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Authors: J. Alcocer, L. A. Oseguera, E. Escobar, L. Peralta, and A. Lugo

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Phytoplankton Biomass and Water Chemistry in Two High-Mountain Tropical Lakes in Central Mexico

J. Alcocer,*

L. A. Oseguera,*

E. Escobar,†

L. Peralta,* and

A. Lugo*

*Proyecto de Investigación en Limnología Tropical, FES Iztacala, UNAM. Av. de los Barrios No. 1, Los Reyes Iztacala. 54090 Tlalnepantla, Edo. de Mexico, Mexico. jalcocer@servidor.unam.mx

†Instituto de Ciencias del Mar y Limnología, UNAM. Apdo. Postal 70-305, Coyoacán 04510, Mexico, D.F., Mexico.

Abstract

In this work we report the vertical phytoplankton biomass distribution (chlorophyll *a* depth-profiles) and the integrated phytoplankton biomass (chlorophyll *a* per unit area) of two high-mountain Mexican Lakes: El Sol and La Luna (19°06'N, 99°45'W, 4200 m a.s.l.). El Sol and La Luna are transparent, nonglacier-fed lakes. Both lakes are continuous warm polymictic with a uniform vertical distribution of phytoplankton biomass. Slight heterogeneities were observed in El Sol with a deep-water chlorophyll maximum above the sediments (maximum difference 0.71 $\mu\text{g L}^{-1}$) associated to phytoplankton sunken cells and the presence of filamentous benthic algae. Phytoplankton biomass per unit area was low in both lakes (El Sol 1.91–8.36 and La Luna 1.13–4.80 mg Chl *a* m^{-2}), and similar to that of temperate high-mountain lakes. The temporal variations in the phytoplankton biomass were attributed mainly to a combined effect of nutrient input and zooplankton grazing pressure; the effect of low pH is also considered in La Luna.

Introduction

Global Climate Change (GCC) is being successfully studied in temperate and polar alpine lakes through diverse programs (e.g., MOLAR–Mountain Lake Research; EMERGE–European Mountain Lake Ecosystems: Regionalization, diagnostic & socio-economic Evaluation). However, almost no information is available regarding the limnology of tropical high-mountain (i.e. high-altitude, alpine) lake ecosystems and their potential value as GCC indicators. This is in part due to the high-mountain lakes have not been the subject of much limnological study in tropical regions, except for Lake Titicaca, Peru/Bolivia. Understanding of tropical, high-altitude limnology is fundamental if “natural” changes (i.e. baseline) are to be distinguished from anthropogenic changes, a distinction that is crucial to GCC studies.

The present contribution is part of a larger project aiming to analyze the suitability of high-mountain Mexican lakes as indicators in monitoring global as well as local/regional climate change. In this work we report the phytoplankton biomass (expressed as Chl *a* per unit area) and the vertical phytoplankton biomass distribution of Lakes El Sol and La Luna. This information will help to establish the baseline for GCC studies in Mexico based on high-mountain lakes. It also contributes to the understanding of tropical, high-mountain limnology.

Mexico has few high-mountain lakes (i.e. above the timberline, >3800 m; Löffler, 1972). There are just two perennial lakes (El Sol and La Luna, Nevado de Toluca volcano, Central Mexico), a temporary pond in Iztaccihuatl volcano, and probably some other(s) pond(s) associated to the highest elevations of Central Mexico.

Of special interest to aquatic ecosystems are primary producers. Annual primary production in lakes declines from the tropics to the poles (Lewis, 1996; Talling and Lemoalle, 1998). However, although there is a wide range of phytoplankton biomass values in tropical lakes, no effect of latitude on chlorophyll *a* (Chl *a*) concentrations or production has been detected within the tropics (Melack, 1981).

Although estimates of phytoplankton biomass in tropical high-mountain lakes are few (Payne, 1986), available data are spread over a wide range. Some cold lakes in highland regions of the tropics such as Lake Titicaca (Widmer et al., 1975) can have quite appreciable rates of production; in contrast, others such as Lake Mucabaji and Laguna Negra, Venezuela, had a very low rate (Lewis and Weibezahn, 1976).

