

# Climate-induced input of turbid glacial meltwater affects vertical distribution and community composition of phyto- and zooplankton

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Receding glaciers are among the most obvious changes caused by global warming, and glacial meltwater entering lakes generally forms plumes of particles. By taking vertical samples along a horizontal gradient from such a particle source, we found that photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) attenuated 20–25% faster close to the inflow of suspended particles compared with the more transparent part of the gradient. All sampled stations had a deep chlorophyll *a* (Chl *a*) maximum at 15–20 m which was more distinct in the transparent part of the horizontal gradient. Picocyanobacteria increased in abundance in more transparent water and their numbers were tightly correlated with the intensity of the deep Chl *a* maxima. Motile species of phytoplankton had a deeper depth distribution in transparent versus less transparent water. Yet other species, like *Chrysochromulina parva*, that can withstand high PAR intensities and low nutrient concentrations, increased in abundance as the water became more transparent. Also copepods increased in abundance, indicating that they are more successful in transparent water. We conclude that sediment input into lakes creates horizontal gradients in PAR and UVR attenuation which strongly affect both distribution and behavior of phyto- and zooplankton. The input of glacial flour creates a sub-habitat that can function as a refuge for species that are sensitive to high PAR and UVR exposure. When the glacier has vanished, this habitat may disappear. During the melting period, with heavy sediment input, we predict that competitive species in transparent waters, like *Chrysochromulina*, picocyanobacteria and copepods, will become less common. The deep Chl *a* maxima is also likely to become less developed. Hence, glacier melting will probably have profound effects on both species composition and behavior of several planktonic taxa with potential effects on the food web.

**KEYWORDS:** glacier melting; transparency; zooplankton; phytoplankton; community composition; vertical migration; UVR; PAR

## INTRODUCTION

Global warming will have serious consequences for all kinds of ecosystems, increasing temperatures and altered precipitation patterns being the most obvious primary changes. As a result of these climatic changes, glaciers in many regions of the world are now melting rapidly (Rignot *et al.*, 2003). The meltwater, carried by rivers, contains high amounts of suspended sediment particles forming longitudinal gradients in lakes and estuaries from very turbid water close to the discharge to clear water far away from the river inflow (Joint and Pomroy, 1981). Sediment transport may also vary seasonally within and between systems by as much as a factor of 1000 (Eisma, 1993).

Turbidity-induced attenuation of photosynthetically active radiation (PAR) can affect the ecosystem strongly, by, for example, reducing primary production and phytoplankton biomass (Joint and Pomroy, 1981; Cloern, 1987). PAR intensity and spectral composition change with depth (Kirk, 1994), and phytoplankton adapt to these changes in PAR quantity and quality. This has been studied extensively, and one of the potential adaptations to dim light in deep waters are deep chlorophyll *a* (Chl *a*) maxima that sometimes are formed in clear oligotrophic waters (Fee, 1976; Pérez *et al.*, 2002; Callieri *et al.*, 2007). Apart from PAR, other factors like UVR avoidance and nutrient availability may also be important for the formation of deep Chl *a* maxima (Sommaruga and Psenner, 1997; Modenutti *et al.*, 2004; Saros *et al.*, 2005). In these deep metalimnetic layers, PAR and temperature are relatively low, while the availability of nutrients may be higher than in the epilimnion (Saros *et al.*, 2005). Particles in turbid waters also have an important role in increasing the attenuation of ultraviolet radiation (UVR; Belzile *et al.*, 2002). UVR attenuation is furthermore highly dependent on the dissolved organic carbon content of the water (DOC; Scully and Lean, 1994; Morris *et al.*, 1995).

Intense PAR and UVR exposures can lead to photo-inhibition and cell damage among phytoplankton and zooplankton may experience high UVR-induced mortality in surface waters (Williamson *et al.*, 1994, 2001; Villafane *et al.*, 1999). However, both phyto- and zooplankton have several ways of avoiding damage from UVR and intense light (Helbling and Zagarese, 2003; Hansson and Hylander, 2009a). For instance, some phytoplankton migrate downwards at noon and ascend during the afternoon and night (Tilzer, 1973; Richter *et al.*, 2007). Zooplankton also migrate to deep waters or accumulate different blends of UVR protective compounds to reduce potential damage (Sommaruga, 2001; Leech and Williamson, 2001; Hansson and Hylander,

2009b; Hylander *et al.*, 2009a). Both *Daphnia*, copepods and rotifers have been shown to migrate vertically to avoid UVR (Rhode *et al.*, 2001; Oberegger *et al.*, 2008; Hylander *et al.*, 2009b) and to accumulate different UVR protective compounds (Moeller *et al.*, 2005; Hansson *et al.*, 2007; Hylander *et al.*, 2009a).

There are large fitness benefits for planktonic organisms that can optimize their vertical position in relation to an environment that changes in terms of PAR, UVR and ratios between the two. Different phytoplankton species indeed withstand different intensities of PAR before inhibition occurs (Ryther and Menzel, 1959; Belay, 1981). Several studies have assessed the effects of horizontal turbidity gradients on primary production in estuaries (Joint and Pomroy, 1981; Cloern, 1987), but few studies have focused on changes in species composition and vertical distribution in freshwater systems. In Lake Mascaradi, a deep oligotrophic lake in the Patagonian Andes, sediment particles originating from a receding glacier form a plume with turbid water near the glacier outlet. This plume was used as a natural experiment where the effects of different PAR and UVR exposure were studied by taking vertical samples at different distances from the meltwater inflow. This is an excellent opportunity to study how large-scale climatic effects, like glacier melting with consequent sediment transport, affect lake ecosystems. We hypothesize that a changing light climate, through input of turbid glacial meltwater, affects the depth and intensity of the deep Chl *a* maximum. The horizontal light gradient is also hypothesized to affect the vertical distribution and species composition of phyto- and zooplankton.

## METHOD

### Study site

Lake Mascaradi in the Andes of Argentina is a deep oligotrophic lake of glacial origin (41°15′–41°25′ S; 71°28′–71°39′ W; maximum depth 218 m; Modenutti *et al.*, 2001 and references therein). The northwestern end of the lake receives meltwater from a receding glacier at Tronador Mountain (3554 m a.s.l.). This glacier has decreased in size considerably during the last decades, and during the warm months it discharges large amounts of suspended glacial flour (Modenutti *et al.*, 2001). These suspended particles are transported to the lake via River Manso, and when the river enters the lake, a sediment plume can be observed. Since the particle content of the water gradually decreases with increasing distance from the river input, a horizontal gradient in water turbidity is formed. By sampling at

different distances from the river input, we evaluated the effects of the meltwater inflow on the transparency of the water (PAR and UVR), the formation of deep Chl *a* maxima as well as phyto- and zooplankton vertical distribution and abundance.

