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Freshwater Phytoplankton of Argentina

# Optical characterization of Argentinean lakes, from deep Andean lakes to shallow Pampean ones

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With 8 figures and 5 tables

**Abstract:** The purpose of this article is to aboard phytoplankton community as an optically active particulate component of water systems. Mayor concepts of hydrologic optics such as water components and processes that determine the nature of underwater light field were briefly revised. A detailed optical characterization of several contrasting Argentinean lakes is presented. From large deep oligotrophic Andean lakes to very shallow eutrophic Pampean lakes, I describe these aquatic systems using bio-optical properties (i.e., inherent and apparent optical properties) together with optically active substances (i.e., TSS, DOC and Chl *a*). Spatial variability of optically active substances and their optical properties were used to confront different group of lakes. Finally, throughout the study of phytoplankton absorption coefficients, acclimation and adaptation processes in contrasting lakes were revised.

**Keywords:** Phytoplankton, optical characterization, lakes, shallow lakes, phytoplankton absorption coefficients

## Introduction

Almost half of all the photosynthetic activity on Earth occurs in the aquatic environment (Falkowski & Raven 1997). Within aquatic ecosystems, phytoplankton is the photoautotrophic part of the plankton and a major primary producer of organic carbon in the pelagic of the seas and inland waters (Reynolds 2006). There are only a handful of biological mechanisms extant for the reduction of inorganic carbon, being photosynthesis the most important one. This process is the biological conversion of light energy to chemical bound energy that is stored in the form of organic carbon compounds. These compounds contain biologically usable energy and also supply the elements to build complex organic molecules. The cumulative energy fixation in carbon compounds by phytoplankton is one of the most important basis for the majority of oceanic and inland waters food webs and significant contributes

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**Table 1.** Abbreviations of terms and variables used in the text.

| NOTATION | |
|---|---|
| $\boldsymbol{a}_g(\lambda)$ and $\boldsymbol{a}_w(\lambda)$ | Spectral absorption coefficients of chromophoric dissolved organic matter and pure water ($m^{-1}$) |
| $\boldsymbol{a}_p(\lambda)$, $\boldsymbol{a}_d(\lambda)$ and $\boldsymbol{a}_{ph}(\lambda)$ | Spectral absorption coefficients of total particulate matter, non algal matter and phytoplankton ($m^{-1}$) |
| $\boldsymbol{a}_{ph}{}^{*}(\lambda)$ | Spectral T-Chl *a* specific phytoplankton absorption coefficients ($m^2$ mg T-Chl $a^{-1}$) |
| $\boldsymbol{a}_{p\ d\ ph\ w}$ (PAR) | Numerical mean absorption coefficient for PAR ($m^{-1}$) |
| AOPs | Apparent Optical Properties |
| $\boldsymbol{a}_t(\lambda)$ | Spectral total absorption coefficient ($m^{-1}$) |
| $\boldsymbol{b}(\lambda)$ | Spectral scattering coefficient ($m^{-1}$) |
| $\beta(\lambda)$ | Pathlength amplification factor |
| CDOM | Chromophoric Dissolved Organic Matter |
| DOC | Dissolved organic carbon (mg $L^{-1}$) |
| IOPs | Inherent Optical Properties |
| $I_{z\ mean}$ | Mean irradiance in the water column (W $m^{-2}$) |
| *K*d (PAR) | Vertical diffuse attenuation coefficient for PAR ($m^{-1}$) |
| $K\mathrm{d}_{(av)}$ (PAR) | Modeled vertical attenuation coefficient assuming total absorption and water scattering ($m^{-1}$) |
| $\lambda$ | Wavelength (nm) |
| OASs | Optically Active Substances |
| OPs | Optical Properties (i.e. apparent and inherent) |
| PAR | Photosynthetic Active Radiation |
| *S*d | Secchi disk (m) |
| T-Chl *a* | Total chlorophyll *a* concentration (Chl *a* + phaeophytin *a*) (µg $L^{-1}$) |
| $\boldsymbol{T}_n$ | Nephelometric turbidity (NTU) |
| TSS | Total suspended solids (mg $L^{-1}$) |
| $Z_{eu}$ | Depth of the euphotic zone (m) |
| *Z* | Water column depth (m) |

with the global biological economy of Earth that is based on the chemistry of carbon. In this sense, the study of phytoplankton has a central importance from an ecological and economic point of view.

In the present article I will address the study of freshwater phytoplankton through their optical properties. Phytoplankton, as a fraction of suspended particulate matter, is one of the optical active substance (OASs) present in aquatic ecosystems. OASs are materials (dissolved and particulate) that absorb and scatter light, i.e. chromophoric dissolved organic matter (CDOM) (commonly estimated as DOC concentration), tripton (inanimate particulate matter), particulate detritus, heterotrophic microorganisms and phytoplankton (commonly estimated as chlorophyll *a* concentration). See Table 1 for a list of symbols, units and definitions. These optical active constituents have inherent optical properties (IOPs) that are determined by the concentration of the different contents of water and by their specific features. IOPs (i.e., absorption and scattering) are additive and linear obeying Lambert-Beer Law, and are significant determining apparent optical properties (AOPs). AOPs (i.e., diffuse attenuation coefficient and reflectance) do not only depend upon absorption and scattering processes, but also are determined by ambient light field (i.e., solar zenith angle, cloud cover, or atmospheric aerosol content) (Preisendorfer 1961).

There are marked differences in the concentrations of optically active substances, their inherent optical properties and therefore their relative contributions to underwater light propagation among water environments. For instance, CDOM concentration and their absorption properties have been observed to strongly govern the UV and PAR attenuation in some lakes (Morris et al. 1995, Bukaveckas & Robbins-Forbes 2000, Belzile et al. 2002). In oceans and in clear oligotrophic lakes with low DOC concentration, phytoplankton and their derivative products are optically dominant (waters classified as Case 1) (Morel & Prieur 1977, Sommaruga & Psenner 1997, LaPerriere & Edmundson 2000). On the other hand, in optically complex waters (i.e. coastal waters, estuaries and lakes) a mixture of OASs, rather than phytoplankton alone, actively absorbs and scatters light (waters classified as Case 2). In optically complex waters, non-algal suspended solids originated from external inflows and wave-induced sediment resuspension could become major factors determining optical properties, and may cause light limitation of phytoplankton production and biomass (Malone 1977, Cloern 1987, V.-Balogh et al. 2009). Particularly, in some lakes and rivers, concentrations of OAS may be so high that they exceed the limits of classifications based on field data from the seas and oceans (Reinart et al. 2003, Reinart & Valdmets 2007). In addition, lakes deserve special attention because of the high temporal and spatial variability of their water properties. OASs concentrations and related optical properties can widely differ within a single lake and between lakes (e. g. Kirk 1980, Nolen et al. 1985, Paavel et al. 2008, Pérez et al. 2002, Reinart et al. 2004).

The wide variability in OASs concentration and optical properties observed in lakes greatly complicates the mathematical analysis of radiative transfer and the building of numerical models (Gallegos 1990, Reinart et al. 2003, Reinart et al. 2004). In estuaries and turbid lakes, generally, the lack of a theoretical framework has led to reliance on empirical regressions between measured optical properties and water-quality parameters (i.e., Pierce et al. 1986, Gallegos et al. 2005). In addition, algorithms that retrieve pigment concentrations from optical properties should give global application in Case 1 waters. However, the use of site-specific or regional algorithms relating IOPs to AOPs and water quality constituents has been reported to be necessary in optically complex waters (Morris et al. 1995, Raaj et al. 2008, Reinart et al. 2003, Xu & Chao 2005).

In this article, I present a detailed optical characterization of several contrasting Argentinean lakes attempting to describe the important gradient of optical properties that could be observed in inland waters. From large deep oligotrophic Andean lakes to very shallow eutrophic Pampean lakes, I describe these aquatic systems using inherent and apparent optical properties together with measurements of OASs concentration.

The aims of this article are: (i) to describe the spatial variability of optical active substances between lakes (ii) to confront the obtained relationship between OASs, IOPs and

AOPs within different group of lakes (iii) to describe and analyze the variability in phytoplankton and chlorophyll specific phytoplankton absorption spectra in different groups of lakes.

## Studied lakes

This study presents a compilation of optical and limnological data set of lakes corresponding to two contrasting geographic areas of Argentina. This group of lakes was selected to encompass a wide range of trophic, chemical and biologic conditions.

One group of lakes is located in the Pampa Plain (35°32'S – 36°48'S and 57°47'W – 58°07'W, lay at < 20 m a.s.l.), Buenos Aires province, situated in the Warm Temperate Region (Fig. 1a). These lakes were sampled in several surveys carried out from 2006 to 2008. Pampean lakes present high levels of nutrients (Quirós & Drago 1999) and their ionic composition is dominated by sodium-bicarbonate (Fernández Cirelli & Miretzky 2002). These lakes are shallow ($Z_{max} < 5$ m), typically polymictic and present different states (clear vegetated or turbid states). The climate of the region is temperate, being the mean annual temperature of about 15.3°C and winds having a mean annual speed of 10.1 km $h^{-1}$ (Torremorell et al. 2007). The region presents a mean annual precipitation of about 935 mm, but with marked annual variability between wet and dry periods (Sierra et al. 1994).

The second group of lakes is located in the North Andean Patagonian region (40°27´ and 42°49´S, lay between 202 and 826 m a.s.l.) (Fig. 1b) corresponding to the Glacial lakes district of the Southern Andes (Iriondo 1989). Patagonian lakes were sampled in two surveys, one during 2002 and during 2006. In addition, literature data reported by Morris et al. (1995) were utilized to complete limnological and optical data for Patagonian lakes. The climate of this region is temperate cool with a mean annual temperature of 8.7°C, predominance of westerly winds, and annual precipitation of 1500 mm (Paruelo et al. 1998). The sampled area is included within three National Parks: Nahuel Huapi, Puelo and Los Alerces, and it is characterised by a profuse hydrographic system including large deep monomictic lakes (area > 5 $km^2$; $Z_{max} > 100$ m) and small shallow lakes (area < 1 $km^2$; $Z_{max} \leq 12$ m), the last ones without a stable stratification during summer months.