It seems that the principal difference between these lakes is not temperature but nutrient content (i.e. lakes with higher mineral content are more productive).

The vertical phytoplankton stratification is influenced by reproduction rate (light and nutrient dependent), passive sinking, resuspension and active migrations (all influenced by water turbulence). Whenever thermal stratification occurs, there is some concomitant stratification of phytoplankton, whereas turbulent mixing can impose vertical patterns favoring homogeneous distribution (Moss, 1980).

The great variation in light penetration into tropical inland waters implies a corresponding variation in the depth range of photosynthetic activity (Talling and Lemoalle, 1998). A characteristic of the Chl *a* depth-profiles (i.e. the vertical distribution of phytoplankton biomass) is the severe surface inhibition caused by the high levels of UV radiation experienced at high altitudes (e.g., Lake Titicaca; Widmer et al., 1975). Moreover, data from high-mountain lakes of the Alps (Sommaruga and Garcia-Pichel, 1999; Sommaruga et al., 1999) indicate two contrasting Chl *a* depth-profiles. A chlorophyll maximum at depth (i.e. close to the bottom) characterizes transparent, nonglacier-fed lakes. In turbid, glacier-fed lakes the maximum is close to the surface.

Study Area

Lakes El Sol and La Luna are inside the crater of the Nevado de Toluca volcano (19°06'N, 99°45'W, 4200 m a.s.l.), Central Mexico (Fig. 1). Both lakes are perennially astatic, this is, their levels rise and fall as a result of the precipitation-evaporation balance, but do not dry up. Twenty-year data (1921–1980) from the “Nevado de Toluca” weather station (19°07'N, 99°45' W, 4,140 m a.s.l.) report average monthly mean temperatures ranged between 2.8°C in February and 5.8°C in April, with an annual mean temperature of 4.2°C. Total annual precipitation is 1243.5 mm, ranging from 17.2 mm in December to 270 mm in July (García, 1988). The narrow temperature range resembles the high-mountain wet zones termed “Paramos” (Löffler, 1964).

Maximum depth of El Sol is 15 m (mean depth 6 m), with a surface area of 237,321 m^2 (length 795 m, width 482 m). Maximum depth of La Luna is 10 m (mean depth 5 m) with a surface area of 31,083 m^2 (length 227 m, width 209 m) (Alcocer et al., unpublished data).

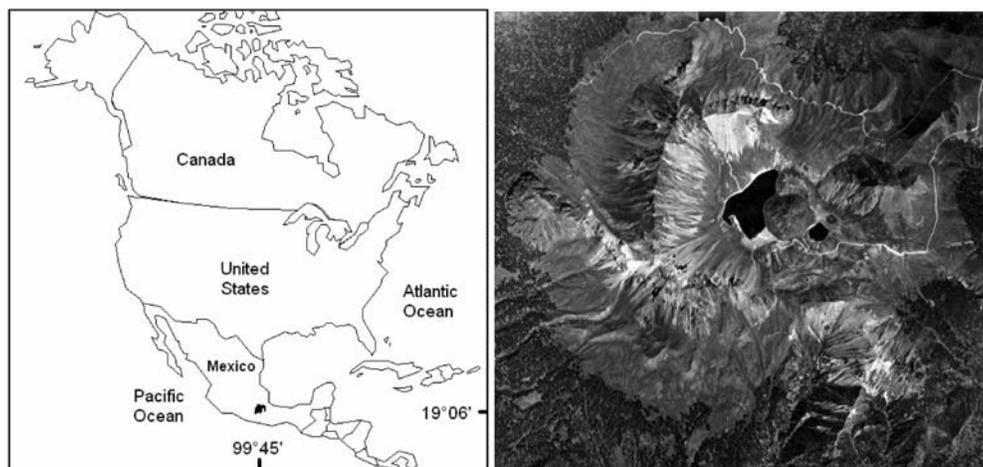


FIGURE 1. Geographic location of (left) Lake El Sol and (right) Lake La Luna, Nevado de Toluca, Mexico.