### Sampling and analysis

Six stations at different distances from the meltwater input were sampled during summer stratification at noon (within 2–3 h; Fig. 1A; January 2009). At each station, vertical profiles of natural fluorescence, temperature and downward irradiance of PAR, UVA (at 340 nm) and UVB (at 320 nm) were measured with a submersible radiometer (PUV 500B, Biospherical Instruments). PAR compensation depths and UVR attenuation depths are used here as proxies of water transparency at different stations. Natural fluorescence output from the radiometer was used as a proxy for Chl *a* and this is an established method used in several previous studies (e.g. Modenutti *et al.*, 2004; Pérez *et al.*, 2007). To calibrate the fluorescence measurements to true Chl *a* values, we filtered 1 L of water from each station onto glass-fiber filters (Whatman GF/C). Chlorophyll extractions followed Nush (Nusch, 1980) and readings were conducted using a Turner AU 10 fluorometer calibrated against spectrophotometric readings. Chl *a* values were generally low  $0.5 \pm 0.07 \mu\text{g L}^{-1}$  (mean  $\pm$  SD). The natural fluorescence profiles from the PUV-meter were then adjusted to the true Chl *a* values obtained from the filtration and extraction procedure. We did not include natural fluorescence readings from the top 5 m, since it is difficult to measure this parameter in surface waters (Garcia-Mendoza and Maske, 1996).

At each station, sampling was conducted at depths of 0.5, 15, 30 and 45 m with a water sampler (van Dorn bottle and Schindler Patalas trap). Even though light is attenuated at shallower depths, it is important to sample as deep as 45 m if organisms perform vertical migration to avoid surface waters. About 0.5 L water was sampled for dissolved phosphorus and analyzed according to conventional methods (APHA, 1995). Zooplankton from each depth were filtered from 12 L (50  $\mu\text{m}$  mesh size) and all samples were preserved in Lugol's solution. They were then counted under a dissecting microscope (Leica Wild M8; Copepods: *Boeckella gracilipes* and Cladocerans: *Daphnia commutata* at 50 $\times$ ) and a copepod to *Daphnia* ratio was calculated to compare their relative contribution to the zooplankton community. From each depth, a sample for phytoplankton (0.5 L) was preserved in Lugol's solution and a subsample (20 mL) for counting picocyanobacteria was preserved with

formaldehyde-cacodylate 2% vol/vol and stored in darkness at  $-20^\circ\text{C}$  (Kemp *et al.*, 1993). Picocyanobacteria in this latter sample were counted in a 3 mL subsample on black membrane filters (Poretics; 0.2  $\mu\text{m}$  pore size) at 1250 $\times$  magnification under an epifluorescence microscope under blue light (Olympus BX50; U-MWB filter). Phytoplankton were counted according to the Utermöhl (Utermöhl, 1958) technique under an inverted microscope (Olympus IX70). Samples were poured into counting chambers (volume 42 mL), in which the phytoplankton were left to sediment for a minimum of 24 h. The most common taxa were identified as *Rhodomonas* sp., *Chrysochromulina parva*, *Ochromonas* sp., *Gymnodinium varians*, *Gymnodinium paradoxum*, *Cryptomonas reinhardtii* and *Mallomonas* sp. and one unidentified Chlorophyceae. Dinoflagellates were counted in transects across the counting chambers at 200 $\times$ , while nanoflagellates in at least 20 fields of view (400 $\times$  or 1000 $\times$ ) and the remaining species in the entire chamber (200 $\times$ ). Mixotrophic ciliates (*Ophrydium naumannii* and *Strobilidium* spp.) were also present, but they were not counted.

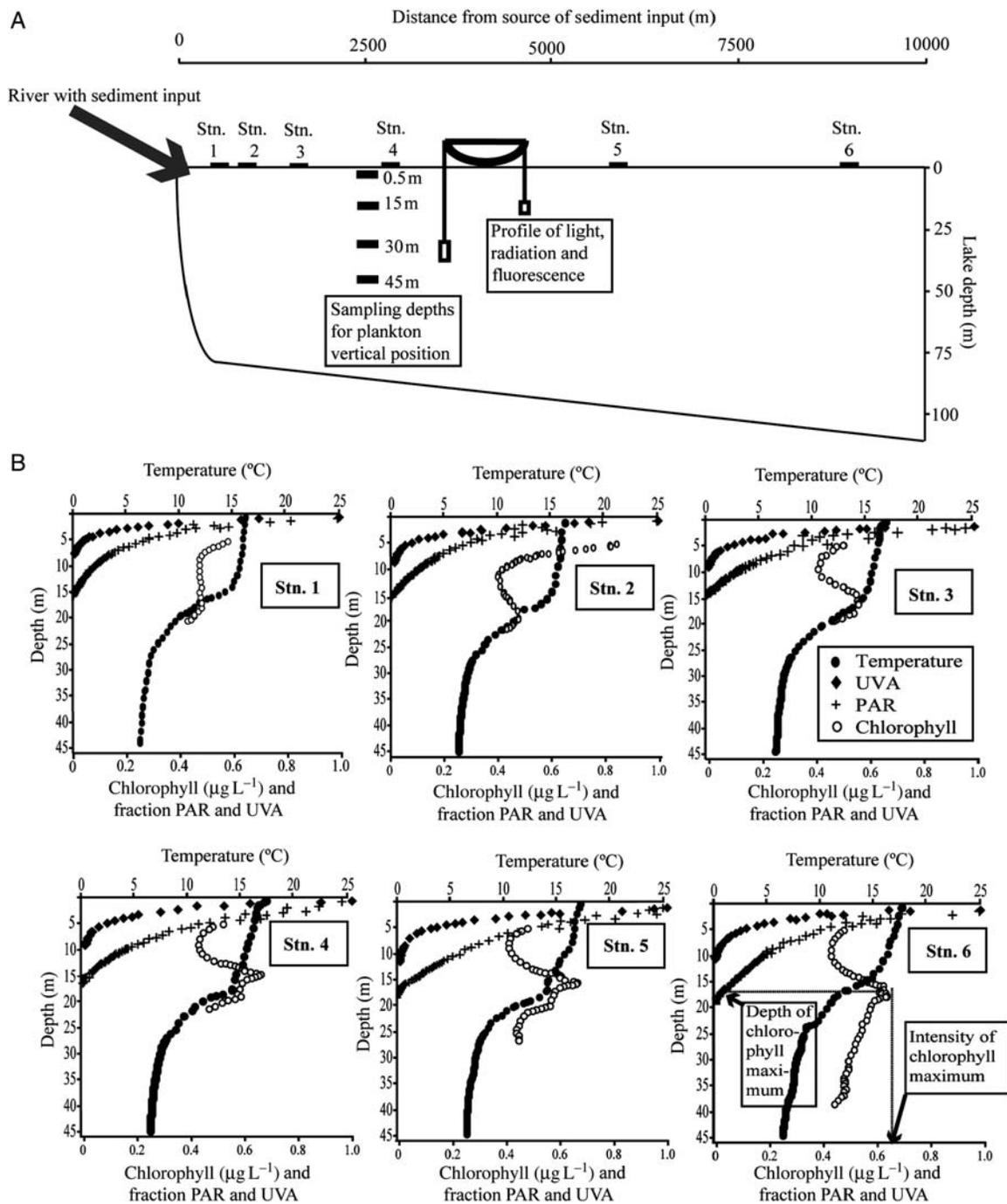
### Statistical methods and calculations