## Optical characteristics analyzed

The following inherent optical properties (IOPs) (i.e., absorption coefficients and nephelometric turbidity), as well as apparent optical propertied (AOPs) (i.e., downward irradiance and vertical light attenuation), were assessed in this article. The absorbance of chromophoric dissolved organic matter (CDOM), ag(λ), was determined by measuring the absorbance of filtered (0.22 μm) water samples from 380 to 750 nm (Kirk 1994a, Shooter et al. 1998). Particulate absorption coefficients, ap (λ), were determined using the filter-pad technique (Trüper & Yentsch 1967) on the material collected onto GF/F filters. Absorption coefficients were estimated according to Mitchell & Kiefer (1988) and the amplification factor vector, β (λ), was calculated according to Bricaud & Stramski (1990). Within the particulate fraction, we further distinguished between (i) the absorption due to phytoplankton absorption, $\boldsymbol{a}_{ph}$ (λ)

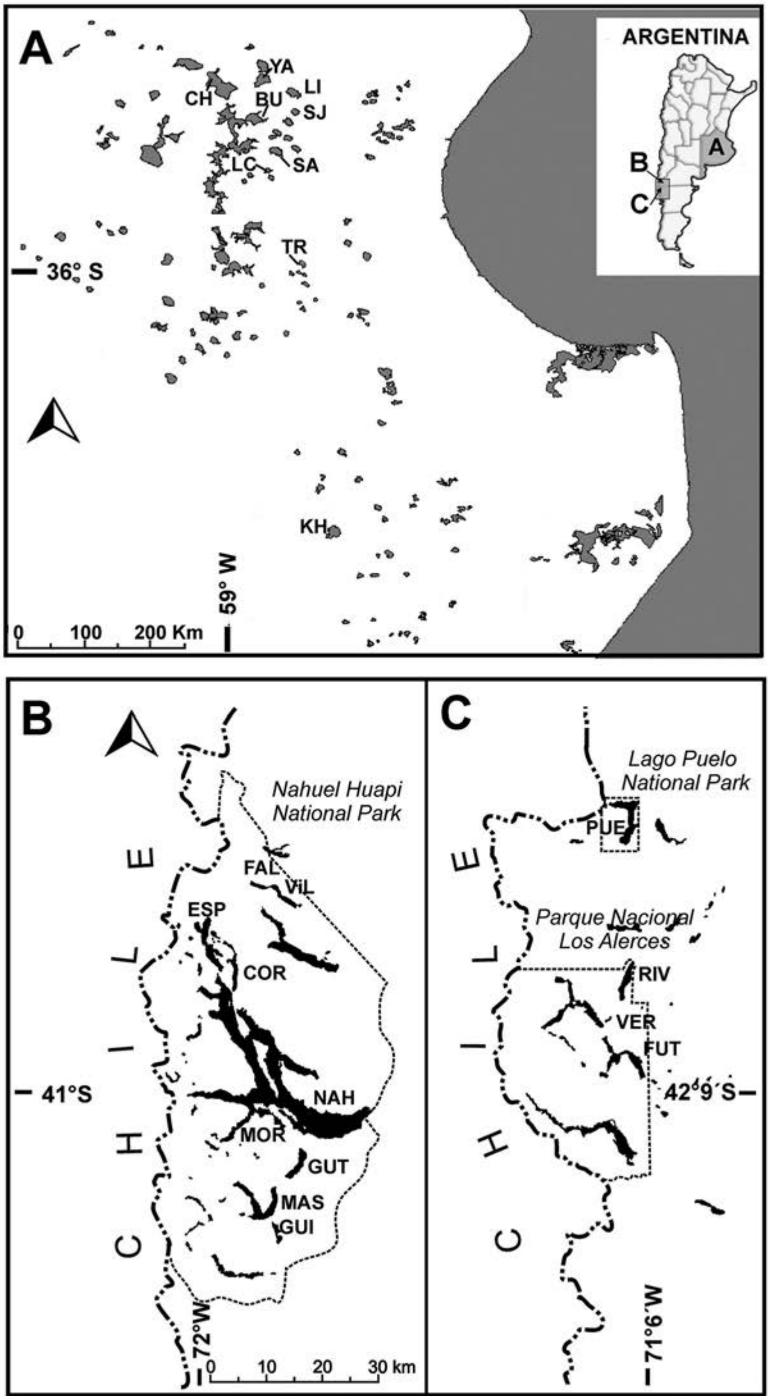

**Fig. 1**. Location of studied Argentinean lakes in: (a) Pampean lakes, and (b) Patagonian lakes.

and (ii) the absorption due nonliving organic particles, inorganic particles and heterotrophic microorganisms [hereinafter, non-pigmented absorption, $\boldsymbol{a}_{\mathrm{d}}$ (λ)]. Non-pigmented absorption was estimated by Kishino´s method (Kishino et al. 1985); based on absorbance measurements performed after pigments extraction in absolute methanol. Total absorption coefficients, $\boldsymbol{a}_{\mathrm{t}}$ (λ), were estimated as the sum of the absorption coefficients by particulates, dissolved matter and pure water (Kirk 1994a). Chlorophyll *a* specific phytoplankton absorption coefficients, $\boldsymbol{a}_{\mathrm{ph}}*$ (λ), were estimated as the quotient between $\boldsymbol{a}_{\mathrm{ph}}$ (λ) and Chl *a*. The broadband absorption coefficients $\boldsymbol{a}_{\mathrm{i}}$ (PAR), where calculated as arithmetic averages between 400–700 nm (the Photosynthetic Active Radiation, range). The contribution (in percent) of each fraction to total absorption spectrum was estimated following Zhang et al. (2007). Nephelometric turbidity , $\boldsymbol{T}_{\mathrm{n},}$ as a proxy for scattering, was measured using a. SCUFA (Turner®) submersible turbidimeter referenced to a bench-top 2100P (Hach®) turbidimeter. Data of $\boldsymbol{T}_{\mathrm{n}}$ were only available for Pampean lakes and for some shallow Patagonian lakes.

In Pampean lakes, downward irradiance vertical profiles were performed using a USB2000 (Ocean Optics) spectroradiometer. The measurements were performed around noon inside a black plastic container (50 x 50 x 40 cm) filled with freshly collected lake water (Torremorell et al. 2009, Pérez et al. 2011). Particularly, in Patagonian lakes downward irradiance was measured using a PUV 500B submersible radiometer (Biospherical Instruments). Vertical diffuse attenuation coefficients for PAR, *K*d (PAR), were determined following (Kirk 1994a). Additionally, a complete data set of *K*d (PAR) values for Patagonian lakes were also obtained from (Morris et al. 1995). The depth of the photic layer ($Z_{\mathrm{eu}}$) was calculated as 4.6/*K*d (PAR).

To examine the relative contribution of scattering and absorption by the dissolved and particulate fractions to light attenuation, the relationship obtained by Kirk (Kirk 1984, 1994b) was used to model $K\mathrm{d}_{\ (\mathrm{av})}$ (PAR); the vertical diffuse attenuation coefficient assuming the absorption by particulate plus CDOM and only the scattering by water itself [$\boldsymbol{b}_{\mathrm{w}}$ (PAR)]. The relative contribution of total absorption and scattering was calculated by computing the ratio between measured *K*d (PAR) and the calculated $K\mathrm{d}_{\ (\mathrm{av})}$ (PAR).

Among optical active substances (OASs), total suspended solids concentration (TSS) was determined accordingly APHA (1998). Dissolved organic matter (DOC) was measured on filtered water samples using the high temperature Pt catalyst oxidation method (Shimadzu TOC-5000) following Sharp et al. (1993). Chlorophyll *a* concentration (Chl *a*) was measured by ion pairing reverse-phase HPLC. The method applied has been described in detail by Laurion et al. (2002), modified from Mantoura & Llewellyn (1983). For pigment identification and quantification we used standard from Sigma Inc. (Buchs, Switzerland). Particularly for some Patagonian lakes, a complete data set of OASs was taken from Morris et al. (1995).

## Optical active substances (OASs)

Complete data sets of OASs from studied Argentinean lakes were taken from Morris et al. (1995), Pérez et al. (2010) and G. Pérez (unpubl. data). Descriptive statistics of OASs are shown in Table 2.