Methods and Material

Sampling took place once each month (El Sol: 0900–1100 h, La Luna: 1300–1400 h) in the central and deepest part of the lakes during a 13-mo period. During this study, El Sol bottom depths at sampling sites ranged between 10 and 12 m and in La Luna between 7 and 9 m. On each sampling occasion, four profiles of Chl a concentration and PAR (Photosynthetic Active Radiation, roughly 400–700 nm) were evaluated for each lake by means of a Biospherical® PNF-300 vertical profiler (discrete readings every second). Chlorophyll concentrations (Chl in $\mu\text{g L}^{-1}$) were calculated according to the PNF-300 user's manual (Biospherical Instruments Inc., 1996), from the natural fluorescence flux, F_f , and the incident irradiance—which are highly correlated (Chamberlain et al., 1990)—according to:

$$\text{Chl} = F_f / {}^{\circ}\text{ac}(\text{PAR}) * \Phi_f * E_o(\text{PAR}) \quad (1)$$

There are two important optical assumptions used in this: ${}^{\circ}\text{ac}(\text{PAR})$ is the chlorophyll-specific absorption coefficient (absorption normalized to chlorophyll concentration) and Φ_f is the quantum yield fluorescence. These values were treated as constants in the software for the PNF-300 with values of $0.04 \text{ m}^2 \text{ mg}^{-1}$ and $0.045 \text{ mE fluoresced per mE absorbed}$, respectively.

Scalar irradiance over PAR, $E_o(\text{PAR})$, is defined as:

$$E_o(\text{PAR}) = \int_{400}^{700} L_{4\pi}(\theta, \Phi) d\omega d\lambda \quad (2)$$

where L is radiance, ω is the solid angle response of the collector (all 4π for scalar), and θ and Φ are the zenith and azimuthal angles of the radiant flux.

Chl a is usually used as an indirect parameter for biomass; Sommaruga et al. (1999) found Chl a and direct estimations of biomass in high-mountain lakes of the Austrian Alps to be highly significantly correlated. To record the total abundance, phytoplankton biomass was expressed per unit area ($\text{mg Chl}a \text{ m}^{-2}$) rather than per unit volume, since the phytoplankton is rarely homogeneously distributed (Payne, 1986) and hence the concentration per unit volume varies with depth.

Profiles *in situ* of temperature, dissolved oxygen, pH, and conductivity (K_{25}) were obtained with a calibrated Hydrolab® DS4/SVR4 multiparameter water-quality data logger and logging system (discrete readings every meter). Three water samples (1 m below the surface, mid-water, and 1 m above the sediment) of each lake were obtained for nutrient (N-NH $_4$, N-NO $_2$, N-NO $_3$, P-PO $_4$, Si-SiO $_4$) analysis with a Niskin water sampler following standard methods

(Strickland and Parsons, 1972) adapted to an autoanalyzer (Føyn et al., 1981) Skalar Sanplus segmented flow analysis (SFA) system.

Results

ENVIRONMENTAL VARIABLES

Secchi disc depth (Z_{SD}) ranged from 3 to 7.4 m ($4.6 \pm 1 \text{ m}$) in El Sol, and between 4 and 9 m ($7.7 \pm 1.5 \text{ m}$) in La Luna (in La Luna, from September to March $Z_{SD} = Z_{max}$). The entire water column was considered a euphotic zone since PAR at the bottom was $> 1\%$ of the surface PAR throughout the year in both lakes.

Annual mean water temperature in El Sol was 8.5°C , with the maximum (11°C) in September and the minimum (5°C) in January. Annual mean water temperature in La Luna was 8.5°C , with the maximum (11.5°C) in July and the minimum (5.5°C) in January. At the times of sampling, the surface layer was slightly warmer, but differences between surface and bottom temperatures were small, indicating well-mixed water columns. In El Sol, the maximum surface-bottom difference was 0.66°C and the minimum 0.07°C , with an annual mean difference of $0.34 \pm 0.18^\circ\text{C}$. In La Luna the maximum surface-bottom difference was 1.61°C and the minimum 0.09°C , with an annual mean difference of $0.9 \pm 0.43^\circ\text{C}$.

