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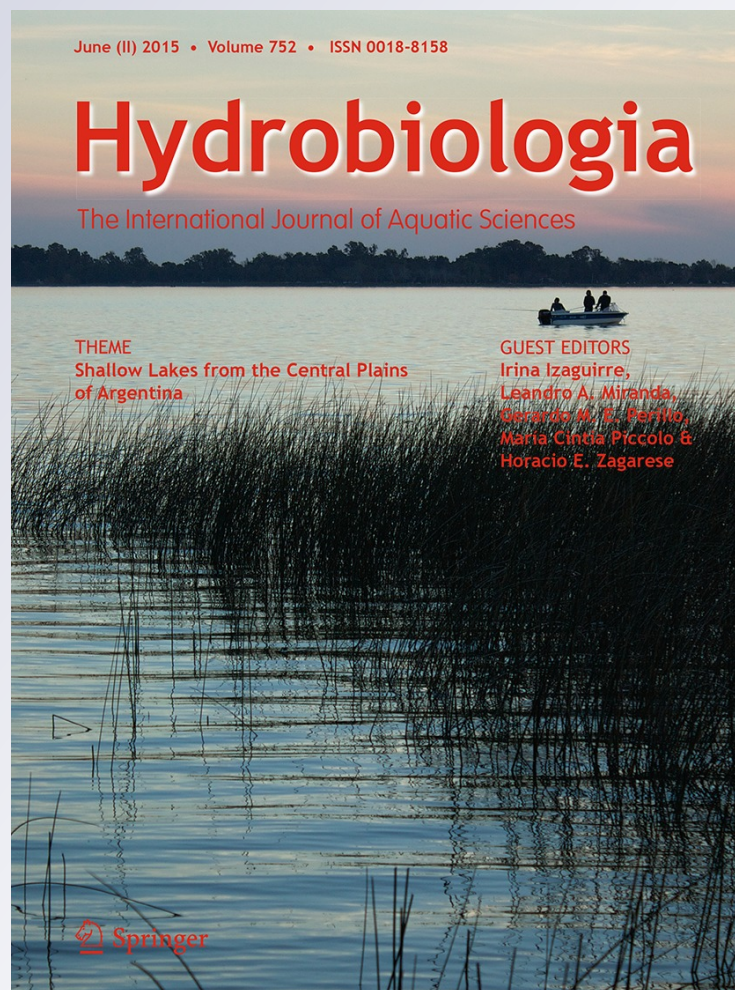
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Which environmental factors trigger the dominance of phytoplankton species across a moisture gradient of shallow lakes?

Irina Izaguirre · María Laura Sánchez · M. Romina Schiaffino · Inés O'Farrell · Paula Huber · Nora Ferrer · Josefina Zunino · Leonardo Lagomarsino · Miguel Mancini

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Abstract We investigated nine Pampean shallow lakes (Argentina) across a moisture gradient (mean annual precipitation 1,000–500 mm), under the framework of a network project of lake monitoring whose main objective was to analyse the responses of ecosystems to different stressors associated with human activities. We postulate that species bloom in different shallow lakes will be determined mainly by local optical features, nutrients and salinity. We analysed the phytoplankton structure during the warm season 2012–2013, identifying those species and functional groups that proliferate in the lakes. Most lakes showed high phytoplankton biomass, except a saline lake located in the driest part of the gradient and an inorganic turbid lake. In some lakes, cyanobacteria blooms occurred in summer, persisting until autumn. Small colonial cyanobacteria and small

fast-growing chlorophytes were abundant in most turbid enriched and anthropogenically impacted systems. Low-est species and functional diversity occurred in the saline lake. Multivariate analysis indicated that the phytoplankton structure was mainly defined by conductivity, transparency and variables associated with the trophic state, also reflecting the importance of the geographical location. Our results evidenced the vulnerability of most shallow lakes in the region to water level fluctuations, eutrophication and canalization.

Keywords Phytoplankton · Shallow lakes · Pampa plain · Algal blooms · Functional groups: functional diversity

Introduction

Shallow lakes, the most abundant lake types in the global landscape (Downing, 2006), share one essential property: much or all the bottom sediment surface is

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frequently, if not continuously, contiguous with the open-water phase of the habitat (Padisák & Reynolds, 2003). This characteristic determines some of their important features: (i) depending on the clarity of the water, the bottom surface may support epilithic and epipelic algae or rooted macrophytes and (ii) finer sediments are liable to entrainment by turbulence, resulting in increased turbidity and light-scattering (Reynolds, 2006). One of the paradigms in shallow lake ecology is that such ecosystems may alternate between two alternative stable states: macrophyte-dominated versus turbid waters (Scheffer et al., 1993; Scheffer et al., 2003), depending on factors such as lake depth and size, climate and nutrients (Scheffer & Carpenter, 2003; Scheffer & Van Nes, 2007; Scheffer, 2009). For the Pampean shallow lakes, O'Farrell et al. (2011) demonstrated that a vegetated floodplain lake shifted between a free-floating plant regime and a phytoplankton regime and, in one shallow lake of the Salado River Basin, alternations of turbid and clear-vegetated conditions were observed within one year (Casco et al., 2009; Solari & Mac Donagh, 2014).

According to data reported by INTA (Instituto Nacional de Tecnología Agropecuaria), the Pampa region of Argentina has about 13,800 shallow lakes with a surface area >10 ha, a number that increases up to 146,000 if also small lakes and temporary ponds are considered (Geraldi et al., 2011). Most of these environments are subjected to a progressive eutrophication due to a combination of human activities in their catchment, leading the lakes to eutrophic or hypertrophic conditions (Quirós & Drago, 1999; Quirós et al., 2006; Diovisalvi et al., this special volume). Such situation determines that most of the shallow lakes of the region have high phytoplankton biomass and a tendency to develop algal blooms (Izaguirre et al., 2012). In recent years, algal blooms have shown an extended growing season, even into late autumn, in some lakes (personal observation).

