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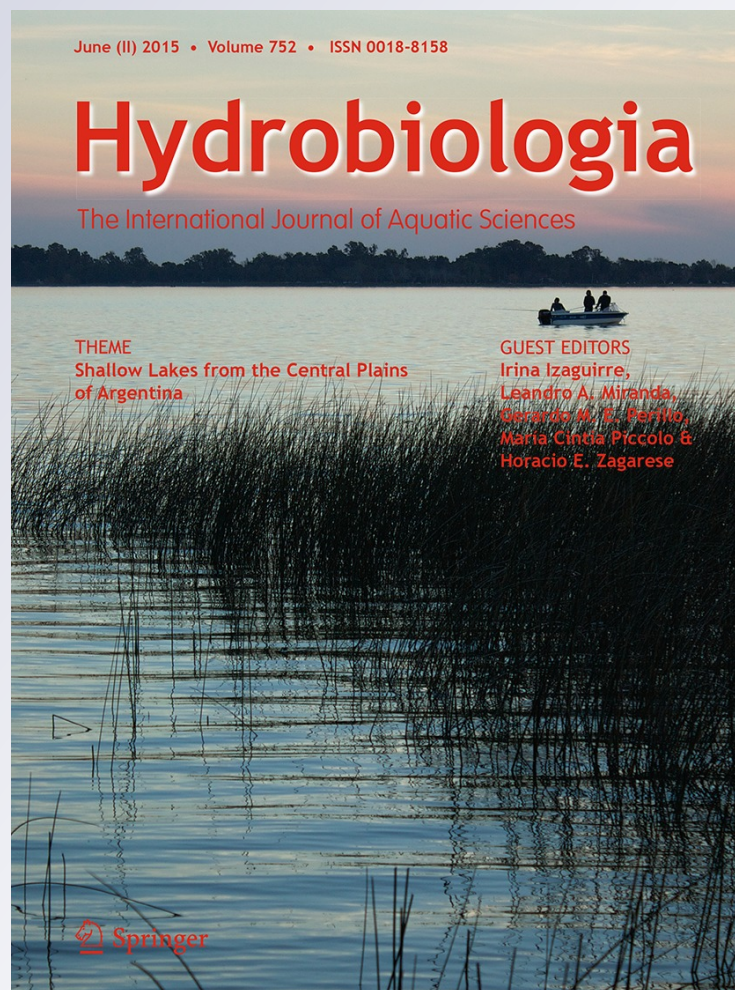
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Light limitation helps stabilize the phytoplankton assemblage steady-state in a temperate and highly turbid, hypertrophic shallow lake (Laguna Chascomús, Argentina)

Clara M. Iachetti · María Eugenia Llames

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Abstract We performed a 30-month field study in a highly turbid, hypertrophic shallow lake from the Pampa Plain (Argentina) in order to investigate the occurrence of steady-state phases of phytoplankton, with an emphasis on the effect of subtle, but measurable, increase in light availability. The results revealed that a steady-state condition prevailed during the first 14 months, during which *Aphanocapsa* cf. *delicatissima* represented, on average, 91% of the total phytoplankton biomass. The statistical analyses provide support for the hypothesis that low light availability in the water column regulates the structure of the algal assemblage in this lake. Our results agree with predictions of the light-limited growth theory (i.e. the observed increase in light supply promoted an

increase in algal density) and are also consistent with the notion that environmental constraints influence the dominant morphological traits in phytoplankton assemblages, particularly, that small organisms and/or attenuated forms are favoured under very poor light conditions. Nevertheless, further work is needed to get a full understanding of the processes controlling phytoplankton dynamics in this lake, including careful studies of the ecophysiology of the colonies comprising pico-sized cells of *Aphanocapsa* cf. *delicatissima* that dominated the assemblage during all the studied period.

Keywords Phytoplankton · Steady-state · Shallow lake · Cyanobacteria · Turbid systems

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Introduction

In many lakes, the phytoplankton seasonal succession involves a series of distinctive stages, each of which is characterized by the presence of a few dominant species. On each of these stages, the biomass of the dominant species remains fairly constant, but after a certain time, they are replaced by other species (Ortega-Mayagoitia et al., 2003; Padisák et al., 2003). Non-equilibrium theory establishes that in unstable environments, disturbances occur with sufficient frequency to disrupt the course of competitive exclusion; as a consequence, competitive interactions

are minimal and populations are limited by environmental constraints (Harris, 1986). On the contrary, the equilibrium model posits that the absence of disturbance promotes niche segregation as a consequence of competition, and diversity is reduced to minimal levels by exclusion of all but the superior competitors (Hardin, 1960; Petersen, 1975; Tilman et al., 1982).

Despite their opposite assumptions (i.e. perturbed vs. unperturbed environments), both views predict that temporal changes in community structure can, eventually, achieve a stable assemblage characterized by growth and loss processes occurring simultaneously and resulting in an invariant assemblage through time. When these stages or phases, dominated by a handful of species, extend for long periods, they are referred to as steady-state periods of the phytoplankton community (Naselli-Flores et al., 2003). Operatively, Sommer et al. (1993) established the criterion for the identification of these steady-state phases in natural systems: a maximum of three species contributing to, at least, 80% of total biomass for more than 2 weeks without considerable variation in total biomass (Padisak et al., 1993).

Selection of dominant phytoplankton species depends upon an unpredictable and complex combination of factors that include the physical structure of the system, the availability of nutrients and biotic interactions, among others (Rojo & Alvarez-Cobelas, 2003). The ecological interest in detecting steady-state phytoplankton assemblages lies in the establishment of patterns among different systems and to analyse whether the observed associations are similar to a certain functional group (Reynolds et al., 2002).

Previous results indicate that, in general terms, steady-state conditions are expected to occur especially in highly resilient environments (Naselli-Flores et al., 2003). Such conditions are more frequently found in large and deep lakes (Morabito et al., 2003; Salmaso, 2003; Becker et al., 2008), where long-lasting stratification allows phytoplankton assemblage to complete the process of competitive exclusion, or in tropical (e.g. Soares et al., 2009) or polar systems (e.g. Allende & Izaguirre, 2003) in which seasonal changes vary over a narrow range promoting relatively stable physical conditions that favour the development of steady-state phases.

