

Effect of volcanic eruption on nutrients, light, and phytoplankton in oligotrophic lakes

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Abstract

Volcanic eruptions that shape the earth's surface can have major effect on ecosystems and, as natural experiments, can yield insights into ecological dynamics. On 04 June 2011, a mega-eruption in the Puyehue volcanic complex (Chile) discharged massive amounts of ash and pumice. Using long-term data from five North Andean Patagonian lakes (Espejo, Correntoso, Nahuel Huapi, Gutiérrez, and Mascardi) that received differing levels of ash, we show that, in Lakes Espejo, Correntoso, and Nahuel Huapi, these inputs resulted in 1.5- to 8-fold increases in total suspended solids, light extinction, phosphorus concentrations, and phytoplankton biomass relative to pre-eruption conditions. Although ashes affected light scattering, the ultraviolet: photosynthetically active radiation ratio remained ~ 0.30 – 0.35 in all the lakes and no changes were seen in dissolved organic carbon in the affected lakes post-eruption. Thus, no differential specific absorption of the different light wavelengths occurred due to ash input. The results of multiple regression analysis identified light extinction coefficient of PAR (K_{PAR}) as the primary variable that was associated with variation in phytoplankton biomass (chlorophyll). Furthermore, incubation experiments demonstrated significant effects of photoinhibition on phytoplankton growth in these lakes at ambient pre-eruption light intensities. Thus, we infer that increased phytoplankton biomass following the eruption likely reflects nutrient (phosphorus) loading and attenuation of excessive light intensities.

Volcanic eruptions have shaped much of Earth's surface over geological time, but they also, in the shorter term, affect ecosystems at local, regional, and even global scales due to ejection and emission of gases, ashes, pumice, and lava. Thus, eruptions present unique opportunities for scientific discovery though such studies are often hindered by a lack of pre-eruption and post-eruption data that allow comprehensive assessment of their effects and the mechanisms of those outcomes (Lindenmayer et al. 2010; Larson 2011). Past studies of the effect of eruptions on aquatic ecosystems have emphasized fertilization by ash-borne elements such as phosphorus and iron (Hamme et al. 2010; Lin et al. 2011). Studies in marine environments have shown that, after volcanic eruptions, the concentrations of chlorophyll, as a proxy of phytoplankton biomass, increase (Hamme et al. 2010; Lin et al. 2011). Paleolimnological evidence from a lake in Iceland also shows that, after a volcanic eruption that deposited considerable amounts of tephra, there was an increase in chlorophyll-derived pigments in sediments, indicating an increase in phytoplankton biomass following volcanic ash deposition (Einarsson et al. 1993). However, increased concentrations of suspended particles in the water column, such as volcano-derived ashes, also increase light scattering and so decrease light penetration (Kirk 1994). In many situations such shading would be expected to negatively affect phytoplankton growth by reducing photosynthesis to levels where it does not exceed respiration (Huisman 1999; Huisman et al. 2002). However, in extremely transparent oligotrophic and ultraoligotrophic aquatic systems, high

light intensities in the upper levels of the water column are known to reduce phytoplankton growth because of photoinhibition (Alderkamp et al. 2010; Gerla et al. 2011), consistent with the possibility that, in highly transparent systems at least, increased light attenuation by abiotic particles such as ash may positively affect phytoplankton growth by reducing photoinhibition.

Despite widespread recognition that pelagic ecosystem function reflects the joint effects of dynamic light and nutrient supplies modulated by water column physical structure and internal food web interactions (Sterner et al. 1997; Falkowski and Raven 2007), the effect of light has been largely neglected in studies regarding volcanic eruption. The 04 June 2011 explosion of Puyehue-Cordón Caulle (40°35'S, 72°07'W) in southern Chile (Fig. 1A) provided a unique chance for assessing such dimensions, as the event deposited massive amounts of ash into a set of nearby lakes in Argentine Patagonia that has been extensively studied for 17 yr (Morris et al. 1995; Callieri et al. 2007; Corno et al. 2009). These temperate Andean lakes (located in North-Patagonia around 41°S) are characterized by high transparency and high ultraviolet radiation (UVR) penetration (Morris et al. 1995), where planktonic organisms living in surface waters are chronically exposed to high light intensity and irradiation at damaging wavelengths (Modenutti et al. 2004, 2005). Such an eruption presents not only an opportunity to evaluate how volcanic eruptions affect lakes but also serves as a "natural experiment" to test the roles of nutrient and light in the ecological functioning of large pelagic ecosystems that cannot otherwise be experimentally manipulated. To assess these effects, we documented optical, chemical, and

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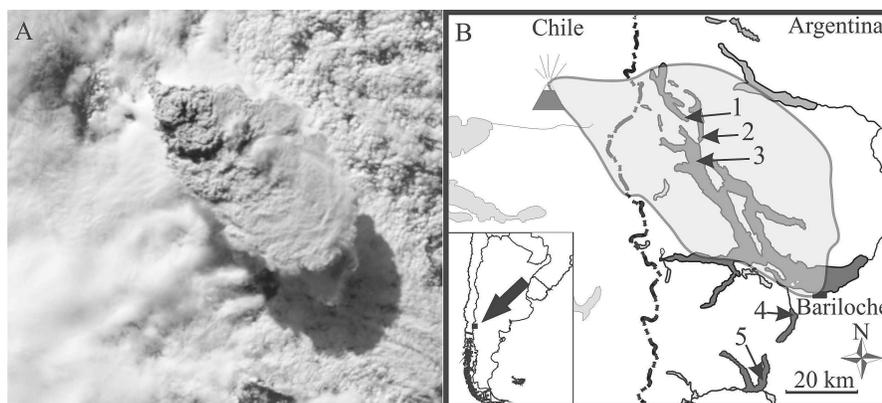


Fig. 1. (A) Satellite view of the eruption in the Puyehue-Cordón Caulle volcanic complex at 18:45 h Universal Time Coordinated (UTC) on 04 June 2011 (Source: <http://earthobservatory.nasa.gov>). (B) The five main study lakes in relation to the eruption site; the silhouette indicates the cloud seen in (A). 1 = Espejo; 2 = Correntoso; 3 = Nahuel Huapi (NW sampling site indicated); 4 = Gutiérrez; 5 = Mascardi.

biological properties in five lakes receiving different levels of ash input and compared these to values from pre-eruption data. To test for the mechanisms involved, we also performed incubation experiments for two lakes, one strongly affected by the eruption (Lake Espejo) and one relatively unaffected (Lake Mascardi), assessing the relative effects of overall light intensity, light quality (e.g., UVR), and nutrients on phytoplankton growth rate.