Differences in vertical distribution and abundance of phyto- and zooplankton along the horizontal gradient were assessed by linear regressions and *t*-tests. For *t*-tests, stations 1–3 (close to meltwater input) and 4–6 (further away from meltwater input) were pooled. Relative estimates of the mean depths of phytoplankton and zooplankton were determined by the formula:  $\sum(\mathcal{N}_d \times d) / \mathcal{N}_{\text{tot}}$ , where  $\mathcal{N}_d$  is the number of individuals at each depth, *d* the sampling depth (1, 15, 30 and 45 m) and  $\mathcal{N}_{\text{tot}}$  the total number of sampled individuals at that station. This mean depth is not a true mean depth and is only used for comparisons of depth distribution along the horizontal gradient, i.e. if depth distribution increased along the sampled gradient. Differences in diffuse attenuation coefficient among radiation types (i.e. PAR, UVA and UVB) were tested by ANCOVA analysis followed by Bonferroni's corrected multiple comparisons (distance from meltwater source as the covariate). All analyses were performed in SPSS 15.0.

## RESULTS

### Abiotic factors along the horizontal gradient

Water transparency for both PAR and UVR gradually increased along the horizontal gradient with  $\sim 20$ –25%



**Fig. 1.** (A) Schematic picture of the lake and the sampling stations. All stations were sampled at the depths indicated at station 4. Distances to sampling stations 1–6 from the river mouth were 630, 948, 1729, 2969, 5949 and 8993 m, respectively. (B) Profiles of PAR, UVA ( $E_{d(340)}$ ), temperature and Chl *a* at the six sampling stations. PAR and UVA are presented as fraction in relation to surface irradiance (surface irradiance = 1). For clarity, features of the deep chl *a* maxima are only shown in the subfigure for station 6. Chl *a* was not estimated for the top 5 m since it is difficult to measure natural fluorescence in surface waters (see Method).

higher penetration in the transparent part of the gradient compared with the less transparent part (Table I). The diffuse attenuation coefficient ( $K_d$ ) for PAR ranged from 0.4 to 0.2 and for UVA from 0.7 to 0.5, close to

the meltwater inflow and in the transparent part, respectively (Fig. 2). Overall, UVB had the highest  $K_d$ , followed by UVA and PAR (ANCOVA;  $F_{2,14} = 132.7$ ;  $P < 0.001$ ; all multiple comparisons  $P < 0.01$ ). There

Table I: Optical characteristics of sampled stations

Station	$K_d$ ( $m^{-1}$ )	Depth where fraction radiation remain		
		1% (m)	10% (m)	50% (m)
<b>PAR</b>				
1	0.4	13.2	6.6	2.0
2	0.3	13.4	6.7	2.0
3	0.4	12.1	6.0	1.8
4	0.3	13.8	6.9	2.1
5	0.3	15.3	7.7	2.3
6	0.2	19.6	9.8	3.0
<b>UVA</b>				
1	0.7	6.7	3.3	1.0
2	0.6	7.2	3.6	1.1
3	0.6	7.4	3.7	1.1
4	0.6	7.6	3.8	1.2
5	0.5	8.9	4.5	1.3
6	0.5	8.6	4.3	1.3
<b>UVB</b>				
1	0.8	5.5	2.8	0.8
2	0.8	5.8	2.9	0.9
3	0.7	6.2	3.1	0.9
4	0.7	6.5	3.3	1.0
5	0.6	7.2	3.6	1.1
6	0.6	7.6	3.8	1.1

UVA is measured at 340 nm and UVB at 320 nm.

was a tight relationship between water transparency and the distance from the meltwater inflow illustrated by regressions between  $K_d$  for PAR and UVR and the distance in meters from the river inflow [Fig. 2; PAR ( $r^2 = 0.86$ ;  $F_{1,4} = 24.4$ ;  $P = 0.008$ ;  $y = -0.000014x + 0.37$ ), UVA ( $r^2 = 0.80$ ;  $F_{1,4} = 16.5$ ;  $P = 0.015$ ;  $y = -0.000018x + 0.66$ ), UVB ( $r^2 = 0.89$ ;  $F_{1,4} = 33.8$ ;  $P = 0.004$ ;  $y = -0.000025x + 0.81$ )].

The thermocline was located at 16–20 m and did not display any change along the horizontal gradient (Fig. 1B;  $r^2 < 0.001$ ;  $F_{1,4} < 0.001$ ;  $P = 0.99$ ). Dissolved phosphorus content ranged from 1.3 to 2.3  $\mu\text{g L}^{-1}$  and there was no relationship between mean phosphorus content and distance from the meltwater inflow ( $r^2 = 0.23$ ;  $F_{1,4} = 1.2$ ;  $P = 0.33$ ). However, dissolved phosphorus content was generally higher above (i.e. 0–15 m) than below the thermocline (i.e. 30–45 m;  $t = 8.0$ ,  $P < 0.001$ ,  $df = 5$ ). Finally, there was a trend toward an increasing light to nutrient ratio along the horizontal gradient (compensation depths for PAR divided by the mean content of dissolved phosphorus content per station;  $r^2 = 0.57$ ;  $F_{1,4} = 5.4$ ;  $P = 0.081$ )

### Deep chlorophyll maxima

The deep Chl *a* maxima were most pronounced at stations 4–6, but there were also small maxima at stations 2 and 3 and a tendency to a maximum at 15–

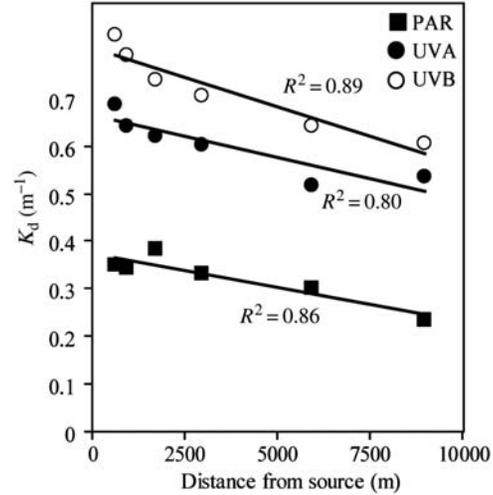


Fig. 2. Diffuse attenuation coefficient ( $K_d$ ) for PAR, UVA and UVB at different distances (m) from the inflow of glacial meltwater to Lake Mascardi.