In contrast, temperate shallow lakes tend to be more susceptible to stochastic events as they are more responsive to meteorological and hydrological

variations due to their particular morphometry and hydrology. In fact, rapid and unpredictable phytoplankton changes are more frequently observed in these fast-changing ecosystems (Naselli-Flores et al., *op. cit.*).

The Pampa plain of Argentina contains several thousand shallow lakes, locally termed “lagunas” (Quirós & Drago, 1999), many of which have progressively undergone increasing loads of nutrients from anthropogenic activities, such as cattle breeding, agriculture and urban discharges (Quirós et al., 2002, 2006). Presently, the area comprises a mosaic of shallow lakes interconnected by fluvial networks. The early work by Scheffer et al. (1993) showed that shallow lakes could alternate between two distinctive regimes: a clear one, characterized by high water transparency, low phytoplankton biomass and the presence of macrophytes; and a turbid regime, characterized by low transparency, often associated with phytoplankton blooms and the absence of rooted vegetation. Laguna Chascomús (35°36'S, 58°02'W) is one of the most extensively studied lakes in the area. For the last two decades, this large (3,014 ha) shallow lake has been stabilized in a phytoplankton turbid state; it is well mixed and it is virtually devoid of rooted vegetation. The lake is hypertrophic, typically registering high chlorophyll-*a*, total phosphorus and total nitrogen concentrations (Torremorell et al., 2007).

It is well known that in shallow, well-mixed eutrophic ecosystems, characterized by non-limiting nutrient concentration, primary producers typically compete for light (Scheffer, 1998). Theory predicts that under light-limiting conditions, as is the case in Laguna Chascomús, there exists a feedback between phytoplankton density dynamics and the light climate in the water column during which, as population increases, overall light conditions become less favourable; growth rates are affected and the successful species are selectively favoured on the basis of having superior light-harvesting properties (Huisman and Weissing, 1994; Huisman, 1999; Huisman et al., 1999). In this context, Llamas et al. (2009) assessed the robustness of the theoretical predictions of light limitation theory using a mesocosm-level experiment comprising complex natural plankton communities. They confirmed that light, rather than other naturally co-varying variables, is a major driver of Laguna

Chascomús' dynamics and metabolism. They also provided evidence that light availability modified total phytoplankton yields without affecting significantly the relative proportions of the dominant species across the light treatments. Also, correlation analyses based on field data have shown that annual patterns of phytoplankton primary production as well as total suspended particle dynamics (Torremorell et al., 2007), water transparency (Torremorell et al., *op. cit.*) and the phosphorus content of seston (Lagomarsino et al., 2011) are driven by seasonal fluctuations in the incident irradiance (I_0). In other words, whenever more light is available, the growth of photoautotrophs is stimulated, resulting in the formation of additional particulates, which in turn reduce water transparency. These non-algae particulate matter corresponds to heterotrophic components of the food chain that develop at the expense of phytoplankton primary production. In addition, transparency is not correlated with wind speed (Torremorell et al., 2007). This suggests that even when resuspension of sedimented material is likely to contribute to water turbidity (Scheffer, 1998), it may not be involved in the fine tuning of water transparency.

On the other hand, Pérez et al. (2011) confirmed that the absorption of incident PAR in Laguna Chascomús was largely dominated by particulate matter. Within the particulate fraction, both phytoplankton pigments and unpigmented components contributed similarly to particulate absorption. Interestingly, and somehow counter-intuitively, the major process controlling light availability in this shallow lake is not phytoplankton self-shading, but the depletion of radiant energy caused by absorption and scattering due to non-algal particulates (i.e. background light attenuation).

In this paper, we studied the phytoplankton assemblage (i.e. nano- and microphytoplankton fractions) during a 30-month period. During the best part of the study, most environmental conditions, including nutrient levels and light limitation, remained fairly stable. However, by the end of the study, a regional scale drought caused a decline of the lake depth (Lagomarsino et al., 2011). Although Laguna Chascomús remained in a phytoplankton turbid state (Scheffer et al., 1993), the decrease in mean lake depth affected the underwater radiation conditions (Lagomarsino et al., *op. cit.*). Decreasing water depth

represents one way of systems' light enrichment and has a complex influence in lake dynamics (Diehl, 2007), as well as on the outcome of competition between phytoplankton species (Litchman & Klausmeier, 2001 and references therein, Litchman, 2003) and directly affects specific algal production and growth rates (Diehl, 2002; Litchman, *op. cit.*; Zohary et al., 2010). In this approach, we focused in the occurrence of steady-state phases in terms of species composition (as defined by Sommer et al., 1993), and we also considered the structure of the assemblage in terms of functional groups (*sensu* Reynolds et al., 2002), as functional diversity may be a stronger determinant of ecosystem processes than species diversity (Hooper & Vitousek, 1997; Huston, 1997; Tilman et al., 1997).

As light is the main driving factor of these lake processes, in this analysis, we emphasized on the importance of subtle, but measurable, changes in light availability in the maintenance of steady-state phases due to decreased lake's maximum depth.

Study site

Laguna Chascomús (35°36'S 58°02'W) (Fig. 1) is a large (area = 30.1 km²), shallow lake (mean depth *c.* 1.9 m) located in the Pampa region of Argentina. It belongs to the Salado River catchment, a large floodplain area (801 km²) characterized by a poorly developed drainage. The climate is temperate, with mean annual temperature ranging from 13 to 16°C, and an annual precipitation is of about 900 mm year⁻¹ (Iriondo & Drago, 2004). This shallow lake is turbid, hypertrophic and typically alkaline and registers high chlorophyll-*a* and dissolved organic matter concentrations (Conzono & Fernandez Cirelli, 1988; Conzono & Claverie, 1990; Izaguirre & Vinocur, 1994; Conzono & Fernandez Cirelli, 1996; Lagomarsino et al., 2011). The water column is homogeneous in temperature and shows high dissolved oxygen values (Conzono & Claverie, 1990; Diovisalvi et al., 2010) due to constant mixing by the persistent wind shear (Torremorell et al., 2007; Diovisalvi et al., *op. cit.*). The biotic community of Laguna Chascomús comprises hundreds of microbial (autotrophic and heterotrophic) species, zooplankton grazers and over 20 species of fish (Torremorell et al., 2009).