Many investigations have evaluated the impact exerted by human activities (climate change, agricultural and urban land use, water overexploitation, among others) on phytoplankton in different lake types around the world, evidence exists on the trade-offs between climate change and other human-induced stresses (Salmaso et al., 2012 and cites therein). For example, the effects of warming on the development of cyanobacteria blooms have been demonstrated by different authors (e.g. Paul, 2008; Paerl & Huisman,

2009; Paerl & Paul, 2012). Under such scenarios, the morpho-functional phytoplankton approaches (i.e. Reynolds et al., 2002; Salmaso & Padisák, 2007; Kruk et al., 2010), have been successfully applied in different lakes (e.g. Tolotti et al., 2005; Zohary et al., 2010; Izaguirre et al., 2012) with the purpose of understanding the phytoplankton patterns in anthropogenic impacted systems. These approaches have the potential to be used to assess the functional diversity, as was shown by Borics et al. (2012).

Despite the common shallowness of all the Pampean lakes, particular environmental characteristics of the different ecozones in the region may influence the limnological characteristics of the aquatic ecosystems. Consequently, it is to be expected that successful algal groups in a given lake will be influenced by the particular environmental characteristics (climatic, geological, anthropogenic) of the ecozone where the ecosystem is located. In this paper, we investigated nine Pampean shallow lakes which are located at different positions in relation to environmental moisture gradient (mean annual precipitation 1,000–500 mm) and temperature (mean annual mean temperature 18–15°C). We aimed to identify the phytoplankton species and functional groups that proliferate during the warm season in the different shallow lakes over the gradient. We analyzed the main environmental factors that regulate the dominance of species and functional groups in them. We postulate that proliferation of particular algal species during the warm season in different shallow lakes of the gradient will be determined mainly by optical features, nutrients and salinity of the lakes.

We evaluated the existence of steady states during the warm season, defining them as phases characterized by the dominance of 2–3 species, which together contribute more than 80% of the standing biomass and their coexistence persist for at least 2 weeks (e.g. Naselli-Flores et al., 2003; Rojo & Álvarez-Cobelas, 2003).

Study area

The shallow lakes studied are encompassed in the Pampean Region of Argentina, covering a wetness gradient (33°25'–39°27'S; 58°48'–62°53'W). All the selected lakes are included in a monitoring network project of shallow lakes carried on in Argentina

(PAMPA²), whose main objective was to analyse the responses of the Pampean shallow lakes to forcing variables, such as climate change, changes in land use and other anthropogenic impacts.

This study in particular was conducted in nine shallow lakes, whose geographic position is shown in Fig. 1, where also the isohyets of the region are indicated. Among these shallow lakes, six belong to the Salado River Basin: Gómez (GO), El Carpincho (CA), Chascomús (CH), El Triunfo (TR), La Limpia (LI), La Salada de Monasterio (SM); one to the Parano-Platense Basin and is included in a natural reserve in the wettest part of the gradient: Laguna Grande in the Reserve of Otamendi (OT); one at the Northwestern part of the region is located in Córdoba Province in a zone of wetlands with permanent and temporary water bodies: La Helvecia (HE); the southernmost lake is a saline water body, which is situated at the driest part of the gradient: La Salada de Pedro Luro (SA). The different wetland zones of the Pampas were described by Gómez & Toresani (1998).

All the shallow lakes of the Salado River Basin have high nutrient levels, are polymictic and their ionic composition is dominated by sodium-bicarbonate (Fernández Cirelli & Miretzky, 2002; Allende et al., 2009); among these lakes, La Limpia was classified as inorganic turbid due to its high concentration of suspended inorganic matter (Allende et al., 2009; Izaguirre et al., 2012); another of the lakes (El Triunfo) is a clear example of a system that has changed its regime, from clear with submerged macrophytes (until 4 years ago) to turbid, condition that shows nowadays. The shallow lake located in the Otamendi Reserve is surrounded by marshy vegetation, temporarily and partially covered by floating macrophytes; it is characterized by waters of brownish colour due to high concentration of dissolved organic substances (O'Farrell et al., 2011). La Helvecia, located in the Pampa from Córdoba Province, is a turbid shallow lake with hard hipohaline waters; it is placed in a region where dredging and pipelines have caused a significant reduction of the wetlands (Mancini et al., 2013).

