

Light climate and plankton in the deep chlorophyll maxima in North Patagonian Andean lakes

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*The light climate at the deep chlorophyll maxima (DCM) was analysed in a set of lakes of the North Patagonian Andean region. Apparent and inherent optical properties in relation to the chlorophyll a vertical distribution were investigated in seven lakes including deep ($Z_{max} > 90$ m) and shallow ($Z_{max} < 12$ m) ones. Sampling was carried out during the thermal stratification period (summer) of the deep lakes since in the shallower lakes no stable thermal stratification was detected. The large deep lakes presented very low diffuse attenuation coefficients of photosynthetically active radiation ($K_d PAR$), and a DCM situated at 0.98–2% of surface PAR irradiance, coinciding with the maximum abundance of the mixotrophic ciliate *Ophrydium naumanni* and autotrophic picoplankton. Both fractions seemed to be favoured by dim light conditions of particular wavelengths, since at these DCM layers mainly green and blue wavelengths prevailed (<600 nm). In contrast, shallow lakes showed higher $K_d PAR$ values, with a higher concentration of dissolved yellow substances, which caused substantial differences in the spectral quality that may have contributed to explain the absence of this ciliate population in these lakes.*

INTRODUCTION

Light is considered as one of the most important ecological factors regulating aquatic ecosystems (Kirk, 1994; Huisman and Weissing, 1995; Mur and Schreurs, 1995). In this sense, phototrophs are expected to be abundant in well-illuminated layers, although many species prefer, or are adapted to, very low light levels (Smayda, 1970; Smayda and Mitchell-Innes, 1974; Sournia, 1982a,b; Gervais *et al.*, 1997). A great number of phototrophic organisms, including small and large flagellates, coccoid and filamentous forms, and colonies, have been observed to occur in relatively deep layers conforming to depth maxima in lakes and in the sea [(Lindholm, 1992) and references therein].

The North Patagonian Andean lakes of Argentina (41°S) are included in the Araucanian Lakes district (Thomasson, 1963), comprising large deep and small shallow lakes of glacial origin. Large lakes have been described as very transparent and with very low dissolved organic carbon and nutrient concentrations (Pedrozo *et al.*, 1993; Morris *et al.*, 1995). Interestingly, a particular

assemblage of two large mixotrophic ciliate species (*Ophrydium naumanni* Pejler and *Stentor araucanus* Foissner and Wöflf) has been observed to be restricted to these ultra-oligotrophic large lakes (Modenutti, 1997; Modenutti *et al.*, 2000). In particular, high *O. naumanni* densities were the cause of a deep chlorophyll maximum (DCM) situated at levels near the lower limit of the euphotic zone in the deep Lake Moreno Oeste (Queimaliños *et al.*, 1999). On the other hand, Modenutti and Balseiro (Modenutti and Balseiro, 2002) have recently indicated that phototrophy is the primary mode of nutrition for *O. naumanni*, while phagotrophy may provide some elemental requirements. Therefore, light seems to be one of the most important factors determining the ciliate success in these ultra-oligotrophic lakes.

The aim of this study was to determine the light climate at the DCM levels of these North Patagonian lakes. In order to elucidate how light climate may influence the settlement of these DCM, we analysed the optical properties of large and small North Patagonian lakes, comparing the main light-absorbing components of these environments. As the dissolved organic carbon

concentration has been found to be higher in the shallow lakes (Modenutti, 1997; Modenutti *et al.*, 2000), it can be expected that underwater light quality would differ between deep and shallow lakes, creating, in consequence, different conditions for the development of photo-synthetic organisms.

STUDY AREA

This study was carried out in seven Andean lakes, between 40 and 42°S, included in the Nahuel Huapi National Park, Patagonia, Argentina (Figure 1). Four of the selected lakes are large (area > 5 km²) and deep ($Z_{\max} \geq 90$ m), while the other three are small (area < 1 km²) and shallow ($Z_{\max} \leq 12$ m) (Table I). The climate is temperate cool with an annual precipitation of 1500 mm and a mean annual temperature of 8.7°C (Paruelo *et al.*, 1998). The surrounding vegetation is constituted by a mixed forest of *Nothofagus dombeyi* (Mirb.) Blume and *Austrocedrus chilensis* (D. Don) Florin et Boutleje.