20 m at station 1 (although Chl *a* was higher in surface waters at stations 1 and 2). The maxima were for all stations located at a depth of  $\sim 15$ –20 m (Fig. 1B), but the depth of the maxima did not display any trends along the horizontal gradient (linear regression between distance from source and depth of Chl *a* maxima ( $r^2 = 0.05$ ;  $F_{1,4} = 0.2$ ;  $P = 0.69$ ). However, the intensity of the deep Chl *a* peak tended to increase with distance from the meltwater inflow at the first four stations, but then leveled off at a Chl *a* concentration of  $\sim 0.6 \mu\text{g L}^{-1}$  (Fig. 1B).

### Species composition and depth distribution of phytoplankton

The phytoplankton species composition did not vary along the horizontal gradient and the most common species were *Rhodomonas* sp., *Chrysochromulina parva* and *Ochromonas* sp. *Chrysochromulina parva* was the only phytoplankton species that displayed a pattern along the gradient, with increasing abundance along the horizontal gradient (Fig. 3A;  $r^2 = 0.74$ ;  $F_{1,4} = 11.1$ ;  $P = 0.029$ ;  $y = 6.90x + 16$ ). This species also displayed a distinct depth pattern and was generally most abundant at 15 m (Fig. 3B). Throughout the horizontal gradient, the total number of phytoplankton cells was always low in surface waters, higher at 15 or 30 m and then lower again in deep waters. The deep Chl *a* maximum was situated at the cell concentration maximum at stations 1 and 5. At the other stations, the cell concentration maximum was located at the 15 or 30 m sampling

depths, i.e. slightly above or below the deep Chl *a* maximum.

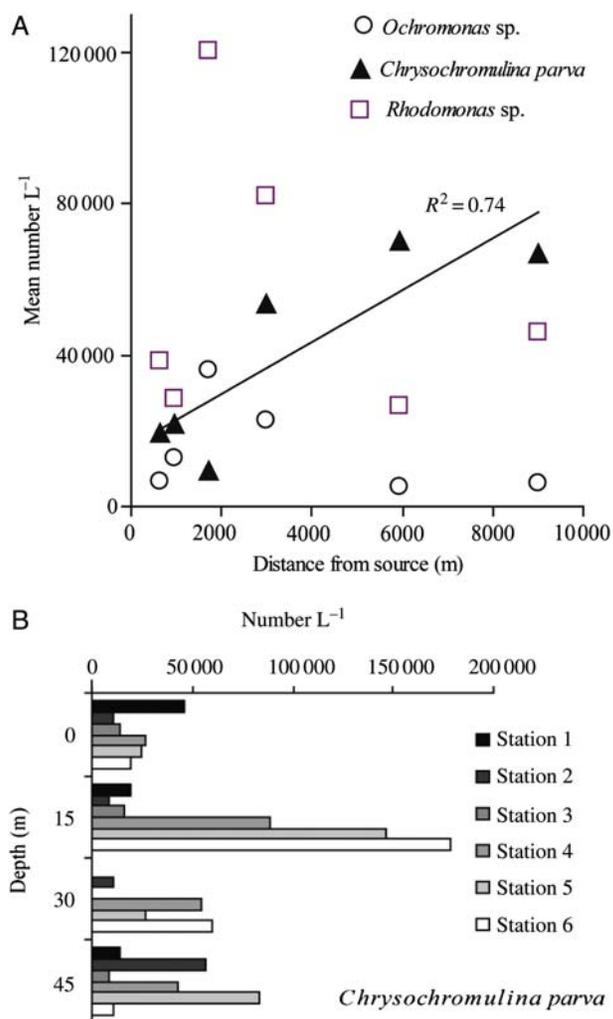
All common species, except *Ochromonas* sp. and *G. varians*, showed a tendency for greater depths at stations far away from the meltwater inflow (stations 4–6) compared with stations close to the inflow (stations 1–3). When pooling all species, phytoplankton occurred deeper far away from the river inlet (stations 4–6) compared with stations close to the inflow (stations 1–3;  $t = 3.1$ ,  $P = 0.035$ ,  $df = 4$ ). Testing the individual species, differences were only significant for *Cryptomonas* sp. ( $t = 8.1$ ,  $P = 0.001$ ,  $df = 4$ ) and slightly for *Rhodomonas* sp. ( $t = 2.4$ ,  $P = 0.071$ ,  $df = 4$ ).

Mean abundance of phycoerythrin-rich cells (picocyanobacteria) also increased along the horizontal

