Annual patterns of phytoplankton density and primary production in a large, shallow lake: the central role of light

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SUMMARY

1. We studied the seasonal dynamics of suspended particulate matter in a turbid, large shallow lake during an annual period (2005–06). We relate the patterns of seston concentration (total suspended solids), phytoplankton biomass and water transparency to the seasonal pattern of incident solar radiation (I_0). We also report the seasonal trends of phytoplankton primary production (PP) and photosynthesis photoinhibition due to photosynthetically active radiation (PAR) and ultraviolet radiation (UVR) (I_β and UV_{50}).
2. We first collected empirical evidence that indicated the conditions of light limitation persisted during the study period. We found that the depth-averaged irradiance estimated for the time of the day of maximum irradiance ($I_{mean-noon}$) was always lower than the measured onset of light saturation of photosynthesis (I_k).
3. We then contrasted the observations with theoretical expectations based on a light limitation scenario. The observed temporal patterns of seston concentration, both on a volume and area basis, were significantly explained by I_0 ($R^2 = 0.39$ and $R^2 = 0.37$ respectively). The vertical diffuse attenuation coefficient (kd_{PAR}) ($R^2 = 0.55$) and the depth-averaged irradiance (I_{mean}) ($R^2 = 0.66$), significantly increased with the I_0; while the irradiance reaching the lake bottom (I_{out}) significantly decreased with the incident irradiance ($R^2 = 0.49$). However, phytoplankton biovolume maxima were not coincident with the time of the year of maximum irradiance.
4. A significant positive relationship was observed between PP estimated on an area basis and I_0 ($R^2 = 0.51$, $P < 0.001$). In addition, the parameters describing the photosynthetic responses to high irradiances displayed marked seasonal trends. The photosynthesis photoinhibition due to PAR as well as to UV were significantly related to incident solar radiation (PAR: $R^2 = 0.73$; UV: $R^2 = 0.74$). These results suggest adaptation of the phytoplankton community in response to changes in incident solar radiation.

Keywords: light limitation, photosynthesis photoinhibition, shallow turbid lake, water transparency

Introduction

Light is a major energy source in freshwater ecosystems. Many studies have contributed to develop a consistent body of theory that describes the physics of light transmission through the aquatic medium and the resultant underwater light field (Talling, 1971; Kirk, 1994), the biochemical basis of light-harvesting

photosynthetic systems (see Falkowski & Raven, 1997; Geider & MacIntyre, 2002), the physiological responses of algae under different light fields (e.g. Reynolds, 1983; Reynolds, Harris & Gouldney, 1985; Tilzer, 1987; Neale *et al.*, 1991; Litchman, 2000; Litchman, Klausmeier & Bossard, 2004) and the ecological implications of different underwater light climates (Scheffer *et al.*, 1993).

Light has long been known to limit phytoplankton primary production (PP) in intensive or extensive aquaculture systems, in which all necessary nutrients for algal growth are supplied in excess (see De Pauw *et al.*, 1980; for a paradigmatic example). More recently, several studies have investigated the role of light limitation on algae growth and interspecific competition using laboratory experiments (Huisman & Weissing, 1994; De Nobel *et al.*, 1998; Huisman, 1999; Huisman *et al.*, 1999, 2002) and outdoor mesocosms (Petersen, Chen & Kemp, 1997; Diehl *et al.*, 2002; Ptacnik, Diehl & Berger, 2003). In natural systems, mixing poses an obstacle to assessing the extent of light limitation, since individual algal cells experience varying degrees of light limitation as they move up and down within the water column. Nevertheless, the phytoplankton community as a whole may become limited by light under certain combinations of mixing depth, nutrient availability and background turbidity (Ptacnik *et al.*, 2003; Berger *et al.*, 2006; Dickman, Vanni & Horgan, 2007). Light limitation may be evaluated by comparing the onset of light saturation (I_k) (Talling, 1957) with the mean light level averaged over the mixing layer (I_{mean}) (Ferrero *et al.*, 2006): the lower the ratio of I_{mean}/I_k, the higher the probability for the system to be limited by light (although particular mixing regimes may alleviate the extent of light limitation (Neale, Helbling & Zagarese, 2003 and references therein). An alternative approach was adopted by Scheffer (1998, p. 89), who examined field patterns of vertical light attenuation and mean lake depth and suggested that light limitation is likely to occur when the optical density of the mixed layer (i.e. the product of the light attenuation coefficient and mixing depth) approaches or exceeds 16. Published examples of light limited aquatic environments include: nutrient rich, eutrophic lakes (Visser *et al.*, 1996; Phlips *et al.*, 2000); turbulent waters, where non-photosynthetic particulates are responsible for much of their turbidity, such as estuaries and shallow coastal areas, and silt-rich lakes (Kromkamp & Peene, 1995; Cloern, 1999); humic lakes, where dissolved organic matter accounts for a large proportion of light absorption (Nürnberg & Shaw, 1998); and large, deep, wind-exposed lakes, that develop deep epilimnia, in which the water itself contributes much to light absorption (Soto, 2002).

In a previous study (Torremorell *et al.*, 2007), we suggested that the light-limited theory (Scheffer, 1998; Huisman *et al.*, 2002) provides a convenient theoretical framework to interpret the seasonal patterns of suspended particulates in a large, shallow lake (Laguna Chascomús, Argentina). Here, we present results obtained during a subsequent annual period. We relate the patterns of suspended particulates, phytoplankton biomass and water transparency with the seasonal pattern of incident solar radiation. We also report the seasonal trends of phytoplankton PP and photoinhibition of photosynthesis.