Dissolved oxygen (DO) in each lake was below saturation most of the year. El Sol annual mean DO was 96% saturation (6.8 mg L^{-1}), with the minimum (82%, 5.57 mg L^{-1}) in August and the maximum (110%, 7.82 mg L^{-1}) in November. La Luna annual mean DO was 95% (6.77 mg L^{-1}), with the minimum (83%, 6.26 mg L^{-1}) in March at the beginning of the sampling program and the maximum (132%, 9.49 mg L^{-1}) in March, at the end of the sampling program. On all sampling occasions, DO concentrations were slightly higher in the surface water layer but surface-bottom differences were negligible, supporting the evidence from the temperature profiles that the water columns were well mixed. In El Sol maximum vertical difference was 9.9% (0.61 mg L^{-1}) and the minimum 0.5% (0.11 mg L^{-1}), whereas in La Luna the maximum was 18% (0.99 mg L^{-1}) and the minimum 1.3% (0.01 mg L^{-1}). Lowest water temperatures allowed the maximum DO concentrations while the highest water temperatures were related to the minimum DO concentrations.

The mean pH in El Sol was 5.5, with a maximum of 7.0 in April and a minimum of 5.0 in February. The mean in La Luna was 4.7, with the maximum (5.6) and minimum (4.5) pH values being observed at the same time as in El Sol (April and February, respectively). The range of pH values found in El Sol and La Luna (4.5–7.0) is similar to

TABLE 1

Nutrient concentration ($\mu\text{mol L}^{-1}$) of Lakes El Sol and La Luna, Nevado de Toluca, Mexico. (DIN, dissolved inorganic nitrogen, $\text{N-NH}_4 + \text{N-NO}_2 + \text{N-NO}_3$)

Nutrient	El Sol			La Luna		
	Mean	Max	Min	Mean	Max	Min
N-NH ₄	2.89	5.95	0.98	2.79	6.71	0.82
N-NO ₂	0.20	1.15	0.03	0.05	0.20	0.02
N-NO ₃	4.70	10.26	0.08	22.61	26.11	16.47
DIN	7.60	13.48	0.94	25.63	29.85	18.05
P-PO ₄	0.20	0.50	0.01	0.13	0.83	0.01
Si-SiO ₄	2.50	8.51	0.45	0.62	5.86	0.05

those (4.9–6.0) found in the eight acid lakes studied by the MOLAR Water Chemistry Group (1999).

Specific conductivity (K_{25}) in El Sol was $16 \mu\text{S cm}^{-1}$, with a range between 15 and $18 \mu\text{S cm}^{-1}$ (second March and January, respectively). Mean K_{25} in La Luna was $14 \mu\text{S cm}^{-1}$, with a range between 13 and $15 \mu\text{S cm}^{-1}$ (second March and January, respectively). The range of K_{25} values found in El Sol and La Luna ($13\text{--}18 \mu\text{S cm}^{-1}$) is similar to those ($10.2\text{--}21.8 \mu\text{S cm}^{-1}$) found in the 11 lakes clustered into group 3 studied by the MOLAR Water Chemistry Group (1999).

El Sol and La Luna had similar N-NH₄ and P-PO₄ concentrations (Table 1). However, El Sol showed higher N-NO₂ and Si-SiO₄ (four-fold) than La Luna; conversely, La Luna had higher N-NO₃ (four-fold) than El Sol (Table 1).

CHLOROPHYLL *a* VERTICAL DISTRIBUTION

Chl *a* concentration in each lake was low but similar to that of other high-mountain lakes (Table 2). It fluctuated between 0.14 and $1.62 \mu\text{g L}^{-1}$ (mean $0.51 \mu\text{g L}^{-1}$) in El Sol, and between 0.13 and $0.89 \mu\text{g L}^{-1}$ (mean $0.33 \mu\text{g L}^{-1}$) in La Luna. The vertical distribution of Chl *a* in the two lakes was similar (Fig. 2). The surface-bottom difference was rather small ($< 0.8 \mu\text{g L}^{-1}$); accordingly, the general pattern of Chl *a* distribution could be considered homogeneous (a straight line) (Fig. 2). However, El Sol exhibited higher concentrations close to the bottom (Fig. 2a).