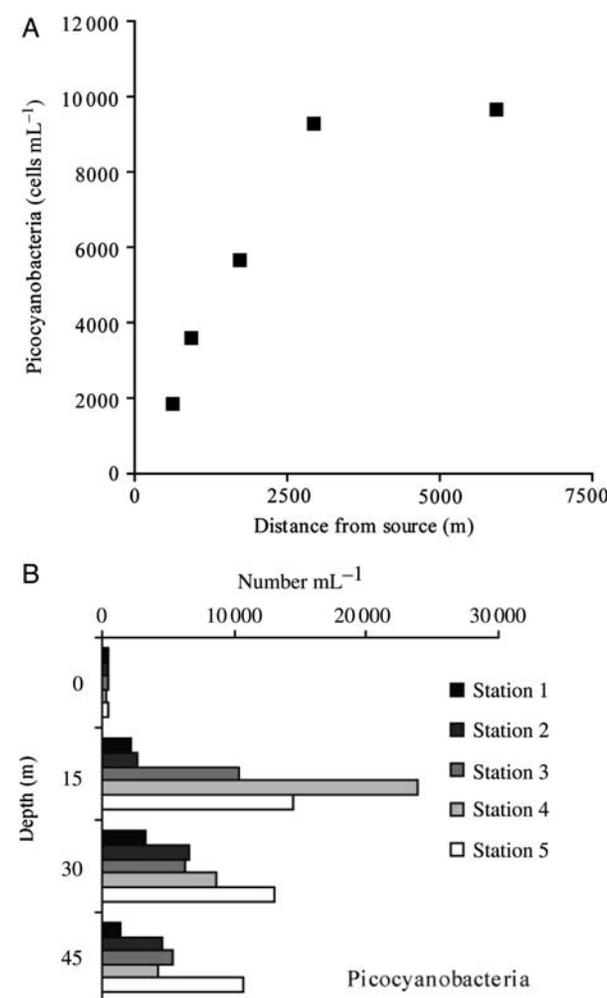
gradient at stations 1–4 but then leveled off at station 5. Sampling for picocyanobacteria unfortunately failed at station 6. There was a trend toward a linear increase in the abundance of cells along the horizontal gradient (Fig. 4A;  $r^2 = 0.76$ ;  $F_{1,3} = 9.6$ ;  $P = 0.053$ ). The abundance of picocyanobacteria was highest at 15–30 m depth (Fig. 4B). There was also a tight correlation between the intensity of deep Chl *a* peak and abundance of picocyanobacteria (Fig. 5; Pearson's correlation  $r = 0.97$ ,  $P = 0.008$ ,  $n = 5$ ).

### Species composition and depth distribution of zooplankton

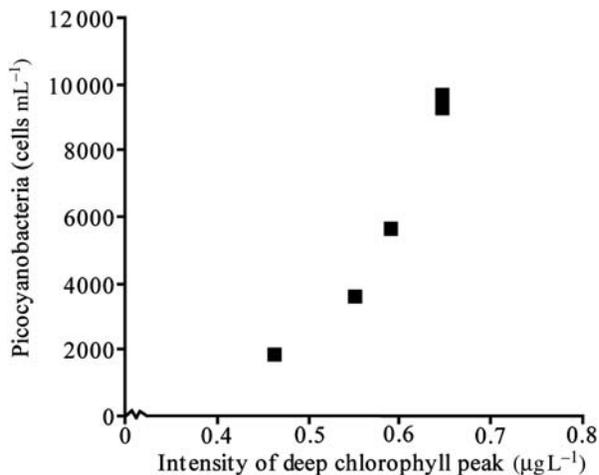
Zooplankton relative species composition changed along the horizontal gradient with more copepods



**Fig. 3.** (A) Mean number of phytoplankton at different distances from the meltwater inflow (mean based on all sampling depths at each station). Significant relationship (*C. parva*) is indicated by a line. (B) Depth distribution of *C. parva* at the different sampling stations.



**Fig. 4.** (A) Mean numbers of picocyanobacteria along the horizontal gradient. Note that sampling at station 6 failed for picocyanobacteria. (B) Number of picocyanobacteria at different sampling depths and at different stations.

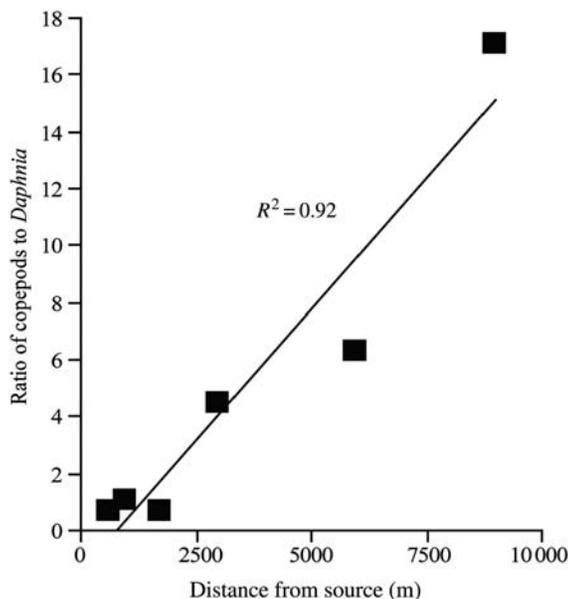


**Fig. 5.** Relationship between mean numbers of picocyanobacteria and the Chl *a* intensity of the deep Chl *a* peak ( $\mu\text{g L}^{-1}$ ).

compared with *Daphnia* with increasing distance from the meltwater inflow. This was manifested by a positive relationship between copepod to *Daphnia* ratio and the distance from the meltwater inflow (Fig. 6;  $r^2 = 0.92$ ;  $F_{1,4} = 44.1$ ;  $P = 0.003$ ;  $y = 0.0018x - 1.46$ ). Virtually, no zooplankton were present in the surface samples, and peaks in zooplankton abundance usually occurred at a depth of 15–30 m. Copepods tended to occur deeper down in the transparent part of the horizontal gradient compared with the less transparent part, but there was no significant relationship (regression between mean depth of copepods and distance from meltwater inflow  $r^2 = 0.51$ ;  $F_{1,4} = 4.2$ ;  $P = 0.109$ ). *Daphnia* did not display any changes in vertical position along the horizontal gradient ( $r^2 = 0.15$ ;  $F_{1,4} = 0.7$ ;  $P = 0.44$ ) and were always most abundant at 15 m.

## DISCUSSION

Our data indicate that glacial meltwater inflows affected several abiotic and biotic factors. We found that PAR and UVR penetrated  $\sim 20$ – $25\%$  deeper in the transparent part of the horizontal gradient. Hence, within 10 km in the same lake, glacial flour creates subhabitats in terms of PAR and UVR transparency. The changes in PAR transparency are in the same range as the differences that can be observed on a seasonal basis in other lakes, e.g. in L. Huron and L. Superior (Jerome *et al.*, 1983). Particles enhance scattering of PAR and UVR which increases the pathway for photons and hence the overall attenuation (Kirk, 1994; Belzile *et al.*, 2002). Other studies have also shown that particles may contribute significantly to UVR attenuation both by



**Fig. 6.** The ratio between numbers of copepods and *Daphnia* along the sampled horizontal gradient.

scattering and absorption of UVR photons (Belzile *et al.*, 2002). Nutrient content was generally higher above than below the thermocline without any trends along the horizontal gradient. Oligotrophic lakes generally display rather homogeneous phosphorus content at different depths (Wetzel, 2001). The observed pattern may be due to harsh conditions for organisms in surface waters of this very transparent lake, leading to potentially lower nutrient consumption above the thermocline. In these surface waters, intense PAR and UVR exposures may lead to zooplankton mortality, inhibition of photosynthesis or induction of vertical migration. These UVR effects on zoo- and phytoplankton have also been observed in other transparent systems (Williamson *et al.*, 1994; Villafane *et al.*, 1999; Modenutti *et al.*, 2004). However, the pattern of higher nutrient content above the thermocline could also be due to inflow of dense and cold nutrient-poor water coming from rivers going directly into the hypolimnion.