The large deep lakes (Nahuel Huapi, Moreno Oeste, Mascaradi Catedral and Guillermo) exhibit a warm monomictic thermal regime, with thermal stratification during late spring and summer (Quirós and Drago, 1985; Baigún and Marinone, 1995; Queimaliños *et al.*, 1999). On the contrary, the shallow lakes (Morenito, El Trébol and Escondido) do not show a stable stratification during summer months, and these lakes freeze in very hard winters (Balseiro and Modenutti, 1990; Modenutti *et al.*, 2000). Therefore, during the major part of the year, the

temperature is homogeneously distributed through the water column. As all these lakes present ultra-oligotrophic or oligotrophic conditions, the oxygen concentration is always found at saturation levels, and total phosphorus concentration fluctuates around 4–11 µg l⁻¹, in deep and shallow lakes, respectively (Modenutti *et al.*, 2000; C. P. Queimaliños, personal observation). Moreover, large deep lakes present an orthograde oxygen distribution, typical of ultra-oligotrophic lakes, while nutrients are homogeneously distributed throughout the water column (Modenutti *et al.*, 2000; C. P. Queimaliños, personal observation). However, shallow lakes show a slight increase in nutrient concentration towards the bottom, while oxygen remains at saturation levels through the water column (Díaz and Pedrozo, 1993; Balseiro *et al.*, 1997; Modenutti *et al.*, 2000).

METHOD

The lakes were sampled during the warm season (December 2000). Samples were obtained in a central sampling point located at the deepest part of each basin. All sampling was carried out in triplicates, at mid-day, 1 h before astronomic noon.

Vertical profiles of temperature, photosynthetically active radiation (PAR; 400–700 nm) and *in situ* chlorophyll (Chl) *a* distribution on the basis of the natural fluorescence were measured with a PUV 500B submersible radiometer (Biospherical Instruments). Underwater light quality was measured with the radiometer equipped with coloured glass filters. Blue and green filters were band pass filters with a maximum transmittance at 484 and 520 nm, respectively, while the red one was a high pass filter with a maximum transmittance >600 nm. Separate profiles were conducted with each filter. The measurements obtained with these filters were only used for the calculation of the diffuse attenuation coefficients for each band. Diffuse attenuation coefficients of PAR (400–700 nm) ($K_{d\text{PAR}}$) and of the three filter colours ($K_{d\text{BLUE}}$, $K_{d\text{GREEN}}$, $K_{d\text{RED}}$) for each lake were calculated by regressing log-transformed light with depth, between the surface and the depth of 1% surface PAR irradiance. Concurrently, water samples of 12 l were obtained with a Schindler–Patalas trap from 0 to 60 m at each 5 or 10 m interval in large deep lakes, and from 0 to 8 m at each 2 m in shallow lakes. Each water sample was transferred to 5 l polypropylene containers, which were kept in darkness and thermally isolated, and immediately carried to the laboratory.

At the laboratory, direct measurements of Chl *a* concentration were carried out. Chlorophyll *a* concentration was determined spectrophotometrically by extraction with hot 90% ethanol following Nusch (Nusch, 1980). Corrections for phaeophytin were performed by

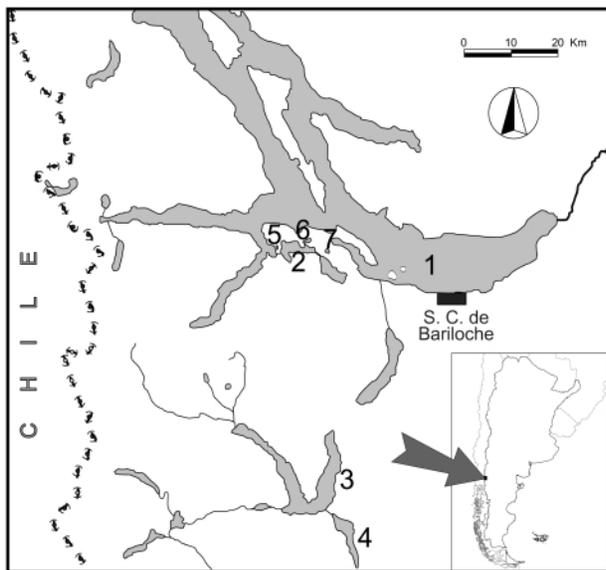


Fig. 1. Geographical location of the seven studied lakes. 1, Lake Nahuel Huapi; 2, Lake Moreno Oeste; 3, Lake Mascaradi Catedral; 4, Lake Guillermo; 5, Lake Escondido; 6, Lake Morenito; 7, Lake El Trébol.