Methods

Study site

Laguna Chascomús (35°36′S 58°W) is a large (area = 30.1 km^2), shallow lake (mean depth *c.* 1.9 m) located in the Pampa region of Argentina. It belongs to the river Salado catchment, a large (801 km^2) floodplain area characterized by a poorly developed drainage. Climate is warm temperate, with mean annual temperature ranging from 13 to 16 °C, and an annual precipitation of about 900 mm year^{-1} (Iriondo & Drago, 2004) Laguna Chascomús is a eutrophic, alkaline lake (Conzonno & Claverie, 1990) which is constantly mixed by the persistent wind shear (Torremorell *et al.*, 2007). The biotic community of Laguna Chascomús is extremely rich and diverse, including hundreds of microbial (autotrophic and heterotrophic) species, zooplankton grazers and over 20 species of fish.

Weather and solar radiation measurements

Atmospheric pressure, temperature, humidity, rainfall and wind direction and speed were constantly recorded by a weather station located near the shore of Laguna Chascomús. During PP measurements, solar radiation was recorded on site, using an Eldonet radiometer (Real Time Computers, Inc., Erlangen, Germany). In addition, daily solar radiation was recorded with a GUV 511 radiometer (Biospherical

Instruments, Inc., San Diego, CA, U.S.A.) located in Buenos Aires city (c. 100 km northeast from Laguna Chascomús). Both radiometers measured broadband (400–750 nm) photosynthetically active radiation (PAR) and ultraviolet radiation (UVR). The GUV 511 has four narrow channels in the UV region, centered at 305, 320, 340 and 380 nm; while the Eldonet has two broad band channels, one for UVA (315–400 nm) and another for UVB (280–315 nm).

Lake sampling and chemical analyses

Laguna Chascomús was sampled every two weeks from July 2005 to September 2006. Subsurface water samples were collected at a central point of the lake using a van Dorn bottle and transported in 10 L polypropylene containers. Routine measurements of lake depth, water temperature, pH (Orion pH-meter; ATI Orion, VWR Scientific, Boston, MA, U.S.A.), conductivity (Hach conductimeter; Hach Company, Loveland, CO, U.S.A.) and Secchi disc readings were measured *in situ*. Dissolved oxygen concentration was measured using a YSI 5000 meter; YSI Incorporated, Dayton, OH, U.S.A.

Vertical profiles of downward irradiance (350–750 nm) were obtained with a spectroradiometer (USB2000, Ocean Optics, Dunedin, FL, U.S.A.) attached to a fibre optic probe. Profiles were performed at noon inside a ($50 \times 50 \times 40$ cm) black container filled with freshly collected lake water. This procedure was adopted to increase the accuracy of the measurements by eliminating the noise due to wave action observed in *in situ* profiles. Diffuse vertical attenuation coefficients for PAR, kd_{PAR}, were calculated by regressing log-transformed irradiance measurements against depth.

Nutrient concentrations were estimated from filtered (Whatman GF/F, Whatman International Ltd., Maidstone, England) water samples. Total phosphorus (TP), nitrate, nitrite and ammonia were estimated following APHA (1998). Organic nitrogen (N_{org}) was determined by semi-micro-Kjeldahl method (APHA, 1998). Total suspended solids (TSS) were estimated after filtration onto weighed and precombusted GF/F filters, dried until constant weight at 103–105 °C (APHA, 1998). Chlorophyll-*a* (Chl-*a*) concentration was determined by acetone extraction (Lopretto & Tell, 1995). Alkalinity was determined by titration with 0.1 N H_2SO_4 (APHA, 1998).

Micro and nano-phytoplankton determination and quantification

Phytoplankton samples were collected with a 15-μm net and preserved in 4% formalin for later qualitative analyses. Quantitative algal samples were collected directly from the lake into PVC flasks and preserved with 1% acidified Lugol's iodine solution. Counts were performed according to Utermöhl (1958). Replicate chambers were allowed to sediment for a minimum of 24 h. A maximum counting error of 20% was accepted in estimating the abundance of each major algal group (Venrick, 1978). In all cases individuals were counted, and for colonial or filamentous algae the size and/or number of cells corresponding to a standard individual was established. Species diversity (Shannon & Weaver, 1949), species evenness (Pielou, 1977) and species richness were calculated. Phytoplankton biomass was estimated by calculating species biovolume following the criteria and formulae proposed by Hillebrand *et al.* (1999). Biovolume was estimated based on cell dimensions measured obtained previously from Pampean shallow lakes.

Phytoplankton primary production

On each sampling date, production versus irradiance curves (*P* versus *I*) were estimated from outdoor incubations, using the ^{14}C technique (Steeman-Nielsen, 1952). Lake water aliquots were placed into acid-washed quartz tubes (45 mL capacity) and inoculated with 1 μCi labelled sodium bicarbonate incubations were performed during 3 h around noon within a water bath. Two series of parallel incubations were performed: (i) full solar spectrum (PAR + UV incubations) and (ii) solar spectrum without UVR (PAR incubation). In the PAR incubations, the UV wavelengths were excluded by covering the tubes with 3 mm thick polycarbonate sheet (cutoff c. 395 nm). For each series of incubations, eight different light intensities (transmittance ranging from 100% to <2%) were obtained by covering the tubes with different layers of neutral density filters. In addition, one tube was wrapped in aluminum foil and served as a dark control. All treatments were run in two replicates. At the end of the incubation, samples were filtered onto Whatman GF/F glass fibre filters. The filters were subsequently placed in 4 mL scintillation vials in an

HCl-saturated atmosphere and allowed to dry overnight. The activity was measured in a scintillation counter (Beckman LS 5000TD, Fullerton, CA, U.S.A.) after adding 2.5 mL of OptiPhase 'HiSafe'3 scintillation solution (Holm-Hansen & Helbling, 1995).