Methods

Lake sampling—The field study comparing pre- and post-eruption data was carried out in five lakes: Espejo, Correntoso, Nahuel Huapi, Gutiérrez, and Mascardi (Fig. 1B; Table 1), which are part of the glacial lakes district of the North-Patagonian Andes. Lakes Espejo and Correntoso are closer to the eruption and were subjected to considerable ashfall during the initial explosion and via subsequent runoff (Fig. 1). Lake Nahuel Huapi is a large, morphologically complex lake whose northwestern arm (hereafter: NW Nahuel Huapi) received direct surface inputs of ash as well as inputs from inflow streams (Fig. 1). Lakes Gutiérrez and Mascardi received little ash and allow us to assess variability in the absence of eruption (Fig. 1).

Throughout the post-eruption study period, lakes were sampled at a standard deep-water station at approximately 2–3 week intervals during the austral growing season (October 2011–March 2012). Vertical temperature and light profile measurements were taken in the upper 50 m of the

water column using a PUV500B submersible radiometer (Biospherical Instruments™). The profiler was lowered at 0.2 m s^{-1} and, at this descent rate, the temperature resolution was $> 0.1^\circ\text{C}$. The light profile included ultraviolet (UV) bands (305, 320, 340, and 380 nm) as well as photosynthetically active radiation (PAR; 400–700 nm). Water samples were taken using a closing sampler at 0, 10, 20, 30, and 45 m depth in the water column. Water samples were carried to the laboratory in thermally isolated containers within 3 h after sampling, and processed immediately after arrival to the laboratory. A volume of 200 mL was immediately fixed with acid Lugol's solution for phytoplankton enumeration. A volume of 50 mL of lake water was collected for enumeration of autotrophic picoplankton in sterile tubes and fixed with $0.2 \mu\text{m}$ filtered formaldehyde buffered with 0.1 mol L^{-1} sodium cacodylate (final concentration 2% vol:vol), stored in darkness at 4°C , and processed within 2 weeks (Callieri and Stockner 2002). For chlorophyll determinations, a volume of 200 mL from each sampling depth was filtered onto Whatman GF/F filters; in a more restricted set of samples, we also filtered onto $0.2 \mu\text{m}$ pore-size polycarbonate filters (Nuclepore). All filters were frozen until extraction.

Laboratory determinations—The readily available P content of ashes freshly collected at Bariloche during the initial ash fall was measured by suspending 1 g of ashes in 50 mL of MilliQ™ water for 1 h and then evaluating soluble reactive phosphorus by the molybdate reaction

Table 1. Location and morphometric characteristics of the studied North-Patagonian Andean lakes. Abbreviations: masl, meters above sea level; Z_{max} , maximum depth of the lake.

Lake	Location	Altitude (masl)	Area (km ²)	Z_{max} (m)	Watershed	Volcanic effect
Espejo	40°40'S, 71°42'W	800	30.0	245	Atlantic	high
Correntoso	40°43'S, 71°39'W	764	19.5	>120		high
Nahuel Huapi	40°47'S, 71°40'W	764	557	464		variable
Gutiérrez	41°10'S, 71°24'W	785	16.4	111	Pacific	low
Mascardi	41°20'S, 71°30'W	750	39.2	218		low

(APHA 2005). For each sampling depth in routine sampling, measurements of total phosphorus (TP; unfiltered lake water) and total dissolved phosphorus (TDP; Whatman GF/F-filtered lake water) concentrations were performed using the molybdate reaction after persulfate digestion of the sample. Dissolved organic carbon (DOC) was determined on filtered lake water (pre-combusted GF/F Whatman filters) using a Shimadzu™ total organic carbon analyzer.

Chlorophyll *a* (Chl *a*) was extracted in hot ethanol following Nusch (1980) and determined by fluorometric analysis (Turner Designs™ 10AU fluorometer) with acid correction. Total suspended solids (TSS) were estimated by filtering 1 liter of lake water onto pre-weighed GF/F filters that were then dried at 60°C for 48 h and reweighed. The two filter types (GF/F and 0.2 μm Nucleopore) gave very similar values in Chl *a* (no significant differences). Finally, filters for seston C analysis were prepared by filtering lake water onto pre-combusted Whatman GF/F glass-fiber filters; these were dried and held in a desiccator until later analysis on a Thermo Finnigan EA1112 elemental analyzer.

Autotrophic picoplankton, mainly picocyanobacteria, were counted on black polycarbonate filters (Poretics, 0.2 μm 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).

Phytoplankton were enumerated to genus and/or species level using 50 mL settling chambers with an inverted microscope. The four dominant phytoplankton types enumerated and analyzed reflect the species typically found in Andean lakes over the past four decades (Thomasson 1963; Callieri et al. 2007). These are *Chrysochromulina parva* (Haptophyceae), *Rhodomonas lacustris* (Cryptophyceae), *Aulacoseira granulata* and *Cyclotella stelligera* (Bacillariophyceae), and *Gymnodimium paradoxum* and *Gymnodimium varians* (Dinophyceae). The presence of *Tabellaria flocculosa* in the post-eruption samples was confirmed by microscopic analysis (Koppen 1975).

Incubation experiments—To test the dependence of phytoplankton growth rate on nutrients and light in both Lake Mascaradi (unaffected by ash inputs) and Lake Espejo (affected by ash), we ran two outdoor incubation experiments. A full 2 (unenriched, enriched) × 2 (full solar radiation [FSR]; PAR) × 5 (100%, 75%, 33%, 11%, and 3% of solar radiation) factorial design (five replicates per treatment) was carried out in 500 mL polypropylene bags arranged in a 1 m³ water bath. Nutrients were enriched using the freshwater culture medium COMBO (Kilham et al. 1998) to increase P by 15 μg L⁻¹; note that COMBO contains N (as NO₃; N:P = 44 by mass) as well as a mix of trace metals. Light was manipulated in two different ways, quality and quantity. The quality, or PAR treatment, was produced using cut-off filters to remove wavelengths shorter than 400 nm (Courtgard™, CPFilms; Doyle et al. 2005). Light quantity was manipulated by reducing irradiance with increasing layers of shade screens to achieve the five levels of incident irradiance. Each bag was filled

with epilimnetic lake water that was diluted 80% with filtered (GF/F glass-fiber filter) lake water to minimize grazing and allow for growth in the unenriched treatment. During the experiment, temperature was maintained at ~ 18 ± 1°C (similar to surface lake temperatures) and incident solar irradiance was monitored with a photoradiometer. Experiments were run for 72 h. Chl *a* was measured at the start and end of the experiment.

The Lake Mascaradi experiment was completed from 25 to 28 January 2012, whereas the experiment for Lake Espejo took place from 02 to 05 February 2012. During this period the skies were generally cloudless; maximum daily incident irradiance for PAR was 2900 μmol photons m⁻² s⁻¹, whereas the daily irradiance dose was 92 mol m⁻² for the 14 h day length. Maximum incident intensities for UVR at 320 and 340 nm were 44 and 74 μW cm⁻² nm⁻¹, respectively, while their respective daily doses were 11 kJ m⁻² and 20 kJ m⁻².

