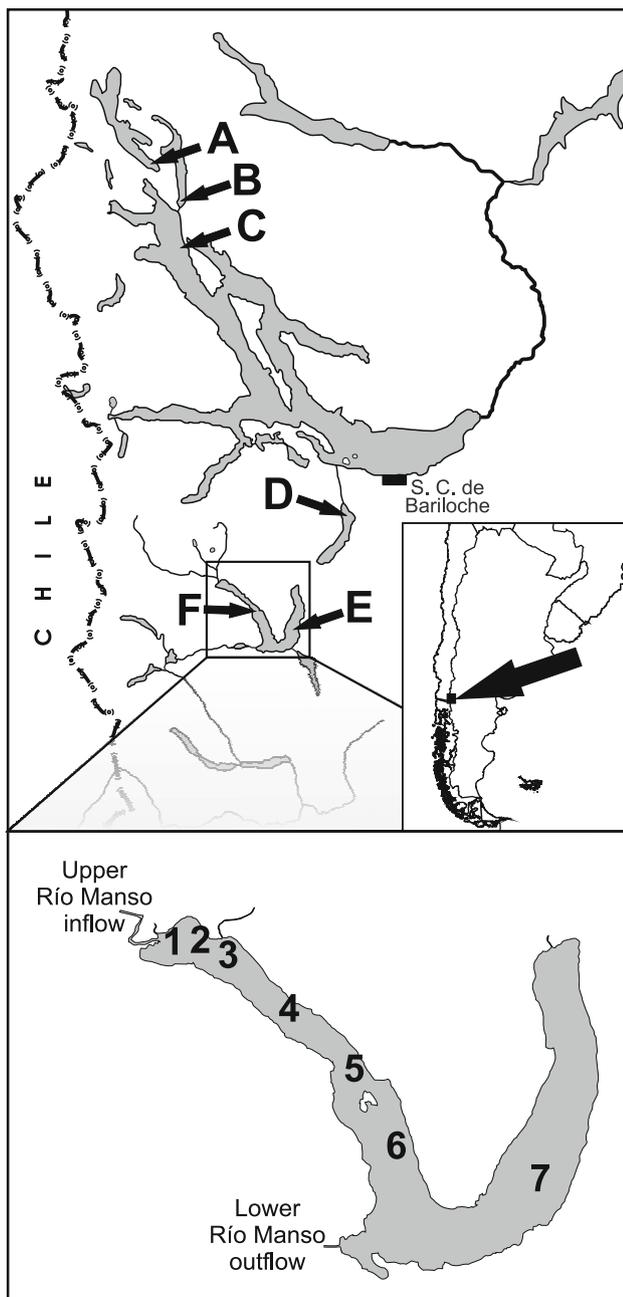
Here, we examine whether the position of DCM can change as a consequence of long-time (global warming: glacial clay input) and short-time (eruption: volcanic ashes) events. We performed different field studies: an interlacustrine analysis of six lakes from different basins and an intralacustrine analysis in which we compared different stations along a transparency gradient in Lake Mascaradi caused by glacial clay input at one end of the gradient. Through these analyses, we document changes in DCM depth and its relationship with different parameters. In addition, the recent volcanic event presents a unique opportunity to evaluate how the vertical position of the DCM responds to unexpected variations in water transparency. For this purpose, we took advantage of a volcanic eruption that heavily affected some of these transparent lakes to evaluate whether this input of inorganic particles affected the DCM of these lakes in a similar manner as the glacial clay from melt water.

## Methods

### Study area

#### *Interlacustrine variation in different watersheds*

We compared data from summer surveys performed in 2002, 2005, 2008 (pre-eruption) and 2012 (post-eruption) in lakes located between 40°40' and 41°07'S in the North Andean Patagonian region (Argentina) (Fig. 1; Table 1) corresponding to the glacial lakes district of the Southern Andes (Iriondo 1989). This area is characterized by a profuse hydrographic system that includes large and deep lakes ( $Z_{\max} \geq 150$  m) that belong to Atlantic or Pacific watersheds (Modenutti et al. 1998, 2010). The studied lakes were Espejo, Correntoso, Nahuel Huapi, and Gutiérrez (Nahuel Huapi Basin) of the Atlantic watershed and Mascaradi Catedral and Mascaradi Tronador (Manso Basin) of the Pacific watershed (Fig. 1, upper panel). The two arms of Lake Mascaradi (Catedral and Tronador) were considered to be two separate lakes since the two arms differ in their hydrology because of three headwater glaciers (Manso, Overo and Alerce glaciers) draining only into Mascaradi Tronador (Modenutti et al. 2000). The post-eruption data (2012) included three lakes: Espejo,



**Fig. 1** Study site. *Upper panel*: interlacustrine comparison. **a** Lake Espejo, **b** Lake Correntoso, **c** Lake Nahuel Huapi, **d** Lake Gutiérrez, **e** Lake Mascardi Catedral and **f** Lake Mascardi Tronador. *Lower panel*: interlacustrine comparison 1–7, Lake Mascardi sampling stations

Correntoso and Nahuel Huapi. The regional climate is temperate cool (mean annual temperature: 8.7 °C) with a predominance of strong westerly winds and a mean annual precipitation of 1,500 mm (Paruelo et al. 1998). Vegetation corresponds to the Andean-Patagonic temperate forest, dominated by evergreens of *Nothofagus dombeyi* and *Austrocedrus chilensis*.

### Intralacustrine variation

The V-shaped Lake Mascardi has different light features in the two arms (Tronador and Catedral). The northwestern end of the Tronador arm receives meltwater from the glaciers at Tronador Mountain (41°S; 71°W; 3,554 m asl). Glacier fluctuations at this mountain have been observed since 1976 (Rabassa et al. 1978), and the Frías, Alerce, Castaño Overo and Ventisquero Negro glaciers have shown continuous and maintained recession (Leiva 1999; Masiokas et al. 2008). Meltwater from the Ventisquero Negro and Castaño Overo glaciers is transported by the Manso Superior River to Lake Mascardi (Iriondo 1974). These suspended sediment particles produce a longitudinal light gradient along the Tronador arm of Lake Mascardi (Bonetto et al. 1971; Modenutti et al. 2001; Balseiro et al. 2007). We established seven sampling stations: six in the Tronador arm along the longitudinal gradient and one in the clear Catedral arm (Fig. 1, lower panel). In this case, we compared data from 1994, 1998, 2002, 2009, 2010 and 2011.