Also many biotic factors changed along the horizontal gradient. As the water became more transparent, the depth distribution and relative abundance of phytoplankton and zooplankton changed. Motile phytoplankton species like *Cryptomonas* sp. had a deeper depth distribution far away from the meltwater inflow, suggesting that these species are able to fine tune their vertical position in response to the PAR and UVR climate. Mixotrophs, like *Cryptomonas* sp., may also feed on picocyanobacteria (Modenutti and Balseiro, 2002; Modenutti *et al.*, 2008), which were abundant in deep

waters of the more transparent part of the horizontal gradient. Among the phytoplankton, *C. parva* increased in abundance along the horizontal gradient. *C. parva* is motile and due to its small cell size, it utilizes nutrients efficiently, making it competitive in oligotrophic systems (Dahl *et al.*, 2005). This genus mainly occurs in marine systems and several species form toxic algal blooms affecting other algae negatively, and also disrupting grazing rate and reproduction of zooplankton (Nielsen *et al.*, 1990). Toxic effects among freshwater *Chrysochromulina* sp. are not well studied, but occasional fish kills may be related to mass occurrences of the species (Hansen *et al.*, 1994). *C. parva* occurred at relatively shallow depths in L. Mascaradi, and increased in abundance as the water became more transparent, indicating that the species is competitive under high PAR and UVR exposure. Regarding toxicity, we cannot draw any conclusions since there is no information on potential toxicity of the studied strain.

Picocyanobacteria became more and more important with increasing transparency. This underlines their importance for the deep Chl *a* maximum also reported in other studies (Modenutti and Balseiro, 2002; Callieri *et al.*, 2007). Mixotrophic ciliates can be common in the deep Chl *a* maxima contributing to the Chl *a* content and also ingesting pico-sized cells (Modenutti and Balseiro, 2002; Pérez *et al.*, 2002). Sampling for ciliates was not included in this study, making it difficult to assess their importance to the Chl *a* maximum in L. Mascaradi. Picocyanobacteria in clear systems have been shown to contain the pigment phycoerythrin which allows them to use dim blue–green light (Gervais *et al.*, 1997; Stomp *et al.*, 2004). This may be beneficial for them in clear waters where they can utilize niches in deep layers with dim light conditions (Pérez *et al.*, 2002; Modenutti *et al.*, 2004). Small phycoerythrin-rich cells, like picocyanobacteria, can also have a competitive advantage over larger phototrophs since nutrient uptake is more efficient under low nutrient conditions in small-sized cells (Gervais *et al.*, 1997). Along the horizontal gradient, increasing PAR and UVR were responsible for a tendency toward an increasing radiation to nutrient ratio. This changing ratio may explain the observed differences in relative abundance in the phytoplankton community. We suggest that taxa that can tolerate high radiation (PAR and UVR) to nutrient ratios and taxa that are adapted to growth in dim blue–green light, like picocyanobacteria, will become less dominant if glacial melting and sediment transport increase. Another explanation to the observed pattern could, however, also be increasing *Daphnia* grazing in the turbid part of the horizontal gradient reducing the number of picocyanobacteria.

The deep Chl *a* maxima tended to be more distinct in clear versus turbid water. However, the depth of the maxima did not change. Deep Chl *a* maxima generally appear near 1% surface PAR irradiance (Modenutti and Balseiro, 2002; Pérez *et al.*, 2002, 2007) and arise *in situ* (Fee, 1976) or by sinking cells (Shortreed and Stockner, 1990). The adaptive benefits of deep Chl *a* maxima have been suggested to be reduced UVR damage due to surface avoidance (Sommaruga and Psenner, 1997; Modenutti *et al.*, 2004) or greater nutrient availability for the phytoplankton in proximity to the thermocline (Saros *et al.*, 2005). The deep Chl *a* maxima in L. Mascaradi was at ~17 m, ruling out UVR avoidance as the primary explanation for the formation of the deep Chl *a* maximum in our study, since all UVA attenuated the first 6–9 m and UVB attenuated in the first 5–6 m. The thermocline was situated at ~18 m and nutrient availability was slightly higher above than below the thermocline, suggesting that the most profitable area for growth regarding temperature and nutrients in this case would be above the thermocline. In L. Mascaradi, the deep Chl *a* maxima indeed occurred slightly above the thermocline. But a vertical position above the thermocline can expose cells to mixing (Modenutti *et al.*, 2004; Callieri *et al.*, 2007). This suggests that phytoplankton in the deep Chl *a* maxima in L. Mascaradi may experience photoinhibition due to mixing if they do not seek refuge at or below the thermocline when wind speeds increase. Wind speeds change rapidly in these systems and mixing regimes are indeed important for the competition and niche overlap for phytoplankton and ciliates (Modenutti *et al.*, 2004, 2008). A position in or below the thermocline represents a refuge from mixing with higher survival due to less photoinhibition, but, on the other hand, cell-specific net primary production may be lower due to low light conditions (Modenutti *et al.*, 2004).

Zooplankton abundance also changed along the sampled horizontal gradient in Lake Mascaradi, and especially *B. gracilipes* became more abundant compared with *D. commutata* as the water became more transparent. *Daphnia* has a higher UVR sensitivity compared with copepods (Leech and Williamson, 2000; Hansson and Hylander, 2009a). We suggest that the higher copepod abundance in the transparent part of the horizontal gradient might be driven by this difference in UVR sensitivity. All zooplankton were also virtually absent in surface samples (0.5 m), suggesting that they avoided UVR damages by migrating to depth refuges. UVR avoidance has indeed been observed among several groups of zooplankton (Rhode *et al.*, 2001; Hansson and Hylander, 2009b; Hylander *et al.*, 2009b). The adaptive benefit of vertical migration has

traditionally been explained as avoidance of fish predators (Lampert, 1989) and L. Mascardi has a population of Galaxiid fish that may affect the vertical distribution of the zooplankton (Balseiro *et al.*, 2007). However, recent studies indicate that UVR avoidance may in some cases be the primary factor driving vertical migration (Obertegger *et al.*, 2008), especially in very transparent lakes where fish predation is low (Kessler *et al.*, 2008).