Table I: Morphometric and optical characteristics of the seven studied lakes

Lakes	Area (km ²)	Z _{max} (m)	K _d PAR (m ⁻¹)	K _d BLUE (m ⁻¹)	K _d GREEN (m ⁻¹)	K _d RED (m ⁻¹)	Z _{1% PAR} (m)
<i>Deep lakes</i>							
Nahuel Huapi	557.00	464	0.090 (± 0.001)	0.096 (± 0.001)	0.090 (± 0.001)	0.141 (± 0.001)	51.0
Moreno Oeste	5.22	90	0.126 (± 0.001)	0.158 (± 0.002)	0.142 (± 0.001)	0.220 (± 0.001)	36.4
Mascardi Catedral	39.20	218	0.169 (± 0.001)	0.189 (± 0.002)	0.168 (± 0.002)	0.221 (± 0.002)	27.2
Guillermo	5.40	107	0.157 (± 0.001)	0.173 (± 0.001)	0.150 (± 0.002)	0.201 (± 0.001)	29.3
<i>Shallow lakes</i>							
Morenito	0.83	12	0.424 (± 0.002)	0.592 (± 0.002)	0.400 (± 0.003)	0.533 (± 0.002)	10.8
El Trébol	0.30	12	0.322 (± 0.004)	n.a.	n.a.	n.a.	14.3
Escondido	0.08	8	0.592 (± 0.005)	0.739 (± 0.003)	0.599 (± 0.001)	0.620 (± 0.002)	7.7

Values are given as average ± SE. n.a., data not available.

acidification with HCl. The estimates of the *in situ* Chl profiles from the radiometer were adjusted to these direct determinations. The upper 5 m of the *in situ* measurements in the deep lakes were not considered as these readings could not be trusted near the surface (Kiefer *et al.*, 1989).

Absorption measurements of the major light-absorbing components were carried out on each water sample (each depth of every lake), within 2 h after sampling. Optical densities were measured with a Metrolab 1700 spectrophotometer in the spectral range of 400–750 nm at 5–10 nm intervals. Dissolved yellow substances (gilvin substances) (Kirk, 1994) were operationally defined as components of the fraction that passed through 0.22 µm Millipore filters (Kirk, 1976). The absorption spectrum of this material was measured in glass cuvettes (0.1 m path length) against a distilled water blank. The true *in situ* absorption coefficients due to yellow substances [$a_g(\lambda)$; units m⁻¹] were obtained by converting the measured values of base 10 to base e logarithms following Kirk (Kirk, 1994). Absorbance at 750 nm, where absorption can be considered negligible, was assumed to be due to residual scattering in the filtrate, and was subtracted from the absorbance values at all other wavelengths in order to calculate $a_g(\lambda)$ after Shooter *et al.* (Shooter *et al.*, 1998). As the dissolved organic carbon mostly absorbs in the blue region of the spectrum, $a_g(440)$ is considered a suitable parameter to indicate its concentration.

The absorption spectra of particulate matter [$a_p(\lambda)$] were measured by the filter pad technique using GF/F filters (Trüper and Yentsch, 1967). Two or three litres of lake water were filtered, and optical densities were measured directly on the wet filters against a blank of a clean filter wet on distilled water. The path length amplification factor (β factor) was determined according to Mitchell and Kiefer (Mitchell and Kiefer, 1988a) and Bricaud and Stramski (Bricaud and Stramski, 1990). During the scan, the wetness of the filters remained unchanged. The absorption at 750 nm was also considered negligible (Bricaud and Stramski, 1990).

After measurement of the absorption spectra of total particulate matter, the spectral absorption by non-algal material [$a_d(\lambda)$] was measured separately following the method of Kishino *et al.* (Kishino *et al.*, 1985). In this case, the GF/F filter was placed in absolute methanol at 4°C for 45–60 min in order to extract pigments. The bleached filter was dried and then soaked again in filtered lake water for 1 h. The same treatment was applied in parallel to a reference filter as blank.

The absorption coefficients of viable phytoplankton, $a_{ph}(\lambda)$, were obtained by subtracting the absorption by the bleached matter, $a_d(\lambda)$, from the absorption by total particulate matter, $a_p(\lambda)$. Finally, these coefficients were converted into Chl-specific coefficients [$a_{ph}^*(\lambda)$], by dividing them by the Chl *a* concentration (Bricaud and Stramski, 1990), previously determined by the extraction method.

The value of the water spectrum [$a_w(\lambda)$] was taken from Morel and Prieur (Morel and Prieur, 1977).

In order to determine phytoplanktonic and *O. naumanni* abundances, 250 ml of the lake water at each depth were fixed with acid Lugol solution. Phytoplankton and *Ophrydium* abundances were quantified with an inverted microscope following the Utermöhl technique (Utermöhl, 1958), in 50 ml chambers. The limit between nano- and netphytoplankton was considered as 20 μm GALD (greatest axial linear dimension).