### Sampling

We performed the same sampling procedures in all lakes and sampling stations in a central sampling point located at the deepest part of each lake. Sampling was performed in all cases during the summer (January or February). Vertical profiles (0–70 m) of UVR bands (305, 320, 340 and 380 nm), PAR (400–700 nm), and temperature were measured using a PUV 500B submersible radiometer (Biospherical Instruments). Water samples (2 L) were collected with a Ruttner bottle within the euphotic zone (0, 5, 10, 20, and 45 m depth, approximately at 100, 50, 10 and 1 % of the surface PAR irradiance, respectively). In the field, 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. A volume of 150 mL of water from each depth was preserved with acid Lugol solution for phytoplankton enumeration. The remaining sampled volume (~1.4 L) was transferred to polypropylene acid-washed containers. The containers were kept in the dark and thermally insulated, and carried immediately to the laboratory to determine the total suspended solids, nutrients (phosphorus) and dissolved organic carbon (DOC) concentrations. All sampling was performed in triplicate at mid-day, 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

**Table 1** Location and morphometric characteristics of the studied North-Patagonian Andean lakes

Lakes	Location		Altitude (m asl)	Area (km <sup>2</sup> )	Z <sub>max</sub> (m)	Watershed	Type of study
Espejo	40°40'S	71°42'W	800	30.00	245	Atlantic	Interlacustrine
Correntoso	40°43'S	71°39'W	764	19.50	>100		Interlacustrine
Nahuel Huapi	40°47'S	71°40'W	764	557.00	464		Interlacustrine
Gutiérrez	41°10'S	71°24'W	785	16.40	111		Interlacustrine
Mascardi Catedral	41°20'S	71°30'W	750	39.20	218	Pacific	Interlacustrine Intralacustrine
Mascardi Tronador	41°15'S 41°19'S	71°38'W 71°34'W	750	39.20	118		Intralacustrine

In the case of Lake Mascardi Tronador, the coordinates indicate both ends of the sampled gradient

potassium persulfate at 125 °C at 1.5 atm for 1 h, and the concentrations were analyzed according to the ascorbate-reduced molybdenum method (APHA 2005). DOC concentration was measured in 50 mL of filtered lake water (GF/F precombusted filters) using a Shimadzu analyzer (TOC 5000A). Chl<sub>a</sub> was extracted in hot ethanol following Nusch (1980) and was measured with a 10-AU fluorometer (Turner design) with previous calibration against spectrophotometric measurements. Total suspended solids (TSS) were estimated by filtering 1 L of lake water through pre-weighed GF/F filters. The filters were then dried at 60 °C for 48 h and reweighed.

Enumeration of phytoplankton and mixotrophic ciliates was performed following the Utermöhl technique with an inverted microscope (Olympus IX70) using 50 mL Utermöhl chambers. Endosymbiotic *Chlorella* abundance was considered as the number of cells inside the peritrich ciliate *Ophrydium naumanni* measured according to Modenutti et al. (2008). The picoplankton contribution to the total chlorophyll data from the different lakes was taken from Callieri et al. (2007) and Callieri et al. (2009).

Inorganic particle size distribution (glacial clay and volcanic ashes) was estimated with an inverted microscope after decantation of lake water in 50 mL Utermöhl chambers. A minimum of 500 particles per sample was measured and processed with an image analysis system (Image ProPlus; Media Cybernetics).

#### Statistical analysis

The diffuse attenuation coefficients (K<sub>d</sub>) were estimated as regression coefficients from light profiles obtained with a radiometer in the field along the whole euphotic zone. Nutrient concentrations were analyzed using a two-way analysis of variance (ANOVA) (lakes and depth). A forward stepwise regression analysis was performed with DCM depth (m) as the dependent variable and the diffuse attenuation coefficients of the different UVR wavelengths

(305, 320, 340 and 380 nm) and PAR irradiances, thermocline depth, and P-TDP concentrations as independent variables. Co-correlation between the different wavelengths ranged from  $r^2 = 0.57$  (K<sub>d</sub><sub>320</sub>–K<sub>d</sub><sub>PAR</sub>) to  $r^2 = 0.94$  (K<sub>d</sub><sub>320</sub>–K<sub>d</sub><sub>340</sub>). Thermocline depth was considered the depth of the mixing layer (i.e., top of the discontinuity layer  $\geq 1$  °C m<sup>-1</sup>) according to vertical temperature profiles obtained with the PUV radiometer. Slopes of the regression lines obtained between the TSS and K<sub>d</sub> depths and the TSS and DCM depths were compared with an analysis of covariance (ANCOVA). Differences in particle size between clay and ash were assessed with a Mann–Whitney test because the normality assumption was not met. In all ANOVAs, the normality and homoscedasticity of the data were previously confirmed. All statistical analyses were performed using the SigmaStat 3.1 and SPSS 18 statistical packages.

## Results

### Interlacustrine comparison

In summer (January or February), all the lakes were thermally stratified with a thermocline varying between 6 and 35 m (Table 2). The studied lakes exhibited high transparency and extended euphotic zones (Table 2, see pre-eruption data). In all lakes, the 1 % surface PAR (Z<sub>1%</sub> PAR) exceeded the thermocline depth; thus the epilimnion, the metalimnion and the upper part of the hypolimnion were included in the euphotic zone. The DCM was mainly located in the upper illuminated hypolimnion (Table 2). This situation changed dramatically after the 2011 volcanic eruption. Because volcanic ash precipitation came from the northwest (Chile), there was a gradient in the impact, with lakes Espejo, Correntoso and northwest Nahuel Huapi receiving higher amounts of particles. Thus, the transparency of lakes Espejo, Correntoso and Nahuel Huapi sharply