INTEGRATED CHLOROPHYLL *a*

Chl *a* per unit area was slightly higher in El Sol (1.91 to 8.36 mg m^{-2}) than in La Luna (1.13 and 4.80 mg m^{-2}). El Sol displayed one major and two minor phytoplankton biomass peaks (Fig. 3): the main peak (8.36 mg m^{-2}) took place in October, and the others were in May and January (4.43 mg m^{-2}). La Luna displayed a different behavior

TABLE 2

Chlorophyll *a* concentration ($\mu\text{g L}^{-1}$) reported from high mountain lakes

Lake	Region	Min	Max	Reference
La Caldera, Spain	Temperate	0.034	0.34	Martínez (1980)
El Sol, Mexico	Tropical	0.14	1.62	This study
La Luna, Mexico	Tropical	0.13	0.89	This study
Wägital, Switzerland	Temperate	0.3	2.7	Schanz et al. (2001)
Eastern Brook, USA	Temperate	1.46	2.62	Thomas et al. (1991)
Milchsee, Easter Alps	Temperate	0.1	4.6	Tait and Thaler (2000)
Austrian Alps	Temperate	0.2	10.6	Sommaruga et al. (1999)
Langsee, Easter Alps	Temperate	0.1	14.5	Tait and Thaler (2000)
Morenito, Patagonia	Temperate	Mean = 5		Queimaliños (2002)
Hagelseewli, Switzerland	Temperate	?	16	Goudsmit et al. (2000)

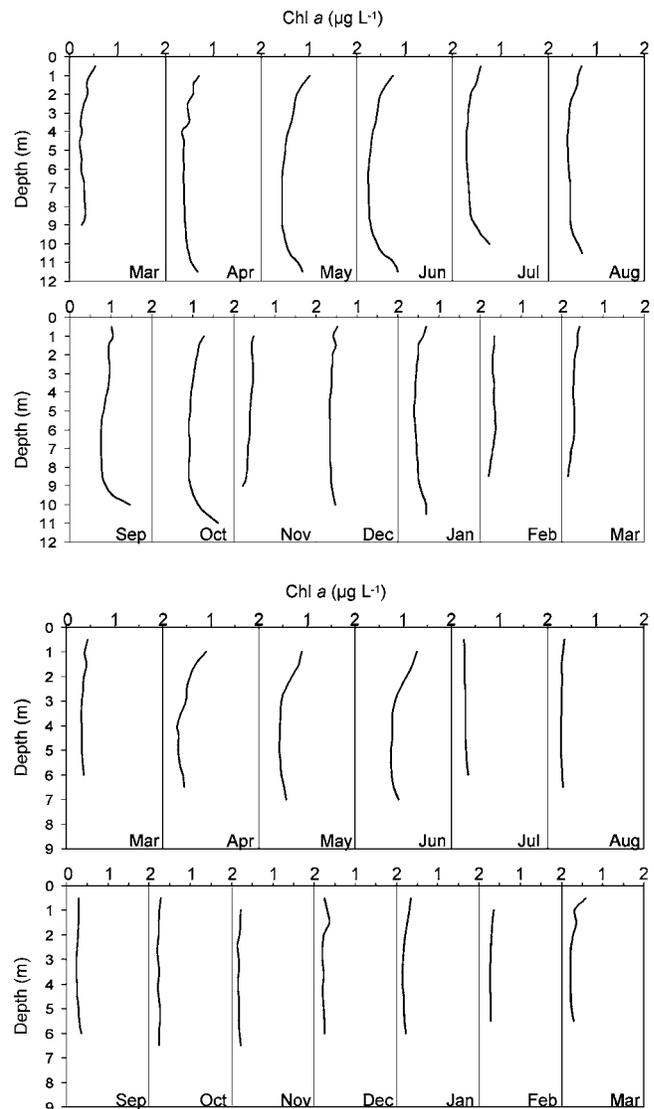


FIGURE 2. Chlorophyll *a* ($\mu\text{g L}^{-1}$) profiles of Lakes El Sol (A) and La Luna (B), Nevado de Toluca, Mexico.

with just one peak in June (4.80 mg m^{-2}); the rest of the year (July–March) phytoplankton biomass in La Luna remained low and constant ($1.13\text{--}2.14 \text{ mg m}^{-2}$).