In the case of lakes Moreno, Guillelmo and Morenito, samples for autotrophic picoplankton (APP) enumeration were also obtained. Samples of 60 ml were fixed with formaldehyde–cacodylate and stored in darkness and refrigerated. Counting of 3 ml subsamples was performed within 2 weeks of sampling on black membrane filters (Poretics; 0.2 μm pore size) at $\times 1000$ magnification in an Olympus BX50 epifluorescence microscope under blue light (U-MWB filter).

RESULTS

The large deep lakes exhibited a thermal stratification with mixed layers up to 32 m depth (Figure 2a), while the shallow ones were not thermally stratified (Figure 2b). Surface PAR irradiance measured during the study ranged from 900 to 1500 $\mu\text{E m}^{-2} \text{s}^{-1}$ in all the lakes (Figure 2a and b). Diffuse attenuation coefficients (K_d) showed a great variation between lakes (Table I), with very low values in large deep ones and higher values in the shallow lakes. Waters in the large deep lakes were extremely transparent: euphotic zones, defined as the depth of 1% surface PAR, ranged from 27 to 51 m. The depth of the euphotic zone was deeper than the mixed layer; as a consequence, a particular scenario can be delimited between the lower boundary of the mixing layer and the depth of the 1% of surface PAR irradiance (Figure 2a, shaded areas). These layers received 0.98 and 2% of the photosynthetically available surface irradiance and DCM were observed to develop (Figure 3a, shaded areas).

In the lakes Moreno Oeste, Mascardi Catedral and Guillelmo, these DCM were dominated by the mixotrophic ciliate, which presented abundances ranging between 6 and 8 individuals ml^{-1} , representing 1500–2000 symbiotic *Chlorella* cells ml^{-1} (Figure 3a), since each ciliate holds 250 *Chlorella* on average (Queimaliños *et al.*, 1999). Unfortunately, there are no available data about the constitution of the observed DCM in Lake Nahuel Huapi. Autotrophic picoplankton exhibited a very low density in the two sampled deep lakes (Figure 3a), and also showed a clear coincidence with *O. naumanni* vertical distribution, indicating that this fraction also contributed

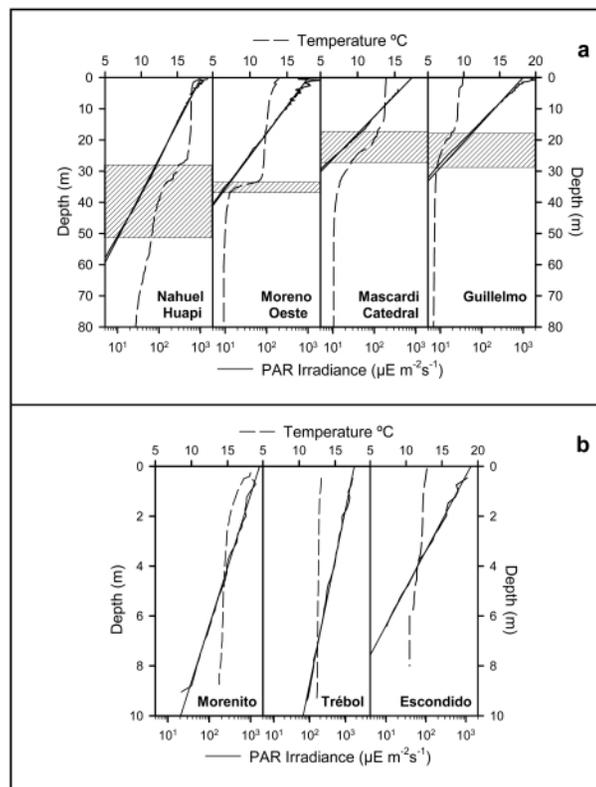


Fig. 2. Temperature and light vertical profiles of (a) large deep lakes and (b) small shallow lakes. The shaded areas are defined by the lower boundary of the mixing layer and the depth of 1% of surface PAR irradiance.

to the observed DCM. In terms of biovolume, the contribution of *Chlorella* (5 μm in diameter) inside the ciliates reached 131 $\text{mm}^3 \text{m}^{-3}$, this biomass representing 3-fold that of APP (1 μm in diameter). On the other hand, phytoplankton did not contribute substantially to this DCM in terms of cell abundance, since the nanoplanktonic fraction showed an even distribution around 200–300 cells ml^{-1} along the water column (Figure 4a) and the netphytoplankton fraction presented a slightly heterogeneous vertical distribution, reaching 50 cells ml^{-1} (Figure 4a).

On the contrary, the shallow lakes did not present such vertical heterogeneity in the Chl *a* distribution (Figure 3b) and the mixotrophic ciliate *O. naumanni* was not present. Autotrophic picoplankton abundances were higher in Lake Morenito than in the deep lakes and no differential distribution in the water column was detected (Figure 3b). In addition, both phytoplanktonic fractions were homogeneously distributed throughout the water column (Figure 4b).