**Table 2** Lake summer features: pre-eruption (before 2011) and post-eruption (2012)

Lakes	Z <sub>therm</sub> (m)	DCM (m)	Z <sub>1%PAR</sub> (m)	K <sub>d305</sub> (m <sup>-1</sup> )	K <sub>d320</sub> (m <sup>-1</sup> )	K <sub>dPAR</sub> (m <sup>-1</sup> )	TDP (μg P L <sup>-1</sup> )
Espejo Pre-eruption	6–15	40	41–42	0.42	0.41–0.44	0.10–0.11	1.05 ± 0.04–1.46 ± 0.25
Espejo Post-eruption	7	15	17	0.7214	0.6945	0.2687	4.30 ± 0.21
Correntoso Pre-eruption	13–15	37–46	43–44	0.46	0.37–0.40	0.09–0.10	0.96 ± 0.05–1.95 ± 0.18
Correntoso Post-eruption	13	20	33	0.5391	0.4617	0.1361	4.63 ± 0.09
NH Pre-eruption	32–45	42–51	43–48	0.42	0.33–0.34	0.09–0.10	1.77 ± 0.23–2.67 ± 0.18
NH Post-eruption	35	25	40	0.3664	0.3013	0.1144	1.87 ± 0.09
Gutiérrez	11–22	29–35	31–37	0.46	0.39–0.41	0.13–0.14	1.30 ± 0.06–2.8 ± 0.45
Mascardi Catedral	14–18	24–26	27–31	0.61	0.61–0.65	0.14–0.17	1.80 ± 0.25–2.47 ± 0.08

Thermocline depth (Z<sub>therm</sub>), Deep Chlorophyll Maxima (DCM), euphotic zone (depth of 1 % surface irradiances (Z<sub>1 %</sub>) of PAR), light attenuation coefficients (K<sub>d</sub>) of UVR (305 and 320 nm), and PAR and total dissolved phosphorus (TDP) concentrations of the studied lakes

Pre-eruption data are given as minimum and maximum values of the 2002–2005 and 2008 samples; post-eruption: 2012 sampling

TDP concentrations are expressed as mean ± standard error of the vertical profile data (3–5 points), and given for the maximum and minimum of the three pre-eruption samples (2002–2005–2008) and post-eruption data from 2012

NH Nahuel Huapi

decreased (Table 2, a more than twofold K<sub>dPAR</sub> increase in Lake Espejo). The decrease in transparency was significant in the three affected lakes (*t* test for each lake,  $P < 0.001$ ). Nutrient concentrations, in particular dissolved phosphorus, were very low, independently of their basin or watershed, and we did not observe any variation along the water column (Table 2, see low s.e.,  $P > 0.05$  for differences between lakes and depths in the pre-eruption dataset). This situation also changed after the volcanic eruption, with a significant increase in P concentration in the affected lakes (Lakes Espejo and Correntoso,  $P < 0.0001$ ). In the large and extremely deep Lake Nahuel Huapi (Table 1, see area and depth), however, the P increase was not significant ( $P > 0.05$ ). Dissolved organic carbon content also showed minor variations among the lakes, and values were always below 0.6 mg L<sup>-1</sup> (Table 3). No changes in DOC were observed in the post-eruption data (Table 3).

We analyzed the dependence of DCM depth before the eruption on the following ecological factors: thermocline depth, TDP concentration, and the extinction coefficients of the different UV wavelengths (305, 320, 340, and 380 nm) and PAR. A forward stepwise multiple regression analysis showed that the only significant variables in the model were K<sub>d</sub> 320 nm and K<sub>d</sub> PAR (for K<sub>d</sub> 320 nm,  $r^2 = 0.788$ ,  $P = 0.0001$ , for K<sub>d</sub> PAR (cumulative),  $R^2 = 0.828$ ,  $P = 0.031$ ) (Fig. 2). In all cases, thermocline depths and nutrients were not significant and, therefore, not included in the model.

Because the volcanic eruption caused a decrease in transparency and, consequently, a decrease in DCM depth (Table 2; Fig. 3, see arrows), we included the post-eruption data in our forward stepwise analysis. This analysis showed

that the factors determining DCM depth remained unchanged (for 320 nm,  $R^2 = 0.653$ ,  $P = 0.005$ , for PAR,  $R^2 = 0.722$ ,  $P = 0.014$ ). Thus, after the catastrophic event that occurred in a short time period, 320 nm and PAR were again factors that explained the position of the DCM.

#### Intralacustrine variation

Lake Mascardi Tronador presented a transparency gradient, and thus K<sub>d</sub> decreased along the sampling stations from the Upper River Manso inflow (station one) to the Catedral arm (station seven) (Fig. 1, lower panel; Table 3). An increase in transparency towards station seven was observed for all the studied wavelengths (Table 3). Thermocline depth did not change significantly along the Tronador arm; however the thermocline was deeper in the Catedral arm. TDP did not vary significantly along the gradient or in the vertical distribution at each station (Table 3). A forward stepwise multiple regression analysis showed that the only variables included in the model were 320 nm and PAR (for PAR,  $r^2 = 0.737$ ,  $P = 0.002$ , for 320 nm (cumulative),  $R^2 = 0.828$ ,  $P = 0.007$ ) (Fig. 4). Indeed, we observed an inverse relationship between total suspended solids caused by glacial clay and the Chl<sub>a</sub> concentration at the DCM ( $r^2 = 0.47$ ,  $P = 0.003$ ).

#### Phytoplankton composition and TSS relationships

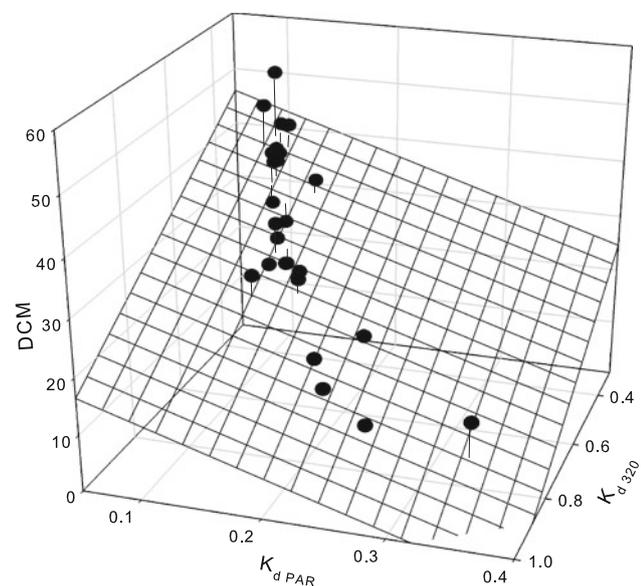
The DCM of all study lakes mainly consisted of mixotrophic nanoflagellates (dominated by *Chrysochromulina parva* and *Rhodomonas lacustris*), mixotrophic ciliates (endosymbiotic *Chlorella*) and picocyanobacteria (Table 4). Lake Gutiérrez