In Pampean lakes, two groups clearly differed in OASs contents (i.e., Turbid vs. Clear Vegetated lakes) (Table 2, Fig. 2). Note that in Fig. 2, Chl *a* contribution was multiplied by $10^{\ 3}$ for comparative purposes. Turbid lakes were characterized by high concentration of

**Table 2**. Descriptive statistics of Optically Active Substances (OASs).

| OASs | Mean ± SD | Min. | Max. | C.V. (%) |
|---|---|---|---|---|
| **PAMPEAN LAKES** | | | | |
| **Clear Vegetated** | | | | |
| DOC (mg L$^{-1}$) | 50.75 ± 17.13 | 22.90 | 80.00 | 34 |
| TSS (mg L$^{-1}$) | 19.45 ± 22.86 | 1.00 | 69.00 | 118 |
| Chl *a* (μ L$^{-1}$) | 15.78 ± 18.72 | 1.55 | 63.24 | 119 |
| Chl *a* / TSS (%) | 0.13 ± 0.13 | 0.02 | 0.55 | 103 |
| **Turbid Organic** | | | | |
| DOC (mg L$^{-1}$) | 35.70 ± 17.41 | 17.60 | 58.95 | 49 |
| TSS (mg L$^{-1}$) | 135.91± 82.02 | 55.00 | 330.00 | 60 |
| Chl *a* (μ L$^{-1}$) | 194.85 ± 135.59 | 31.02 | 513.00 | 69 |
| Chl *a* / TSS (%) | 0.18 ± 0.16 | 0.03 | 0.46 | 87 |
| **Turbid Inorganic** | | | | |
| DOC (mg L$^{-1}$) | 35.04 ± 25.01 | 15.50 | 68.30 | 71 |
| TSS (mg L$^{-1}$) | 274.00 ± 86.38 | 129.00 | 361.00 | 32 |
| Chl *a* (μ L$^{-1}$) | 23.44 ± 10.83 | 11.15 | 37.13 | 46 |
| Chl *a* / TSS (%) | 0.01 ± 8 10$^{-3}$ | 4.0 10$^{-3}$ | 2.4 10$^{-2}$ | 71 |
| **PATAGONIAN LAKES** | | | | |
| DOC (mg L$^{-1}$) | 1.49 ± 1.98 | 0.24 | 8.10 | 132 |
| TSS (mg L$^{-1}$) | 0.79 ± 1.13 | 0.02 | 5.28 | 143 |
| Chl *a* (μ L$^{-1}$) | 0.62 ± 0.73 | 0.10 | 2.90 | 122 |
| Chl *a* / TSS (%) | 0.14 ± 0.21 | 0.01 | 0.90 | 153 |

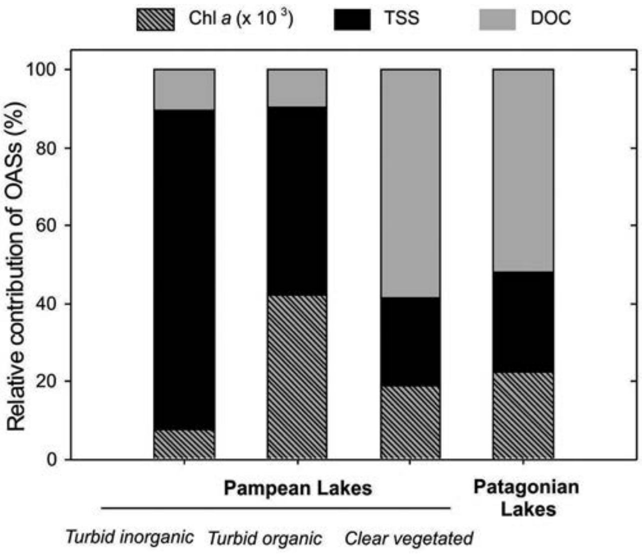

**Fig. 2.** Relative mass contribution of OASs for Pampean and Patagonian lakes. Note that Chl *a* was multiply by 10$^3$ to be discernable.

TSS, contributing between 40 to 80% of OASs mass. Particularly, turbid inorganic lakes showed high concentration of TSS and low concentration of Chl *a*, though turbid organic ones were characterized by high concentration of both TSS and Chl *a* (Table 2, Fig. 2). In turbid lakes, DOC concentration was comparatively low. In average, DOC was roughly five fold lower than TSS concentration. On the other hand, clear vegetated lakes commonly presented higher DOC than TSS concentration. In these lakes, DOC contributed in average to almost the 60% of OASs mass (Fig. 2) and Chl *a* concentration was comparatively lower than that observed in turbid organic lakes. Regarding the contribution of phytoplankton biomass to TSS (assessed as Chl *a*/TSS in %), in average, turbid inorganic lakes (i.e., LI and YA, see abbreviations in Fig. 1) presented lower values (0.01%). In contrast, turbid organic lakes (i.e., CH, SJ and BU) showed higher contribution (0.18%) (Table 2). Middle values of Chl *a*/TSS quotient was observed for clear vegetated Pampean lakes, at an average of 0.13%.

In Patagonian lakes, DOC was generally the most important mass contributor to OASs concentration (~ 55%), presenting an average of 2 fold higher concentration than TSS (Fig. 2, Table 2). Exceptions among studied Patagonian lakes were Lake Mascardi and Puelo (deep lakes with important inputs of glacial flour). Commonly shallow Patagonian lakes (lakes: TRE, ESQ, ESC, FAN, JUV and PAT) showed higher concentration of OASs than deep Patagonian lakes. On average, Patagonian lakes presented values of Chl *a*/TSS quotient around 0.14%.

## Absorption coefficients

Examples of spectral absorption coefficients of different components obtained from studied lakes are shown in Figures 3 and 4 (take notice of dissimilar y scales). Important variation in amplitude and spectral shape of total absorption, $\boldsymbol{a}_t$ (λ), was observed among lakes. For instance, Pampean lakes showed very high total absorption coefficients, $\boldsymbol{a}_t$ (PAR), averaging 7.05 $m^{-1}$ (± 6.13 s.d.). In contrast, Patagonian lakes presented low values of $\boldsymbol{a}_t$ (PAR), on average 0.28 $m^{-1}$ (± 0.45 s.d.), being 25 fold lower than that registered from Pampean lakes (Table 3).

Among Pampean lakes, turbid lakes (organic and inorganic) showed higher values of $\boldsymbol{a}_t$ (PAR) than clear vegetated lakes (on average about 3.8 fold). Among turbid organic lakes particulate absorption coefficients, $\boldsymbol{a}_p$ (PAR), were on average 1.7 fold higher than CDOM absorption, $\boldsymbol{a}_g$ (PAR), (Table 3). Particulate matter contributed with more than 60% of total absorption of light, being phytoplankton the dominant particulate fraction (Fig. 3, pie charts). The dominant phytoplankton absorption contribution elicited pigment-shaped spectral curves of $\boldsymbol{a}_t$ (λ) (Fig. 3). In turbid inorganic lakes (YA and LI), CDOM and non-pigmented absorption coefficients, $\boldsymbol{a}_d$ (PAR), presented similar values, being about 17 fold higher than phytoplankton absorption coefficients, $\boldsymbol{a}_{ph}$ (PAR), (Table 3). In these lakes, either CDOM or non-pigmented particles were the major contributors to light absorption (Fig. 3, pie charts). The co-dominant contribution of dissolved and non-pigmented particulate absorption elicited a spectral shape of $\boldsymbol{a}_t$ (λ) resembling an exponential decay curve (Fig. 3).

More diluted waters were observed for clear vegetated lakes (Fig. 3, take notice of the contribution by water itself). In lakes TR and KH, CDOM absorption coefficients were on average 4 fold higher than particulate absorption, contributing mostly to light absorption

**Table 3.** Descriptive statistics of Inherent Optical Properties (IOPs) – In Patagonian deep lakes, values of IOPs were calculated as the average of epilimnetic and metalimnetic layers. (*) $\boldsymbol{T_n}$ values were only available for some shallow Patagonian lakes.

| IOPs | Mean ± SD | Min. | Max. | C.V. (%) |
|---|---|---|---|---|
| **PAMPEAN LAKES** | | | | |
| **Clear Vegetated** | | | | |
| $a_t$ (PAR) ($m^{-1}$) | 2.79 ± 1.07 | 1.33 | 5.14 | 38 |
| $a_g$ (PAR) ($m^{-1}$) | 1.79 ± 1.03 | 0.49 | 3.94 | 58 |
| $a_d$ (PAR) ($m^{-1}$) | 0.40 ± 0.27 | 0.12 | 0.96 | 66 |
| $a_{ph}$ (PAR) ($m^{-1}$) | 0.41 ± 0.51 | $5\ 10^{-2}$ | 1.61 | 124 |
| $T_n$ (NTU) | 9.24 ± 10.21 | 0.84 | 32.33 | 111 |
| **Turbid Organic** | | | | |
| $a_t$ (PAR) ($m^{-1}$) | 7.99 ± 2.29 | 5.16 | 12.15 | 28 |
| $a_g$ (PAR) ($m^{-1}$) | 1.80 ± 0.60 | 1.06 | 3.02 | 32 |
| $a_d$ (PAR) ($m^{-1}$) | 2.09 ±1.25 | 0.58 | 4.14 | 59 |
| $a_{ph}$ (PAR) ($m^{-1}$) | 3.92 ± 1.64 | 2.01 | 7.13 | 42 |
| $T_n$ (NTU) | 120.71 ± 58.79 | 60.68 | 232.00 | 49 |
| **Turbid Inorganic** | | | | |
| $a_t$ (PAR) ($m^{-1}$) | 13.64 ± 9.23 | 5.16 | 34.45 | 68 |
| $a_g$ (PAR) ($m^{-1}$) | 6.67 ± 6.99 | 0.50 | 21.90 | 105 |
| $a_d$ (PAR) ($m^{-1}$) | 6.69 ± 2.59 | 3.94 | 12.29 | 39 |
| $a_{ph}$ (PAR) ($m^{-1}$) | 0.39 ± 0.20 | 0.15 | 0.75 | 51 |
| $T_n$ (NTU) | 222.99 ± 87.81 | 95.46 | 347.70 | 39 |
| **PATAGONIAN LAKES** | | | | |
| $a_t$ (PAR) ($m^{-1}$) | 0.28 ± 0.45 | $7\ 10^{2}$ | 1.73 | 159 |
| $a_g$ (PAR) ($m^{-1}$) | 0.20 ± 0.40 | 0.04 | 1.42 | 194 |
| $a_d$ (PAR) ($m^{-1}$) | $6\ 10^{2} \pm 7\ 10^{2}$ | $5\ 10^{3}$ | 0.27 | 122 |
| $a_{ph}$ (PAR) ($m^{-1}$) | $1.9\ 10^{2} \pm 7\ 10^{2}$ | 0.01 | 0.07 | 34 |
| $T_n$* (NTU) | 1.03 ± 0.75 | 0.38 | 2.03 | 65 |

(more than 40%) (Fig. 3, pie charts). These lakes showed $\boldsymbol{a}_t$ (λ) shape like an exponential decay curve, due to the CDOM dominant absorption contribution. Particularly, two clear vegetated lakes (LC and SA), showed a mixture contribution of CDOM, phytoplankton, and non-pigmented matter. These contributions elicited total absorption spectra more similar to that observed in turbid organic lakes, though with lower amplitudes (Fig. 3, pie charts).