A few studies have also shown that zooplankton may ingest silt and clay particles, which leads to a lower net intake of food since the stomach gets full of inorganic particles (Kirk, 1991; Jönsson *et al.*, 2011). Furthermore, clay particles can clog the filtering appendages, making them less efficient (Kirk, 1991). Especially, filter-feeding cladocerans, like *Daphnia*, are negatively affected by particles while copepods are less affected (Koenings *et al.*, 1990). Overall, this would potentially lead to a lowered food intake in the less transparent part of the horizontal gradient. We did not observe any reduction in cladocerans in the less transparent part of the gradient, indicating that current levels of particles did not significantly affect the zooplankton in Lake Mascardi.

We conclude that glacier melting with following sediment input into lakes creates horizontal gradients in PAR and UVR transparency which strongly affect phyto- and zooplankton relative species abundance and behavior. Based on our study, we may predict that species that are competitive in transparent waters, like *Chrysocromulina parva* and picocyanobacteria, will become less abundant if sediment input from melting glaciers increases due to climate change. The phenomenon of deep Chl *a* maxima is also suggested to become less developed. Changing PAR and UVR to nutrient ratios may be one of the mechanisms producing these changes in the planktonic community. Looking at the results in another way, sediment input into lakes creates a subhabitat that could function as a refuge for species that are sensitive to high PAR and UVR exposure. When the glacier has vanished, this habitat may disappear. Future studies need to elucidate the mechanisms behind the observed patterns and apart from the above-mentioned factors, other factors like grazing and nutrient mixing may be of importance. In conclusion, we suggest that glacier melting will have profound effects on both species composition and behavior of several planktonic taxa with potential effects on the entire food web.

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## REFERENCES

- APHA. (1995) *Standard Methods*, 19th edn. American Public Health Association, Washington, DC.
- Balseiro, E., Modenutti, B., Queimalinos, C. *et al.* (2007) *Daphnia* distribution in Andean Patagonian lakes: effect of low food quality and fish predation. *Aquat. Ecol.*, **41**, 599–609.
- Belay, A. (1981) An experimental investigation of inhibition of phytoplankton photosynthesis at lake surfaces. *New Phytol.*, **89**, 61–74.
- Belzile, C., Vincent, W. F. and Kumagai, M. (2002) Contribution of absorption and scattering to the attenuation of UV and photosynthetically available radiation in Lake Biwa. *Limnol. Oceanogr.*, **47**, 95–107.
- Callieri, C., Modenutti, B., Queimalinos, C. *et al.* (2007) Production and biomass of picophytoplankton and larger autotrophs in Andean ultraoligotrophic lakes: differences in light harvesting efficiency in deep layers. *Aquat. Ecol.*, **41**, 511–523.
- Cloern, J. E. (1987) Turbidity as a control on phytoplankton biomass and productivity in estuaries. *Cont. Shelf Res.*, **7**, 1367–1381.
- Dahl, E., Bagoien, E., Edvardsen, B. *et al.* (2005) The dynamics of *Chrysocromulina* species in the Skagerrak in relation to environmental conditions. *J. Sea Res.*, **54**, 15–24.
- Eisma, D. (1993) *Suspended Matter in the Aquatic Environment*. Springer, Berlin.
- Fee, E. J. (1976) Vertical and seasonal distribution of chlorophyll in lakes of Experimental-Lakes-Area, Northwestern Ontario—implications for primary production estimates. *Limnol. Oceanogr.*, **21**, 767–783.
- García-Mendoza, E. and Maske, H. (1996) The relationship of solar-stimulated natural fluorescence and primary productivity in Mexican Pacific waters. *Limnol. Oceanogr.*, **41**, 1697–1710.
- Gervais, F., Padisák, J. and Koschel, R. (1997) Do light and low nutrient concentration favour picocyanobacteria below the thermocline of the oligotrophic Lake Stechlin? *J. Plankton Res.*, **19**, 771–781.
- Hansen, L. R., Kristiansen, J. and Rasmussen, J. V. (1994) Potential toxicity of the fresh-water *Chrysocromulina* species *C. parva* (Prymnesiophyceae). *Hydrobiologia*, **287**, 157–159.
- Hansson, L.-A. and Hylander, S. (2009a) Effects of ultraviolet radiation on pigmentation, photoenzymatic repair, behavior, and community ecology of zooplankton. *Photoch. Photobio. Sci.*, **8**, 1266–1275.
- Hansson, L.-A. and Hylander, S. (2009b) Size-structured risk assessments govern *Daphnia* migration. *Proc. R. Soc. B.*, **276**, 331–336.
- Hansson, L.-A., Hylander, S. and Sommaruga, R. (2007) Escape from UV threats in zooplankton: a cocktail of behavior and protective pigmentation. *Ecology*, **88**, 1932–1939.
- Helbling, E. W. and Zagarese, H. (eds.) (2003) *UV Effects in Aquatic Organisms and Ecosystems*. The Royal Society of Chemistry, Cambridge.
- Hylander, S., Boeing, W., Granéli, W. *et al.* (2009a) Complementary UV protective compounds in zooplankton. *Limnol. Oceanogr.*, **54**, 1883–1893.