Calculations—For comparing pre- and post-eruption data for TP and Chl *a*, the multiple depths in the water column were averaged. Note that because our sampling depths are approximately evenly spaced across the upper water layers and encompassed the deep chlorophyll maximum, average chlorophyll concentration (per unit volume) is essentially equivalent to integrated chlorophyll concentration from 0–45 m (per unit area). Long-term data for all parameters were then analyzed by calculating an overall, pre-eruption, average for each parameter for each 4 week interval during the October–February period. All individual data points were then normalized to that average (by dividing) for each 4 week data bin; thus, a value in an interval that does not differ from the overall pre-eruption dynamics would have a value of 1. We then calculated averages and 95% confidence intervals for these normalized, pre-eruption data for each data bin. To plot the data on a common graph for more than one lake (e.g., for the two unaffected lakes, Mascaradi and Gutiérrez), we plotted the maximum confidence limits for each 4 week data period. We normalized each post-eruption data point to its pre-eruption mean for the appropriate temporal bin and plotted those data along with the normalized pre-eruption confidence intervals; statistically significant deviations from historical dynamics were assessed by determining if post-eruption values were outside of these 95% confidence bands. The dependence of Chl *a* on light and TP concentration was assessed with forward and backward stepwise regression.

In addition, we analyzed light transparency and phytoplankton composition of the pre- and post-eruption data set for the lake thermal stratified period (December–February). Light attenuation coefficients (*K*) were estimated from the vertical light profiles as the slope of log_e-transformed irradiance data with depth. To evaluate possible UV wavelength-specific changes relative to PAR absorption due to suspended ashes, we also analyzed the ratio of the 1% depth of 320 nm UV relative to the 1% depth of PAR following Rose et al. (2009).

For calculation of the mean light intensity in the mixed layer (*I*_m; Sterner et al. 1997) for all sampling dates, we used

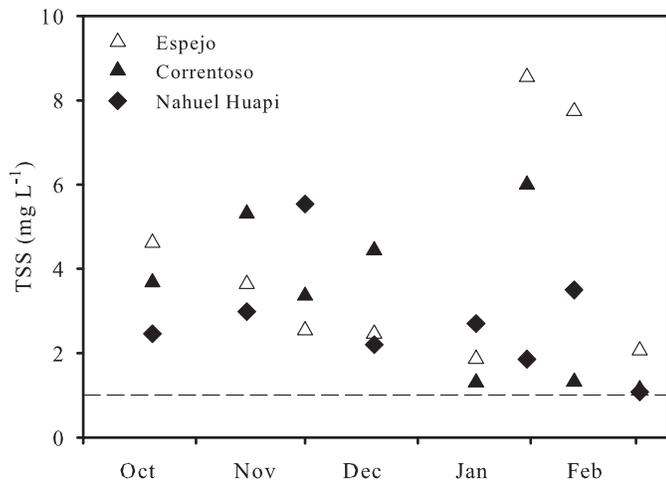


Fig. 2. Post-eruption dynamics of TSS in the affected lakes, relative to typical pre-eruption values that never exceeded 1 mg L^{-1} for a 15-yr record (horizontal line).

light extinction coefficients (K_{PAR}) obtained as described above along with estimates of the depth of the mixing layer (Z_m) from the vertical temperature profile obtained at the same time. Z_m was determined as the depth above the temperature discontinuity (temperature difference $> 1^\circ\text{C m}^{-1}$) identified by direct inspection of the continuous vertical temperature profiles obtained with the PUV radiometer. Since the lakes were generally sampled on calm days in this windy region, small thermal gradients ($< 1^\circ\text{C}$) due to temporary diurnal microstratification were ignored in estimating Z_m on a given day; note that most of our sampling was relatively early in the morning so that such temporary stratification events were uncommon in the data.

I_m was then estimated as in previous work (Sterner et al. 1997) as:

$$I_m = \frac{1 - e^{-K_{\text{PAR}} \times Z_m}}{K_{\text{PAR}} \times Z_m}$$

Note that calculation of I_m yields a value for the average light experienced across the entire mixed layer as a fraction of surface irradiance; this I_m varies from 0 to 1.

The incubation experiment data were analyzed as growth rates based on Chl *a* data. Growth rate (GR) for each replicate for the 3-d incubation was calculated as:

$$\text{GR}(\text{d}^{-1}) = \frac{\ln(\text{Chl } a_f) - \ln(\text{Chl } a_i)}{3}$$

where Chl a_i and Chl a_f are the initial and final concentrations of Chl *a*. GR data were then analyzed with a three-way factorial analysis of variance (ANOVA). Normality and homoscedasticity were confirmed prior to the ANOVA; the data did not require transformation.

Results

In situ dynamics—Immediately after the eruption, concentrations of TSS increased, reaching levels in July

2011 of $\sim 14 \text{ mg L}^{-1}$ in Lakes Espejo, Correntoso, and NW Nahuel Huapi, relative to values typically closer to $\sim 0.5 \text{ mg L}^{-1}$ (maximum: $\sim 1 \text{ mg L}^{-1}$) in these lakes before eruption and in Lakes Gutiérrez and Mascardi both before and after the eruption. During summer 2011–2012, TSS levels in the affected lakes (Espejo, Correntoso, and Nahuel Huapi) were 2–8 times higher than typical pre-eruption levels (Fig. 2). Ash inputs had major effects on various other limnological variables in the affected lakes (Fig. 3). Prior to eruption, the five lakes were very transparent, with light extinction coefficients (K_{PAR}) generally $0.10\text{--}0.15 \text{ m}^{-1}$ (Table 2); however, post-eruption data showed that K_{PAR} increased 1.5- to 2.5-fold after the eruption in Lakes Espejo, Correntoso, and Nahuel Huapi, while remaining at the same historical levels in Mascardi and Gutiérrez (Fig. 3A).

In two of the affected lakes (Lakes Espejo and Correntoso), TP concentrations increased up to > 3 -fold post-eruption (Table 2; Fig. 3B); increasing from values of $\sim 2.0\text{--}3.4 \mu\text{g P L}^{-1}$ to $\sim 4.2\text{--}8.4 \mu\text{g P L}^{-1}$, a result that likely reflects direct contributions of suspended ash, as chemical analysis of fresh ash collected during the 04 June 2011 event indicated an available P content of 0.009% by mass. There was no such increase in TP concentrations in Lake Nahuel Huapi after the eruption (Table 2; Fig. 3B; from $3.9\text{--}4.5 \mu\text{g P L}^{-1}$ to $5.6 \mu\text{g P L}^{-1}$). The unaffected Lakes Gutiérrez and Mascardi retained typical TP concentrations of $1.6\text{--}4.3 \mu\text{g P L}^{-1}$ (Table 2; Fig. 3B). TDP showed a similar pattern to that of TP, including an absence of nutriclines in the vertical profiles. In two of the affected lakes (Espejo and Correntoso), TDP increased from $1.1\text{--}2.3 \mu\text{g P L}^{-1}$ before the eruption to $\sim 4.0\text{--}4.5 \mu\text{g P L}^{-1}$ after the eruption, whereas TDP in Lake Nahuel Huapi did not change appreciably ($2.0\text{--}2.8 \mu\text{g P L}^{-1}$ before to $3.5 \mu\text{g P L}^{-1}$ after). The unaffected Lakes Gutiérrez and Mascardi always had very low values of TDP ($1.0\text{--}2.4 \mu\text{g P L}^{-1}$).