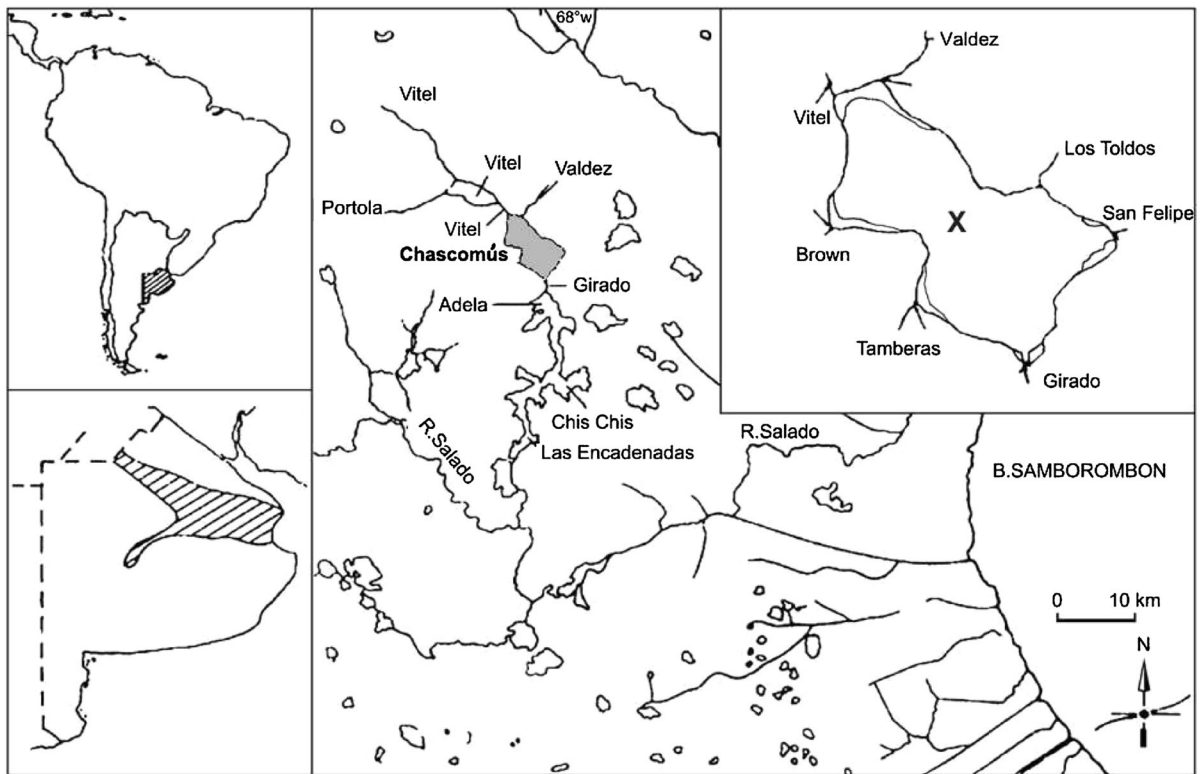


Fig. 1 Geographical location and sampling site in Laguna Chascomús

Methodology

Lake sampling and chemical analyses

Integrated water samples were collected every 2 weeks, during 30 months, from July 2005 to December 2007 at a central point of the lake.

Routine measurements of the lake's depth, water temperature, pH (Orion pH-meter; ATI Orion, VWR Scientific, Boston, MA, USA), conductivity (Hach conductimeter; Hach Company, Loveland, CO, USA) and Secchi disc readings were measured in situ. Dissolved oxygen (DO) concentration was measured using a YSI 5000 meter, YSI Incorporated, Dayton, OH, USA. Alkalinity was determined by titration according to Gran's method (Wetzel & Likens, 2000).

Samples for dissolved nutrient analyses were filtered through Whatman GF/F and the concentration of soluble reactive phosphorous (SRP), and nitrate, nitrite and ammonia (DIN, dissolved inorganic nitrogen) were estimated following APHA (1992). Samples for total nutrient determination were pre-digested in

acid conditions. Total phosphorous (TP) was estimated following APHA (1992). Organic nitrogen (NK) was determined by semi-micro-Kjeldahl method (APHA, *op. cit.*). Total nitrogen (TN) was defined as the sum of (NK + nitrate + nitrite). Total suspended solids (TSS, also referred to as seston) were estimated after filtration onto weighed and precombusted GF/F filters, and dried until constant weight at 103–105°C (APHA, 1992). The ash fraction (inorganic matter content; IM) was estimated by reweighing the GF/F filters after combustion at 530°C for 3 h following APHA (1992). The organic matter content of seston (OM) was estimated as the difference of (TSS – IM). Chlorophyll-*a* concentration corrected for phaeopigments was determined by acetone extraction (Marker et al., 1980).

Solar radiation measurements and optical variables estimation

Incident solar radiation (I_0) was recorded continuously on site, using an IL 1700 radiometer (Biospherical

Instruments, Inc., San Diego, CA, USA). The instrument was connected to a computer and the data acquisition occurred with a 5 min frequency.

Vertical profiles of downward irradiance (350–750 nm) were obtained with a spectroradiometer (USB2000, Ocean Optics, Dunedin, FL, USA) attached to a fibre optic probe. Diffuse vertical attenuation coefficients for PAR (kd_{PAR}) were calculated by regressing log-transformed irradiance measurements against depth. The depth of the photic layer (Z_{eu}) was calculated as $4.6/kd_{PAR}$, and the ratio of euphotic depth to mixing depth (Z_{eu}/Z_{mix}) was estimated as a measure of the light gradient in the water column (Huisman, 1999). Previous results of the thermal structure of the water column indicate that for Laguna Chascomús, the mixing depth (Z_{mix}) coincides with the maximum depth (Z) of the lake (Diovisalvi et al., 2010).