The photosynthetic parameters for the PAR treatment were estimated from *P* versus *I* curves by fitting an exponential model (Platt, Gallegos & Harrison, 1980):

$$P = P_S \times \left(1 - e^{\frac{-\alpha \cdot I}{P_S}} \right) \times e^{\frac{-\beta \cdot I}{P_S}} \qquad (1)$$

where *P*, the photosynthetic rate at a given irradiance *(I)*; P_S, the maximum light-saturated photosynthetic rate; α, the photosynthesis light efficiency at sub-saturating irradiances; β, corresponds to the negative slope of the curve at high PAR irradiance (i.e. photoinhibition). In addition, the onset of light saturation ($I_k = P_S/\alpha$) and the index of photoinhibition by PAR ($I_\beta = P_S/\beta$) (Harrison & Platt, 1986) were derived from the parameterized equation.

The photoinhibition due to ultraviolet radiation was estimated from the PAR + UV curve, which was fitted to the following model:

$$P = P_S \times \left(1 - e^{\frac{-\alpha \cdot I}{P_S}} \right) \times e^{\frac{-\beta \cdot I}{P_S}} \times \frac{a}{a + UV^b} \qquad (2)$$

In this case, P_S, α and β were substituted by the values obtained for the PAR curve, while the con-

stants '*a*' and '*b*' were estimated by nonlinear regression. From eqns 1 & 2, we estimated the index of photoinhibition by UV (UV_{50}) as the UVA irradiance required to reduce PP by 50% as compared to the PAR curve (see Table 1 and Fig. 1 for definitions and units).

For assessing the degree of light limitation in Laguna Chascomús, we compared the onset of light saturation (I_k) to the depth-averaged light intensity ($I_{mean-noon}$) as:

$$I_{mean-noon} = \frac{I_{0-noon} \times e^{-kd_{PAR} \cdot Z}}{kd_{PAR} \cdot Z} \qquad (3)$$

where I_{0-noon}, the incident PAR irradiance, kd_{PAR}, the attenuation coefficient of PAR; *Z*, the average lake depth. In this case, the I_{0-noon} value corresponds to the 2-h period around noon. It was noted that this is a very stringent condition, then if $I_{mean-noon} < I_k$, we can be sure that the lake is limited by light at any other time of the day (Knoll, Vanni & Renwick, 2003).

The daily integrated phytoplankton PP was estimated using the full model (eqn 2). For each sampling date, calculations were made using the parameterized model corresponding to that day, and the mean daily PAR and UVR irradiances averaged over the whole water column. For the days between sampling dates, we used a parameterized model

Table 1 Symbols and units used in the text

| Name	Definition	Unit
Optical properties		
I_0	Mean daily PAR incident irradiance	W m^{-2}
I_{mean}	Mean water column irradiance	W m^{-2}
$I_{mean-noon}$		W m^{-2}
I_{out}	Irradiance reaching lake bottom	W m^{-2}
PAR	Photosynthetic active radiation (400–700 nm)	
UV-A	Ultraviolet radiation (320–400 nm)	
SD	Secchi disc	m
kd_{PAR}	Vertical PAR diffuse attenuation coefficient	m^{-1}
Primary production parameters		
P^b	Fixation rate	mg C mg^{-1} Chl h^{-1}
P_s^b and P_{max}^b	P_s, the maximum, potential, light-saturated photosynthetic rate. When $\beta = 0$, $P_s \cong P_{max}$	mg C mg^{-1} Chl h^{-1}
α^b	Light limited slope, photosynthesis efficiency at sub-saturating irradiances	mg C mg^{-1} Chl h^{-1} W^{-1} m^2
β^b	Negative slope at high irradiance characterizing photoinhibition	mg C mg^{-1} Chl h^{-1} W^{-1} m^2
^{b}superscript	Denoted Chl-*a* normalization	
I_k	Onset of light saturation. $I_k = (P_S/\alpha)$	W (PAR) m^{-2}
I_β	Index of photoinhibition by PAR. $I_\beta = (P_S/\beta)$	W (PAR) m^{-2}
UV_{50}	Index of photoinhibition by UVR	W (UVA) m^{-2}
PP	Daily areal primary production	g C m^{-2} day^{-1}
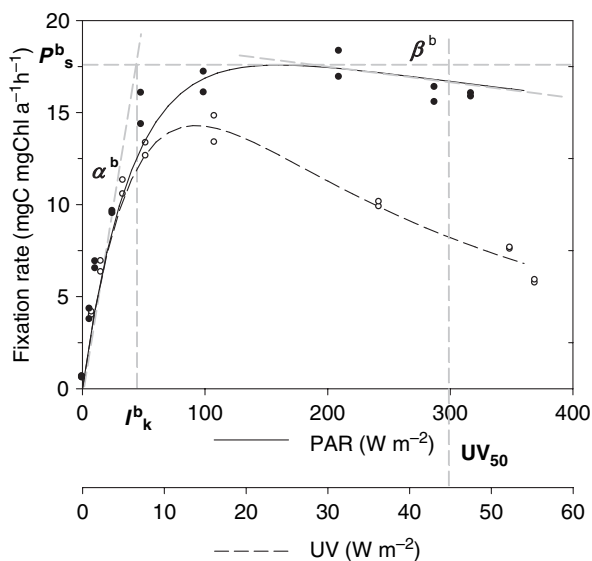
Fig. 1 Example of *P* versus *I* curves obtained with PAR (filled circles) and PAR plus UVR (open circles) treatments. Photosynthetic parameters are indicated in the figure.

corresponding to the previous sampling date, but the PAR and UVR irradiances corresponding to the actual day. The annual phytoplankton PP was estimated as the sum of the daily estimates over the entire year.

Statistical analyses

Simple and multiple linear regression analyses were performed to investigate the relationships between biological response variables (seston concentration, phytoplankton biovolume, phytoplankton PP, photoinhibition indexes) and potential external forcing variables [mean incident daily irradiance (I_0) and wind speed]. We also used this approach to relate underwater optical properties to TSS, phytoplankton biovolume and Chl-*a*. Here we assumed that instantaneous measurements of optical properties were controlled by the water content of TSS, phytoplankton biovolume and Chl-*a*, and not vice versa. This, of course, is not true over longer time-scales.