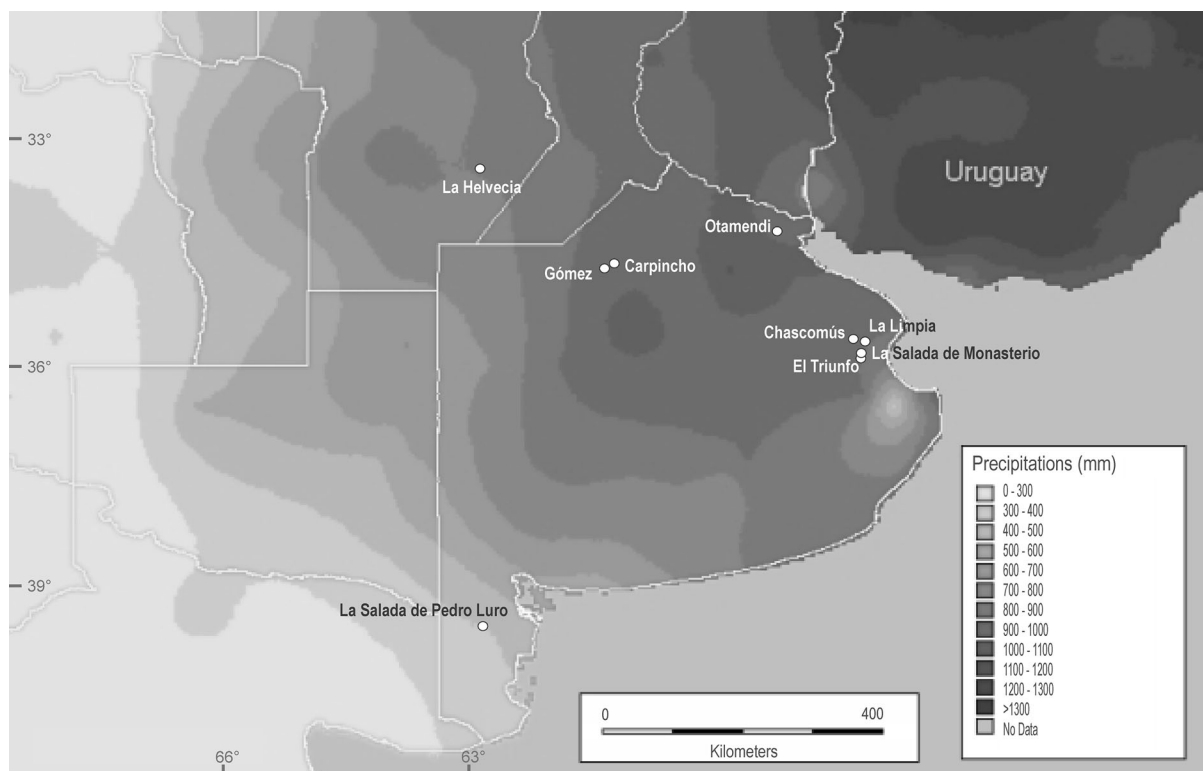


Fig. 1 Geographic position of the studied shallow lakes, and isohyets

Table 1 Geographic position, main morphometric features and type of catchment of the studied shallow lakes

| Shallow lake | | Geographic position | Surface area (km ²) | Mean depth (m) | Max. depth (m) | Type of catchment |
|----------------------|----|---------------------|---------------------------------|----------------|----------------|-----------------------|
| La Helvecia*** | LH | 32°25' S 62°53' W | 0.9 | 1.75 | 2.16 | Exorheic |
| Laguna Grande** | OT | 34°13' S 58°52' W | 1.6 | <1 | 1.20 | Exorheic ^a |
| Gómez***** | GO | 34°39' S 61°01' W | 36.6 | 1.1 | 1.9 | Exorheic |
| El Carpincho***** | CA | 34°34' S 60°54' W | 4.4 | 1.2 | 1.4 | exorheic |
| Chascomús* | CH | 35°36' S 58°02' W | 28.7 | 1.5 | 1.9 | Exorheic |
| La Limpia* | LI | 35°37' S 57°48' W | 5.6 | 1.9 | 2.3 | Exorheic |
| Salada Monasterio*** | SM | 35°47' S 57°52' W | 6.0 | 1.3 | nd | Exorheic |
| El Triunfo* | TR | 35°51' S 57°52' W | 1.5 | nd | nd | Exorheic |
| Salada (Pedro Luro) | SA | 39°27' S 62°41' W | 4 | nd | nd | Endorheic |

Data obtained from: * Izaguirre et al. (2012); ** Chaparro et al. (2011); *** Mancini et al. (2013); ***** Quirós (1988; 2004)

nd no data

^a Floodplain lake communicated through the water table with the Paraná River delta

Finally, La Salada (Pedro Luro) is a mesosaline lake located at the South of Buenos Aires Province, and its water level is maintained discharging water from the Colorado River. The main morphometric characteristics of the shallow lakes, their geographic coordinates and the type of catchment are summarized in Table 1.

Climatic and geological information of the region was reported in Viglizzo et al. (2006) and Allende et al. (2009). In general, the shallow lakes of the region are subjected to a progressive eutrophication due to different human activities in their catchments, among them: agriculture, livestock, urbanization, canalization, damming and fish introduction (Quirós et al., 2006). For a deeper description of the environmental characteristics of the Pampean shallow lakes and their geomorphological features see also the first article of this special issue (Diovisalvi et al., this special volume).

Materials and methods

The nine selected lakes are being visited since October 2012 with a monthly periodicity, under the framework of the above-mentioned network project. Buoys installed in four of them (HE, OT, CH, SA), provide high frequency data of some water and meteorological variables. In this study, we have analysed samples collected during a warm season particularly from October 2012 to May 2013 (mid-spring–mid-autumn). We decided to include part of the autumn in our analysis because in some shallow lakes of the region

algal blooms continue until May. In all cases, samples were collected in the pelagial zone of the lakes.

In addition to the environmental variables continuously monitored by the buoys, the following physical and chemical variables were measured monthly in each lake: water temperature, pH, dissolved oxygen, conductivity (with different portable instruments available at each participant laboratory: Horiba D-54 meter, Horiba U-10, Hach HQ30D, YSI 57, Lutron IK-22 ct, Lutron D-5510, Altronix TPA-II, ADWA AD32); water transparency was estimated with Secchi disk. Total suspended solids (sston) were determined from water samples filtrated through pre-combusted WhatmanTM GF/F. Total phosphorus (TP) from unfiltered water samples was converted to soluble reactive phosphorus (SRP) after an acid digestion with potassium persulfate. In turn, SRP was determined as molybdate reactive P according to standard analytical procedures APHA AWWA WEF (2005). Total organic nitrogen (TN) was determined from unfiltered water by Kjeldahl method. All these determinations were performed following the protocols given in APHA AWWA WEF (2005).