Concerning Patagonian lakes, CDOM absorption coefficients were on average roughly two fold higher than particulate absorption (Table 3). Among Patagonian lakes, shallow lakes presented higher values of $\boldsymbol{a}_t$ (PAR) than deep lakes (Fig. 4). Primarily three spectral shapes of $\boldsymbol{a}_t$ (λ) were observed from Patagonian lakes. Shallow lakes ESC and ESQ presented $\boldsymbol{a}_t$ (PAR) dominated by CDOM absorption, and therefore a total absorption spectra similar to an exponential decay curve (Fig. 4). In these lakes CDOM contributed on average with more than 55% of light absorption; followed by water itself with > 26% (Fig. 4, pie chart). On the other hand, shallow lakes TRE and JUV showed an u-shaped total absorption spectra, where

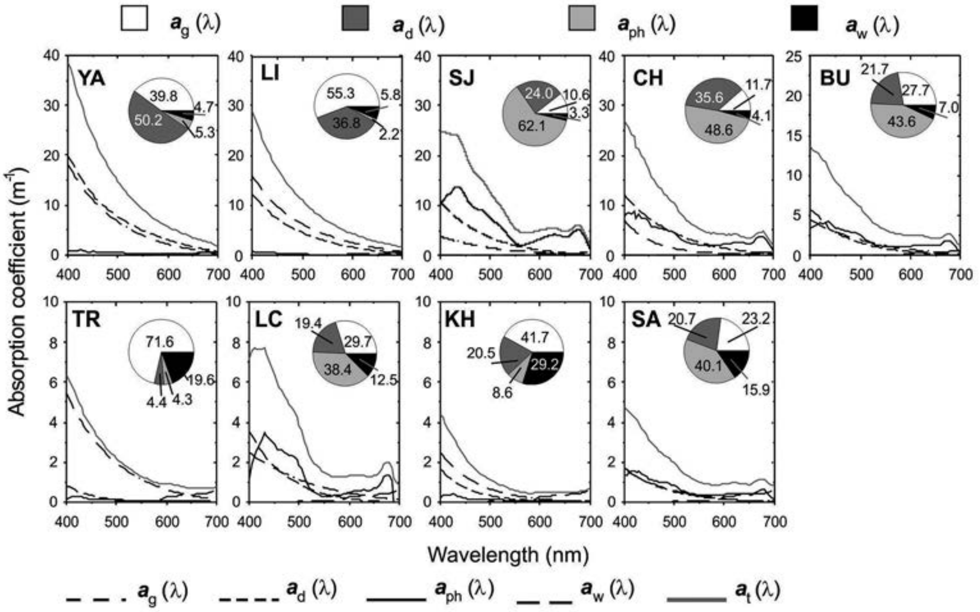

**Fig. 3.** Examples of absorption spectra of different fractions obtained for Pampean lakes. In pie chart percentage contribution of each component to total absorption spectra in the PAR range.

maxima values were registered at blue and red ends of the spectra (Fig. 4). In these lakes, similar contribution to light absorption by particular matter plus CDOM (55% in average) and water itself (45% in average) was observed. The remaining deep Patagonian lakes presented a j-shaped total absorption spectra, where water itself was the most important contributor to $\boldsymbol{a}_t$ (PAR) (Fig. 4, pie charts). In these lakes water itself contributed, on average, to the 51% of total PAR absorption coefficients, followed by CDOM with a contribution of 30%.

## Phytoplankton absorption coefficients

Phytoplankton spectral absorption coefficients showed a large variability either in amplitude or spectral shape among studied lakes. Examples of obtained phytoplankton absorption coefficients are shown in Figure 5 (take notice of dissimilar *y* scales). Overall, in Argentinean lakes $\boldsymbol{a}_{ph}$ (PAR) averaged 1.77 $m^{-1}$ (± 1.59 s.d.), with values varying seventy fold between eutrophic Pampean lakes and oligotrophic Patagonian ones (Table 4).

In Pampean lakes, noticeable differences in phytoplankton spectral absorption coefficients were observed among turbid organic, turbid inorganic and clear vegetated lakes (Fig. 5a, b and c). Particularly, in turbid inorganic lakes obtained absorption at the blue part of the spectra, were not consistent with normal phytoplankton absorption signature (Fig. 5b). Representative phytoplankton absorption spectrum has two diagnostic absorption peaks in the blue and in the red part of the spectrum corresponding to Chl *a* absorption bands. In turbid inorganic lakes (i.e., LI and YA), non-pigmented matter dominated total particulate

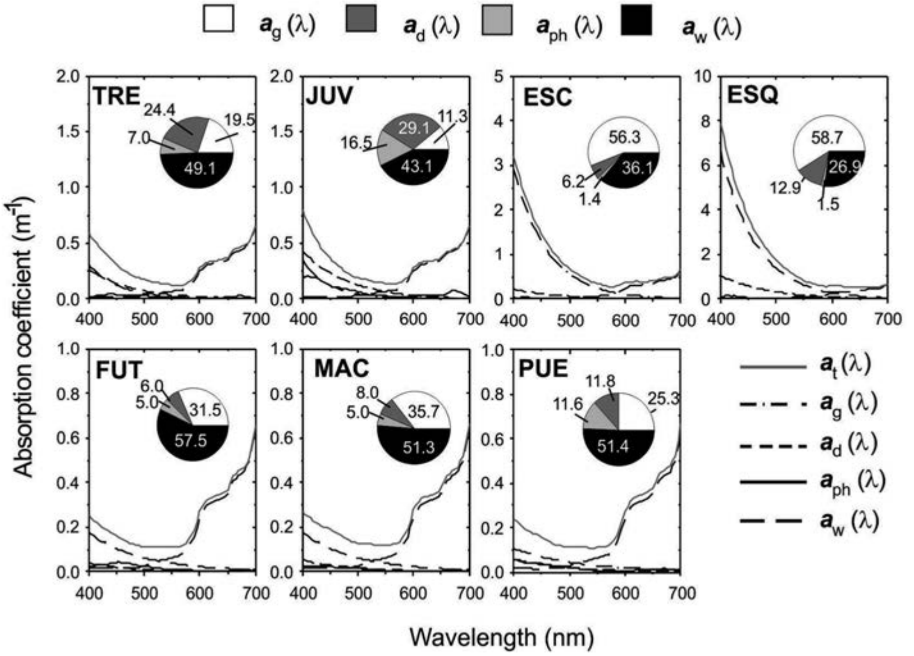

**Fig. 4.** Examples of absorption spectra of different fractions obtained for Patagonian lakes. In pie chart percentage contribution of each component to total absorption spectra in the PAR range.

**Table 4**. Phytoplankton absorption and Chlorophyll specific absorption coefficients.

| LAKES | $a_{ph}$ (PAR) m$^{-1}$ | $a_{ph}$ (blue) m$^{-1}$ | $a_{ph}$ (red) m$^{-1}$ | $a_{ph}$* (PAR) m$^2$mg Chl *a* $^{-1}$ | $a_{ph}$* (blue) m$^2$mg Chl *a* $^{-1}$ | $a_{ph}$* (red) m$^2$mg Chl *a* $^{-1}$ |
|---|---|---|---|---|---|---|
| **Pampean lakes** | 1.64 ± 1.95 | 3.52 ± 4.61 | 1.54 ± 1.75 | 2.1 $10^{-2}$ ± 1.2 $10^{-2}$ | 4.5 $10^{-2}$ ± 3.0 $10^{-2}$ | 1.7 $10^{-2}$ ± 1.0 $10^{-2}$ |
| Clear Vegetated | 0.41 ± 0.51 | 0.97 ± 1.19 | 0.39 ± 0.51 | 2.5 $10^{-2}$ ± 1.6 $10^{-2}$ | 6.0 $10^{-2}$ ± 4.0 $10^{-2}$ | 1.8 $10^{-2}$ ± 8.0 $10^{-3}$ |
| Turbid Organic | 3.92 ± 1.64 | 8.23 ± 4.07 | 3.61 ± 1.43 | 2.0 $10^{-2}$ ± 5.0 $10^{-2}$ | 4.0 $10^{-2}$ ± 9.0 $10^{-3}$ | 2 $10^{-2}$ ± 6. 1 $10^{-3}$ |
| Turbid Inorganic | 0.39 ± 0.20 | 0.95 ± 0.54 | 0.45 ± 0.28 | 1.1 $10^{-2}$ ± 7.0 $10^{-3}$ | 2.8 $10^{-2}$ ± 2.0 $10^{-2}$ | 1.3 $10^{-2}$ ± 9.0 $10^{-3}$ |
| **Patagonian lakes** | 1.9 $10^{-2}$ ± 1.0 $10^{-2}$ | 3.7 $10^{-2}$ ± 5.0 $10^{-2}$ | 1.6 $10^{-2}$ ± 3.0 $10^{-2}$ | 2.1 $10^{-2}$ ± 6.0 $10^{-3}$ | 4.9 $10^{-2}$ ± 2.0 $10^{-3}$ | 2.1 $10^{-2}$ ± 1.0 $10^{-3}$ |

absorption spectra hindering the resolution of phytoplankton absorption. Phytoplankton absorption averaged 0.39 m$^{-1}$ (± 0.20 s.d.), being in average 17 fold lower than non-pigmented matter absorption (Table 3). In contrast, turbid organic lakes displayed representative phytoplankton spectra with two main peaks in the blue (~ 430–438 nm) and in the red (~ 675–677 nm) part of the spectrum (Fig. 5a). In these lakes, values of $a_{ph}$ (PAR) averaged 3.92 m$^{-1}$ (± 1.64 s.d.), ranging 3.5 folds. Values of $a_{ph}$ (blue) and $a_{ph}$ (red) averaged