- Hylander, S., Larsson, N. and Hansson, L.-A. (2009b) Zooplankton vertical migration and plasticity of pigmentation arising from simultaneous UV and predation threats. *Limnol. Oceanogr.*, **54**, 483–491.
- Jerome, J. H., Bukata, R. P. and Bruton, J. E. (1983) Spectral attenuation and irradiance in the Laurentian Great-Lakes. *J. Great Lakes Res.*, **9**, 60–68.
- Joint, I. R. and Pomroy, A. J. (1981) Primary production in a turbid estuary. *Estuar. Coast. Shelf Sci.*, **13**, 303–316.
- Jönsson, M., Ranåker, L., Nicolle, A. *et al.* (2011) Glacial clay affects foraging performance in a Patagonian fish and cladoceran. *Hydrobiologia*, **663**, 101–108.
- Kemp, P. F., Sherr, B. F., Sherr, E. B. *et al.* (eds) (1993) *Handbook of Methods in Aquatic Microbial Ecology*. Lewis Publishers, Boca Raton, Florida.
- Kessler, K., Lockwood, R. S., Williamson, C. E. *et al.* (2008) Vertical distribution of zooplankton in subalpine and alpine lakes: ultraviolet radiation, fish predation, and the transparency-gradient hypothesis. *Limnol. Oceanogr.*, **53**, 2374–2382.
- Kirk, K. L. (1991) Inorganic particles alter competition in grazing plankton—the role of selective feeding. *Ecology*, **72**, 915–923.
- Kirk, J. T. O. (1994) *Light & Photosynthesis in Aquatic Ecosystems*, 2nd edn. Cambridge University Press, Cambridge.
- Koenings, J.P., Burkett, R.D. and Edmundson, J.M. (1990) The exclusion of limnetic Cladocera from turbid glacier-meltwater lakes. *Ecology*, **71**, 57–67.
- Lampert, W. (1989) The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.*, **3**, 21–27.
- Leech, D. M. and Williamson, C. E. (2000) Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency? *Ecol. Appl.*, **10**, 1530–1540.
- Leech, D. M. and Williamson, C. E. (2001) In situ exposure to ultraviolet radiation alters the depth distribution of *Daphnia*. *Limnol. Oceanogr.*, **46**, 416–420.
- Modenutti, B. E. and Balseiro, E. G. (2002) Mixotrophic ciliates in an Andean lake: dependence on light and prey of an *Ophrydium nautmanni* population. *Freshwater Biol.*, **47**, 121–128.
- Modenutti, B., Balseiro, E., Callieri, C. *et al.* (2004) Increase in photosynthetic efficiency as a strategy of planktonic organisms exploiting deep lake layers. *Freshwater Biol.*, **49**, 160–169.
- Modenutti, B. E., Balseiro, E. G., Callieri, C. *et al.*, (2008) Light versus food supply as factors modulating niche partitioning in two pelagic mixotrophic ciliates. *Limnol. Oceanogr.*, **53**, 446–455.
- Modenutti, B., Perez, G., Balseiro, E. *et al.* (2001) The relationship between light attenuation, chlorophyll a and total suspended solids in a Southern Andes glacial lake. *Int. Assoc. Theor. Appl. Limnol.*, **27**, 2648–2651.
- Moeller, R. E., Gilroy, S., Williamson, C. E. *et al.* (2005) Dietary acquisition of photoprotective compounds (mycosporine-like amino acids, carotenoids) and acclimation to ultraviolet radiation in a freshwater copepod. *Limnol. Oceanogr.*, **50**, 427–439.
- Morris, D. P., Zagarese, H., Williamson, C. E. *et al.* (1995) The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnol. Oceanogr.*, **40**, 1381–1391.
- Nielsen, T. G., Kiorboe, T. and Bjornsen, P. K. (1990) Effects of a *Chrysochromulina-polytepis* subsurface bloom on the planktonic community. *Mar. Ecol. Prog. Ser.*, **62**, 21–35.
- Nusch, E. A. (1980) Comparison of different methods for chlorophyll and phaeopigment determination. *Arch. Hydrobiol.*, **14**, 14–36.
- Obertegger, U., Flaim, G. and Sommaruga, R. (2008) Multifactorial nature of rotifer water layer preferences in an oligotrophic lake. *J. Plankton Res.*, **30**, 633–643.
- Peréz, G. L., Queimalinos, C. P. and Modenutti, B. E. (2002) Light climate and plankton in the deep chlorophyll maxima in North Patagonian Andean lakes. *J. Plankton Res.*, **24**, 591–599.
- Peréz, G. L., Queimalinos, C. P., Balseiro, E. *et al.* (2007) Phytoplankton absorption spectra along the water column in deep North Patagonian Andean lakes (Argentina). *Limnologia*, **37**, 3–16.
- Rhode, S. C., Pawlowski, M. and Tollrian, R. (2001) The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*. *Nature*, **412**, 69–72.
- Richter, P. R., Hader, D. P., Goncalves, R. J. *et al.* (2007) Vertical migration and motility responses in three marine phytoplankton species exposed to solar radiation. *Photochem. Photobiol.*, **83**, 810–817.
- Rignot, E., Rivera, A. and Casassa, G. (2003) Contribution of the Patagonia Icefields of South America to sea level rise. *Science*, **302**, 434–437.
- Ryther, J. H. and Menzel, D. W. (1959) Light adaptation by marine phytoplankton. *Limnol. Oceanogr.*, **4**, 492–497.
- Saros, J. E., Interlandi, S. J., Doyle, S. *et al.* (2005) Are the deep chlorophyll maxima in alpine lakes primarily induced by nutrient availability, not UV avoidance? *Arct. Antarct. Alp. Res.*, **37**, 557–563.
- Scully, N. M. and Lean, D. R. S. (1994) The attenuation of ultraviolet radiation in temperate lakes. *Arch. Hydrobiol. Beih.*, **43**, 135–144.
- Shortreed, K. S. and Stockner, J. G. (1990) Effect of nutrient additions on lower trophic levels of an oligotrophic lake with a seasonal deep chlorophyll maximum. *Can. J. Fish. Aquat. Sci.*, **47**, 262–273.
- Sommaruga, R. (2001) The role of solar UV radiation in the ecology of alpine lakes. *J. Photochem. Photobiol. B*, **62**, 35–42.
- Sommaruga, R. and Psenner, R. (1997) Ultraviolet radiation in a high mountain lake of the Austrian Alps: air and underwater measurements. *Photochem. Photobiol.*, **65**, 957–963.
- Stomp, M. J., Huisman, F., de Jongh, A. J. *et al.* (2004) Adaptive divergence in pigment composition promotes phytoplankton biodiversity. *Nature*, **432**, 104–107.
- Tilzer, M. M. (1973) Diurnal periodicity in phytoplankton assemblage of a high mountain lake. *Limnol. Oceanogr.*, **18**, 15–30.
- Utermöhl, H. (1958) Zur vervollkommnung der quantitativen phytoplankton-methodik. *Mitt. Int. Ver. Theor. Angew. Limnol.*, **9**, 1–38.
- Villafane, V. E., Andrade, M., Lairana, V. *et al.* (1999) Inhibition of phytoplankton photosynthesis by solar ultraviolet radiation: studies in Lake Titicaca, Bolivia. *Freshwater Biol.*, **42**, 215–224.
- Wetzel, R. G. (2001) *Limnology: Lake and River Ecosystems*. Academic Press, London.
- Williamson, C. E., Neale, P. J., Grad, G. *et al.* (2001) Beneficial and detrimental effects of UV on aquatic organisms: implications of spectral variation. *Ecol. Appl.*, **11**, 1843–1857.
- Williamson, C. E., Zagarese, H. E., Schulze, P. C. *et al.* (1994) The impact of short-term exposure to UV-B radiation on zooplankton communities in north temperate lakes. *J. Plankton Res.*, **16**, 205–218.