Phytoplankton biomass as indicated by Chl *a* increased strongly after the eruption in Lakes Espejo, Correntoso, and NW Nahuel Huapi, with Chl *a* as much as four times higher (Fig. 3C; Table 2), increasing from concentrations typically $< 0.6 \mu\text{g L}^{-1}$ for Correntoso and Espejo and $< 0.9 \mu\text{g L}^{-1}$ for NW Nahuel Huapi. However, Chl *a* in the unaffected lakes (Gutiérrez, Mascardi) did not deviate from pre-eruption dynamics, maintaining concentrations $< 0.85 \mu\text{g L}^{-1}$ (Fig. 3C; Table 2).

To assess the relative contributions of light attenuation and nutrient loading to observed increases in lake phytoplankton biomass, we performed stepwise multiple regression. Both forward and backward algorithms relating Chl *a* to K_{PAR} and TP for all data from the five lakes indicated that TP was eliminated and only K_{PAR} remained in the final model ($r^2 = 0.41$) with a highly significant ($p < 0.001$) and positive association with Chl *a*. The same overall result was obtained when the analysis was confined to only the affected lakes following the eruption, during which time K_{PAR} would be dominated by light extinction contributed by ash particles. In addition, a similar result was obtained if TDP rather than TP was used in the multiple regression analysis; only K_{PAR} was retained.

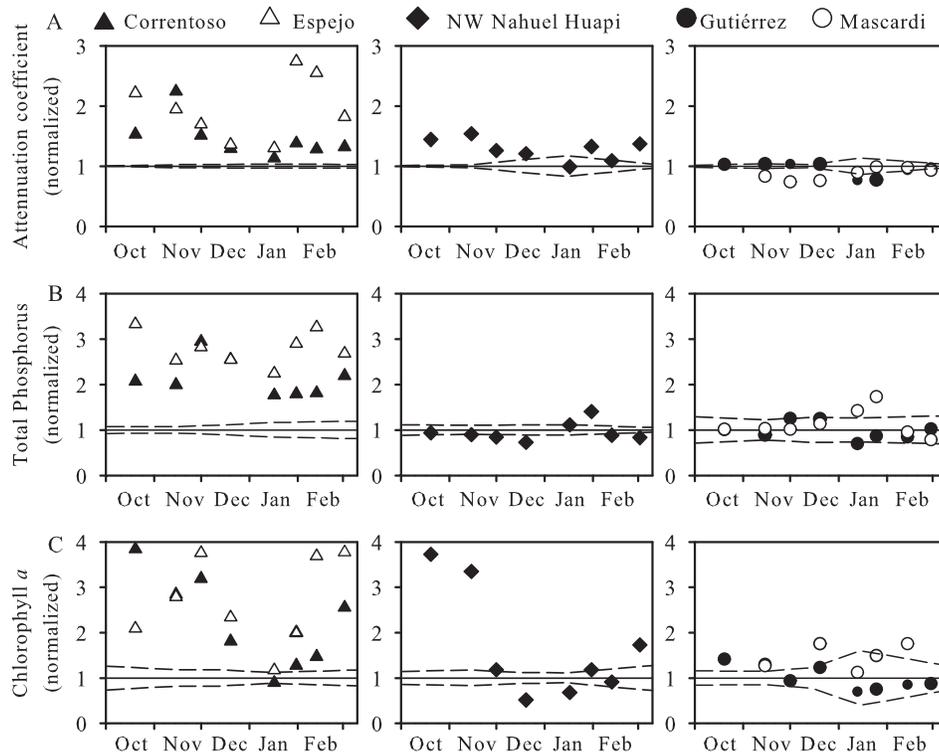


Fig. 3. Post-eruption changes in (A) optical (light extinction coefficient [K_{PAR}]), (B) chemical (total phosphorus concentration [TP]), and (C) biological (phytoplankton biomass as indexed by chlorophyll a concentration [Chl a]) properties in the lakes, normalized to pre-eruption values from ~ 17 yr of monitoring (data in Table 2). Thus, a value of 1 indicates no change relative to the corresponding pre-eruption interval. Dotted lines indicate 95% confidence limits for each month's pre-eruption data.

More detailed analysis of vertical profiles shows that light penetration changed up to 2.7-fold in the affected lakes, particularly in Lakes Espejo and Correntoso (Fig. 4). As an average for the summer stratification period, in Lake Espejo the depth of 1% light penetration ($Z_{1\%}$) for PAR decreased from ~ 40 m to 20 m (Fig. 4A,B) and in Lake Correntoso from 42 m to 25 m (Fig. 4C,D). Because thermal structure of the lakes did not change after the eruption, these increases in light attenuation also caused decreases in the mean irradiance of the mixing layer (I_m), from $> 60\%$ of surface irradiance in Espejo and Correntoso before the eruption to $\sim 30\%$ afterwards. Notably, average I_m in Lake Nahuel Huapi over the summer thermal stratification period did not decrease to the same degree as in the other two lakes because mean K_d

increased only ~ 1.5 -fold during the early part of the growing season in the post-eruption period in this lake (Fig. 3A). In addition, we note that Lake Nahuel Huapi has a considerably deeper thermocline compared with the other two affected lakes; this causes a different physical structure in which the euphotic zone is coincident with or near the upper limit of the mixolimnion (Fig. 4E,F).

The ratio between UV wavelength-specific changes relative to PAR showed that the ash inputs affected all wavelengths equally and thus no shift was found before and after the eruption, with the UV:PAR ratio remaining ~ 0.30 – 0.35 in all the lakes. This result likely reflects the lack of change in DOC in the affected lakes post-eruption; pre-eruption DOC concentration did not exceed 0.6 mg L^{-1} (Morris et al. 1995) and these values were maintained after

Table 2. Pre-eruption mean values of chlorophyll (Chl a ; $\mu\text{g L}^{-1}$), total dissolved phosphorus (TP; $\mu\text{g L}^{-1}$), and light extinction coefficient (K_{PAR} ; m^{-1}) for each month for each lake, used for standardization in Fig. 3. Data are from 1994–2010.