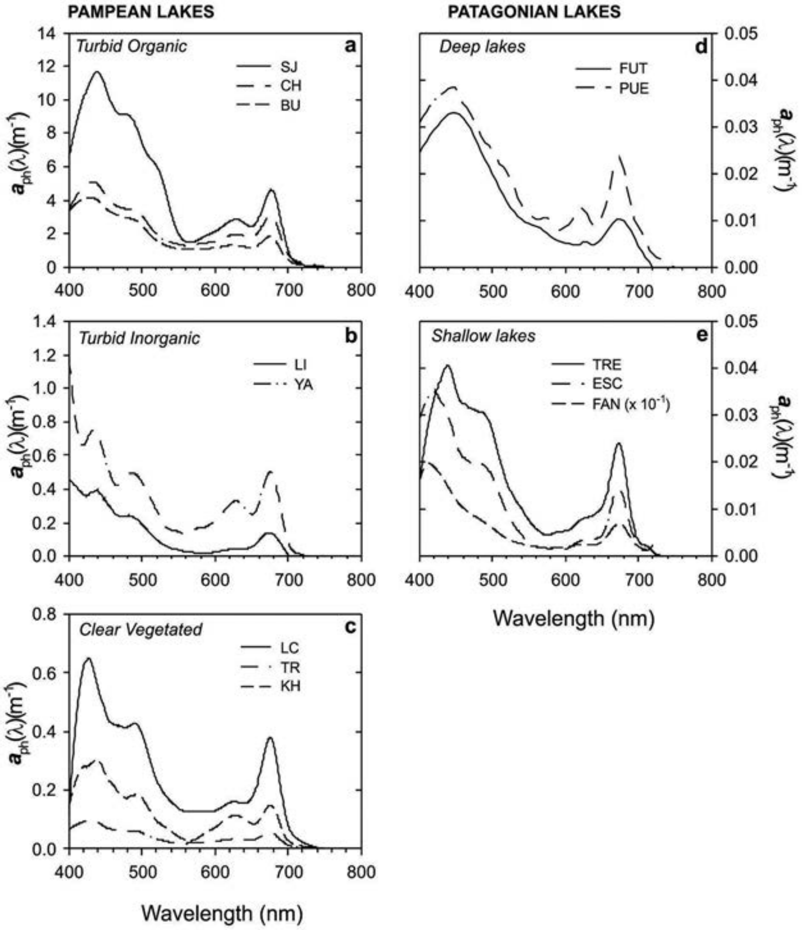

**Fig. 5.** Examples of phytoplankton absorption spectra in the PAR range obtained for Pampean lakes (a, b, c) and for Patagonian lakes (d, e, f).

8.23 $m^{-1}$ (± 4.07 s.d.) and 3.61 $m^{-1}$ (± 1.43 s.d.), respectively (Table 4). Phytoplankton spectral absorption showed also distinctive secondary peaks at 485–490 nm, 520 nm and 625–628 nm, corresponding to accessory pigments absorption bands (Fig. 5a). On the other hand, clear vegetated Pampean lakes showed around 9 fold lower $\boldsymbol{a}_{ph}$ (PAR) than turbid organic lakes, with values averaging 0.41 $m^{-1}$ (± 0.51 s.d.) (Table 4). In these lakes, phytoplankton spectral absorption showed peaks at blue band shifted towards lower wavelength (~ 420–427nm) (Fig. 5c). Values of $\boldsymbol{a}_{ph}$ (blue) and $\boldsymbol{a}_{ph}$ (red) averaged 0.97 $m^{-1}$(± 1.19 s.d.) and 0.39 $m^{-1}$ (± 0.51 s.d.), respectively (Table 4). Secondary peaks were observed around 485 nm and 625 nm (Fig. 5c).

Among the studied Patagonian lakes, obtained values of $\boldsymbol{a}_{ph}$ (PAR) were much lower, averaging 1.9 $10^{-2}$ $m^{-1}$ (± 1 $10^{-2}$ s.d.) (Table 4) and varying around 7 fold (Fig. 5d and e, see *y* scales). Diagnostic peaks at blue band were commonly observed at 435–440 nm, though in

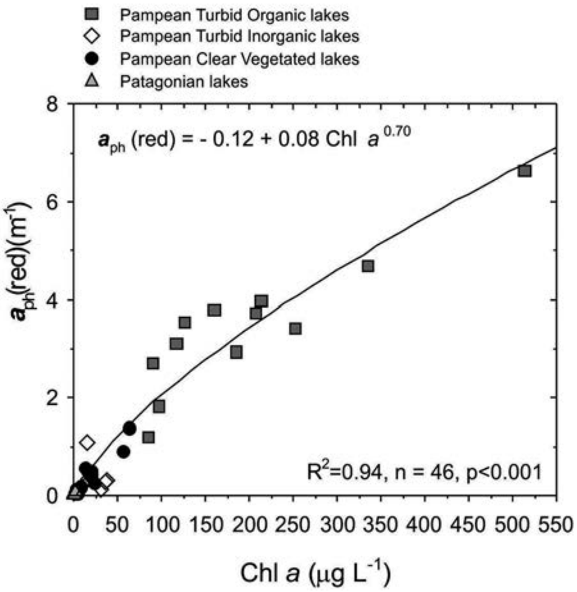

**Fig. 6.** Obtained non linear relationship between $a_{ph}$ (red) and Chl *a* for Pampean and Patagonian lakes.

shallow lakes ESC and FAN, peaks shifted towards lower wavelength (~ 420 nm) (Fig. 5 e). Values of $\boldsymbol{a}_{ph}$ (blue) and $\boldsymbol{a}_{ph}$ (red) averaged 3.7 $10^{-2}$ $m^{-1}$ (± 5 $10^{-2}$ s.d.) and 1.6 $10^{-2}$ $m^{-1}$ (± 3 $10^{-2}$ s.d.), respectively. Deep Patagonian lakes presented secondary absorption peaks at 520 nm, 575 nm and 620 nm, while Shallow lakes showed secondary peaks at 480 nm and 620 nm (Fig. 5d and e).

Considering the entire data set (Pampean and Patagonian lakes), a significant strong power relationship was obtained between $\boldsymbol{a}_{ph}$ (red) and Chl *a* concentration (Fig. 6). Around the 94 % of observed variability in $\boldsymbol{a}_{ph}$ (red) was explained by differences in Chl *a* concentration, showing a decrease in the increment of $\boldsymbol{a}_{ph}$ (red) per unit of Chl *a* at high chlorophyll values.

Variation in phytoplankton Chl *a* specific spectral absorption represents differences in phytoplankton absorption mainly caused by differences in accessory pigment concentration and due to package effect, which is caused by the phytoplankton size and intracellular pigment concentration. Overall, in Argentinean lakes values of $\boldsymbol{a}_{ph}$* (PAR) averaged 2.5 $10^{-2}$ ($m^2$mg Chl $a^{-1}$) (±1.2 $10^{-2}$ s.d.) ranging around 5 folds. Among Pampean lakes, was observed an important variation in $\boldsymbol{a}_{ph}$* within different group of lakes (Fig. 7a). However, in average turbid lakes showed lower values of $\boldsymbol{a}_{ph}$* (PAR) than clear vegetated lakes, and turbid inorganic lakes depicted lowest values (Table 4).

Patagonian lakes presented similar values of specific phytoplankton absorption coefficients than that observed in Pampean lakes (Fig. 7b, Table 4). Interestingly, Deep lakes presented slightly lower values of $\boldsymbol{a}_{ph}$* (PAR) than clear vegetated Pampean ones (Fig. 7).

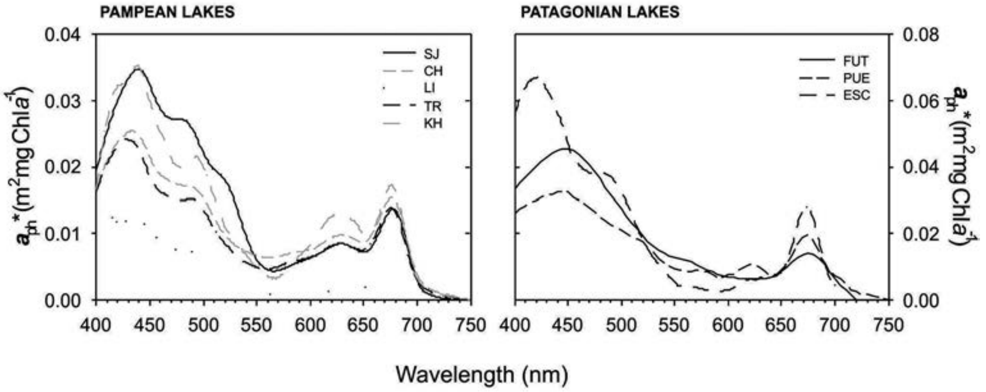

**Fig. 7.** Examples of Chl *a* specific phytoplankton absorption coefficients obtained for Pampean and Patagonian lakes.

## Turbidity

Readings of nephelometric turbidity were available for all Pampean lakes and only for some shallow Patagonian lakes (Table 3). In Pampean lakes, values of $\boldsymbol{T}_{\mathrm{n}}$ averaged 93.08 NTU (± 98.13 s.d.) and ranged from around 1 NTU in clear-vegetated lakes to 350 NTU in turbid lakes. Patagonian shallow lakes showed values of $\boldsymbol{T}_{\mathrm{n}}$ in average around 1 NTU.

## PAR and spectral diffuse attenuation coefficients

Water transparency measured as vertical diffuse light attenuation coefficient, *k*d (PAR), showed a broad variability among the studied Argentinean lakes (Table 5). Overall, values of *k*d (PAR) ranged from 0.10 $m^{-1}$ in deep Patagonian lakes to 47 $m^{-1}$ in turbid inorganic Pampean lakes.