Mean incident daily irradiance (I_0) corresponds to irradiance measurements averaged over the 24 h prior to sampling, whereas wind values correspond to the average wind speed over the 9 h before sampling [$W_{speed}^{(9\,h)}$]. The choice of these time windows is preliminary since we have not conducted a thorough time-series analysis, but produced reasonable fits to the data.

Before each analysis, Kolmogorov–Smirnov test and Spearman's rank correlation were run to test data for normality and homoscedasticity respectively. Whenever necessary, the raw data were transformed to meet the assumptions of the statistical model. When multiple linear regressions were applied, a stepwise, backward procedure was performed in order to identify the variables that contributed the most to explain the variance in the dependent variable.

Results

During the study period the maximum depth of Laguna Chascomús varied between 1.72 and 2.16 m, but remained below the overflow (*c.* 3.3 m; Torremorell *et al.*, 2007). Water temperature varied seasonally, with maximum and minimum values recorded during summer and winter, respectively, while dissolved oxygen concentration showed the opposite pattern (data not shown). The pH was typically alkaline and conductivity values were always high, and both showed little variation through the year. TP and nitrogen concentrations were within the eutrophic to hypereutrophic range. Accordingly, the Chl-*a* concentration was high and also within the hypereutrophic range. The average annual wind speed was high (*c.* 10 km h^{-1}) and tended to be slightly higher in spring and summer (data not shown). The mean daily incident PAR irradiance ranged from 22 to 162 W m^{-2} (Table 2).

Eighty-eight different algal entities, including species and varieties of microphytoplankton and nanophytoplankton were recorded. In terms of species richness, Chlorophyceae were best represented (38 taxa), followed by Cyanobacteria (22 taxa) and Bacillariophyceae (15 taxa). The remaining taxa belonged to the classes Zygophyceae, Euglenophyceae, Xanthophyceae and Cryptophyceae. Considering the structure of the algal assemblage, the phytoplankton community mainly comprised colonies formed by small cells of *Aphanocapsa delicatissima* W. West & G. S. West, co-occurring with filamentous Cyanobacteria (i.e. *Planktolyngbya contorta* Lemmermann and *P. limnetica* Lemmermann), small chlorococcales (i.e. *Monoraphidium* spp. and *Scendesmus* spp.) and the diatom *Synedra berolinensis* Lemmermann. Total algal density ranged from 210×10^3 to 616×10^3 ind mL^{-1} (Table 2). Quantitatively,

Table 2 Mean values and range of main physical, chemical and biological parameters, measured during the study period

Parameters	Mean	Minimum	Maximum
Physical and chemical parameters			
Temperature (°C)	15.4	7.0	23.3
DO (mg L^{-1})	9.2	5.1	13.8
Wind speed (daily average) (km h^{-1})	9.4	3.5	14.6
$W_{speed}^{(9h)}$ (average 9 h before sampling) (km h^{-1})	7.6	1.4	16.4
I_0 mean daily incident PAR irradiance (W m^{-2})	77	22	162
pH	8.9	8.4	9.2
Conductivity (mS cm^{-1})	1.7	1.4	1.9
Alkalinity ($\mu E\ L^{-1}$)	6787	5095	8325
Z_{mix} (water column level) (m)	1.9	1.7	2.2
Seston (TSS) (mg L^{-1})	227	75	536
Areal TSS (g m^{-2})	439	133	1099
kd_{PAR} (m^{-1})	23	10	36
SD (m)	0.1	0.1	0.2
Optical density	45	19	74
I_{mean} (PAR) (W m^{-2})	1.7	0.5	3.2
$I_{mean-noon}$ (PAR) (W m^{-2})	5.3	1.1	9.7
I_{mean} (UV-A) (W m^{-2})	0.1	0.2	0.0
TN (mg L^{-1})	1.0	0.5	2.4
TP (mg L^{-1})	0.5	0.3	0.8
Biological parameters			
Chl-*a* ($\mu g\ L^{-1}$)	257	122	516
Phytoplanktonic biovolume (phyto-biovolume) (mm^3 mL^{-1})	0.37	0.15	0.65
Phytoplanktonic density (10^3 ind mL^{-1})	395	211	617
Cyanobacteria (10^3 ind mL^{-1})	251	135	435
Chlorophyceae (10^3 ind mL^{-1})	111	48	316
Bacillariophyceae (10^3 ind mL^{-1})	29	8	104
Species diversity (Shannon–Weaver)	2.8	2.2	3.4
Richness (number of species)	26	19	37
Daily areal PP (g C m^{-2} day^{-1})	8.5	2.7	16.6

DO, dissolved oxygen; PAR, photosynthetically active radiation; TSS, total suspended solid; TN, total nitrogen; TP, total phosphorus; Chl-*a*, chlorophyll-*a*; PP, primary production.

A. delicatissima dominated phytoplankton density during most of the study period, except on 15 November 2005 when *Monoraphidium minutum* Nägeli (Chlorophyceae) was the dominant species. Phytoplankton biovolume ranged from 0.15 to 0.65 mm^3 mL^{-1}. Overall, Cyanobacteria comprised more than 50% of the biovolume, followed by Chlorophyceae and Bacillariophyceae. The seasonal trends of phytoplankton density and biovolume (Fig. 2a) were similar and both peaked by early spring instead of midsummer. Interestingly, this pattern and that of the incident solar radiation appears to be offset by roughly two months, with the fluctuations in phytoplankton biovolume preceding the pattern of solar radiation (Fig. 2a). The TSS concentration displayed a marked seasonal pattern that tracked the variations in incident solar radiation (Fig. 2b). Significant positive relationships were obtained for TSS concentration and ln of I_0 (Table 3). Adding wind speed (as a potential driver of sediment resuspension) to the regression model did not significantly improve the fit ($P > 0.5$).