**Table 3** Average of dissolved organic carbon (DOC) concentration in the lakes included in the interlacustrine comparison analysis (January (Summer) sampling)

Lake	DOC (mg L <sup>-1</sup> ) 1994 (1)	DOC (mg L <sup>-1</sup> ) 2008 (2)	DOC (mg L <sup>-1</sup> ) 2012 (3)
Espejo	NA	0.33	0.35
Correntoso	0.25	0.25	0.39
NH	0.44	0.50	0.36
Gutiérrez	0.71	0.62	0.80
Mascardi Catedral	0.38	0.47	0.60
Mascardi Tronador	0.44	0.36	0.52

Pre-eruption data: (1) Morris et al. (1995), (2) Corno et al. (2009), (3) this study

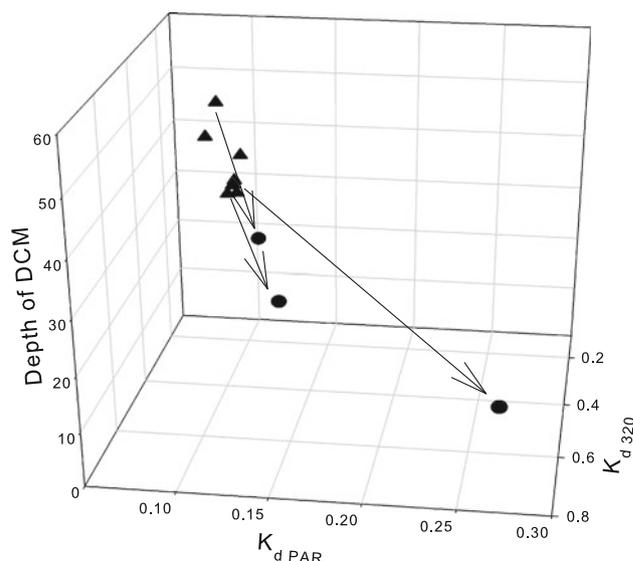
NA data not available



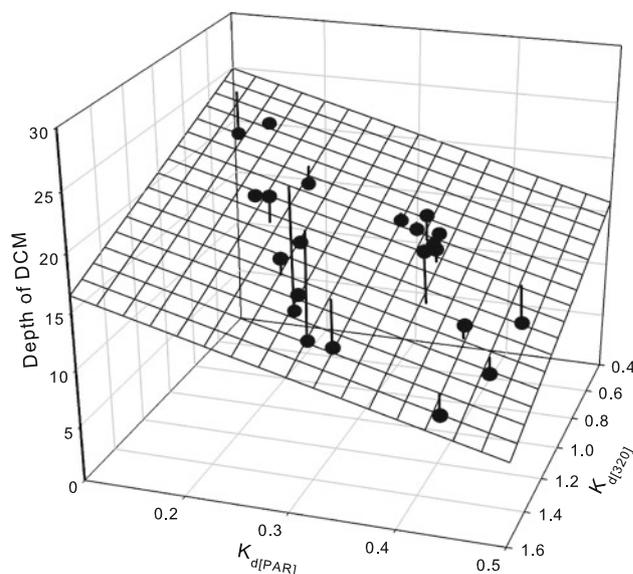
**Fig. 2** DCM depth in relation to the extinction coefficient of 320 nm and PAR ( $K_{d320}$  and  $K_{dPAR}$ ) in the pre-eruption interlacustrine comparison. For statistical significance, see the text

diatoms, particularly *Cyclotella meneghiniana*, also increased their abundance at the DCM.

Total suspended solids showed a gradient along the Mascardi Tronador arm and an increase after the volcanic event in lakes Espejo, Correntoso and Nahuel Huapi. Particle size analysis showed that the suspended glacial clay had smaller particles in a narrower range size than volcanic ashes (clay =  $1.25 \mu\text{m} \pm 1.20$ ; ashes =  $2.55 \mu\text{m} \pm 2.00$ , mean  $\pm$  SD), and the differences were significant (Mann-Whitney,  $P < 0.00001$ ) (Fig. 5). We observed that the  $K_{dPAR}$ -TSS relationship differed between clay and ash (ANCOVA:  $F_{1,27} = 11.58$ ,  $P = 0.0021$ ) (Fig. 6a). However,



**Fig. 3** DCM depth in relation to the extinction coefficient of 320 nm and PAR ( $K_{d320}$  and  $K_{dPAR}$ ), comparing pre-eruption (triangles) and post-eruption (circles) data of lakes Espejo, Correntoso and Nahuel Huapi. Arrows indicate change in the position of the DCM



**Fig. 4** DCM depth in relation to the extinction coefficient of 320 nm and PAR ( $K_{d320}$  and  $K_{dPAR}$ ) in the Lake Mascardi intralacustrine gradient. For statistical significance, see the text

we observed an inverse relationship between TSS and DCM depth with two different regression lines, one for glacial clay and one for volcanic ash (Fig. 6b). The statistical analysis showed that, although both lines had different origins ( $F_{1,44} = 19.34$ ,  $P < 0.001$ ), the slopes of both regression lines did not ( $F_{1,43} = 0.140$ ,  $P = 0.70$ ), indicating a comparable effect of TSS on DCM depth.

**Table 4** Features of Lake Mascardi sampling stations

Sampling stations	$Z_{\text{therm}}$ (m)	DCM (m)	$Z_{1\% \text{ PAR}}$ (m)	$K_{d305}$ ( $\text{m}^{-1}$ )	$K_{d320}$ ( $\text{m}^{-1}$ )	$K_{d\text{PAR}}$ ( $\text{m}^{-1}$ )	TDP ( $\mu\text{g P L}^{-1}$ )
1	5–8	8–10	10–12.5	1.21–1.28	0.47–1.01	0.37–0.46	$1.89 \pm 0.19$ – $2.15 \pm 0.19$
2	5–8	9–13	11–13	0.94–1.27	0.51–0.74	0.35–0.42	$1.75 \pm 0.32$ – $1.97 \pm 0.37$
3	5–8	10–16	12.5–15	0.86–1.2	0.37–0.64	0.30–0.37	$1.52 \pm 0.36$ – $2.08 \pm 0.12$
4	5–8	15–17	13–17	0.77–1.1	0.35–0.62	0.27–0.35	$2.31 \pm 0.28$ – $2.02 \pm 0.16$
5	5–8	16–18	15–18	0.75–1.0	0.32–0.58	0.25–0.31	$1.36 \pm 0.26$ – $1.98 \pm 0.13$
6	6–9	18–20	18.5–22	0.70–0.95	0.31–0.55	0.21–0.25	$1.47 \pm 0.32$ – $1.50 \pm 0.06$
7	14–18	25–30	27–33	0.67–0.75	0.30–0.52	0.14–0.17	$1.48 \pm 0.19$ – $1.52 \pm 0.03$