Chlorophyll *a* (Chl *a*) concentrations were estimated from water samples filtered through glass-fibre filters (GF/F WhatmanTM); filters were stored in aluminium foil at −20°C; Chl *a* was extracted using 90% acetone in darkness, and overnight storage at 4°C; then the extracts were cleared by centrifugation at 3,000 rpm for 3 min, and the analyses were performed with a spectrophotometer; concentrations

of Chl *a* free of phaeopigments were calculated using the equations given by Marker et al. (1980).

Water samples for quantitative phytoplankton analyses were taken from the upper 30 cm of the water column in each shallow lake, and fixed with 1% acidified Lugol's iodine solution. Phytoplankton counts were performed with the inverted microscopes available at each laboratory (Olympus CKX41 and Nikon TMS-F) at 400 of magnification, following Utermöhl (1958). Counting error was estimated according to Venrick (1978). Individual algae were considered as the unit and the cell numbers per colony or filament was estimated in all cases. Biovolumes were calculated using appropriate geometric formulae (Hillebrand et al., 1999; Sun & Liu, 2003). In case of colonial organisms, biovolumes were calculated including mucilage. Algal biomass was estimated from biovolume, assuming unit specific gravity.

Numerical analyses

Phytoplankton species were classified into the functional groups using the classification of Reynolds et al. (2002) updated by Padisák et al. (2009). As we were focused on the more abundant species, the analysis was performed excluding rare species occurring in less than 10% in all samples. Then, a Canonical Correspondence Analysis (CCA) was applied to analyse how much variance of the abundance of the phytoplankton functional groups was explained by the environmental variables. Previously, we performed a detrended correspondence analysis (DCA) in order to establish the distribution of the biological data, and as we found unimodal response, CCA was applied. Calculations were performed with the program CANOCO (ter Braak, 2002). The statistical significance of the first axis and all the axes were tested by Monte Carlo permutation test, and the significance of the environmental variables was assessed by forward selection.

We calculated the Simpson diversity of the functional groups expressed as reciprocal ($1/D$) (Magurran, 2008) for each water body and sampling date. For the dominant species in each lake, we analysed the correlation with the environmental variables (Pearson).

In order to compare the magnitude of the temporal variations in the total phytoplankton abundance during the warm season among the shallow lakes, the variation coefficient (VC) was calculated for each lake.

Results

Limnological variables

Although all the shallow lakes investigated are located in the Pampa region, noticeable differences in their limnological features were observed, reflecting the particular characteristics of the ecozones where they are emplaced. Ranges of the physical and chemical variables measured in this study, and mean values are shown in Table 2.

Average depths of the shallow lakes varied between 0.77 and 2.36 m, with the maximum value corresponding to the lake SA, and the minimum one to LI. Taking into account the shallowness of the water bodies, considerable changes were observed during the period of our study as the depth amplitude varied from 0.19 to 0.65 m (Fig. 2). Most shallow lakes of the Salado River Basin (CH, LI, GO, CA) showed their highest hydrometric levels in late spring and the lowest at the end of the summer. Unfortunately, we do not have data of depth for SM, but the pattern was similar. The shallow lake belonging to the Paraná Basin (OT) had two periods of higher level (spring and autumn), and also the lowest hydrometric level in summer. On the contrary, in the southernmost shallow lake SA, the maximum depth was as observed in summer (February).

Most shallow lakes of the gradient studied are in a turbid state (except SA). The most turbid lakes were CH and LI, with extremely low values of Secchi depths (mean values 10.7–10.9 cm). At the opposite extreme, the more transparent water body SA showed an average Secchi depth of 124.9 cm (Fig. 3). In the rest of the lakes, mean Secchi values ranged from 17.5 to 31.4 cm.

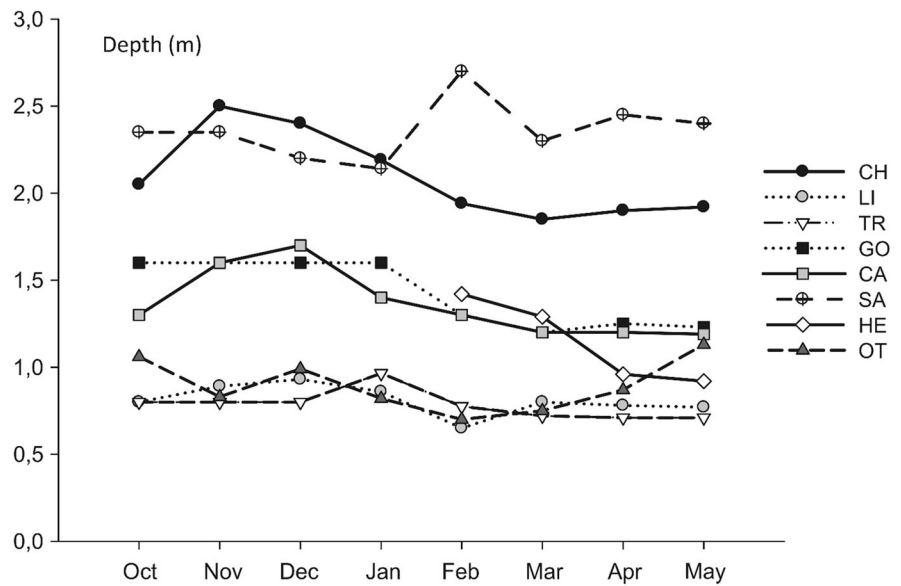
Over the period of our study, mean water temperatures ranged from 18.9 to 24.8°C, registering the lowest values in SA due to its location at the South of the gradient, and the highest ones in TR, probably because of its very low water level. As our study comprised a warm season extending to the autumn, seasonal variations in temperature were observed, with maximum values in mid-summer (February) and minimum ones in autumn (May).