The mean daily PP averaged for the set of 23 sampling dates was 8.5 g C m^{-2} day^{-1} (±4.2 SD) (Table 2). The annual PP of Laguna Chascomús, estimated on the basis of daily irradiance measurements, was 2835 g C m^{-2} year^{-1}. The maximum values of PP occurred in late spring (16.6 g C m^{-2} day^{-1}) and early summer, while the minimum occurred in winter (2.7 g C m^{-2} day^{-1}). A significant positive relationship was observed between PP and I_0 ($R^2 = 0.51$) (Table 3, Fig. 2c).
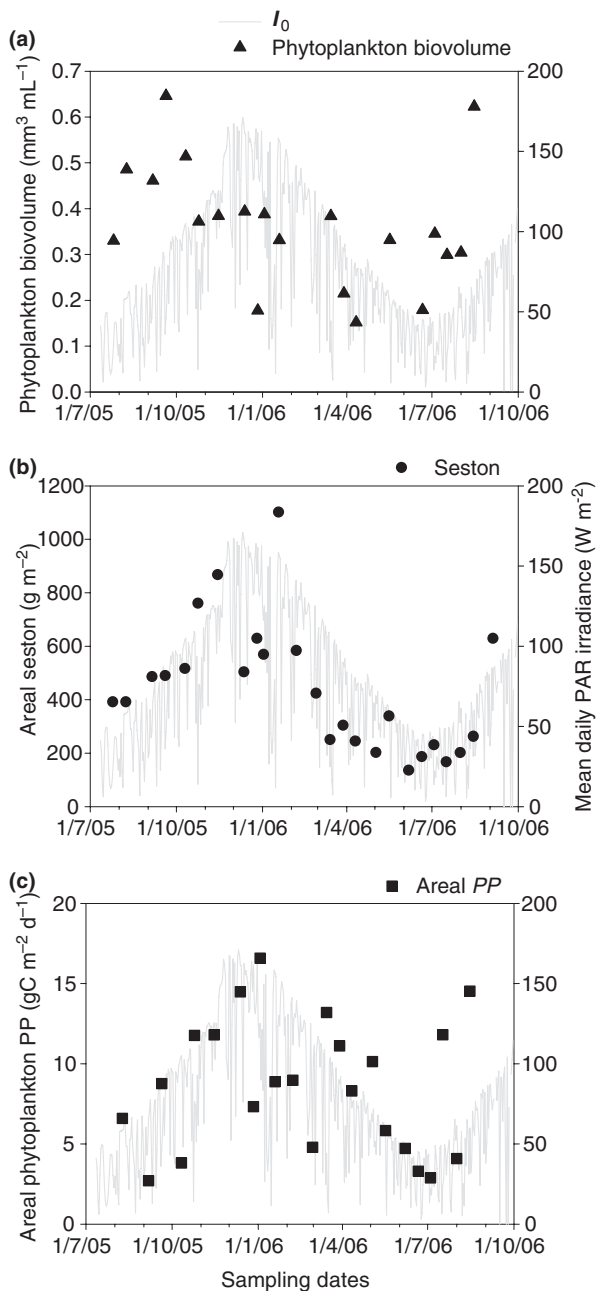
Fig. 2 The development during the study period of (a) phytoplankton biovolume, (b) seston and (c) phytoplankton primary production. The faint solid line represents the daily incident PAR irradiance, averaged over 24 h.

The photosynthetic parameters that describe the behaviour of PP at low light intensities varied haphazardly over the year, without displaying clear seasonal trends. The maximum, potential photosynthetic rate, P_s^b, averaged 12.2 mg C mg^{-1} Chl h^{-1} (range: 4.7–27.5 mg C mg^{-1} Chl h^{-1}) (Table 4).

The light-limited photosynthetic efficiency, α^b, averaged 0.5 mg C mg^{-1} Chl h^{-1} W^{-1} m^2 (range: 0.2–1.4 mg C mg^{-1} Chl h^{-1} W^{-1} m^2). The onset of light saturation (I_k) ranged between 15.4 and 34.4 W m^{-2}, and was the least variable parameter, with a coefficient of variation of only 21%.

In contrast, the photosynthetic parameters that describe the behaviour of PP at high light intensities showed marked seasonal trends that correlated with the levels of incident solar radiation (Fig. 3). The index of photoinhibition by PAR, I_β, averaged 745 W m^{-2} (range: 179–2295 W m^{-2}) and was significantly positively explained by the incident solar radiation ($r^2 = 0.73$) (Table 3). On the other hand, the index of photoinhibition by UV, UV_{50}, averaged 25.2 W m^{-2} (range: 7.5–73.8 W m^{-2}) (Table 4) and was significant positively explained by the incident solar radiation ($r^2 = 0.74$) (Table 3).

The vertical diffuse attenuation coefficient for PAR, kd_{PAR}, remained high during the whole study period (average: 23.2 m^{-1} ± 7.0 SD) (Fig. 4, Table 2), which translated into estimated euphotic depths that ranged from 0.13 to 0.44 m. In addition, Secchi disc averaged 0.11 m (±0.28 SD) and optical density presented elevated values, with a mean value of 44 (±15 SD) and a range of 19 (in winter) to 74 (in summer) (Table 2). These values of transparency correspond to extremely turbid waters. Moreover, the mean light intensity averaged over the lake depth for the period of maximum irradiance (i.e. the 2-h around noon), ($I_{mean-noon}$) varied between 1.1 and 9.7 W m^{-2} and was always lower than the onset of light saturation, I_k (Table 2, Fig. 5). This confirmed that phytoplankton PP in Laguna Chascomús was permanently limited by light.