	Espejo			Correntoso			NW Nahuel Huapi			Gutiérrez			Mascardi		
	Chl a	TP	K_{PAR}	Chl a	TP	K_{PAR}	Chl a	TP	K_{PAR}	Chl a	TP	K_{PAR}	Chl a	TP	K_{PAR}
Oct	0.45	2.13	0.10	0.39	2.65	0.10	0.85	3.96	0.10	1.02	1.90	0.10	1.32	1.64	0.15
Nov	0.43	2.25	0.11	0.52	2.96	0.10	0.90	4.03	0.10	0.84	2.01	0.11	0.68	2.07	0.14
Dec	0.46	2.04	0.11	0.61	2.25	0.11	1.93	4.48	0.10	0.99	2.45	0.11	0.58	2.65	0.15
Jan	0.80	2.90	0.11	0.95	3.45	0.10	0.98	3.99	0.11	0.92	4.39	0.13	0.77	3.46	0.14
Feb	0.47	2.09	0.11	0.49	2.32	0.11	1.26	4.57	0.10	1.01	2.33	0.11	0.60	4.25	0.15

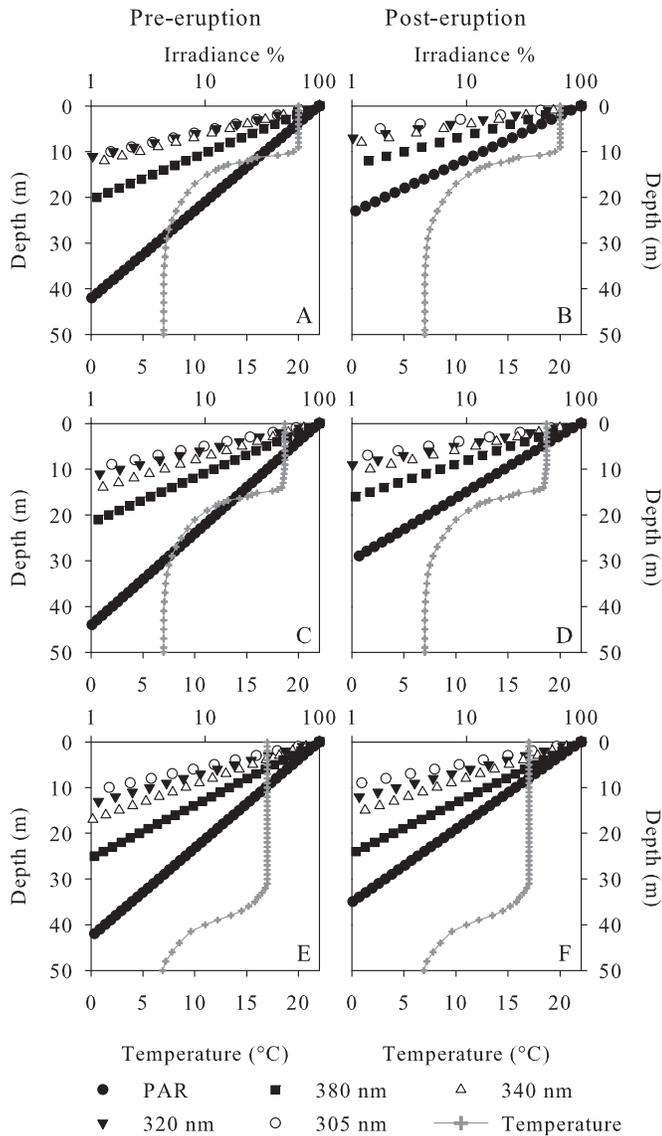


Fig. 4. Depth profiles for mean percent irradiance for 305, 320, 340, and 380 nm UV, and PAR and temperature for (A,C,E) pre-eruption and (B,D,F) post-eruption periods. Pre-eruption data are average of 2000–2008 summer (Dec–Feb). Post-eruption data are averages of December 2011–February 2012 sampling dates. References: A and B: Lake Espejo, C and D: Lake Correntoso, E and F: Lake Nahuel Huapi.

the eruption (Espejo = $0.52 \pm 0.15 \text{ mg L}^{-1}$, Correntoso = $0.51 \pm 0.14 \text{ mg L}^{-1}$, and Nahuel Huapi = $0.51 \pm 0.11 \text{ mg L}^{-1}$).

The Chl *a*:C ratio ($\mu\text{g}:\text{mg}$) averaged 10–12 in the affected lakes as well as in the unaffected Lakes Gutiérrez and Mascardi (Fig. 5). Furthermore, we found no significant differences in Chl *a*:C between lakes (ANOVA, $F_{4,35} = 1.43$, $p = 0.24$), although Lake Nahuel Huapi had more variable Chl *a*:C ratios (Fig. 5).

Previous quantitative data on summer phytoplankton taxa in Lakes Espejo, Correntoso, and Nahuel Huapi indicated dominance by picocyanobacteria and the nano-flagellate *Chrysochromulina parva* (Haptophyceae; cell

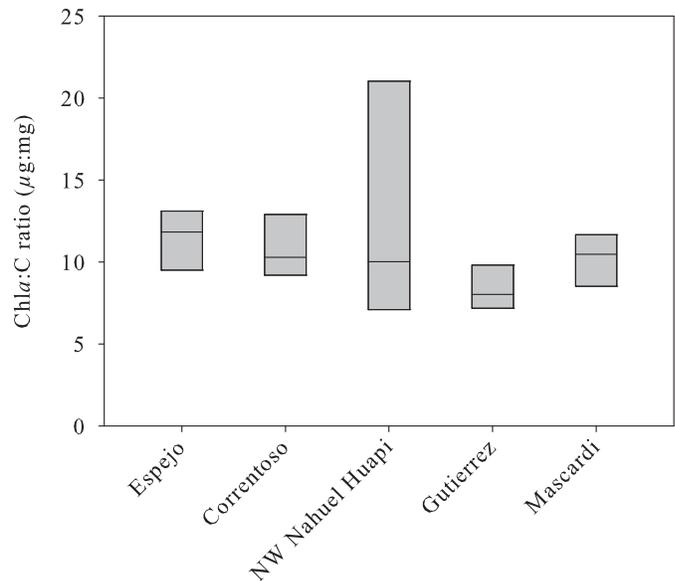


Fig. 5. Box plot of the chlorophyll *a*:sestonic C (Chl *a*:C) ratio ($\mu\text{g}:\text{mg}$) for the study lakes during 2011–2012 sampling period. Box limits indicate 25th and 75th percentiles; horizontal line in the box represents the median.

average length = $3.78 \pm 0.5 \mu\text{m}$) with increased abundances of both towards 45 m depth (Fig. 6A,B; see pre-eruption graphs). However, examination of post-eruption samples indicated that, whereas picocyanobacteria remained the dominant component of the phytoplankton (Fig. 6B; see post-eruption graphs), there was a noticeable change in the structure of the phytoplankton community (Fig. 6A; see post-eruption graphs). In Lakes Correntoso and Espejo we observed an increase in the abundance of Cryptophyceae, in particular of *Rhodomonas lacustris* (cell average length = $8.7 \pm 0.7 \mu\text{m}$). In Lake Nahuel Huapi we noted a decrease of *C. parva* with a concomitant increase in the abundance of *R. lacustris* and diatoms (*Tabellaria flocculosa* and *Aulacoseira granulata*; Fig. 6A; see post-eruption graphs). After the volcanic event we observed that the increase in phytoplankton biomass occurred both in the deep chlorophyll maxima (DCM) and in the mixing layer, and that the mean depth of the maximum cell abundance of both phytoplankton components moved upwards to around 20 m depth, especially in Espejo and Correntoso (Fig. 6).