Mean absorption spectra of the light-absorbing components showed clear differences in relation to both lake

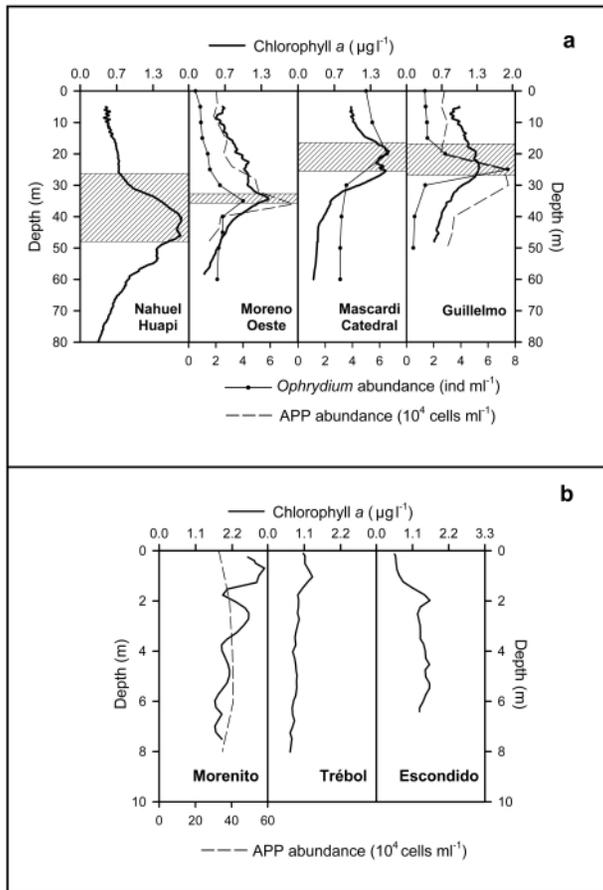


Fig. 3. (a) Chlorophyll *a*, *O. naumanni* and autotrophic picoplankton (APP) abundances in the large deep lakes (shaded areas as in Figure 2). (b) Chlorophyll *a* and APP abundance in the small shallow lakes.

types. The large deep lakes presented the maximum absorption values at the red end of the spectra (Figure 5a), and in these systems the contribution of water itself [$a_w(\lambda)$] at longer wavelengths was large. At short wavelengths, the absorption values were low and were caused by both dissolved yellow material (a_g) and particulate matter (a_p), with values of $a_g(440)$ ranging from 0.06 to 0.13 m^{-1} , and $a_p(440)$ varying between 0.06 and 0.09 m^{-1} (Figure 5a). Following the classification of Kirk (Kirk, 1980, 1994), the large deep lakes Moreno Oeste, Mascardi Catedral and Guillermo belong to Type W.

On the contrary, in shallow lakes, the maximum absorption values were high and were obtained in the violet–blue end of the spectra (Figure 5b). In these waters, the contribution of $a_g(\lambda)$ at lower wavelengths was large, with mean $a_g(440)$ ranging from 0.27 to 1.96 m^{-1} , values that were considerably higher than those obtained for large deep lakes; in addition, mean $a_p(440)$ varied between 0.19 and 0.21 m^{-1} (Figure 5b).

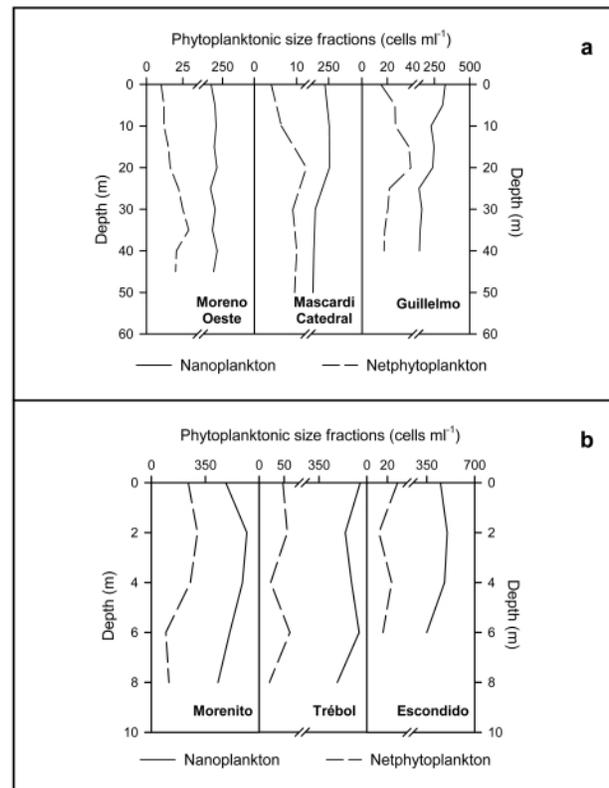


Fig. 4. Nanoplankton and netphytoplankton abundances in (a) large deep lakes and (b) small shallow lakes.