Thermocline depth ( $Z_{\text{therm}}$ ), deep chlorophyll maxima (DCM), euphotic zone (depth of 1 % surface PAR irradiance =  $Z_{1\%}$ ), light attenuation coefficients ( $K_d$ ) of UVR (305 and 320 nm), and PAR and total dissolved phosphorus (TDP) concentrations of the studied lakes

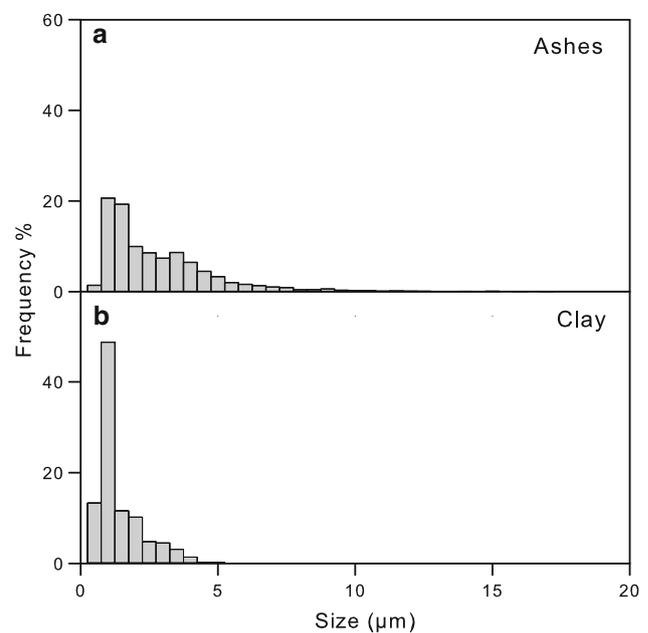
Data are given as minimum and maximum values of the 1998–2009–2010 and 2011 samples

TDP concentrations are given as maximum and minimum of the sampling years (1998–2009–2010 and 2011) as mean  $\pm$  standard error of the vertical profile data (three points)

## Discussion

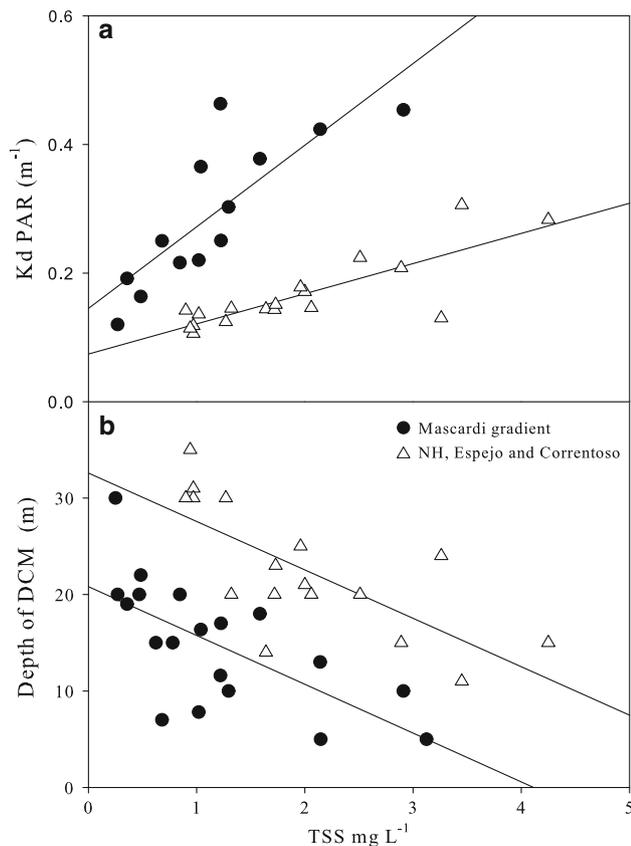
Our results indicate that in North-Patagonian Andean lakes during the stratification period, DCM occurs at or below the thermocline, with a strong relation to light quality and quantity. In particular, PAR and UV-A (320 nm) wavelengths seemed to have a major importance in determining DCM depth. The presence of a DCM has been indicated as a characteristic of many alpine lakes, and UVR avoidance has been proposed as one of the mechanisms explaining its development (Sommaruga and Psenner 1997; Sommaruga 2001). Therefore, the observed pattern may result from strong photosynthetic inhibition at the surface, as early studies have recognized that UVR can strongly inhibit algal photosynthesis (Neale et al. 1998; Montesinos et al. 1997; Villafañe et al. 1999). In the North Patagonian Andean transparent lakes, it has been demonstrated that photosynthetic inhibition is due to both UV-A and UV-B (Villafañe et al. 2004; Callieri et al. 2007). However, if the only reason for the vertical chlorophyll distribution is UVR, then the depth of the mixing layer should provide a good prediction of DCM depth, as cells included in the mixing layer are dragged to the surface layer with damaging UV irradiance, while those below the mixing layer are safe from damage by UV radiation. A correlation between thermocline depth and DCM position was not observed in our data set, although the DCM was always deeper than the mixing layer, resulting in the thermocline depth being excluded in the multiple regression model (Fig. 2). DCM was observed depending on light and was located mainly in the illuminated upper part of the hypolimnion.

Constitution of the DCM in the Andean lakes includes phytoplankton made of motile and mainly mixotrophic cells (*Chrysochromulina parva*, *Gymnodinium paradoxum*, *Rhodomonas lacustris*, *Gymnodinium* spp) (Modenutti et al. 2004; Callieri et al. 2007). Motile nanoflagellates are



**Fig. 5** Particle size distribution in **a** volcanic ashes suspended in Lake Espejo and **b** glacial clay suspended in Lake Mascardi Tronador (station 2)

able to move to lower depths, developing DCM in alpine lakes (Sommaruga and Psenner 1997); thus, in a similar way, motile mixotrophic nanoflagellates would develop in Andean lakes by exploiting the upper hypolimnetic levels of euphotic zones. Previous data obtained from static incubations in North Patagonian Andean lakes indicated that the cell-specific production of phytoplankton was higher at 10 % of surface PAR than at the DCM depth (approximately 1 % of the surface PAR) (Modenutti et al. 2004; Callieri et al. 2007), suggesting that epilimnetic light levels are more suitable for primary production, although species maximum abundances were located at lower levels.