Discussion

El Sol and La Luna are polymictic according to temperature profiles throughout the year. Löffler (1972) considers tropical high-mountain lakes to be cold polymictic. However, since neither lake had seasonal ice cover, nor each stratified at most for a few hours at a time, they fit Lewis (1983) classification of “continuous warm polymictic.” Similar cases have been found in other tropical high-mountain lakes (e.g., Ecuadorian lakes, Steinitz-Kannan et al., 1983). On the other hand, the orthograde stratification of oxygen found in El Sol and La Luna agrees with Löffler’s (1964) findings in other tropical high-mountain regions.

According to the Redfield (1958) ratio (N:P 16:1) calculated on N-NO₃/P-PO₄, both lakes seems to be P-limited (N:P > 16), La Luna (174) by far more P-limited than El Sol (23.5). The enrichment in nitrogen found in both lakes seems to be related to first, the negative correlation between pH and nitrate—low pH, high nitrates (Barbieri et al., 1999)—that combined with the presence of aluminum can

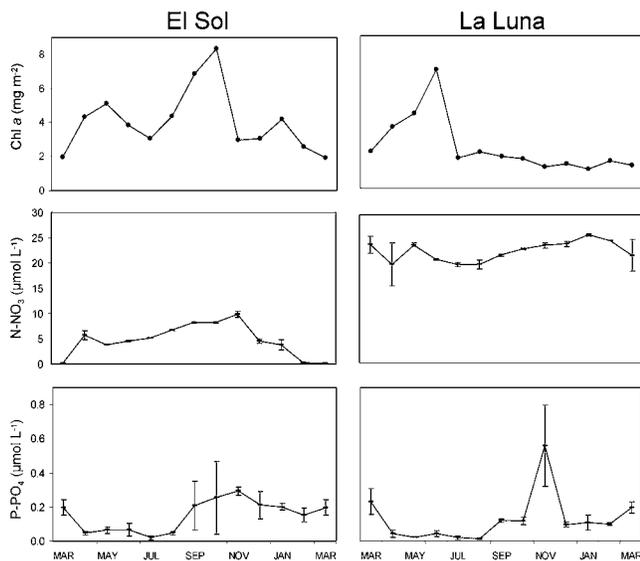


FIGURE 3. Temporal variation of chlorophyll *a* per unit area (upper), dissolved inorganic nitrogen–DIN– (center) and phosphates (bottom) of Lakes El Sol (left) and La Luna (right), Nevado de Toluca, Mexico.

partially inhibit the metabolism of algae; and second, the atmospheric deposition of nitrogen compounds as has been found in other high-mountain lakes (e.g., Catalan et al., 1994; Tait and Thaler, 2000).

Tilzer and Bindloss (1980) say that in clear polymictic lakes (i.e. $Z_{\max} < Z_{\text{eu}}$) a uniform vertical distribution of the phytoplankton (i.e. unstratified phytoplankton) might be expected; however, in most cases slight heterogeneities are observed. As mentioned before, El Sol and La Luna Chl *a* profiles showed most of the time a uniform vertical distribution of phytoplankton biomass, although slight heterogeneities were also evident on occasion.

In El Sol we found a chlorophyll maximum just above the sediment; this, along with a weak temperature gradient, is common in transparent, nonglacier-fed, high-mountain and alpine lakes (Sommaruga and Garcia-Pichel, 1999; Sommaruga et al., 1999; Winder and Spaak, 2001). This chlorophyll maximum is probably a combination of phytoplankton sunken cells and the presence of filamentous benthic algae. Cuna et al. (unpublished data) noticed the highest densities of phytoplankton located close to the bottom in addition to the presence of filamentous benthic algae (e.g., *Spyrogira*, *Zignema*, Desmidiaceae; Alcocer, 1980 unpublished report) that are probably being current-driven from the shallow littoral areas where they are plentiful.