As regards the under-water optical climate of Laguna Chascomús, differences in Secchi disc readings were significant and negatively explained by I_0 ($R^2 = 0.47$, Table 3). On the other hand, kd_{PAR} and the mean light intensity averaged over the whole water column, I_{mean}, were significantly and positively related to I_0 ($R^2 = 0.55$ and 0.66, respectively; Table 3). In addition, the irradiance reaching lake bottom, I_{out}, significantly decreased with increasing incident solar radiation ($R^2 = 0.48$, Table 3). Variations in water transparency, expressed as kd_{PAR}, were positively and significantly explained by the concentration of TSS ($R^2 = 0.59$, Table 3).

Table 3 Summary and statistics of linear regression models

Dependent	Independent	Model equation	n	R^2	P-value
TSS	l_0 and $W_{\text{speed}}^{(9\,\text{h})}$	$\text{TSS} = -327.81 + 132.07 \times \ln l_0$	25	0.39	<0.001
Areal TSS	l_0 and $W_{\text{speed}}^{(9\,\text{h})}$	$\text{Areal TSS} = -657.43 + 260.85 \times \ln l_0$	25	0.37	0.001
Areal PP	l_0	$\text{Areal PP} = 3.00 + 0.07 \times I_0$	23	0.51	<0.001
I_β	l_0	$I_\beta = -453.62 + 15.51 \times I_0$	25	0.73	<0.001
UV_{50}	l_0	$\text{UV}_{50} = 3.68 + 0.25 \times I_0$	24	0.74	<0.001
SD	l_0	$\text{SD} = 14.49 – 0.05 \times I_0$	25	0.47	<0.001
$k\text{d}_{\text{PAR}}$	l_0	$k\text{d}_{\text{PAR}} = 14.20 + 0.12 \times I_0$	22	0.55	<0.001
I_{mean}	l_0	$I_{\text{mean}} = 0.75 + 0.01 \times I_0$	22	0.66	<0.001
I_{out}	l_0	$\ln I_{\text{out}} = -22.77 – 0.23 \times I_0$	22	0.49	<0.001
$k\text{d}_{\text{PAR}}$	TSS	$k\text{d}_{\text{PAR}} = 13.401 + 0.0456 \times \text{TSS}$	24	0.59	<0.001

TSS, total suspended solid; PP, primary production; SD, Sacchi disc.

Table 4 Photosynthetic parameters obtained form P versus I curves during the study period

Sampling date	P_s^b	α^b	β^b	I_k	I_β	UV_{50}
26/07/05	5.1 (±0.2)	0.3 (±0.0)	n/e	15.4	n/e	8.8
09/08//05	12.0 (±1.4)	0.7 (±0.1)	0.03 (±0.01)	18.2	364	15.5
06/09/05	20.5 (±4.4)	0.8 (±0.1)	0.06 (±0.04)	27.1	331	18.0
20/09/05	10.4 (±4.3)	0.5 (±0.1)	0.02 (±0.02)	19.2	647	73.8
11/10/05	21.4 (±2.1)	0.8 (±0.1)	0.02 (±0.01)	26.1	930	28.8
25/10/05	7.9 (±1.8)	0.3 (±0.1)	0.01 (±0.01)	28.9	1123	26.0
15/11/05	13.9 (±1.2)	0.5 (±0.1)	0.01 (±0.01)	26.4	1154	24.7
13/12/05	14.1 (±2.5)	0.6 (±0.1)	0.01 (±0.01)	25.5	2020	42.1
27/12/05	14.5 (±1.4)	0.7 (±0.1)	0.01 (±0.01)	21.2	2066	42.5
03/01/06	18.4 (±2.4)	0.7 (±0.1)	0.01 (±0.01)	28.2	2295	46.7
19/01/06	21.5 (±2.3)	0.8 (±0.1)	0.01 (±0.01)	26.7	1794	40.0
07/02/06	6.5 (±0.7)	0.3 (±0.0)	0.00 (±0.00)	25.7	1628	42.1
28/02/06	10.0 (±1.6)	0.4 (±0.1)	0.02 (±0.02)	23.0	455	18.6
15/03/06	9.8 (±1.9)	0.4 (±0.1)	n/e	24.6	n/e	31.0
29/03/06	27.5 (±3.1)	1.4 (±0.2)	0.05 (±0.02)	19.8	561	28.2
11/04/06	14.0 (±2.3)	0.6 (±0.1)	0.01 (±0.02)	22.3	1075	25.0
03/05/06	10.6 (±3.2)	0.6 (±0.1)	0.06 (±0.04)	19.1	179	12.8
17/05/06	10.8 (±2.4)	0.6 (±0.1)	0.01 (±0.02)	19.0	833	14.2
07/06/06	6.9 (±1.8)	0.3 (±0.2)	n/e	22.8	n/e	10.1
21/06/06	4.8 (±1.0)	0.2 (±0.0)	n/e	20.0	n/e	12.0
04/07/06	5.5 (±2.7)	0.3 (±0.0)	n/e	21.0	n/e	13.3
17/07/06	12.3 (±4.1)	0.4 (±0.1)	n/e	32.2	n/e	7.5
01/08/06	4.7 (±0.7)	0.3 (±0.0)	0.01 (±0.01)	15.9	430	9.3
15/08/06	10.6 (±2.2)	0.3 (±0.0)	0.03 (±0.02)	34.4	341	16.4
05/09/06	11.4 (±1.3)	0.6 (±0.1)	0.03 (±0.01)	18.7	394	22.2

See Table 1 for explanation of symbols and units.
n/e, not estimated due to low irradiance levels, particularly in winter.