**Fig. 6** **a** Relationship between total suspended solids (TSS) and extinction coefficient of PAR ( $K_{dPAR}$ ) and **b** relationship between TSS and depth of deep chlorophyll maxima (DCM). *Open triangles* lakes affected by the ashes of the volcanic eruption, *filled circles* Lake Mascardi Tronador intralacustrine gradient. For statistical significance, see the text

However, 10 % of the surface PAR is, in most cases, within the mixing layer, so static incubation does not represent natural conditions where cells are dragged to harmful UVR levels (Modenutti et al. 2005). In addition, photosynthetic efficiency increases toward DCM (Callieri et al. 2007) concurrently with an increase in photosynthetic accessory pigments (Pérez et al. 2007). This pattern would suggest that these motile cells are photo-adapted to these dim layers, and here we showed that they can react rapidly to sudden changes (volcanic eruption) or long-term changes (warming with glacier recession) in transparency.

Theoretical approaches suggest that in poorly mixed environments, motile algae should form a thin layer at a depth determined by nutrient and light co-limitation (Klausmeier and Litchman 2001). Moreover, these models predict that the position of this layer will depend on nutrient availability, being deeper in lower-nutrient environments (Mellard et al. 2011). Analysis of our data showed that light affected the position of the DCM but that nutrients did not. The oligotrophic lakes of Patagonia have an even vertical distribution of nutrients along the euphotic zone (Callieri et al. 2007; Corno et al. 2009), a situation not considered in these theoretical studies. However, as light decreases with depth, the depth of nutrient-light co-limitation still exists in a system without a nutrient gradient. If DCM should appear, at the co-limitation depth, as predicted by theory, then in a series of 6 lakes and different years, nutrient availability should have been a significant factor in determining DCM depth (Table 5).

Recent studies have suggested that nutrient availability may play a more important role than UVR in inducing the

**Table 5** Phytoplankton features at the deep chlorophyll maxima (DCM) in the studied lakes from 2005 and 2008 samples

	Espejo	Correntoso	Nahuel Huapi	Gutiérrez	Mascardi (Catedral)	Mascardi (Tronador)
Total Chl <i>a</i> at DCM ( $\mu\text{g L}^{-1}$ )	$1.13 \pm 0.35$	$1.33 \pm 0.42$	$2.01 \pm 0.53$	$1.78 \pm 0.38$	$1.12 \pm 0.75$	$0.87 \pm 0.53$
Chl <i>a</i> picoplankton to total Chl <i>a</i> (% of contribution)	33.4	23.3	25.6	31.0	19.1	9.00
Phytoplankton > 2 $\mu\text{m}$ (cell $\text{mL}^{-1}$ )	$435 \pm 34.45$	$283 \pm 32.9$	$486 \pm 52.65$	$909 \pm 67.52$	$456 \pm 25.38$	$285 \pm 37.51$
Endosymbiont <i>Chlorella</i> (cell $\text{mL}^{-1}$ )	$420 \pm 40$	$897 \pm 67$	$385 \pm 75$	$195 \pm 27$	$475 \pm 106$	0
Phytoplankton species at DCM (% to total abundance)						
Chrysophyceae mainly <i>Dynobryon</i> spp	2.8	7.6	3.0	0.9	4.0	2.6
Haptophyceae <i>Chrysochromulina parva</i>	59.4	41.0	57.4	45.7	57.0	60.7
Cryptophyceae mainly <i>Rhodomonas lacustris</i>	20.3	42.0	30.8	13.3	26.0	33.2
Dinophyceae mainly <i>Gymnodinium paradoxum</i>	7.3	7.5	1.7	3.0	12.9	3.1
Other Algae						
Mainly <i>Cyclotella meneghiniana</i> <i>Fragilaria</i> sp <i>Staurodesmus</i> sp	10.1	1.8	7.1	37.1	0.0	0.5

Concentration and abundance data are given as mean  $\pm$  standard error

formation of DCM in alpine lakes (Saros et al. 2005). In this sense, it has been suggested that the oligotrophic conditions allow enough light to penetrate to the upper hypolimnion, where nutrient availability is often higher (Camacho 2006). However, three particular conditions should be taken into account in our analysis: (1) in the study lakes, we observed an even nutrient distribution in the epilimnion, metalimnion and hypolimnion, indicating that differential nutrient availability was not the cause of DCM development as was observed in the lakes studied by Saros et al. (2005); (2) the north-Patagonian Andean lakes are much more transparent than those studied by Saros et al. (2005) (mean Z1 %PAR = 33 m, ranging from 15 to 50 m) and this situation causes a deeper DCM location; and (3) the nanoflagellates that dominate the DCM are mainly mixotrophic combining both phototrophy and phagotrophy through photosynthesis and particle uptake. This feeding mode may improve access to scarce nutrients (Nygaard and Tobiesen 1993) and, therefore, should provide a strong advantage in oligotrophic environments, as particle uptake would offer the opportunity to access to scarce elements (Jones and Rees 1994). In the transparent oligotrophic Andean lakes, where light is abundant and the nutrient concentration is very low, mixotrophy may be a key attribute in the functioning of lake food webs (Modenutti et al. 2004, 2008). It has been shown that an understanding of mixotrophy in the euphotic zone of aquatic ecosystems is important for predicting how aquatic ecosystems respond at evolutionary and ecological scales to changing environments (Stoecker et al. 2009). In this sense, our dataset showed that these organisms exhibited a rapid response to environmental change (volcanic eruption and glacial clay input) that modified the light climate of the transparent lakes.

Remarkably, the two natural phenomena compared here (glacier recession and volcanic eruption) did not affect the DOC concentration or CDOM, which can cause severe differential variations in UV attenuation. Many alpine and mountain lakes, including the Andean lakes, have low DOC concentrations and, therefore, are highly transparent to UV wavelengths (Morris et al. 1995). In these lakes, phytoplankton have been observed to be constrained to the lower levels of euphotic zones, where UV irradiance is low (Modenutti et al. 2004). It seems clear that DOC or CDOM did not change due to glacial clay input or volcanic ash; however, UVR attenuation was also increased by suspended particles because of scattering.