Well-oxygenated waters were observed in all lakes, with the mean dissolved oxygen concentrations varying between 7.1 and 12.4 mg l⁻¹. The highest figures were measured in OT, the most vegetated lake among

Table 2 Ranges and mean values (between brackets) of the limnological variables analysed in the shallow lakes during the period of the study

| Shallow lake | Water level (m) | Secchi (cm) | Temperature (°C) | Diss. oxygen (mg l ⁻¹) | pH | Conductivity (mS cm ⁻¹) | TP (mg l ⁻¹) | TN (mg l ⁻¹) | Chl a (µg l ⁻¹) |
|---------------|---------------------|-------------------|---------------------|---------------------------------------|---------------------|--|--------------------------|-----------------------------|--------------------------------|
| La Helvecia | 0.92–1.42 (1.15) | 14–28 (20.8) | 16.1–24.5 (20.6) | 7.1–11.1 (8.98) | 8.12–8.77 (8.35) | 7.34–8.58 (8.02) | 0.310–0.442 (0.401) | 3.41–6.38 (4.70) | 43.7–241 (112.4) |
| Laguna Grande | 0.7–1.13 (0.89) | 19–44.5 (28.6) | 13.1–26.1 (21.9) | 9.1–19.3 (12.45) | 6.87–9.3 (8.55) | 0.46–1.08 (0.83) | 0.360–0.620 (0.483) | 0.50–8.80 (2.55) | 59.9–370.8 (179.5) |
| Gómez | 1.2–1.6 (1.42) | 15–28 (21.2) | 15.2–31 (22.0) | 6.5–12.6 (8.76) | 8.33–9.09 (8.89) | 3.07–5.02 (4.19) | 0.635–1.164 (0.899) | 0.08–7.313 (3.363) | 23.9–155.1 (94.7) |
| Carpincho | 1.19–1.7 (1.36) | 15–20 (17.5) | 18–28.6 (21.6) | 5.5–10.98 (7.98) | 8.54–9.07 (8.84) | 3.03–4.92 (4.18) | 0.561–1.220 (0.859) | 0.06–6.70 (3.628) | 43.5–180.7 (105.9) |
| Chascomús | 1.85–2.5 (2.09) | 7–17 (10.7) | 15–26 (21.0) | 8–10 (9.37) | 8.3–9.3 (8.80) | 1.06–1.7 (1.52) | 0.395–0.791 (0.584) | 3.612–5.398 (4.599) | 105.3–278.1 (209.6) |
| La Limpia | 0.77–0.93 (0.81) | 7–15.5 (10.9) | 13–29 (22.1) | 8.2–10.2 (9.49) | 8.66–9.17 (9.03) | 1.46–2.49 (1.86) | 0.51–1.541 (1.042) | 3.320–6.240 (4.759) | 20.2–139.0 (66.64) |
| Salada | 0.8 | 7–58 | 17–30 | 8–12.2 | 8.74–10.5 | 1.54–3.28 | 0.085–0.666 | 2.910–9.868 | 15–333 |
| Monasterio | | | | | | | | | |
| SM | (0.8) | (23.1) | (22.1) | (10.13) | (9.70) | (2.62) | (0.234) | (6.962) | (200.6) |
| El Triunfo | 0.71–0.96 (0.78) | 11–80 (31.4) | 17–32 (24.8) | 9–14.6 (11.37) | 8.26–9.74 (9.06) | 1.85–2.65 (2.29) | 0.531–1.149 (0.926) | 5.28–11.05 (8.353) | 126–670 (268.7) |
| Salada Pedro | 2.2–2.7 | 63–145 | 16.2–23.2 | 5.1–8.2 | 9.44–10.22 | 49.6–60.4 | 0.044–0.086 | 1.344–7.414 | 0.48–12.8 |
| Luro | | | | | | | | | |
| SA | (2.36) | (124.9) | (18.9) | (7.1) | (9.89) | (53.83) | (0.087) | (5.593) | (7.0) |

Fig. 2 Depth in the pelagial zone (sampling point) for each shallow lake



the studied systems, whereas the lowest concentrations corresponded to the most saline water body SA. In general, all lakes are characterized by alkaline waters (average pH values 8.3–9.9), although OT showed a wider range. Conductivity displayed a strong variation among the lakes (Fig. 3). At one extreme of the gradient, OT exhibited the lowest conductivity (mean 0.83 mS cm^{-1}), whereas at the opposite extreme, SA showed the highest, with typical values of hyperhaline water bodies (mean 53.83 mS cm^{-1}). In general, the shallow lakes belonging to the Salado River Basin are oligohaline (mean $1.52\text{--}4.19 \text{ mS cm}^{-1}$), but clearly, those located at the upper part of the basin (GO and CA) showed the highest conductivity values. Placed at the NW of the studied gradient, HE also exhibited a relatively high conductivity (mean 8.02 mS cm^{-1}), typical of mesohaline waters.

In spite of all these lakes are classified as eutrophic, important differences were found regarding TP (Fig. 3). The shallow lakes of the Salado River Basin showed the highest TP concentrations (mean $0.234\text{--}1.042 \text{ mg l}^{-1}$), with extreme values in the very turbid LI; the lowest concentrations were measured in SA (mean 0.086 mg l^{-1}). The differences among lakes were less marked for TN (Fig. 3), and relatively high concentrations were found in all lakes; SA also showed quite high values of TN (mean 5.593 mg l^{-1}), whereas the lowest concentrations were measured in the vegetated lake OT.

Chl *a* concentrations also displayed clear differences among these lakes (Fig. 3). The lowest Chl *a* values were recorded in SA (mean $7.0 \mu\text{g l}^{-1}$), whereas the highest corresponded to TR (mean $268.7 \mu\text{g l}^{-1}$). Taking into account their nutrient levels, all shallow lakes may be considered eutrophic or hypertrophic (OECD, 1982), although according to Chl *a* data, SA was always in the range of mesotrophic lakes.