Discussion

Previous studies (Izaguirre & Vinocur, 1994; Torremorell *et al.*, 2007) concluded that Laguna Chascomús is a highly turbid, well mixed waterbody. The lake has high nutrient and Chl-*a* concentrations. All these elements suggested that the lake was light-limited, at least during most of the day year^{-1}. In addition, the dynamics of suspended particulates has been shown to be consistent with the expectations of the light-limited chemostat theory. In the present study, we examined the dynamics of suspended particulates and the patterns of PP in more detail during an additional annual period (2005–06).
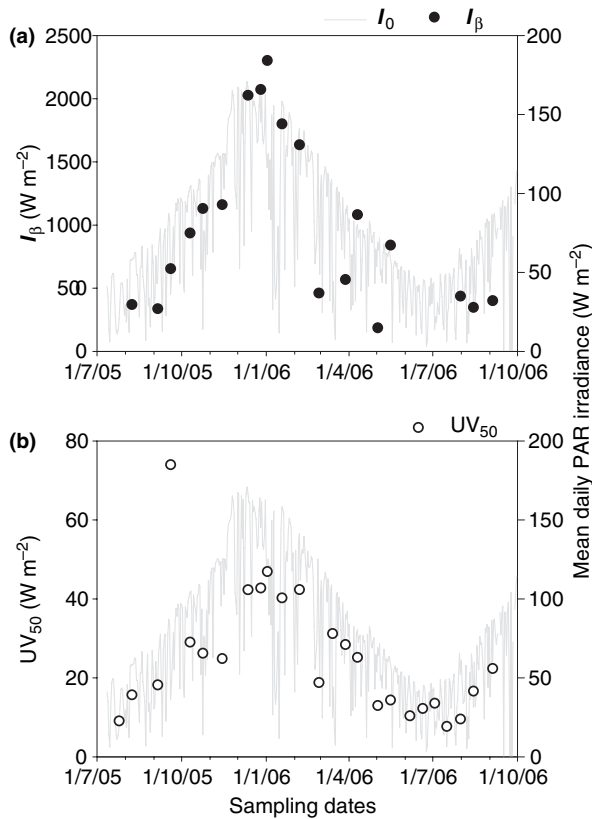
Fig. 3 The development during the study period of (a) photo-inhibition index by PAR (filled circles) and (b) photoinhibition index by UVR (open circles). The faint solid line represents the daily incident PAR irradiance, averaged over 24 h.
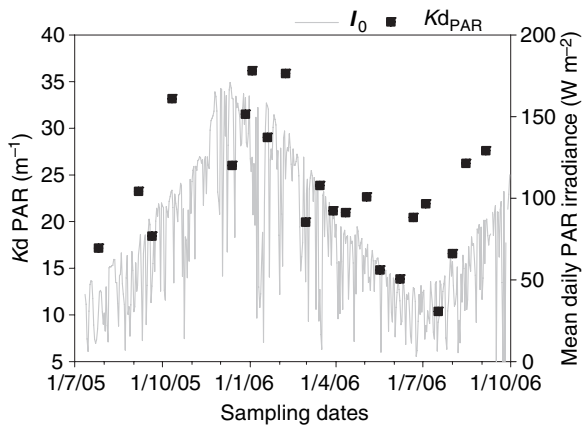

Fig. 4 The development during the study period of PAR attenuation coefficient during the study period. The faint solid line represents the daily incident PAR irradiance, averaged over 24 h.

Several pieces of evidence indicated that conditions of light limitation persisted during this period. First, we found that the mean irradiance averaged over the
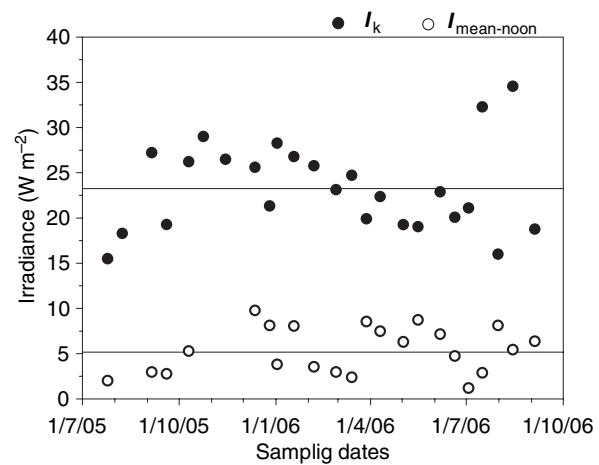

Fig. 5 Mean water column irradiance estimated for the 2-h period around noon ($I_{mean-noon}$) and onset of light saturation (I_k) during the study period. Mean values for each variable are indicated in the figure as horizontal solid lines.

mixing layer ($I_{mean-noon}$) estimated for the time of the day of maximum irradiance (i.e. 2 h around noon) was always lower than the measured onset of light saturation (I_k) (Fig. 5). In fact, $I_{mean-noon}$ was on average 4.4 times lower than I_k and this factor increases sharply at either side of the local noon. Secondly, the analysis of P versus I curves provides indirect evidence for light limitation. We found that the P_s^b values were always high and varied haphazardly over the year. In addition, the results of a preliminary experiment (E. Chornomaz & H.E. Zagarese, unpubl. data) showed that additions of inorganic P failed to stimulate phytoplankton PP. Finally, the optical density of Laguna Chascomús ranged from 19 to 74; so was 1.1- to 4.6-fold higher than the value of 16 suggested by Scheffer (1998) as indicating limitation by light. Although we cannot rule out the possibility that the phytoplankton experienced a certain level of nutrient limitation, particularly when the algae are close to the water surface, the collected evidence suggests a strong role of light in limiting the average phytoplankton PP.