Considering the highly different absorption coefficients obtained at short wavelengths in the different kinds of lake, the availability of blue light in deep waters of the large lakes was noticeably higher than in shallow ones. In this sense, the different K_d obtained with colour filters revealed that at the DCM levels the green and blue wavelengths of the spectrum prevailed (Table I).

The specific absorption coefficients of living phytoplankton in the six lakes showed the two major peaks at 440 and 680 nm, corresponding to the Chl *a* absorbance (Figure 6a and b). The mean values of the water column corresponding to $a_{ph}^*(440)$ and $a_{ph}^*(680)$ ranged from 0.030 to 0.045 $\text{m}^2 (\text{mg Chl } a)^{-1}$ and from 0.010 to 0.019 $\text{m}^2 (\text{mg Chl } a)^{-1}$, respectively, in all lakes (Figure 6a and b). In the large deep lakes (Moreno Oeste, Mascardi Catedral and Guillermo), specific absorption values showed a discontinuity between mixed layers and deep ones, decreasing from the surface to the deep levels (Figure 6a). The pattern obtained indicated that changes in pigment concentration occurred, as was observed at the DCM levels. In opposition, it was very clear that the $a_{ph}^*(440)$ values obtained for the shallow lakes did not present a systematic decrease with increasing depth (Figure 6b).