Mean irradiance in the water column (I_{mean} [$\mu\text{mol photons m}^{-2} \text{s}^{-1}$]) was estimated as:

$$I_{mean} = \frac{I_0 \times (1 - e^{-kd_{PAR} \cdot Z_{mix}})}{kd_{PAR} \cdot Z_{mix}},$$

where I_0 corresponds to the incident PAR irradiance; kd_{PAR} , to the attenuation coefficient of PAR; and Z_{mix} , the mixing depth (Nicklisch et al., 2008).

In order to establish light-limiting environmental conditions, we followed the criteria suggested by Reynolds et al. (2002) and adopted a tolerance threshold value of $17.4 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (i.e. $1.5 \text{ mol m}^{-2} \text{ day}^{-1}$) for mean irradiance levels experienced by algae.

Micro and nano-phytoplankton determination and quantification

Phytoplankton samples were collected with a 20 μm net and preserved in 2% formalin for later qualitative analyses. Quantitative algal samples were collected directly from the lake into 250 ml PVC flasks and preserved with 1% acidified Lugol's iodine solution. Counts were performed according to Utermöhl (1958), and replicate chambers were allowed to sediment for a minimum of 24 h. A scan of the entire chamber bottom at a low magnification was performed in order to analyse the evenness of phytoplankton distribution, and fields were randomly counted. A maximum counting error of 20% was accepted in estimating

the abundance of the most frequent taxon (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 were established. Algae were classified according to their size in nano- (2–20 μm) or microphytoplankton (>20 μm).

Phytoplankton biovolume was estimated based on cell dimension measures obtained previously from Pampean shallow lakes (Allende et al., 2009). We studied the morphometry of pelagic dominant microalgae, and we classified the species according to the set of geometric models proposed by Hillebrand et al. (1999) to be used for the determination of microalgal biovolume. In the case of rare species, biovolume data from bibliography was used (Margalef, 1983; Dokulil, 1988; García de Emiliani, 1993; Seip & Reynolds, 1995). Only species that represented >1% of total density in, at least, one sampling date were taken into account for biovolume estimations.

Steady-state phases were identified according to Sommer et al. (1993), and phytoplankton species were grouped according to their strategies into functional groups following Reynolds et al. (2002) and Padišák et al. (2009).

Species evenness (Pielou, 1977), species richness and Stander's Similarity Index or SIMI (Elber & Schanz, 1989) were calculated based on biovolume estimations.

Statistical analyses

Non-parametric Spearman correlations were calculated in order to investigate the relationship between physical–chemical, optical variables and biological data.

Similarity Percentage Analysis (SIMPER) based on biovolume data was used to differentiate those taxa that contribute most strongly to the dissimilarity between samples (Clarke & Ainsworth, 1993). This test was performed with the software PAST 2.0 (Hammer et al., 2001).

To assess the relative contribution of environmental variables to the determination of the structure of the algal assemblage, we performed a series of ordination analyses that included all the physical and chemical variables (i.e. I_0 , T° , DO, pH, conductivity, alkalinity, Z , seston, OM, IM, DIN, TN, SRP, TP, Secchi disc reading, kd_{PAR} , I_{mean} and Z_{eu}/Z_{mix}) as potential

Table 1 Means and standard deviations of physical–chemical and optical variables in Laguna Chascomús during the sampling period

Physical and chemical variables	Mean	±SD
Temperature (°C)	16	5.7
pH	8.8	0.2
Conductivity (mS cm ⁻¹)	1.8	0.2
Alkalinity (mEq l ⁻¹)	7.3	1.1
Dissolved oxygen (mg l ⁻¹)	9.5	1.8
Depth (m)	2	0.2
Seston (mg l ⁻¹)	225.6	116.4
% Organic matter in seston	36.4	9
Total phosphorous (µg l ⁻¹)	619.4	191.7
Soluble reactive phosphorous (µg l ⁻¹)	10.4	4.3
Total nitrogen (µg l ⁻¹)	2,255	1,619
Dissolved inorganic nitrogen (µg l ⁻¹)	64.1	58.4
Secchi depth (cm)	10.9	3.1
Incident irradiance (W m ⁻²)	79.2	46.1
Vertical attenuation coefficient for PAR (m ⁻¹)	20.8	6
Mean irradiance (W m ⁻²)	2.2	1.3
Euphotic depth to mixing depth ratio	0.122	0.042

explanatory factors. We also include zooplankton abundance data (Diovisalvi, *pers. comm.*) as a proxy for grazing pressure. A preliminary detrended correspondence analyses (DCA) was carried out based on phytoplankton biovolume as biological data. As the analysis evidenced a short gradient length (<2 standard deviations), we performed a redundancy analysis (RDA), a linear response model, for subsequent ordination analyses (ter Braak & Smilauer, 1998).

The importance of each variable was assessed using the forward selection procedure and to evaluate the multicollinearity among explaining variables, we inspected the variance inflation factors and removed those variables with values higher than 20 (ter Braak, 1986). All analyses were performed with CANOCO 4.5 software.

Results

Physical and chemical parameters

In general terms, physical and chemical conditions in Laguna Chascomús ranged within previously registered data for this lake (Table 1). Water temperature ranged

between 7 and 25°C, while mean daily incident PAR irradiance (I_0) ranged between 32.6 and 754.9 µmol photons m⁻² s⁻¹, and both parameters showed a seasonal oscillation. As regards pH, values registered were alkaline while dissolved oxygen concentration (DO) ranged from 5.1 to 14.6 mg L⁻¹, with maximum and minimum values recorded during winter and summer, respectively. Conductivity and alkalinity remained high and evidenced a slightly increasing tendency towards the end of the sampling period. These two parameters were significantly and negatively related to the variation in the maximum depth of Laguna Chascomús ($r_{s\ cond} = -0.75$, $P < 0.001$; $r_{s\ alk} = -0.62$, $P < 0.001$).

Water transparency in Laguna Chascomús was very low during the whole study period. Secchi depth readings (SD) ranged from 6 to 18 cm, while the diffuse attenuation coefficient of the photosynthetically active radiation (kd_{PAR}) varied between 9.4 and 35.7 m⁻¹. Both parameters evidenced a significant relationship ($r_{s\ SD-kd_{PAR}} = -0.86$, $P < 0.0001$) and were also significantly related to the amount of seston (SS) in the water column ($r_{s\ SD-SS} = -0.89$, $P < 0.0001$; $r_{s\ kd_{PAR}-SS} = 0.93$, $P < 0.0001$). In contrast, Chl-*a* was not significantly related to kd_{PAR} , nor to SS or SD.