The observed relationship between DCM depth and light was consistent in time and space. We showed that DCM development was not observed in coincidence with thermocline depth or nutrient distribution. Indeed, our study showed that suspended particles (glacial clay and volcanic ash) can play a crucial role in transparent lakes, affecting lake features such as phototrophic biomass distribution

along the water column. The increase of suspended solids coming either from glacial clay or from volcanic ash produced a comparable effect, provoking a decrease in light and a consequently higher location in DCM development. Analysis of the particle sizes of suspended clay and ash showed that the former are smaller, which would explain the different absolute effects of TSS on DCM depth. Although the scattering effect of particles increases with size, for a given TSS, the amount of particles increases with a decrease in their size, so the net effect on light scattering increases (Kirk 1994). Thus, TSS constituted by smaller particles would have a greater effect on DCM position than larger ones, as was observed in our data comparing glacier clay with volcanic ash.

In summary, DCM development was found to be highly sensitive to global change, such as increased temperatures causing glacier recession or regional changes caused by volcanic eruptions. Both events have occurred repeatedly in geological time in different areas of the world, shaping lakes and oceans through changes in light. These effects, in turn, influence the pelagic community composition in the water column, favoring motile cells that are able to exploit the different light levels.

**Acknowledgments** This work was supported by FONCYT (PICT 2007-01256, PICT 2007-01258 and PICT 2011-2240) and National Geographic Grant NGS9005-11. BM, EB and MSS are CONICET researchers and MBN, CL and FC are CONICET Fellowships.

## References

- APHA (2005) Standard methods for the examination of water and wastewater. American Public Health Association, AWWA, Washington
- Balseiro EG, Queimaliños CP, Modenutti BE (2004) Grazing impact on autotrophic picoplankton in two south andean lakes (Patagonia, Argentina) with different light: nutrient ratios. *Rev Chil Hist Nat* 77:73–85
- Balseiro E, Modenutti B, Queimaliños C, Reissig M (2007) *Daphnia* distribution in Andean Patagonian lakes: effect of low food quality and fish predation. *Aquat Ecol* 41(4):599–609
- Bonetto AA, Dioni W, Depetris P (1971) Informe preliminar sobre las investigaciones limnológicas de la cuenca del Río Manso y Lago Mascardi (Río Negro–Patagonia). *Fundación Bariloche* 4:1–62
- Brooks AS, Torke BG (1977) Vertical and seasonal distribution of chlorophyll a in Lake Michigan. *J Fish Bd Can* 34(12): 2280–2287
- Callieri C, Modenutti B, Queimaliños C, Bertoni R, Balseiro E (2007) Production and biomass of picophytoplankton and larger autotrophs in Andean ultraoligotrophic lakes: differences in light harvesting efficiency in deep layers. *Aquat Ecol* 41(4):511–523
- Camacho A (2006) On the occurrence and ecological features of deep chlorophyll maxima (DCM) in Spanish stratified lakes. *Limnologia* 25(1–2):453–478
- Corno G, Modenutti B, Callieri C, Balseiro E, Bertoni R, Caravati E (2009) Bacterial diversity and morphology in deep ultraoligotrophic Andean lakes: the role of UVR on vertical distribution. *Limnol Oceanogr* 54(4):1098–1112