In Pampean lakes, values of *k*d (PAR) averaged 17.61 $m^{-1}$ (± 12.79 s.d.), varying from 3.36 to 46.99 $m^{-1}$. Turbid lakes presented almost 4 folds higher *k*d (PAR) values than clear vegetated lakes. In turbid lakes *k*d (PAR) averaged 23.62 $m^{-1}$ (± 11.94 s.d.), with larger values in inorganic than organic lakes (Table 5). The observed high values of light attenuation in turbid lakes were translated into narrow euphotic depths varying from 0.10 to 0.48 m. In clear vegetated Pampean lakes values of *k*d (PAR) averaged 6.05 $m^{-1}$ (± 3.54 s.d.), representing euphotic depths ranging from 0.34 m to 1.37 m (Table 5).

Among Patagonian lakes, much lower values of *k*d (PAR) were registered, averaging 0.34 $m^{-1}$ (± 0.45 s.d.) (Table 5). In deep lakes, for example Lake Nahuel Huapi, euphotic layer reached roughly 45 m depth. In contrast, in shallow lakes, euphotic depth could either reach almost 2 m depth or lake's bottom.

**Table 5.** Descriptive statistics of Apparent Optical Properties (AOPs).

| AOPs | Mean ± SD | Min. | Max. | C.V. (%) |
|---|---|---|---|---|
| **PAMPEAN LAKES** | | | | |
| **Clear Vegetated** | | | | |
| *k*d (PAR) ($m^{-1}$) | 6.06 ± 3.54 | 3.36 | 13.50 | 58 |
| $Z_{1\%}$ ($m^{-1}$) | 0.94 ± 0.39 | 0.34 | 1.37 | 41 |
| **Turbid Organic** | | | | |
| *k*d (PAR) ($m^{-1}$) | 17.97 ± 6.48 | 9.60 | 27.6 | 36 |
| $Z_{1\%}$ ($m^{-1}$) | 0.29 ± 0.11 | 0.17 | 0.48 | 37 |
| **Turbid Inorganic** | | | | |
| *k*d (PAR) ($m^{-1}$) | 36.34 ± 12.10 | 21.14 | 47.00 | 33 |
| $Z_{1\%}$ ($m^{-1}$) | 0.14 ± 0.06 | 0.10 | 0.22 | 39 |
| **PATAGONIAN LAKES** | | | | |
| *k*d (PAR) ($m^{-1}$) | 0.34 ± 0.45 | 0.10 | 2.31 | 131 |
| $Z_{1\%}$ ($m^{-1}$) | 25.13 ± 13.01 | 1.99 | 46.05 | 52 |

## Relationship among OASs, IOPs and water transparency

Examples of the relative contribution by absorption and scattering to vertical diffuse light attenuation coefficients are shown in Fig. 8a and b. In turbid organic and inorganic Pampean lakes, scattering by particles, contributed higher to light attenuation than in clear vegetated lakes (Fig. 8a). In turbid lakes both absorption and scattering contributed similarly to light attenuation. In these lakes particulate matter scatter light, increasing considerably the attenuation caused only by absorption (Fig. 8a). For instance, SJ absorption (mainly by phytoplankton) contributed to more than 70%, though in YA (a turbid inorganic lake) scattering contributed largely (Fig. 8a).

On the other hand, in clear vegetated lakes (i.e., TR and KH) absorption (mainly CDOM) contributed mainly to *k*d (PAR) with values higher than 80%. Particularly, LC could show an important variation in scattering contribution reaching values around 40%.

In Patagonian lakes, absorption contribution to light attenuation was commonly dominant with values up to 70% (Fig. 8b). Deep lakes showed light attenuation caused mainly by absorption processes (more than 90 %). Particularly, lakes with glacial clay inputs (i.e. MAS Catedral arm and PUE) showed an increase of scattering contribution to *k*d (PAR). Among shallow Patagonian lakes, scattering contribution to light attenuation could increase (Fig. 8b).

Using OASs concentration to estimate light attenuation coefficients resulted in important differences between the two set of lakes. In Pampean lakes, the 80% of the observed variation in *k*d (PAR) could be significantly explained by TSS ($R^2 = 0.81$, $p < 0.001$, n = 37). The inclusion of Chl *a* and DOC concentration did not add significant additional information to predict the response variable. In contrast, in Patagonian lakes the 97% of the observed variation in *k*d (PAR) was significantly explained by the linear combination of DOC plus Chl *a* ($R^2 = 0.97$, $p < 0.001$, n = 19). In these lakes DOC concentration explained by itself the 95% of the observed differences in *k*d (PAR).

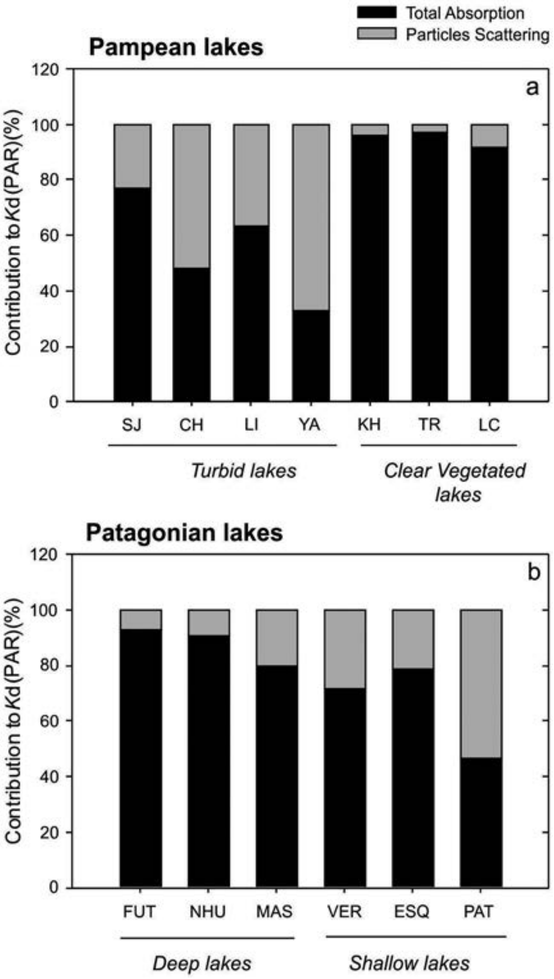

**Fig. 8.** Examples of percentage contribution of total absorption and scattering by particles to vertical diffuse attenuation coefficient in the PAR range.

Regarding obtained relationships between IOPs and water transparency, in Pampean lakes particulate absorption significantly explained almost the 71% of the observed variation in *k*d (PAR) ($R^2 = 0.71$, $p < 0.001$, $n = 34$). CDOM absorption was only important (in addition to particulate absorption) explaining highest *k*d (PAR) values measured in LI and YA. Interestingly, considering only nephelometric turbidity, about the 90% of variation in *k*d (PAR) was explained ($R^2 = 0.90$, $p < 0.001$, $n = 36$). The observed variation in $\boldsymbol{T}_n$ was significantly explained by differences in TSS and Chl *a* ($R^2 = 0.90$, $p < 0.001$, $n = 39$), though Chl *a* contributed little with < 3%. In Patagonian lakes, significant linear relationship was acquired between *k*d (PAR) and CDOM absorption coefficients. Values of ***a***g (PAR) explained 93% of the observed variation in the measured *k*d PAR ($R^2 = 0.93$, $p < 0.001$, $n = 30$). In these lakes, the inclusion of ***a***d (PAR) and ***a***ph (PAR) did not explain additional variation.

## Discussion

The described patterns evidence the enormous variation in concentration of optical active substances and their optical properties among a group of Argentinean lakes that, in some way, depict the marked gradient of bioptical characteristic presented in inland waters around the world.

OASs presented a wide variability between studied Argentinean lakes, stressing important differences in water types. Pampean shallow lakes showed commonly much higher values of Chl *a*, TSS and DOC concentration than Patagonian lakes (Table 2). For instance, considering the entire data set, phytoplankton biomass (as Chl *a*) could vary in average three hundred fold between eutrophic Pampean lakes and oligotrophic Patagonian lakes. Comparing the relative mass contribution of OASs, Pampean turbid lakes presented on average a higher contribution of TSS than DOC. However, among these lakes, turbid organic showed higher values of Chl *a* than Turbid Inorganic, with values of Chl a/TSS averaging 0.18% and 0.01% respectively. Allende et al. (2009) reported high concentration of nutrients in both groups of turbid lakes with an increasing light limitation in turbid inorganic ones. On the other hand, clear vegetated Pampean lakes and Patagonian lakes showed and opposite patter, being, on average, the relative mass contribution of DOC more important than TSS. Both groups of lakes presented low Chl *a* concentration with Chl a/TSS averaging ~ 0.13%. Interestingly, some exceptions in OASs contributions were observed among clear vegetated Pampean lakes. Lakes LC and SA showed comparable values of DOC and TSS with high Chl *a* concentration, characteristics that could represent a transient state between clear and turbid one. Among Patagonian lakes some shallow lakes showed comparable values of DOC and TSS. In addition, TSS could be a more important mass contributor than DOC in deep lakes with large inputs of glacial clay (i.e., Lakes PUE and MAS).