The estimated depth of the euphotic layer ranged from 0.13 to 0.49 m, while the mean PAR irradiance averaged over the whole water column (I_{mean}) was low (10.2 ± 5.6 µmol photons m⁻² s⁻¹) and remained mostly below the tolerance threshold value for light-limiting environmental conditions (Fig. 2).

The availability of light in the water column, expressed by the ratio $Z_{cu}:Z_{mix}$, ranged from 0.06 to 0.25 and showed an increasing tendency during all the studied period (Fig. 3). Interestingly, maximum values of this ratio were always reached during the fall–winter periods (March to September) when the euphotic layer represented, on average, 13.3% of the mixing zone in 2006 and 16.2% in 2007.

Typically, high figures of total phosphorous (TP), total nitrogen (TN) concentration (Table 1) as well as phytoplanktonic Chl-*a* (307.3 ± 158.5 µg L⁻¹) were registered during all the study period. Particularly, TP showed a seasonal pattern presenting maximum values in summer and a slightly increasing tendency towards the end of the sampling period (Fig. 4). This parameter was significantly related to Secchi depth readings

Fig. 2 Mean irradiance (I_{mean}) variation in the water column during the study period. Dashed line indicates the tolerance threshold value suggested by Reynolds et al. (2002) for limiting mean daily irradiance level experienced by the phytoplankton community

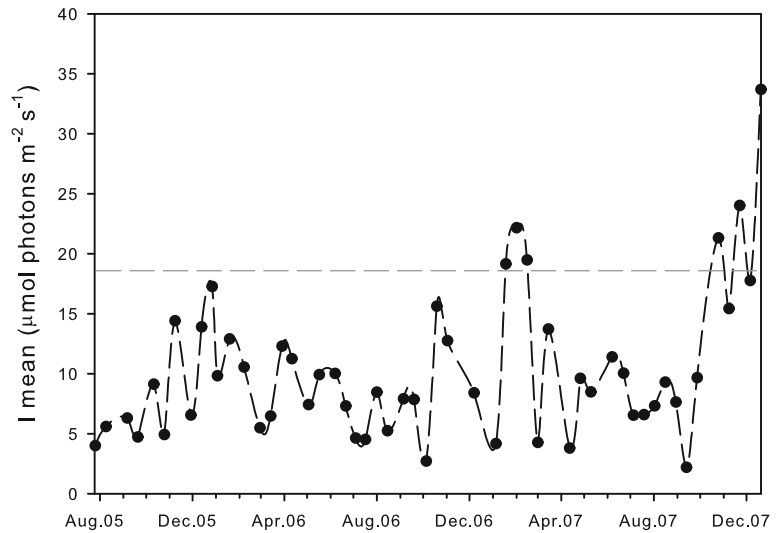
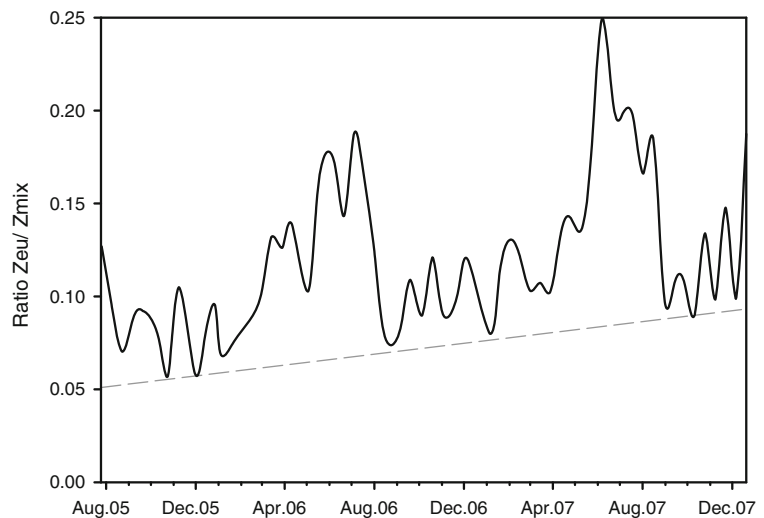


Fig. 3 Temporal variation of the euphotic depth (Z_{eu}) to mixing depth (Z_{mix}) ratio. The dotted line helps evidence the increasing tendency in this parameter



($r_s = -0.72$, $P < 0.001$), seston concentration ($r_s = 0.69$, $P < 0.001$) and kd ($r_s = 0.55$, $P < 0.001$).

Phytoplankton community structure

The analysis of the algal flora revealed a total of 94 specific and infraspecific taxa. Most belonged to Chlorophyceae (44 taxa), Cyanobacteria (21 taxa) and Bacillariophyceae (16 taxa), while a few belonged to the classes Zygnematophyceae, Euglenophyceae, Xanthophyceae and Cryptophyceae. Considering the structure of the algal assemblage, the phytoplankton community mainly comprised colonies of small cells

in the picoalgal range of *Aphanocapsa* cf. *delicatissima*, co-occurring with filamentous Cyanobacteria (i.e. *Raphidiopsis* sp., *Planktolyngbya contorta* and *P. limnetica*), small chlorococcales (i.e. *Monoraphidium* spp. and *Scenedesmus* spp.) and the diatom *Synedra berolinensis*.