Incubation experiments—Our incubation experiments showed that, while nutrient fertilization modestly increased phytoplankton growth, consistent with a role for ash-borne nutrients in stimulating post-eruption chlorophyll concentrations in the affected lakes, there was also a large negative effect of overall light intensity on phytoplankton GR as well as an effect of UV removal (Fig. 7). GR declined at relatively low levels, when FSR intensity exceeded 10% of incident irradiance (or even 3% for the unenriched treatment in Lake Mascardi). Similar, though slightly more modest, negative effects of light intensity were obtained when UVR was removed. Notably, the difference between FSR and PAR treatments was only present in medium to high light intensities, while at low light intensities there was

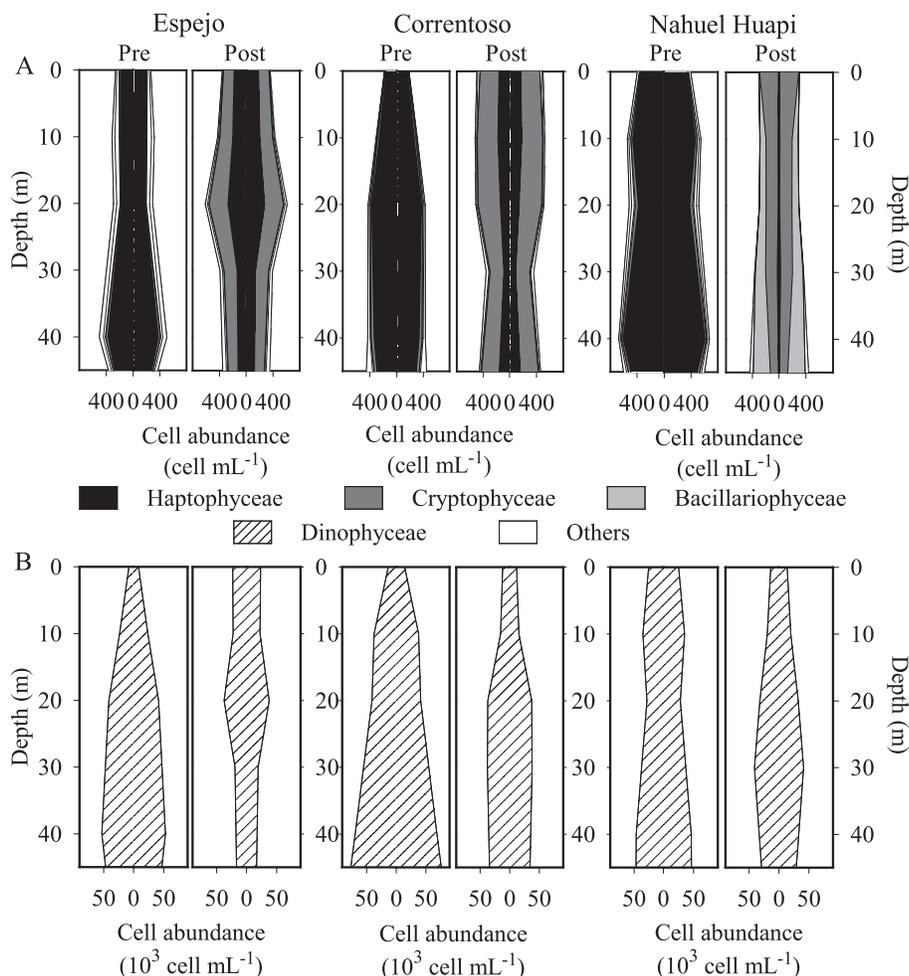


Fig. 6. Vertical profiles of phytoplankton in Lakes Espejo, Correntoso, and NW Nahuel Huapi pre-eruption and post-eruption. (A) Phytoplankton composition and cell abundance, (B) picocyanobacteria cell abundance. Pre-eruption data are average of 2000–2008 summer (Dec–Feb). Post-eruption data are averages of December 2011–February 2012 sampling dates.

little effect of UVR removal, especially in the Espejo experiment. For both lakes, ANOVA indicated highly significant main effects of light quality ($p < 0.0001$), light intensity ($p < 0.0001$), and nutrients ($p < 0.0001$) on GR. We found statistically significant light intensity \times nutrient interactions in both experiments ($p = 0.006$ in Espejo and $p = 0.024$ in Mascardi) but only the Espejo experiment had significant two-way interactions involving light quality, with intensity ($p < 0.0001$) and with nutrients ($p = 0.026$). No significant ($p > 0.05$) three-way interactions were observed.

To interpret these results in light of the Puyehue eruption, we assessed the shading stimulation of phytoplankton GR in light of the observed values of average relative mixed-layer irradiance (I_m expressed as a percentage of surface irradiance) before and after the eruption. I_m was $\sim 42\%$ in Lake Mascardi and did not change after the eruption. In the Lake Mascardi experiment (Fig. 7A), phytoplankton had near-zero or slightly negative growth rates at this I_m , even with nutrient fertilization and UVR removal. In Lake Espejo, I_m declined markedly after the

eruption, from $\sim 62\%$ (brighter than Lake Mascardi) to $\sim 30\%$. This change was nearly entirely due to the increase in K_{PAR} post-eruption, as average mixing depth did not change appreciably following the eruption (Fig. 4A,B). In the Lake Espejo experiment (Fig. 7B), a decline in I_m from 62% to 30% I_m corresponds to a shift from light conditions that strongly inhibited phytoplankton growth (regardless of nutrients or UV) in the experiment to those at which GR was near zero or positive.