In general, the condition of light limitation is maintained through a negative feedback loop involving phytoplankton growth as a function of available light. An increase in light availability stimulates phytoplankton PP. As the periods of maximum phytoplankton PP coincide with the maxima in TSS, we hypothesize that the latter are directly (phytoplankton biovolume) or indirectly (detritus and

heterotrophic microorganisms) derived from algae photosynthesis. The resulting higher TSS translates into increased light attenuation, which eventually lowers the available light for phytoplankton photosynthesis. Thus, if the incoming radiation is higher, a higher level of turbidity can be tolerated (Scheffer, 1998). Although the previous feedback is probably key to maintaining the state of light limitation, other elements contributing to the attenuation of light may affect the concentration and dynamics of the phytoplankton community. For example, an increase in background attenuation (i.e. the fraction of the total photons absorbed by non-algal components, such as water, dissolved organic matter, non-algal particulates) must be compensated by a comparable decrease in phytoplankton attenuation, in such a way that the mean available light averaged over the mixing layer remains the same (Scheffer, 1998). Background attenuation could also increase due to sediment resuspension by wind. However, although that possibility appears quite likely, particularly on windy days, our regression analysis did not identify wind as a significant source of TSS (Table 3).

The results obtained in this study are consistent with a light limitation scenario in Laguna Chascomús. The diffuse attenuation coefficient (kd_{PAR}, a reciprocal measure of water transparency) increased with incident solar radiation (I_0) (Fig. 4; Table 3). In addition, the mean light intensity averaged over the mixing layer (I_{mean}, Table 3) increased with the incident irradiance; while the irradiance reaching the lake bottom, I_{out} decreased with incident irradiance. The kd_{PAR} in Laguna Chascomús is mostly controlled by the amount of TSS, which also increased with incident irradiance (I_0) (Fig. 2b). Interestingly, neither Chl-*a* nor phytoplankton biovolume contributed significantly to explain water transparency.

On the other hand, the phytoplankton biovolume maxima were not coincident with the time of the year of maximum irradiance. In fact, the highest phytoplankton biovolume values occurred roughly 2 months before the summer solstices in both years (Fig. 2a). It is well known that maxima and minima of numbers and biomass of phytoplankton are often out of phase with rates of PP (Wetzel, 2001). At present we do not have a full understanding of the phytoplankton dynamics in Laguna Chascomús. Grazing by herbivorous zooplankton and mussels could influence

the observed pattern of biovolume, as well as contributing to the increase in background light attenuation (the fraction of total attenuation not accounted for by phytoplankton). In fact, an analysis of the optical properties of lake water showed that the contribution of non-chlorophyllous particulates to total absorption is maximum in summer and minimum in wintertime (G.L. Pérez, unpubl. data). Thus, we emphasize that, regardless of the asynchronous pattern displayed by phytoplankton biovolume, PP was closely related to the amount of incident solar radiation.

In laboratory-scale model systems (light-limited chemostat) the so-called critical light intensity, i.e. the amount of light exiting the algae culture chamber (I_{out}), is an important parameter for describing the steady-state condition. In Laguna Chascomús this parameter could not be directly measured as it fell well below the detection limit of any radiometer. However, I_{out} estimates based on kd_{PAR} and depth showed an inverse exponential relationship with I_0 (Table 3).

When expressed on an area basis, Laguna Chascomús has an annual PP of 2835.2 g C m^{-2} year^{-1}, which is extremely high (Takamura *et al.*, 1989) and is only attained in hypereutrophic lakes. The analysis of the responses of phytoplankton PP at low light levels showed little variability and an absence of seasonal trends. In particular, the onset of light saturation, I_k, showed little variability during the whole year (Fig. 5). The estimated I_k values were at the low extreme of the range reported for other phytoplankton communities (Reynolds, 2006), and are similar to those typical of populations growing in low light environments (Brightman & Smith, 1989 and references therein). Nevertheless, the I_k estimates were always higher than the depth-averaged irradiance for the best illuminated time of the day ($I_{mean-noon}$). Considering the extreme degree of light limitation prevailing in Laguna Chascomús, the low I_k values may be interpreted as an adaptive strategy in response to the low light levels that algal cells experience during the best part of their life cycle.

On the other hand, the parameters that describe the photosynthetic responses to high solar irradiances displayed marked seasonal trends. The indexes of photoinhibition by PAR and UVR increased with incident solar irradiance (Fig. 3), indicating that

the autotrophic community becomes more tolerant to photoinhibiting levels of solar radiation as the incident radiation increases. This may be interpreted as a strategy to counteract the photoinhibitory effects of high radiation levels experienced during the short periods of time that the cells spend near the surface, and has very interesting ecological implications. First, it provides a demonstration that UVR affects phytoplankton PP, even in extremely turbid lakes, in which the UV component of solar radiation is removed within the first few centimetres of water column. Secondly, it is a strong indication that the algae do not respond solely to the average irradiance (notice that I_{mean} was always much lower than onset of photoinhibitory radiation), but that they also perceive the vertical light gradient and adapt in response to it. As the phytoplankton assemblage did not display significant variability in species composition during the annual period, the seasonal trend in photosynthesis photoinhibition could have resulted from physiological adaptations of the cells. However, since it is known that mixing may affect the responses of the phytoplankton community to light (Neale *et al.*, 2003), an important caveat to our previous discussion is that all our incubations were performed using a static array of tubes. Nevertheless, as all incubations were performed using the same protocol, the observed changes in photosynthetic parameters reveal a true seasonal response of the algae community, even though its magnitude and impact on the lake PP remains to be evaluated.

Our study demonstrated that light limitation provides a convenient framework for understanding the functioning of shallow, well mixed and highly turbid environments, such as Laguna Chascomús. This concept increases our understanding of these highly complex environments and reaffirms the importance of energy fluxes. It also has important practical implications for lake management, since it suggests that highly turbid systems, such as Laguna Chascomús, may be relatively insensitive to increases in nutrient loads, which on average appear to be in excess. In contrast, turbid systems may be more seriously affected by increases in coloured organic matter loads, which may also represent an important external energy subsidy that may eventually decouple the fine-tune control that solar radiation has on the microbial plankton community.

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