In terms of abundance, total phytoplankton density ($>2 \mu\text{m}$) ranged between 2.1×10^5 and 9.4×10^5 ind. ml^{-1} and higher densities were registered from August 2006 until the end of the sampling period. Phytoplankton biovolume averaged 6.5×10^9 ($\pm 3.5 \times 10^9$) $\mu\text{m}^3 \text{ml}^{-1}$ and species dominance remained rather constant during the 30-month sampling period

Fig. 4 Temporal variation of Total Phosphorous concentration (TP) during the study period. The *dotted lines* indicate the increasing tendency of minimum and maximum values during the studied period

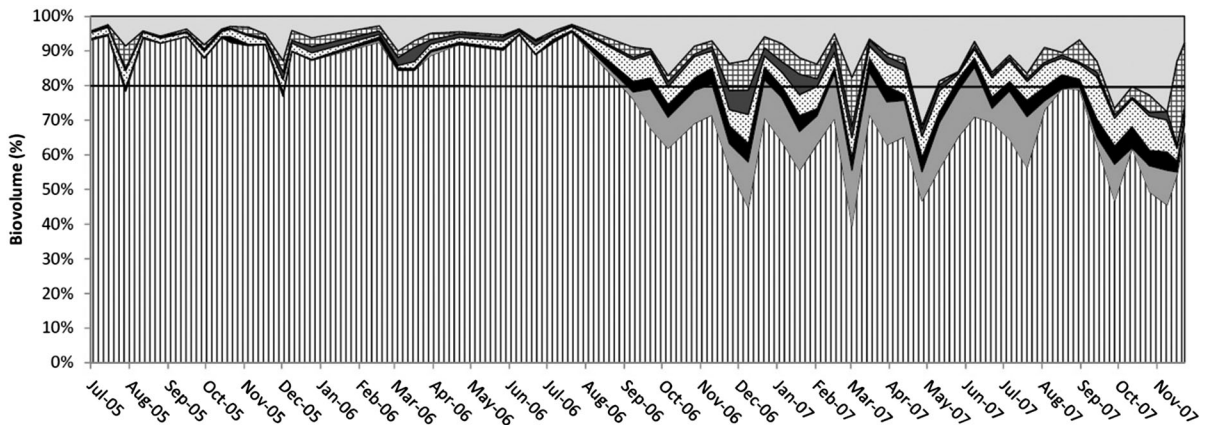
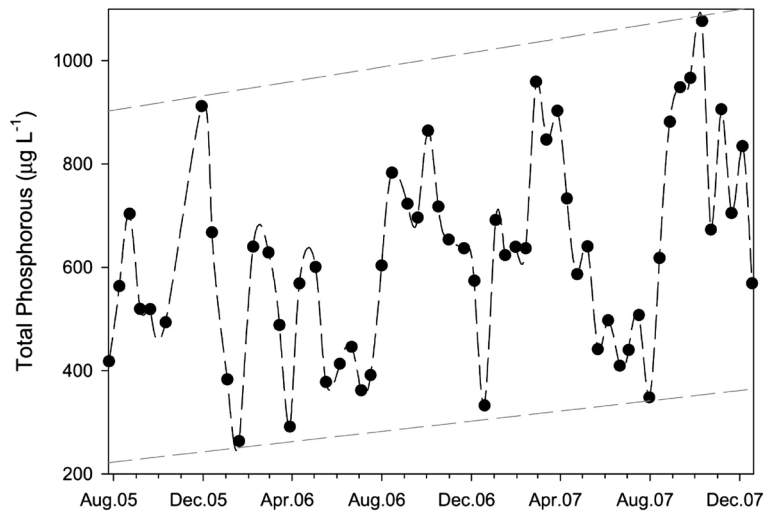


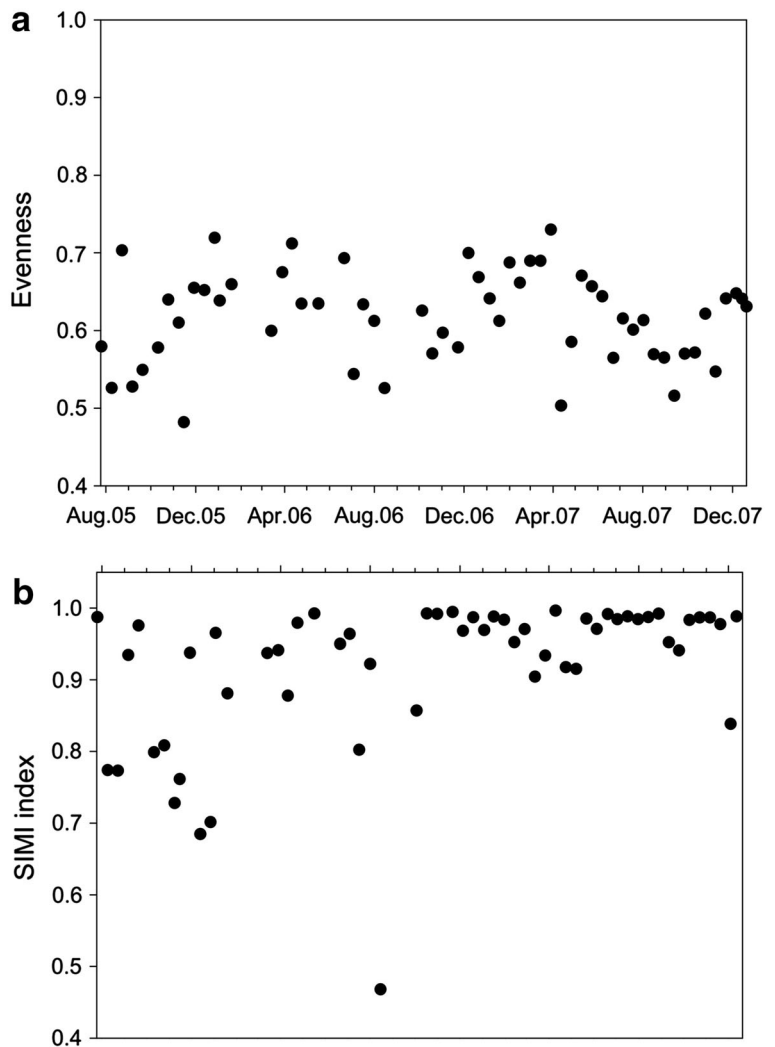
Fig. 5 Temporal variation of phytoplankton biomass. The *solid line* indicate Sommer's criteria of biomass accumulation (80%) (Sommer et al. 1993)

(Fig. 5). Cyanobacteria was the dominant group, being responsible, on average, for 82.7% of total biomass.