Discussion

Overall, lake dynamics after eruption indicate that increased phytoplankton biomass was likely due to combination of an increase in P supplies together with a lowering of light intensities caused by suspended ashes. An indication that mechanisms other than nutrient loading alone appear to be involved was provided by the observation that Chl *a* increased considerably in October and November in NW Nahuel Huapi after the eruption, despite no apparent change in P (Fig. 3; see October and

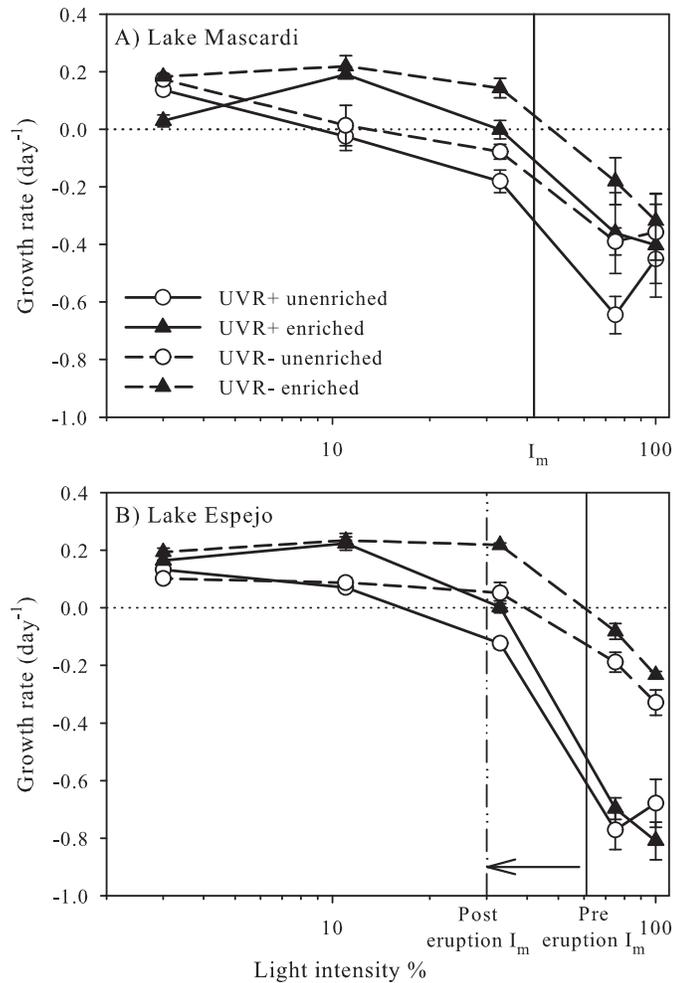


Fig. 7. Results of incubation experiments testing the effects of overall light intensity (UVR+), removal of ultraviolet radiation (UVR-), and nutrients on growth rate of phytoplankton from (A) Lake Mascardi (relatively unaffected by the eruption) and (B) Lake Espejo (strongly affected by the eruption). Error bars on each symbol indicate ± 1 standard error. On each figure, vertical lines indicate the historical 17 yr pre-eruption average mixed-layer light intensity (I_m , as a percentage of incident) as well as the average post-eruption value for 2011. For Lake Mascardi, the pre- and post-eruption values of I_m were essentially identical, but the horizontal arrow in panel B indicates the post-eruption shift seen in Lake Espejo due to shading by suspended ash.

November samples). Furthermore, Chl *a* decreased in early summer (December to January) in Lakes Espejo and Correntoso with no decrease in P (Fig. 3A) but in concert with declining K_{PAR} (increasing light). One possible mechanism for these changes in Chl *a* despite no change in TP is that suspended ash ameliorated exposure of phytoplankton to excessive solar radiation, which previous studies have shown to be damaging in these highly transparent lakes (Morris et al. 1995; Modenutti et al. 2004; Villafaña et al. 2004). Previous to the eruption event, wind-sheltered lakes like Espejo and Correntoso had their whole epilimnia illuminated and exposed to high PAR as well as hazardous UVR (including UV-B and UV-A; Fig. 4). Lake Nahuel Huapi is the largest lake in the area,

and because of its location and the predominance of western winds, has a considerable fetch (Fig. 1) that results in a very deep thermocline (Fig. 4E,F). Nevertheless, almost the whole epilimnion is exposed to UV-A while the upper 40% of the epilimnion is also exposed to UV-B (305 nm; Fig. 4). Indeed, in these North-Patagonian Andean lakes DOC concentrations are very low (Morris et al. 1995) and the lakes have elevated UV:PAR ratios (~ 0.35), indicating that light attenuation is not due to DOC but instead is dominated by attenuation by suspended particles (Rose et al. 2009). The fact that suspended ashes increased K_{PAR} and light scattering at all wavelengths (no changes in UV:PAR ratio were observed) implies an overall reduction in total solar radiation received as well as amelioration of UVR exposure (Fig. 4).

The inference that increased post-eruption chlorophyll at least partially reflects lower light intensities is supported by the results of multiple regression analysis, which identified K_{PAR} as the variable that is primarily associated with variation in Chl *a*, both across all lakes throughout the study period as well as just in the affected lakes during the post-eruption interval. Importantly, this correlation analysis is bolstered by the experimental results (Fig. 7): nutrient enrichment had only modest effect on phytoplankton growth compared with the large positive effect of lowering solar radiation. We note that the modest responses to nutrient enrichment we observed in these experiments are unlikely to reflect possible nutrient release from cells damaged during preparation of filtered lake water for the 80% experimental dilution because measurements of soluble (i.e., filtered) reactive phosphorus samples typically are below our limit of detection of $1 \mu\text{g L}^{-1}$, considerably lower than the $15 \mu\text{g L}^{-1}$ experimental P enrichment. Removal of UVR also had a positive effect on GR, an understandable outcome given that ultraviolet radiation is known to damage phytoplankton and reduce primary production (Holm-Hansen et al. 1993; Neale et al. 1998a). When we removed this damaging wavelength in our experiments, the overall photoinhibition effect was reduced but not eliminated. This result suggests that PAR itself is too high and sufficient on its own to induce photoinhibition and that this effect is not counteracted by nutrient enrichment.

Our inference that excess irradiance is an important ecological factor in these lakes clarifies the observed dynamics in Lake Nahuel Huapi in spring and Lakes Espejo and Correntoso in early summer, where phytoplankton biomass changed significantly despite no apparent change in nutrient levels (Fig. 3) but in concert with shifts in light extinction. Consistent with this interpretation, previous studies in the same lakes have shown that primary production at depths corresponding to 10% of surface irradiance is 5–10 times higher than that in surface layers (Modenutti et al. 2004; Callieri et al. 2007), despite vertical uniformity in nutrient concentrations.

Extrapolation of our experimental results to lake conditions is complicated by the fact that we used a static incubation but, under natural conditions, phytoplankton cells in a lake's mixing layer are continuously brought in and out of near-surface layers where solar radiation is high

and induces photoinhibition (Neale et al. 1998b; Modenutti et al. 2005). Relevant to such mechanisms, our experimental results suggest a stronger negative effect of light on phytoplankton growth rate at irradiances exceeding I_m than below (Fig. 6). This apparent nonlinearity suggests that, compared to cells held at a constant value of I_m (as in our incubation experiment), overall photoinhibitory effects would be larger for circulating cells experiencing light $> I_m$ for part of the day and light $< I_m$ for part of the day. Considering the differences in I_m between Lakes Espejo and Correntoso vs. Lake Nahuel Huapi, it seems that our static experiments could be either under- or overestimating photoinhibitory effects on phytoplankton experiencing in situ I_m . Nevertheless, considering the in situ dynamics following the volcanic natural experiment and our experimental results together, photoinhibition emerges as a candidate factor contributing to dynamics of primary production and phytoplankton biomass under normal (pre-eruption) conditions in these lakes and suggests that excessive irradiance plays a similar role in other water columns of high optical clarity.