Under water light is actively absorbed and scattered by optically active substances and also by water itself. The amount and quality (spectral composition) of available light throughout water column is determined primarily by OASs concentration and by their specific absorption and scattering coefficients. Pampean lakes (turbid and clear vegetated) showed much higher values of total absorption spectra than Patagonian lakes, bringing out differences in OASs concentration and trophic status. Interestingly, we found marked differences in absorption characteristics between turbid organic and turbid inorganic Pampean lakes that could be linked mainly with the composition of particulate matter. In turbid organic lakes CH and BU, phytoplankton and non-pigmented particles contributed similarly to light absorption; while in Lake SJ phytoplankton contributed largely. On the other hand, in turbid inorganic lakes (YA and LI) particulate contribution was dominated by non-pigmented particles; in addition, CDOM could be also an important component to light absorption. In turbid inorganic lakes a strong light competition may be taking place, being phytoplankton actively shaded by non-pigmented particles and CDOM. This scenario of light limitation could explain the low values of Chl *a* measured in these lakes, in spite of the highest attenuation coefficients. In an intermediate term there were turbid organic lakes CH and BU that seem to have concentrations and type of components of non-pigmented particles that allowed higher phytoplankton development (even if competition by light could be restricting its growth) than that observed in inorganic lakes. Phytoplankton competition with non-algal particles is well known in many coastal and estuarial environments (Cloern 1987, Loos & Costa 2010). In Lake CH, Pérez et al. (2011) found that the depletion of radiant energy caused by absorption and scattering due to non-algal particulates was the major process controlling light availability. On the other hand, the turbid organic lake SJ showed a different scenario where phytoplankton self-shading may be the main process. This lake presented highest Chl *a* concentrations in spite of comparatively lower values of nephelometric turbidity than that observed in other turbid lakes. In this sense, light limitation may be mainly determined by phytoplankton absorption; though scattering processes caused a minor increase in light attenuation (i.e., filamentous algae are good at absorbing poor scattering particles). Therefore, higher phytoplanktonic biomass could develop in Lake SJ. On the other hand, in remainder turbid lakes scattering (mainly related to non-pigmented particulate) was able to enhance light attenuation from 36 to 67%, hindering phytoplankton growth. Pampean clear vegetated lakes showed lower total absorption spectra than turbid lakes. In these lakes, light is absorbed and scattered in lower extent, producing waters characterized by elevated transparency among Pampean lakes. Even if CDOM dominates the light absorption in TR and KH lakes (actively removing blue light), light availability seems not to be the determinant factor explaining low Chl *a* concentration observed in these Pampean lakes. Allende et al. (2009) reported lower nutrient concentration in some clear vegetated lakes and related this observation to high nutrient uptake by macrophytes. In addition, phytoplankton biomass in clear vegetated lakes has been suggested to be controlled by several other factors including high pressure by herbivorous zooplankton, elevated piscivore to planktivore density ratios and macrophytes reducing turbulence (Timms & Moss 1984, Scheffer 1998, Jeppesen et al. 2000, among others). On the other hand, submerged macrophytes may also restrict phytoplankton growth shading water column and increasing light attenuation to that actually reported here, measured with the black container methodology (refer to Torremorell et al. 2009 and Pérez et al. 2011). Patagonian lakes were at one end of bioptical gradient observed in this study. These lakes presented the lowest total absorption spectra, being the contribution increased by water itself. CDOM was commonly an important contributor to light absorption, although particulate matter was only significant in some shallow lakes and in lakes with important input of glacial clay. In these lakes, an increase in scattering and related decrease in water transparency was observed. The lowest values of Chl *a* registered in Patagonian lakes were related to the availability of very low nutrient concentrations. The high transparency observed in deep lakes was translated in extended euphotic zones that included the whole epilimnion. Consequently two optic scenarios can be delimited in the water column. First, the epilimnion characterized by irregular light regime (due to turbulence), with high irradiances including hazardous UV-B in the upper levels. Secondly, a subsequent illuminated metalimnion which exhibited a more stable dim-light regime with a prevalence of blue-green light (as a result of CDOM absorption contribution) in which Deep Chlorophyll Maxima may develop (Pérez et al. 2002, Pérez et al. 2007).

An important goal in the field of hydrologic optics has been to predict light attenuation and therefore light availability in the water column from knowledge of optically active substance and IOPs (Morris et al. 1995, LaPerriere & Edmundson 2000, Gallegos 2001, Xu & Chaos 2005, among others). The accuracy in reproduction of light field is a key problem to understand some aspects in the ecology and lakes functioning. The solution of these problems has important implications to implement management strategies, restoration actions and lake monitoring. From the data set of studied lakes, I found that water transparency in Pampean lakes (overall turbid and clear vegetated) could be significantly estimated (> 70%) by the concentration of TSS as well as by particulate absorption coefficients. Concentration of DOC and CDOM absorption coefficients showed to be important predicting *K*d (PAR) in clear vegetated lakes and in some extent in turbid inorganic lakes. Interestingly, measurements of nephelometric turbidity strongly explained light attenuation among Pampean lakes (around 90%). Unlike *K*d (PAR) measurements, $\boldsymbol{T}_\mathrm{n}$ can be recorded automatically and irrespective of the ambient light field (solar zenith angle, cloud cover, atmospheric aerosol content). These results showed that a suitable and practical method to estimate light attenuation, in a wide range of optical water types, could be the use of empirical models based either on TSS, particulate absorption coefficients or $\boldsymbol{T}_\mathrm{n}$ measurements with automated sensors or bench top instruments. On the other hand, in Patagonian lakes DOC measurements as well as the determination of CDOM absorption coefficients showed to be the key in the estimation of water transparency. TSS and particulate absorption coefficient measurements could be important in the optical study of some shallow lakes and deep lakes with presence of glacial clays.

Regarding the study of phytoplankton community, phytoplankton absorption coefficients has been reported to have significant implications in the estimation of pigment concentration and primary production from measurements of AOPs and IOPs (Marra et al. 2007, Le et al. 2009). In addition, relevant information could be obtained from $\boldsymbol{a}_\mathrm{ph}(\lambda)$ and $\boldsymbol{a}_\mathrm{ph}{}^*(\lambda)$ in the study of species composition, physiology and light acclimation of phytoplankton community (Bricaud & Stramsky 1990, Millie et al. 1997, Fujiki & Taguchi 2002). I found a general good positive non linear relationship between $\boldsymbol{a}_\mathrm{ph}$ (red) and Chl *a* concentration, considering the entire data set of studied lakes ($R^2 = 0.94$). This relationship also showed a general decrease of phytoplankton absorption per unit of Chl *a* with increasing trophic status (i.e., at higher Chl *a* values). However, $\boldsymbol{a}_\mathrm{ph}{}^*(\lambda)$ showed an unclear pattern throughout the trophic gradient and light regimens observed among different group of Argentinean lakes. This indicates that several factors seem to determine the variation in specific phytoplankton absorption among contrasting water environments; as previously reported by other authors (Bricaud et al. 1995, Bouman et al. 2003). In addition to ontogenetic and phylogenic light adaptation to light regimens (surface irradiance, light attenuation and water column thermal structure), other factors like temperature, nutrient availability and top down control of phytoplankton community can be considered as important causes of variation in $\boldsymbol{a}_\mathrm{ph}{}^*(\lambda)$. Finally and in a methodological context, the resolution of $\boldsymbol{a}_\mathrm{ph}(\lambda)$ by Kishino´s method yielded inconsistent values around blue wavelengths in lakes with lower Chl *a*/TSS rates. In these lakes, like turbid inorganic Pampean ones, non-algal particles hindered the accurately partitioning of particulate components. However, Kishino´s method seems to be suitable to provide $\boldsymbol{a}_\mathrm{ph}$ values at the red end of the spectrum, which make possible the proper retrieval of Chl *a* concentration from phytoplankton absorption in a broad variation range.

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## References

Allende, L., Tell, G., Zagarese, H., Torremorell, A., Pérez, G., Bustingorry, J., Escaray, R. & Izaguirre, I. (2009): Phytoplankton and primary production in clear-vegetated, inorganic-turbid, and algal-turbid shallow lakes from the pampa plain (Argentina). – Hydrobiologia **624**: 45–60.

APHA (1998): Standard Methods for the examination of water and wastewater. – 1220 Ed. American Publication Health Association., Washington DC.

Belzile, C., Gibson, J. A. E. & Vincent, W. F. (2002): Colored dissolved organic matter and dissolved organic carbon exclusion from lake ice: Implications for irradiance transmission and carbon cycling. – Limnol. Oceanogr. **47**: 1283–1293.

Bouman, H. A., Platt, T., Sathyendranath, S., Li, W. K. W., Stuart, V., Fuentes-Yaco, C., Maass, H., Horne, E. P. W., Ulloa, O., Lutz, V. & Kyewalyanga, M. (2003): Temperature as indicator of optical properties and community structure of marine phytoplankton: Implications for remote sensing. – Mar. Ecol. Prog. Ser. **258**: 19–30.

Bricaud, A. & Stramski, D. (1990): Spectral absorption of living phytoplankton and nonalgal biogenus matter: A comparison between the Peru upwelling area and the Sargasso Sea. – Limnol. Oceanogr. **35**: 562–582.

Bricaud, A., Babin, M., Morel, A. & Claustre, H. (1995): Variability in the chlorophyll-specific absorption coefficients of natural phytoplankton: analysis and parameterization. – J. Geophys. Res. **100**: 13321–13332.

Bukaveckas, P. A. & Robbins-Forbes, M. (2000): Role of dissolved organic carbon in the attenuation of photosynthetically active and ultraviolet radiation in Adirondack lakes. – Freshwat. Biol. **43**: 339–354.

Cloern, J. E. (1987): Turbidity as a control on phytoplankton biomass and productivity in estuaries. – Cont. Shelf Res. **7**: 1367–1381.

Falkowski, P. G. & Raven, J. A. (1997): Aquatic Photosynthesis. – 375 pp., Oxford, Blackwell.

Fernández Cirelli, A. & Miretzky, P. (2002): Lagos poco profundos de la Pampa Argentina. Relación con aguas subterraneas someras. – In: Fernández Cirelli, A. & Chalar Marquisa, G. (eds.): El agua en Iberoamérica. De la limnología a la gestión en Sudamérica.: CYTED XVII, CETA— Centro de estudios Transdisciplinarios del Agua, Facultad de Ciencias Veterinarias, Buenos Aires, Argentina, pp. 43–52.

Fujiki, T. & Taguchi, S. (2002): Variability in chlorophyll a specific absorption coefficient in marine phytoplankton as a function of cell size and irradiance. – J. Plankton Res. **24**: 859–874.

Gallegos, C. L. (2001): Calculating optical water quality targets to restore and protect submersed aquatic vegetation: Overcoming problems in partitioning the diffuse attenuation coefficient for photosynthetically active radiation. – Estuaries **24**: 381–397.