Strictly adhering to Sommer's criteria of an equilibrium phase (i.e. a maximum of three species contributing to, at least, 80% of total biomass for more than 2 weeks without considerable variation in total biomass, Fig. 5—solid line), these conditions were fulfilled during the first 14 months of this study (i.e. from July 2005 to August 2006). During this period, the cumulative biovolume of the most abundant species, namely *Aphanocapsa* cf. *delicatissima*, surpassed by far 80% of total phytoplanktonic biovolume (i.e. mean = $91 \pm 4.8\%$) and was followed by

Scenedesmus quadricauda and *Synedra berolinensis*, which averaged 3.3 and 2.2% of total phytoplankton biovolume, respectively. After that, from September 2006 until the end of the study, a non-steady-state phase began which differed, fundamentally, by changes in species evenness; particularly, we observed a slight decrease in the dominance of *Aphanocapsa* cf. *delicatissima* and an increase, fundamentally, in the biovolume of another Cyanobacteria, i.e. *Raphidiopsis* sp. (Fig. 5). This pattern was reflected in parameters such as evenness that ranged from 0.48 to 0.73 and evidenced a seasonal pattern with maximum values registered during spring–summer (Fig. 6a). Also, the similarity between the species compositions of

Fig. 6 *Upper panel a* temporal variation of the evenness during the sampling period. *Lower panel b* temporal variation of Stander's Similarity Index or SIMI during the sampling period



consecutive samples (SIMI Index) agrees with the distinction of these two periods (Fig. 6b), and the similarity percentage analysis (SIMPER) based on biovolume estimations indicated an overall dissimilarity between these two periods of 51%. This analysis identified *Aphanocapsa* cf. *delicatissima* (39%) and *Raphidiopsis* sp. (3%) as those species that contributed most strongly to the distinction of both periods.

In terms of functional groups, the algal assemblage in Laguna Chascomús was characterized by an overwhelming dominance of the **K** functional group accompanied by **X1**, **S1**, **J** and **C** species assemblage.

Redundancy ordination diagram (RDA) performed on environmental variables and phytoplankton biovolume showed significance (trace = 0.502, $F = 2.313$,

$P = 0.016$) in all four canonical axes (Fig. 7). The first two redundancy axes accounted for 99.5% of the variance represented in a species–environmental variables biplot. The sum of the redundancy eigenvalues, which indicates the proportion of community variation explained by the RDA, was 0.502 (first axis 0.497; second axis 0.003). The forward selection procedure identified three variables with significant contribution and low inflation factors: the $Z_{eu}:Z_{mix}$ ratio ($F = 5.85$, $P = 0.026$), Secchi disc depth (Secchi) ($F = 10.76$, $P = 0.004$) and depth (Z) ($F = 4.30$, $P = 0.04$). Together, these variables accounted for 60% of the total explained variance. The highest scores of the species corresponded to *Aphanocapsa* cf. *delicatissima*, which is a colonial, non gas-vacuolated,

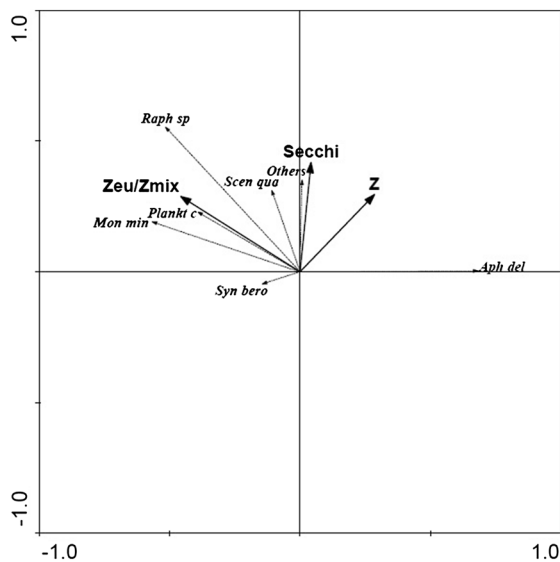


Fig. 7 First and second axes of the RDA based on biomass of phytoplankton species. Significant limnological variables vectors are represented with *solid arrows*, while species vectors are indicated with *dashed arrows*

small-celled Cyanobacteria typically inhabiting shallow, nutrient rich systems, and *Raphidiopsis* sp., which is a strong light competitor, bloom-forming Cyanobacteria. In general terms, we can distinguish two main traits among species: those that showed best performance during periods of higher light availability and water transparency, to a lesser extent, during lower water level (negative side of the first RDA axis) and *A. cf. delicatissima* which contributed with higher biomass during periods of longer dark/light regime, i.e. condition as associated with higher water level and lower light availability (positive side of the first RDA axis).

Discussion

In this paper, we performed a 30-month period analysis of phytoplankton dynamic in a hypertrophic shallow lake in order to search for the occurrence of steady-state phases. We found that, according to Sommer's criteria, a steady-state condition prevailed for a period of 14 months that was characterized by an overwhelming dominance of one species of Cyanobacteria, namely *Aphanocapsa cf. delicatissima* which represented, on average, 91% of total phytoplankton

biomass. This species is characterized by a colonial thallus comprised by small cells, and belongs to the **K** functional group (Reynolds et al., 2002).

According to the statistical analyses, the maintenance of this 1-year steady-state condition in Laguna Chascomús was significantly related to light availability (i.e. $Z_{eu}:Z_{mix}$ ratio and Secchi depth) and parameters that directly affect the light environment (i.e. water depth) (Diehl, 2007; Lagomarsino et al., 2011).

The decrease in depth towards the end of the study period most likely affected the time scale of vertical mixing and promoted a change in the interval length of light fluctuation in the water column which coincided with the end of the steady-state phase.

In fact, the simultaneous increase in the $Z_{eu}:Z_{mix}$ ratio suggests that the algae remained more time within (and were brought more often to) the euphotic layer and these changes in light conditions had a direct effect on the dynamics of the different species (Diehl, 2002; Litchman, 2003; Zohary et al., 2010).