The same should have been the case in La Luna, since the two lakes have similar characteristics. However, in La Luna the maximum near the bottom was not observed. A lower phytoplankton biomass and the absence of filamentous algae over the bottom of the lake could explain the difference.

The first phytoplankton biomass peak found between March and May–June (Fig. 3, upper) seems to be related to P-PO₄ input through snowmelt in March and its later depletion by phytoplankton uptake (Fig. 3, down). In July, both lakes displayed a decline in phytoplankton biomass probably associated to an increase in zooplankton density (Alcocer et al., unpublished data). In August–September, P-PO₄ increases again in both lakes, probably as a result of rainfall. From here on, both lakes follow a different behavior.

In El Sol the phytoplankton biomass increased to the maxima observed in October. This peak resembles Nauwerck's (1980) findings in arctic-alpine lakes where there is usually a summer phytoplankton biomass maximum. Although P-PO₄ concentration in El Sol remained relatively high, phytoplankton biomass diminished. We think this

reduction of biomass was related to zooplankton grazing since high densities of large filter feeders were observed (Alcocer et al., unpublished data). Availability of phytoplankton (October) probably promoted zooplankton increase and then the effect of large grazers depleted phytoplankton (November). However, from November along the cold months, zooplankton is drastically reduced thus allowing a new phytoplankton peak which in turn is probably limited by low temperature and light availability.

After the peak in La Luna, the phytoplankton biomass remained low. We think there are two processes that explain the low phytoplankton biomass found in La Luna: a) low pH values (pH < 5) and b) zooplankton grazing pressure.

Information regarding the effect of acidification on phytoplankton is sparse and often contradictory. Some evidence suggest phytoplankton biomass is reduced in lakes of pH about 4.5 or below, other suggest phytoplankton species diversity is reduced as a result of acidification, whereas total biomass and primary production are relatively unaffected, meanwhile other show the effect of the low pH on the phytoplankton is most clearly seen in a shift of the dominant groups (Lyden and Grahn, 1985; Findlay and Kasian, 1990; Pugnetti and Bettinetti, 1995; Havens and Carlson, 1998). However, Barbieri et al. (1999) mentioned that low pH combined with the presence of aluminum inhibit the metabolism of algae and reduce the assimilation of nitrates. This fact could also explain the high concentration of nitrates in La Luna.

On the other hand, zooplankton data (Alcocer et al., unpublished) suggest grazing pressure could be playing an important role in controlling phytoplankton biomass, particularly from July on when the zooplankton density remained steadily high. The high N-NH₄ concentration in La Luna points to a high zooplankton grazing pressure as an important control of phytoplankton biomass, and also helps to explain the prevalence of low biomass values. The last comment applies also to El Sol.

Concentrations of Chl *a* per unit area found herein (El Sol 1.91–8.36 mg m⁻², La Luna 1.13–4.80 mg m⁻²) are higher than those found in Lake La Caldera, Spain, with 0.7–1.13 mg m⁻² (Martínez, 1980) but much lower than the tropical, deep, monomictic Lake Titicaca, with 0.4–1.2 g m⁻² (Lazzaro, 1981).

Nauwerck (1980) mentioned that as lakes become more oligotrophic, the maximum biomass tends to decrease (max:min usually <30:1); this is the case of El Sol (max:min 4.4:1) and La Luna (max:min 4.3:1). However, the same author also mentions that the seasonal course of biomass in oligotrophic lakes becomes smoother; this seems not to be the case in El Sol (mean $3.85 \pm 1.87 \mu\text{g m}^{-2}$, Coefficient of variation 49%) and La Luna (mean $2.06 \pm 1.02 \mu\text{g m}^{-2}$, Coefficient of variation 50%), which showed large fluctuations.

In conclusion, in spite of their tropical situation, Lakes El Sol and La Luna resembled high-mountain lakes from temperate regions. Chl *a* concentrations found were low. The vertical distribution was homogeneous throughout the year, particularly in La Luna. El Sol tended to display a chlorophyll maximum near the bottom. La Luna showed a phytoplankton biomass maximum at the end of the spring and El Sol in the summer.

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