This inference is strengthened by previous studies in these lakes, which also provide insight into how phytoplankton vertical distributions shifted in response to the eruption. Phytoplankton in clear North Andean-Patagonian lakes often develop DCM, likely due to strong effects of photoinhibition (Modenutti et al. 2004). Therefore, the possibility of a refuge against hazardous wavelengths in deep layers is important in these extremely clear lakes. Previous to the volcanic event, these lakes regularly exhibited DCM, either in the hypolimnion (Espejo and Correntoso) or in the metalimnion (Nahuel Huapi; Modenutti et al. in press). These DCM involve mainly motile mixotrophic cells (Modenutti et al. 2004, in press) that are able to move to deeper layers (Sommaruga and Psenner 1997), exploiting hypolimnetic levels of the euphotic zone. Noticeably, after the eruption event, phytoplankton composition changed, with an increase in the flagellate *R. lacustris* (Cryptophyceae) in Lakes Espejo and Correntoso and an upward shift in the depth of its maximum abundance. This latter change is consistent with a community actively maintaining its position at a desired light intensity. *R. lacustris* is a facultative mixotroph that is very common in less transparent lakes in the area (Balseiro et al. 2004) and the flexibility of such mixotrophs has been suggested as an adaptive advantage that allows them to dominate in plankton communities exposed to variation in light (Laybourn-Parry et al. 1997). This change in flagellate species composition implies a change in cell size (dominance from *C. parva*, cell average length = $3.78 \pm 0.5 \mu\text{m}$, to *R. lacustris*, cell average length = $8.7 \pm 0.7 \mu\text{m}$), which may help in understanding the observed increase in Chl *a* concentrations despite no significant change in cell numbers or Chl *a*:C ratio. On the other hand, the increase of the diatoms *A. granulata* and *T. flocculosa* in Lake Nahuel Huapi and their shift towards deeper levels suggest that these nonmotile cells accumulated at the thermocline because they cannot actively regulate their position in the water column (Cullen 1982). The increase in diatoms may be a result of more silica in the water column from the

volcanic activity. However, diatoms would likely not be supported in Espejo and Correntoso because their shallower mixing layers have low turbulent diffusivity compared to Nahuel Huapi (Huisman et al. 2004).

Picocyanobacteria remained the dominant component in the phytoplankton based on cell abundance both in pre- and post-eruption periods (Fig. 6B). Picocyanobacteria have generally more relative abundance when nutrient concentrations are low (Callieri et al. 2007). For all three affected lakes, the abundance of picocyanobacteria declined after the eruption. Further, and consistent with a decrease in nutrient limitation, the abundance of larger nanoplankton increased. Picocyanobacteria have been reported to perform well under low-intensity, green light because of the presence of phycoerythrin (Stomp et al. 2007). This helps explain increased abundances of phycoerythrin-rich cells previously observed in the DCM of deep ultraoligotrophic Patagonian lakes (Callieri et al. 2007), where blue-green light prevails (Pérez et al. 2002). Since no post-eruption changes were observed in absorption of different wavelengths (Fig. 4), dim, green light conditions after the eruption occurred at a shallower depth (*see* increase around 20 m depth in Fig. 6B post-eruption graphs). Thus, as the same light quality was achieved at shallower depth, picocyanobacteria moved upwards in the water column. These shifts are consistent with previous documentation of the highly variable dynamics of picocyanobacteria in forming DCM in the metalimnion or the hypolimnion (Callieri et al. 2007).

Consistent with an overall view that high light intensities are an important ecological factor in these lakes are the low Chl *a*:C ratios we observed, as low Chl *a*:C ratios are generally considered to be indicative of high irradiance conditions (Geider et al. 1997). While differences in average Chl *a*:C ratios between lakes were not significant, Chl *a*:C ratios in Lake Nahuel Huapi were quite variable (Fig. 5). This variability may be due to several factors. Since different taxonomic groups can differ considerably in the Chl *a*:C ratios (Chan 1980), one possible contributing factor is the greater variability in algal composition and cell size (including nanoflagellates and diatoms, from ~ 3 to $45 \mu\text{m}$ in cell length) in Nahuel Huapi than seen in the other lakes. Another possible contributing factor for the extreme variability in Chl *a*:C ratios in Nahuel Huapi is its deeper thermocline, its complex lake morphometry, and its greater wind exposure than in the other lakes. Together, these may result in the whole euphotic zone being included in the mixing layer, leading to the possibility of a weak photoacclimation because turbulence may drag cells all along the light gradient (Geider et al. 1997) or sporadically move them out of the DCM into the mixed layer.

Beyond documenting volcano effects on lake water quality, our study suggests an unexpectedly contribution of excess light in affecting phytoplankton growth and production in these transparent Patagonian lakes. It has recently been suggested that limiting light conditions are an underappreciated factor in lake ecology (Karlsson et al. 2009). However, the findings of Karlsson et al. are from small, highly colored lakes that, while numerous, do not contain large volumes of surface freshwaters. In such

shallow lakes, colored dissolved organic matter greatly reduces overall light intensity and acts as the “ozone of the underwater world” by selectively removing the shorter wavelengths of light (Williamson and Rose 2010). However, in these clear North Patagonia lakes, dissolved organic matter concentration is extremely low ($< 0.6 \text{ mg L}^{-1}$; Morris et al. 1995; Corno et al. 2009) and high light has been recognized as an important factor structuring lacustrine plankton (Modenutti et al. 2004, 2005). The high-transparency, low-nutrient scenarios typical of our study lakes are likely widespread in many large lakes worldwide; notably, large lakes contain the majority (68%) of global unfrozen surface waters and provide a variety of key ecosystem services (Beeton 2002). Such high light scenarios may also be common in many oceanic regions, leading us to suggest that increasing photoinhibition may be a factor contributing to recently reported declines in oceanic phytoplankton biomass linked to warming surface layers during the last 30 yr (Boyce et al. 2010; but see also McQuatters-Gollop et al. 2011). For lakes, future light environments will depend strongly on possible changes in inputs of colored organic matter. While some early assessments suggested reduced inputs of colored organic materials and thus brighter surface mixed layers during coming decades (Magnuson et al. 1997), more recent studies highlight the possibility of increasing DOC inputs to lakes due to temperature stimulation of DOC mobilization from peatlands (Freeman et al. 2001; Hansson et al. 2012). According to the inferences we make here, such changes might result in increased phytoplankton production in highly transparent lakes by shielding phytoplankton from excessive irradiance. Regardless of the direction of such DOC shifts, our work suggests that understanding the effects of shifts in DOC inputs to lakes will require assessment of how such changes might modulate photoinhibition of lake ecosystem production and interactions with nutrient supply. Thus, our findings should motivate continued work on the role of optical conditions in affecting the functioning of the pelagic ecosystems that are fundamental in global water supplies and biogeochemical cycles.

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