Phytoplankton

Very high phytoplankton abundances were recorded in most of the studied shallow lakes, except in the inorganic turbid lake LI, that presented the lowest total phytoplankton densities ($1,672\text{--}8,300 \text{ ind. ml}^{-1}$) and total algal biomass ($34\text{--}1,285 \text{ mg l}^{-1}$). The saline lake SA also showed rather low algal biomass ($36\text{--}176 \text{ mg l}^{-1}$) and intermediate values of density ($18,972\text{--}108,451 \text{ ind. ml}^{-1}$). In the other lakes, total phytoplankton density ranged from $22,675$ to $645,819 \text{ ind. ml}^{-1}$, registering the lowest figures in HE and the highest ones in TR; total phytoplankton biomass varied from 45 to $17,816 \text{ mg l}^{-1}$, corresponding these extreme values to the extremely fluctuating shallow lake SM.

The biomass of the different algal groups for each water body is depicted in Fig. 4. Cyanobacteria showed the highest biomass in most of the shallow lakes of the Salado River Basin; Chlorophyta co-dominated in the two lakes from the upper basin (GO

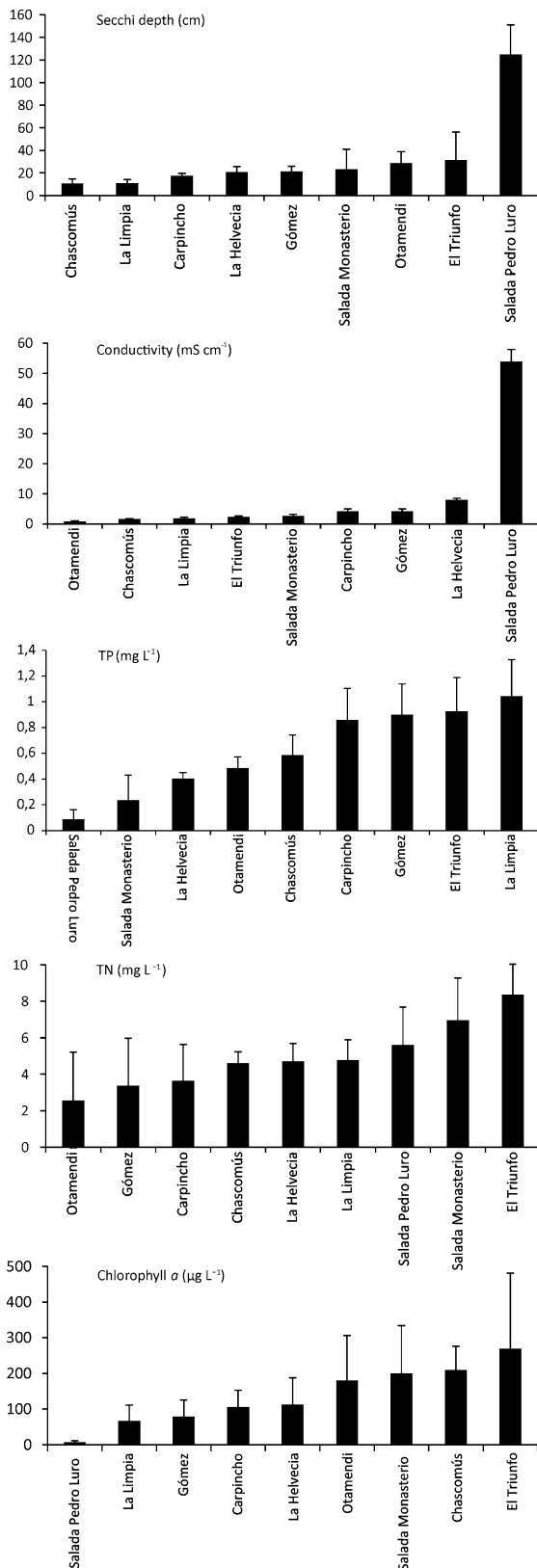


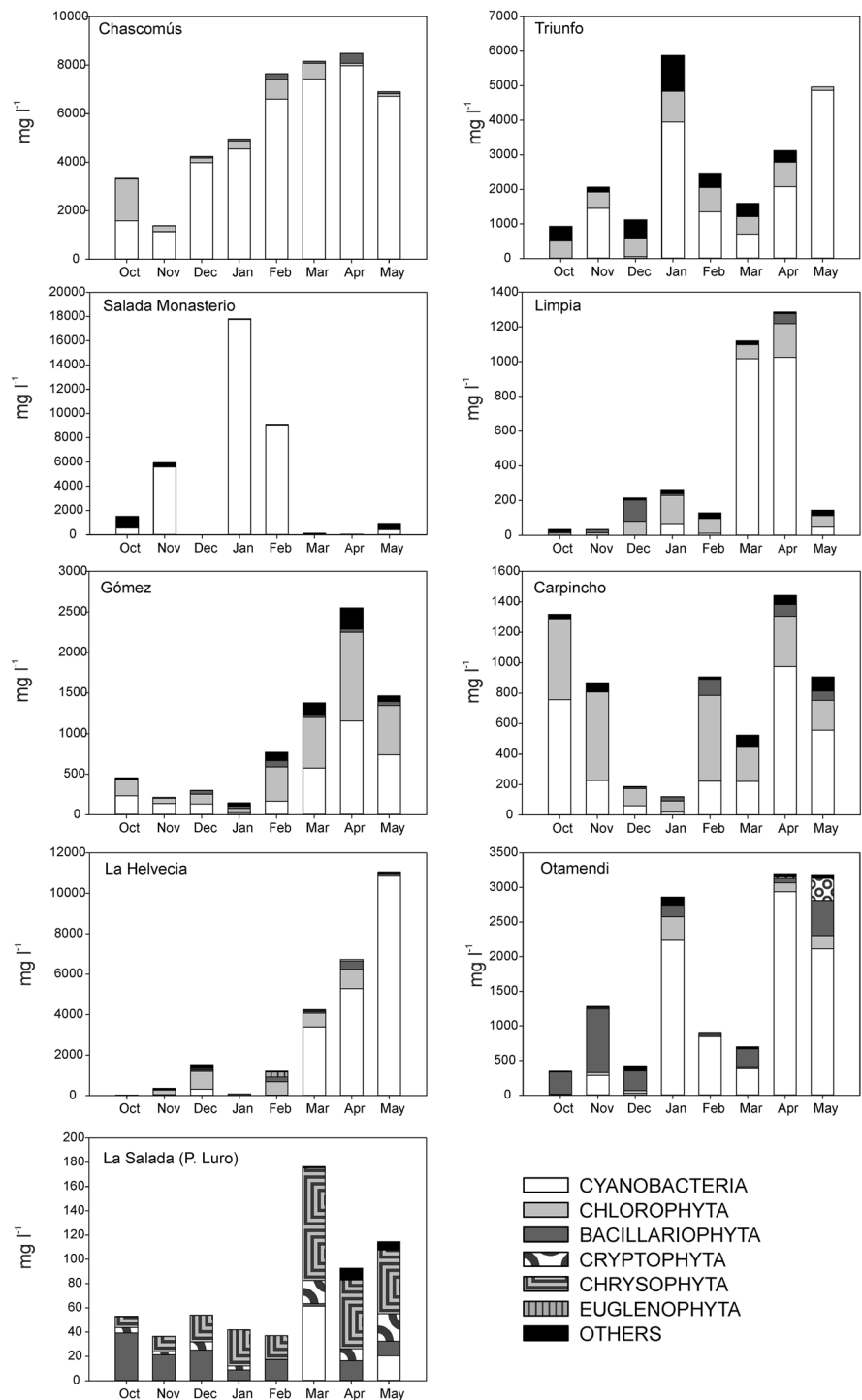
Fig. 3 Main physical and chemical variables measured in the shallow lakes. The water bodies are ordered following increasing values

and CA). Cyanobacteria also dominated in HE. In OT, diatoms dominated in late spring and Cyanobacteria became prevalent from summer to the end of the study period; in this shallow lake, we also observed an increase of cryptophytes in autumn. The saline shallow lake SA showed a very different proportion of algal groups, with dominance of diatoms and chrysophytes for most of the warm period, and an increase of cryptophytes towards the end of the summer.

Changes in total phytoplankton abundance during the warm season varied in magnitude in these lakes, as indicated from the CV values (Fig. 5). The most turbid lakes (CH and LI) presented less pronounced temporal changes, whereas OT and SM exhibited marked temporal variations.