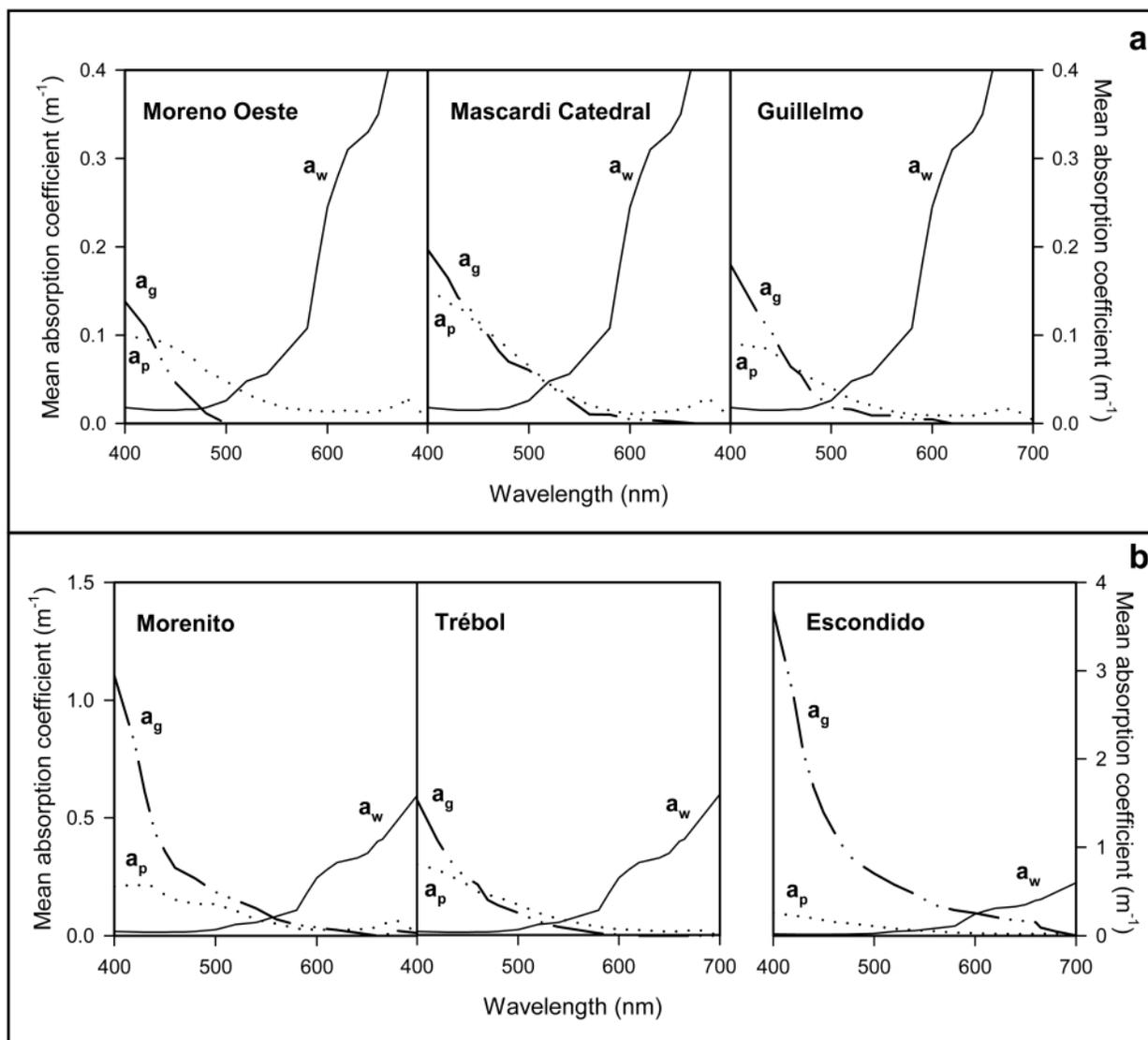


Fig. 5. Absorption coefficients of the main light-absorbing components as a function of wavelength. (a) Large deep lakes and (b) small shallow lakes. In all cases, the absorption spectra were outlined as the average of the whole water column values. a_g , gilvin substances; a_p , particulate matter; a_w , water.

DISCUSSION

The present analysis shows that the light climate is clearly different in Andean deep and shallow lakes, inducing different light availability for photosynthetic activity and for the settlement of a DCM. The pattern of mean specific absorption coefficients obtained in the deep lakes can be associated with the package effect concept (Morel and Bricaud, 1981), described in the Sargasso Sea and in the northeastern Pacific Ocean (Mitchell and Kiefer, 1988b; Bricaud and Stramski, 1990). This effect predicts that the absorption spectrum is ‘flattened’ due to increasing cell or colony size, or pigment concentration (Morel

and Bricaud, 1981), and this situation is due to the observed DCM in the deepest euphotic layers of Andean deep lakes. In other freshwater ecosystems, a similar deep layer with high Chl *a* concentration has also been observed (Larson, 1972; Fee, 1976; Priscu and Goldman, 1983; Coon *et al.*, 1987).

The DCM observed in the present study received 0.98 and 2% of the photosynthetically available surface irradiance and coincided with the distribution of the mixotrophic ciliate *O. naumanni* as well as with APP. The dim light condition probably favours the settlement of this particular DCM, constituted by a symbiotic consortium and the APP, its main prey (Modenutti and Balseiro, 2002).