Gallegos, C. L. (2005): Optical water quality of a blackwater river estuary: The Lower St. Johns River, Florida, USA. – Estuar. Coast. Shelf Sci. **63**: 57–72.

Gallegos, C. L., Correll, D. L. & Pierce, J. W. (1990): Modeling spectral diffuse attenuation, absorption, and scattering coefficients in a turbid estuary. – Limnol. Oceanogr. **35**: 1486–1502.

Iriondo, M. H. (1989): Quaternary lakes of Argentina. – Palaeogeogr. Palaeoclimatol. Paleoecol. **70**: 81–88.

Jeppesen, E., Peder Jensen, J., Søndergaard, M., Lauridsen, T. & Landkildehus, F. (2000): Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. – Freshwat. Biol. **45**: 201–218.

Kirk, J. T. O. (1980): Spectral absorption properties of natural waters: contribution of the soluble and particulate fractions to light absorption in some inland waters of south-eastern Australia. – Aust. J. Mar. Freshw. **31**: 287–296.

Kirk, J. T. O. (1984): Dependence of relationship between inherent and apparent optical properties of water on solar altitude. – Limnol. Oceanogr. **29**: 350–356.

Kirk, J. T. O. (1994a): Light and Photosynthesis in Aquatic Ecosystems. – Cambridge Univ. Press, Cambridge.

Kirk, J. T. O. (1994b): Characteristics of the light field in highly turbid waters: a Monte Carlo study. – Limnol. Oceanogr. **39**: 702–706.

Kishino, M., Takahashi, M. & Okami, N. (1985): Estimation of the spectral absorption coefficients of phytoplankton in the sea. – Bull. Mar. Sci. **37**: 634–642.

Laperriere, J. D. & Edmundson, J. A. (2000): Limnology of two lake systems of Katmai National Park and Preserve, Alaska: Part II. Light penetration and Secchi depth. – Hydrobiologia **418**: 209–216.

Laurion, I., Lami, A. & Sommaruga, R. (2002): Distribution of mycosporine-like amino acids and photoprotective carotenoids among freshwater phytoplankton assemblages. – Aquat. Microb. Ecol. **26**: 283–294.

Le, C., Li, Y., Zha, Y. & Sun, D. (2009): Specific absorption coefficient and the phytoplankton package effect in Lake Taihu, China. – Hydrobiologia **619**: 27–37.

Loos, E. A. & Costa, M. (2010): Inherent optical properties and optical mass classification of the waters of the Strait of Georgia, British Columbia, Canada. – Progr. Oceanogr. **87**: 144–156.

Malone, T. C. (1977): Environmental regulation of phytoplankton productivity in the lower Hudson Estuary. – Estuar. Coast. Mar. Sci. **5**: 157–171.

Mantoura, R. F.C. & Llewellyn, C. A. (1983): The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reverse-phase high-performance liquid chromatography. – Anal. Chim. Acta. **151**: 297–314.

Marra, J., Trees, C. C. & O'Reilly, J. E. (2007): Phytoplankton pigment absorption: A strong predictor of primary productivity in the surface ocean. – Deep-Sea Res. Part I, Oceanogr. Res. Pap. **54**: 155–163.

Millie, D. F., Schofield, O. M., Kirkpatrick, G. J., Johnsen, G., Tester, P. A & Vineyard, B. T. (1997): Detection of harmful algal blooms using photopigments and absorption signatures: A case study of the Florida red tide dinoflagellate, Gymnodinium breve. – Limnol. Oceanogr. **42**: 1240–1251.

Mitchell, B. G. & Kiefer, D. A. (1988): Chlorophyll a specific absorption and fluorescence excitation spectra for light-limited phytoplankton. – Deep-Sea Res. Part A, Oceanogr. Res. Pap. **35**: 639–663.

Morel, A. & Prieur, L. (1977): Analysis of variations in ocean color. – Limnol. Oceanogr. **22**: 709–722.

Morris, D. P., Zagarese, H., Williamson, C. E., Balseiro, E. G., Hargreaves, B. R., Modenutti, B., Moeller, R. & Queimaliños, C. (1995): The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. – Limnol. Oceanogr. **40**: 1381–1391.

Nolen, S. L., Wilhm, J. & Howick, G. (1985): Factors influencing inorganic turbidity in a great plains reservoir. – Hydrobiologia **123**: 109–117.

Paavel, B., Arst, H. & Reinart, A. (2008): Variability of bio-optical parameters in two North-European large lakes. – Hydrobiologia **599**: 201–211.

Paruelo, J., Beltran, A., Jobbágy, E., Sala, O. & Golliuscio, R. (1998): The climate of Patagonia:general patterns and controls on biotic processes. – Ecol. Austral **8**: 85–101.

Pérez, G., Queimaliños, C., Balseiro, E. & Modenutti, B. (2007): Phytoplankton absorption spectra along the water column in deep North Patagonian Andean lakes (Argentina). – Limnologica **37**: 3–16.

Pérez, G. L., Queimaliños, C. P. & Modenutti, B. E. (2002): Light climate and plankton in the deep chlorophyll maxima in north patagonian andean lakes. – J. Plankton Res. **24**: 591–599.

Pérez, G. L., Llames, M. E., Lagomarsino, L. & H. Zagarese, H. (2011): Seasonal Variability of Optical Properties in a Highly Turbid Lake (Laguna Chascomús, Argentina). – Photochem. Photobiol. **87**: 659–670.

Pérez, G. L., Torremorell, A., Bustingorry, J., Escaray, R., Pérez, P., Diéguez, M. & Zagarese, H. (2010): Optical characteristics of shallow lakes from the Pampa and Patagonia regions of Argentina. – Limnologica **40**: 30–39.

Pierce, J. W., Correll, D. L., Goldberg, B., Faust, M. A. & Klein, W. H. (1986): Response of underwater light transmittance in the Rhode River estuary to changes in water-quality parameters. – Estuaries **9**: 169–178.

Preisendorfer, R. W. (1961): Application of radiative transfer theory to light measurements in the sea. – Union Geod. Geophys. Inst. Monogr. **10**: 11–30.

Quirós, R. & Drago, E. (1999): The environmental state of Argentinean lakes: An overview. – Lakes Reserv. Res. Manage. **4**: 55–64.

Raaj, R., Ramalingam, M., Ghosh, S. K. & Kothyari, U. C. (2008): Mapping of suspended sediments using site specific seasonal algorithms. – J. Indian Soc. Remote Sens. **36**: 61–68.

Reinart, A., Herlevi, A., Arst, H. & Sipelgas, L. (2003): Preliminary optical classification of lakes and coastal waters in Estonia and south Finland. – J. Sea Res. **49**: 357–366.

Reinart, A., Paavel, B., Pierson, D. & Strömbeck, N. (2004): Inherent and apparent optical properties of Lake Peipsi, Estonia. – Boreal Environ. Res. **9**: 429–445.

Reinart, A. & Valdmets, K. (2007): Variability of optical water types in Lake Peipsi. – Proc. Est. Acad. Sci. Biol. Ecol. **56**: 33–46.

Reynolds, C. S. (2006): Ecology of Phytoplankton. – Cambridge Univ. Press, Cambridge, U.K.

Scheffer, M. (1998): Ecology of Shallow Lakes. – Chapman & Hall, London.

Sharp, J. H., Peltzer, E. T., Alperin, M. J., Cauwet, G., Farrington, J. W., Fry, B., Karl, D. M., Martin, J. H., Spitzy, A., Tugrul, S. & Carlson, C. A. (1993): Procedures subgroup report. – Mar. Chem. **41**: 37–49.

Shooter, D., Davies-Colley, R. J. & Kirk, J. T. O. (1998): Light absorption and scattering by ocean waters in the vicinity of the Chatham Rise, South Pacific. – Ocean. Mar. Freshwat. Res. **49**: 455–461.

Sierra, E. M., Fernández Long, M. E. & Bustos, C. (1994): Cronologías de inundaciones y sequías en el noreste de la provincia de Buenos Aires 1911-89. – Rev. Facultad Agron. **14**: 241–249.

Sommaruga, R. & Psenner, R. (1997): Ultraviolet Radiation in a High Mountain Lake of the Austrian Alps: Air and Underwater Measurements. – Photochem. Photobiol. **65**: 957–963.

Timms, R. M. & Moss, B. (1984): Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. – Limnol. Oceanogr. **29**: 472–486.

Torremorell, A., Bustigorry, J., Escaray, R. & Zagarese, H. E. (2007): Seasonal dynamics of a large, shallow lake, laguna Chascomús: The role of light limitation and other physical variables. – Limnologica **37**: 100–108.

Torremorell, A., Llames, M. E., Pérez, G. L., Escaray, R., Bustingorry, J. & Zagarese, H. (2009): Annual patterns of phytoplankton density and primary production in a large, shallow lake: The central role of light. – Freshwater Biol. **54**: 437–449.

Trüper, H. G. & Yentsch, C. S. (1967): Use of glass fiber filters for the rapid preparation of in vivo absorption spectra of photosynthetic bacteria. – J. Bacteriol. **94**: 1255–1256.

V.-Balogh, K., Németh, B. & Vörös, L. (2009): Specific attenuation coefficients of optically active substances and their contribution to the underwater ultraviolet and visible light climate in shallow lakes and ponds. – Hydrobiologia **632**: 91–105.

Xu, J., Hood, R. & Chao, S.-Y. (2005): A simple empirical optical model for simulating light attenuation variability in a partially mixed estuary. – Estuar. Coast. **28**: 572–580.

Zhang, Y., Zhang, B., Wang, X., Li, L., Feng, S., Zhao, Q., Liu, M. & Qin, B. (2007): A study of absorption characteristics of chromophoric dissolved organic matter and particles in Lake Taihu, China. – Hydrobiologia **592**: 105–120.