For the entire study period, total species richness varied between 19 and 117, registering the lowest values in the saline shallow lake SA, and the highest one in TR and OT. Table 3 summarizes the list of the most abundant species (in density and/or biomass) for each shallow lake, and their corresponding functional groups. Temporal fluctuations of the density of these taxa are depicted in Fig. 6. The shallow lakes GO and CA shared a similar phytoplankton composition, showing peaks of *Monoraphidium circinale* in mid-spring and beginning of autumn, and a peak of *Chaetoceros* sp. in summer; an important increase of *Raphidiopsis mediterranea* was only found in GO at the end of the summer. The other shallow lakes of the Salado River basin differed in their dominant phytoplankton species: SM showed an important bloom of *R. mediterranea* in mid-summer, followed by a smaller peak of *Planktolyngbya limnetica*; the very turbid shallow lake CH was dominated by small colonial Cyanobacteria (i.e. *Aphanocapsa elachista*, *Chroococcus microscopicus* and *Cyanodictyon* sp.), which showed their maxima at the end of summer and early autumn; on the other hand, the particularly shallow lake TR, which shifted from a clear to a turbid condition over last 7 years, exhibited marked fluctuations in its dominant species with blooms of *Merismopedia minima* and *Monoraphidium minutum* in spring and summer, respectively, and a peak of *Anabaenopsis elenkni* in early autumn; in the inorganic turbid, shallow lake LI diatom species (*Fragilaria construens* and *Cyclotella meneghiniana*) which

Fig. 4 Algal biomass of the different phytoplankton groups in the shallow lakes



were more abundant in late spring and early autumn, dominated together with *Oocystis lacustris* which increased throughout the summer reaching its maximum in April.

In OT, an intense bloom of *Raphidiopsis mediterranea* started in summer (February) and reached its maximum in autumn (April); during the study period, other two species also achieved important numbers,

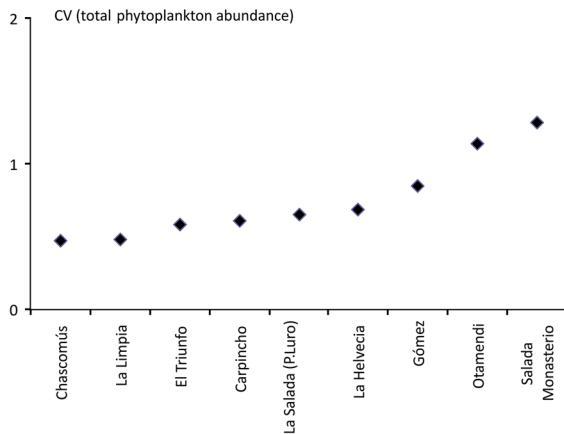


Fig. 5 Variation coefficient of total phytoplankton abundance through the study period for each shallow lake

Anabaena (Dolichospermum) torques-reginae and *C. meneghiniana*, with peaks in January and March, respectively. In HE, the highest abundances of the dominant species were found at the end of the summer and beginning of autumn: peaks of *Ochromonas* sp. and *P. limnetica* in March were followed by a bloom of *Aphanocapsa delicatissima* in May.