- Couture S, Houle D, Gagnon C (2012) Increases of dissolved organic carbon in temperate and boreal lakes in Quebec, Canada. *Environ Sci Pollut Res* 19(2):361–371
- Cullen JJ (1982) The deep chlorophyll maximum: comparing vertical profiles of chlorophyll a. *Can J Fish Aquat Sci* 39(79):1–803
- Fahnenstiel GL, Scavia D (1987) Dynamics of Lake Michigan phytoplankton: primary production and growth. *Can J Fish Aquat Sci* 44(3):499–508
- Falkowski PG, Raven JA (2007) *Aquatic photosynthesis*, 2nd edn. Blackwell Science, Malden
- Fee EJ (1976) The vertical and seasonal distribution of chlorophyll in lakes of the Experimental Lakes Area, northwestern Ontario: implications for primary production estimates. *Limnol Oceanogr* 21(6):767–783
- Gervais F, Padisak J, Koschel R (1997) Do light quality and low nutrient concentration favour picocyanobacteria below the thermocline of the oligotrophic Lake Stechlin? *J Plankton Res* 19(6):771–781
- Helbling W, Zagarese HE (2003) UV effect on aquatic organisms and ecosystems. Royal Society of Chemistry, Cambridge
- Hessen DO (2002) UV radiation and Arctic ecosystems, vol 153. Springer, Berlin
- Iriondo MH (1974) Modelo de sedimentación en el lago Mascardi, provincia de Río Negro. *Rev Asoc Geolog Arg* 29(3):349–358
- Iriondo MH (1989) Quaternary lakes of Argentina. *Palaeogeogr Palaeoclim Palaeoecol* 70:81–88
- Jones R, Rees S (1994) Influence of temperature and light on particle ingestion by the freshwater phytoflagellate *Dynobryon*. *Arch Hydrobiol* 132:203–211
- Kirk JTO (1994) *Light and photosynthesis in aquatic ecosystems*. Cambridge University Press, Cambridge
- Klausmeier CA, Litchman E (2001) Algal games: the vertical distribution of phytoplankton in poorly mixed water columns. *Limnol Oceanogr* 46(8):1998–2007
- Leiva JC (1999) Recent fluctuations of the Argentinian glaciers. *Global Planet Change* 22(1–4):169–177
- Masiokas MH, Villalba R, Luckman BH, Lascano ME, Delgado S, Stepanek P (2008) 20th-century glacier recession and regional hydroclimatic changes in northwestern Patagonia. *Global Planet Change* 60(1–2):85–100
- Mellard JP, Yoshizawa K, Klausmeier CA, Litchman E (2011) Experimental test of phytoplankton competition for nutrients and light in poorly mixed water columns. *Ecol Monogr* 82(2):239–256
- Modenutti BE, Balseiro EG, Queimaliños CP, Añón Suárez D, Diéguez MC, Albariño RJ (1998) Structure and dynamics of food webs in Andean lakes. *Lakes Reserv Res Manage* 3(3–4):179–186
- Modenutti BE, Perez GL, Balseiro EG, Queimaliños CP (2000) Relationship between light availability, chlorophyll a and total suspended solid in a glacial lake of South Andes. *Verh Internat Verein Limnol* 27(5):2648–2651
- Modenutti B, Pérez G, Balseiro E, Queimaliños C (2001) The relationship between light attenuation, chlorophyll a and total suspended solids in a Southern Andes glacial lake. *Verh Internat Verein Limnol* 27(5):2648–2651
- Modenutti B, Balseiro E, Callieri C, Queimaliños C, Bertoni R (2004) Increase in photosynthetic efficiency as a strategy of planktonic organisms exploiting deep lake layers. *Freshw Biol* 49(2):160–169
- Modenutti BE, Balseiro EG, Callieri C, Bertoni R, Queimaliños CP (2005) Effect of UV-B and different PAR intensities on the primary production of the mixotrophic planktonic ciliate *Stentor araucanus*. *Limnol Oceanogr* 50(3):864–871
- Modenutti BE, Balseiro EG, Callieri C, Bertoni R (2008) Light versus food supply as factors modulating niche partitioning in two pelagic mixotrophic ciliates. *Limnol Oceanogr* 53(2):446–455
- Modenutti B, Albariño R, Bastidas Navarro M, Díaz Villanueva V, Souza MS, Trochine C, Laspoumaderes C, Cuassolo F, Mariluán G, Buria L, Balseiro E (2010) Structure and dynamic of food webs in Andean North Patagonian freshwater systems: organic matter, light and nutrient relationships. *Ecol Austr* 20:95–114
- Moll R, Stoermer E (1982) Hypothesis relating trophic status and subsurface chlorophyll maxima of lakes. *Arch Hydrobiol* 94(4):425–440
- Montesinos V, Pizarro G, Martínez G (1997) Optical climate (PAR and UV) and phytoplankton dynamics in a high mountain Andean lake (Laguna Negra, Chile). *Verh Internat Verein Limnol* 26:441–445
- Morris DP, Zagarese H, Williamson CE, Balseiro EG, Hargreaves BR, Modenutti B, Moeller R, Queimaliños C (1995) The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnol Oceanogr* 40(8):1381–1391
- Neale PJ, Cullen JJ, Davis RF (1998) Inhibition of marine photosynthesis by ultraviolet radiation: variable sensitivity of phytoplankton in the Weddell-Scotia confluence during the austral spring. *Limnol Oceanogr* 43(3):433–448
- Nusch EA (1980) Comparison of different methods for chlorophyll and phaeopigment determination. *Arch Hydrobiol Beih Ergeb Limnol* 14:14–36
- Nygaard K, Tobiesen A (1993) Bacterivory in algae: a survival strategy during nutrient limitation. *Limnol Oceanogr* 38:273–279
- Paruelo JM, Beltran A, Jobbágy E, Sala O, Golluscio R (1998) The climate of Patagonia: general patterns and controls on biotic processes. *Ecol Austr* 8(2):85–101
- Paul F, Kääh A, Haerberli W (2007) Recent glacier changes in the Alps observed by satellite: consequences for future monitoring strategies. *Global Planet Change* 56(1–2):111–122. doi:10.1016/j.gloplacha.2006.07.007
- Pérez G, Queimaliños C, Balseiro E, Modenutti B (2007) Phytoplankton absorption spectra along the water column in deep North Patagonian Andean lakes (Argentina): limnology of temperate South America. *Limnologica* 37(1):3–16
- Pick F, Nalewajko C, Lean D (1984) The origin of a metalimnetic chrysophyte peak. *Limnol Oceanogr* 29(1):125–134
- Pilati A, Wurtsbaugh WA (2003) Importance of zooplankton for the persistence of a deep chlorophyll layer: a limnocorral experiment. *Limnol Oceanogr* 48(1):249–260
- Rabassa J, Rubulis S, Suarez J (1978) Los glaciares del Monte Tronador, Parque Nacional Nahuel Huapi, Río Negro, Argentina. *Anales de Parques Nacionales* 14:259–318
- Saros JE, Interlandi SJ, Doyle S, Michel TJ, Williamson CE (2005) Are the deep chlorophyll maxima in Alpine lakes primarily induced by nutrient availability, not UV avoidance? *Arct Antarct Alp Res* 37(4):557–563
- Schindler DW, Curtis PJ (1997) The role of DOC in protecting freshwaters subjected to climatic warming and acidification from UV exposure. *Biogeochemistry* 36(1):1–8. doi:10.1023/a:1005768527751
- Self S (2006) The effects and consequences of very large explosive volcanic eruptions. *Philos Trans R Soc Lond A* 364(1845):2073–2097
- Sommaruga R (2001) The role of solar UV radiation in the ecology of alpine lakes. *J Photochem Photobiol* 62:35–42
- Sommaruga R, Psenner R (1997) Ultraviolet radiation in a high mountain lake of the Austrian Alps: air and underwater measurements. *Photochem Photobiol* 65(6):957–963

- Stoecker DK, Johnson MD, De Vargas C, Not F (2009) Acquired phototrophy in aquatic protists. *Aquat Microb Ecol* 57(3): 279–310
- Villafañe VE, Andrade M, Lairana V, Zaratti F, Helbling EW (1999) Inhibition of phytoplankton photosynthesis by solar ultraviolet radiation: studies in Lake Titicaca, Bolivia. *Freshw Biol* 42(2):215–224
- Villafañe VE, Buma AGJ, Boelen P, Helbling EW (2004) Solar UVR-induced DNA damage and inhibition of photosynthesis in phytoplankton from Andean lakes of Argentina. *Arch Hydrobiol* 161(2):245–266
- Williamson CE, Rose KC (2010) When UV meets fresh water. *Science* 329(5992):637–639
- Williamson CE, Dodds W, Kratz TK, Palmer MA (2008) Lakes and streams as sentinels of environmental change in terrestrial and atmospheric processes. *Front Ecol Environ* 6(5):247–254
- Williamson CE, Saros JE, Vincent WF, Smol JP (2009) Lakes and reservoirs as sentinels, integrators, and regulators of climate change. *Limnol Oceanogr* 54(6):2273–2282
- Zhang Y, Zhang E, Yin Y, van Dijk MA, Feng L, Shi Z, Liu M, Qin B (2010) Characteristics and sources of chromophoric dissolved organic matter in lakes of the Yungui Plateau, China, differing in trophic state and altitude. *Limnol Oceanogr* 55(6):2645–2659