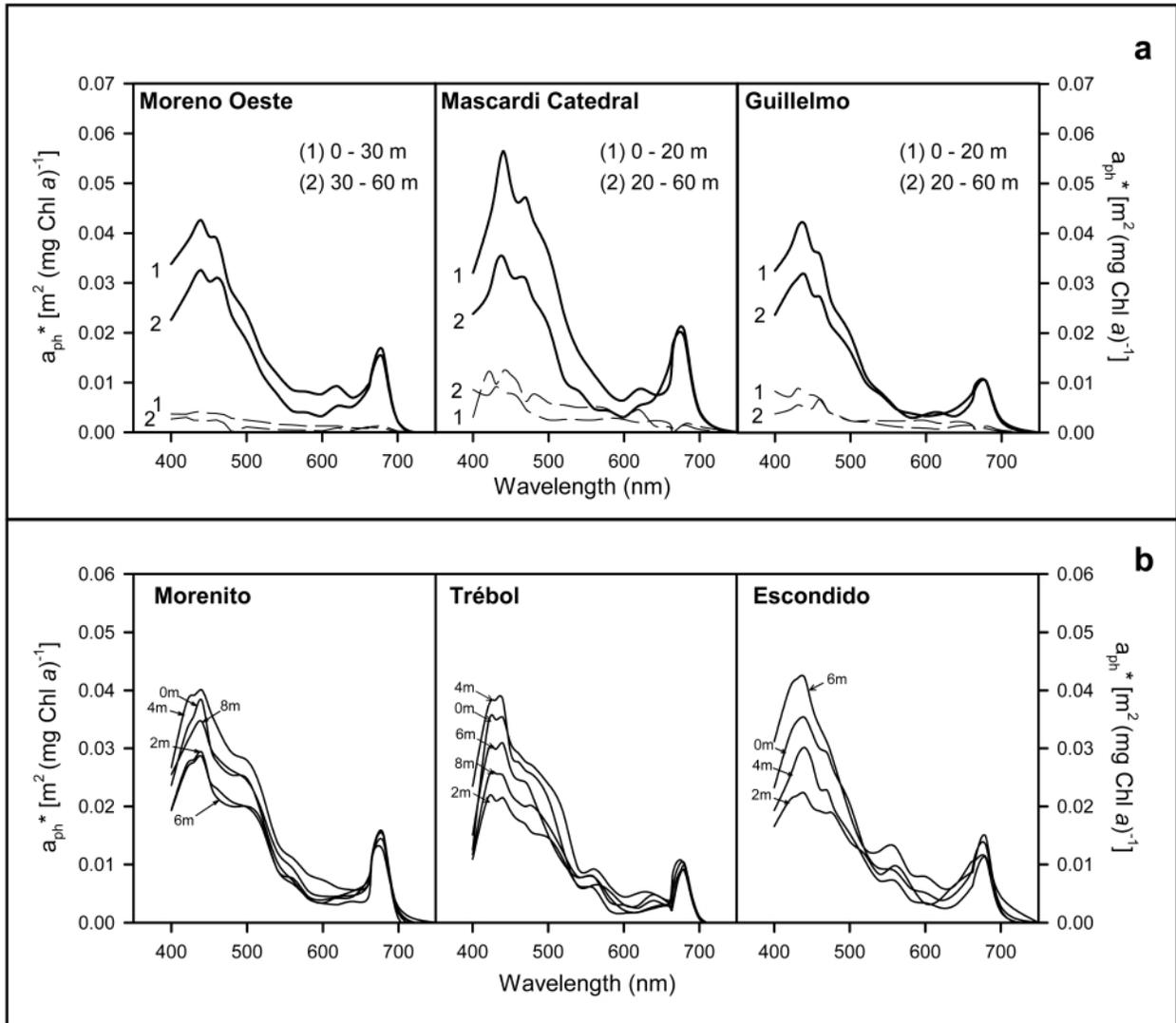


Fig. 6. (a) Mean specific absorption coefficients (solid line) for large deep lakes computed as the average of surface mixed layers (0 to 20 or 30 m) and deeper levels (20 or 30 to 60 m); standard errors (dashed line). (b) Specific absorption coefficients obtained for small shallow lakes.

Phototrophy is the primary mode of nutrition for *O. naumanni* (Modenutti and Balseiro, 2002) and its autotrophic capability lies in a high population of endosymbiotic *Chlorella*, with 250 cells per ciliate on average (Modenutti, 1988; Queimaliños *et al.*, 1999). Therefore, it appears that in this case the light requirements of the mixotrophic ciliate follow essentially those of the endosymbiotic algae. In that sense, in light-limited experiments, *Chlorella* was found to be a great competitor for light, displacing other phototrophic species (Huisman, 1999; Huisman *et al.*, 1999). Thus, *Chlorella* seems to have a clear competitive ability under such poor light.

Following Kirk's optical classification (Kirk, 1980, 1994), our large deep lakes that presented this particular DCM can be considered Type W, in which water itself is

the major light-absorbing component. This situation provokes a higher availability of the green and blue light at the DCM level, which receives almost exclusively wavelengths <600 nm (Table I). In contrast, the spectral quality of underwater light of our shallow lakes, though transparent, was affected by a relatively higher concentration of dissolved yellow substances. Thus, the spectrum at 1% of surface irradiance is not composed only by wavelengths <600 nm, but also by the red end of the spectrum (Table I). The absorption of light by these dissolved compounds may cause direct competition with phytoplankton for capture of available light energy (Kirk, 1976, 1980; Yentsch, 1980). Therefore, it can be expected that the absence of *O. naumanni* in the shallow lakes would be related to light quality, although the transparency would

be enough for the population settlement. However, differences in turbulence intensity may also be another factor in the absence of *O. naumanni* in small lakes.

The importance of light quality for picocyanobacteria has been shown in early studies (Pick, 1991), and these organisms have been observed to be adapted to 1% PAR irradiance (Gervais *et al.*, 1997). In addition, Callieri (Callieri, 1996) indicated a clear relationship between picocyanobacterial types and the extinction coefficient of red, green and blue light. In this sense, phycoerythrin-rich cells are present in the very clear, oligotrophic lakes, whereas in shallow eutrophic lakes, phycocyanin-rich cells dominate (Callieri, 1996). Unfortunately, we do not have data about the phycobiliprotein type of picocyanobacteria in Andean deep and shallow lakes; nevertheless, a similar pattern to those described in the Northern Hemisphere can be expected.

In the large deep lakes, the entire apparent and inherent optical properties produced extended euphotic zones and low values of spectral absorption coefficients, comparable with those obtained in low productive marine coastal waters (Kishino *et al.*, 1984; Kirk, 1994). These conditions brought out deep layers with green and blue light as the major wavelengths of the spectrum, which might favour the existence of this particular DCM.

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