On a biomass basis, the subtle increase in the light availability was coincident with an increase in species evenness, which directly affected species diversity. This result is in agreement with previous results obtained from culture experiments in which the authors demonstrated that variability in light conditions plays a crucial role in sustaining the species diversity of phytoplankton (Litchman & Klausmeier, 2001; Flöder et al., 2002). Particularly, the time scale of light fluctuation of our field survey is comparable with the light intervals used by Flöder and co-workers (*op. cit.*) in their semi-continuous culture experiments. In accordance with our observations, these authors showed that slow fluctuating light at the scale of 3–12 days resulted in an increased diversity index. It is interesting to note that when competing for light, theory predicts that those taxa that reduce the light intensity at the bottom of the water column to the lowest level (i.e. the species with lowest critical light intensity) will displace all other competitors, allowing a few species to persist in the long run (Sommer, 1985; Huisman & Weissing, 1995; Passarge et al., 2006). Then, as critical light intensities for phytoplankton growth are species specific and fall in a very narrow range (e.g. *Aphanizomenon flos-aquae*: $2.44 \mu\text{mol m}^{-2} \text{s}^{-1}$, *Chlorella vulgaris*: $2.75 \mu\text{mol m}^{-2} \text{s}^{-1}$, *Microcystis* sp. $2.85 \mu\text{mol m}^{-2} \text{s}^{-1}$, *Scenedesmus protuberans*: $6.49 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Huisman

et al., 1999), small changes in light supply would promote differences in species composition. Thus, if the critical light intensities of the dominant species in the present work were comparable to the range shown by Huisman et al. (1999), it is likely that the observed increase in light availability has promoted the differences in species evenness evidenced during our study.

On the other hand, in terms of abundance, we observed a significant increase in total phytoplankton density from August 2006 that agrees well with the prediction that in light-limited systems, an increase in light supply promotes an increase in algal density (Huisman, 1999). In analogy to the effects of enrichment with limiting nutrients, the primary effect of the enrichment with light is to fuel phytoplankton primary production; whenever more light is available, the growth of photoautotrophs is stimulated, resulting in the formation of additional particulates, which in turn reduce water transparency, completing a feedback loop that fine-tunes transparency according to the light input (Huisman, *op. cit.*; Scheffer, 1998).

The morphological traits of the dominant algae species provides additional pieces of evidence for the strong influence of the poor underwater light conditions in modulating the phytoplankton assembly in Laguna Chascomús. Kirk (1994) and Reynolds (1997) assert that either very long and thin filaments or small spheres are the most efficient forms in harvesting light and, thus, grow best under sub-optimal light conditions. In agreement with these authors and with previous results obtained by O'Farrell et al. (2007) in another light-limited system of the Pampa plain, the deficient light supply that characterizes this lake favoured the development of small organisms and attenuated forms, such as the small colonies of *Aphanocapsa cf. delicatissima* or the thin filaments of *Raphidiopsis* sp. and *Planktolyngbya contorta*.

The high Cyanobacteria biomass registered in this shallow lake also agrees with this light-limiting and alkaline environment scenario. It is well known that reduced transparency and high pH are important factors that account for Cyanobacteria being especially competitive in this shallow and nutrient rich lake (Tilzer, 1987; Shapiro, 1990; Caraco & Miller, 1998; Havens et al., 1998). Particularly, the dominance of the **K** functional group is expected to occur in shallow, nutrient rich, turbid lakes, such as Laguna Chascomús (Reynolds et al., 2002).

The extremely low light conditions of the water column could have also had an effect on the structure of the assemblage, favouring the development of *Aphanocapsa cf. delicatissima* over other cyanobacterial species. In relation to this species' morphological traits, *A. cf. delicatissima* could be positively selected as it is able to harvest more light per cell or unit carbon than larger cells. In other words, species with increasing cell sizes typically show less efficient light utilization features as a consequence of an increase in the packaging effect, which reduces their pigment absorption efficiency (Sakshaug et al., 1997; Schwaderer et al., 2011).

On the other hand, Torremorell et al. (2009) demonstrated that UV radiation inhibited phytoplankton primary production in this extremely turbid lake and also they found evidence that the algae do not respond solely to the average irradiance, but that they also perceive the vertical light gradient and adapt in response to it. In this regard, and in agreement with the results obtained by Callieri et al. (2011) in culture experiments, formation of microcolonies of *Aphanocapsa cf. delicatissima* could result as a defence strategy to counteract the photoinhibitory effects of high radiation levels experienced during the short periods of time that the cells spend near the surface. In addition, the long persisting dominance of this morphotype could be favoured by the negligible zooplankton grazing pressure that plays no role in controlling phytoplankton biomass in this system (Diovisalvi et al., 2010).

It is interesting to note that these dominant small cyanobacterial colonies are more often registered in cyanobacterial blooms together with larger and more common cyanobacteria of the genus *Microcystis*, *Aphanizomenon* and *Anabaena* (Callieri et al., 2012). Moreover, in shallow, turbid lakes with high nutrient concentrations, cyanobacterial taxa belonging to Oscillatoriales are more often reported (Havens et al., 1998 and references therein). We suggest that the prolonged exposure to low levels of underwater light irradiance promotes the development of *Aphanocapsa cf. delicatissima* over other species present in the lake. Similarly, Havens et al. (1998) analysed the regulation of cyanobacteria species composition by light availability in a shallow subtropical lake. These authors found that certain taxa (i.e. *Planktolyngbya limnetica* and *P. contorta*) were more tolerant to low irradiance than others, particularly *Microcystis* spp. and

Oscillatoria spp. On the other hand, Van Duin et al. (1995) found that after extended periods of mean underwater irradiance below $50 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, the development of *Oscillatoria agardhii* in turbid Dutch lakes was inhibited. Nevertheless, as pointed out by Callieri and co-workers (2012), there are only a few reports on the life history and ecology of colonial picocyanobacteria and, thus, further work is needed in this regard.

In summary, our analysis provides support for the hypothesis that low light availability in the water column regulates the structure of the algal assemblage in this shallow, turbid, hypereutrophic lake and helps stabilize the phytoplankton assemblage in a steady-state phase. Our results were also consistent with the notion that environmental constraints influence the dominant morphological traits in phytoplankton assemblages and, particularly, that small organisms and/or attenuated forms are favoured under very poor light conditions. Nevertheless, further work is needed to get a full understanding of the processes controlling phytoplankton dynamics in this lake, specifically; careful studies of the ecophysiology of the colonies comprising pico-sized cells of *Aphanocapsa* cf. *delicatissima* that dominated the assemblage during all the studied period.

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