Regarding phytoplankton composition, the most unusual lake was SA, where two diatoms associated with saline waters were dominant (*Chaetoceros* cf. *muellerii* and *Cyclotella choctawhatcheeana*), together with a Chrysophyte identified as cf. *Ochromonas* sp. that was very abundant in summer and presented peaks in January and March.

Analysing the biomass of the more abundant species, we were able to identify the existence of steady-states assemblages in some shallow lakes. We adopted the criteria given in Naselli-Flores et al. (2003), where steady states are defined as phases characterized by the dominance of 2–3 species, which together contribute more than 80% of the standing biomass and their coexistence persist for at least 2 weeks. In this sense, the most stable lake was CH, where this condition occurred during the entire warm season with the dominance in biomass of *A. elachista*, *C. microscopicus* and *Cyanodictyon* sp., which together constituted between 81 and 92% of the total algal biomass. SM also showed a sustained steady state from November to May dominated by *R. mediterranea*, *A. delicatissima* and *Oocystis lacustris*. In HE, we observed a steady state from March to May

with *O. lacustris*, *O. parva* and *A. delicatissima*, whereas in OT steady state lasted only during a month (October to November) with *Aulacoseira granulata* and *Cyclotella meneghiniana* dominating. In the saline lake SA, the three dominant taxa, *Chaetoceros* cf. *muellerii*, *Cyclotella choctawhatcheeana* and cf. *Ochromonas* sp. constituted more of 80% of the total biomass from October to February. In the remaining lakes LI, GO, CA and TR, no steady states were identified.

Some of the dominant species showed significant correlations ($P < 0.05$) with the environmental variables analysed here. In three lakes, the small colonial cyanobacteria *A. delicatissima* (abundant in CA, HE) and *A. elachista* (abundant in CH) were inversely correlated with temperature ($r = -0.73$; $r = -0.84$; $r = -0.81$, respectively). *R. mediterranea*, a species that formed blooms in three lakes, was positively correlated with temperature in SM ($r = 0.86$), whereas in GO it showed an inverse correlation ($r = -0.79$) with water level, and a direct one with conductivity ($r = 0.74$). In OT, this species was also directly correlated with conductivity ($r = 0.64$; $P < 0.1$). In the saline lake (SA), *C. choctawhatcheeana* was inversely correlated with the concentration of TN ($r = -0.75$). *M. circinale* showed inverse correlations with pH ($r = -0.83$) in TR, whereas in OT was positively correlated with water level ($r = 0.83$) and negatively with temperature ($r = -0.87$). An inverse correlation was also found between *Ochromonas* sp. and TP in the lake HE ($r = -0.92$).

Most of the shallow lakes shared several phytoplankton functional groups, typical of shallow eutrophic lakes. Particularly, those lakes of the Salado River Basin where there was a similar composition to that previously described for the water bodies of this region (Izaguirre et al., 2012). In turbid lakes with high phytoplankton biomass (CH, SM, GO, CA), species belonging to the following coda dominated: **K** (small-celled non-gas-vacuolated cyanobacteria frequent in shallow enriched waters), **X1** (mainly small chlorococcalean species, typical of eu-hypertrophic lakes), **X2** (unicellular flagellates typical of shallow meso-eutrophic environments), **L₀** (represented in the study lakes by colonial cyanobacteria), **J** (mainly non-gelatinous, non-motile chlorococcaleans prominent in shallow highly enriched systems), **F** (non-motile, near-neutrally-buoyant colonial green algae well adapted to meso-eutrophic lakes). In SM, we also found a great

Table 3 More abundant phytoplankton species in the period of the study and their corresponding functional groups

| Taxa | Codon | CH | LI | SM | TR | GO | CA | OT | HE | SA |
|-------------------------------------|----------------------|----|----|----|----|----|----|----|----|----|
| Cyanobacteria | | | | | | | | | | |
| <i>Anabaena torques-reginae</i> | H1 | | | | | | | x | | |
| <i>Anabaenopsis elenkinii</i> | H1 | | | | x | | | | | |
| <i>Aphanocapsa delicatissima</i> | K | | | | x | x | x | | x | |
| <i>Aphanocapsa elachista</i> | K | x | | | | | | | | |
| <i>Chroococcus microscopicus</i> | L₀ | x | | | | | | | | |
| <i>Cyanodictyon</i> sp. | K | x | | | | | | | | |
| <i>Merismopedia minima</i> | L₀ | | | x | x | | | | | |
| <i>Merismopedia tenuissima</i> | L₀ | | | | | x | x | | | |
| <i>Planktolyngbya limnetica</i> | S1 | | | x | | | | | x | |
| <i>Raphidiopsis mediterranea</i> | S_N | | | x | | x | | x | | |
| Chlorophyceae | | | | | | | | | | |
| <i>Chlamydomonas</i> sp. | X2 | | | x | x | | | | | |
| <i>Monoraphidium circinale</i> | X1 | | | | x | x | x | x | x | |
| <i>Monoraphidium contortum</i> | X1 | | | | | | | x | | |
| <i>Monoraphidium griffithii</i> | X1 | | | | x | | | | | |
| <i>Monoraphidium minutum</i> | X1 | | | | x | | | | | |
| <i>Oocystis lacustris</i> | F | | x | | | | | | x | |
| <i>Tetrastrum komarekii</i> | J | x | | | | | | | | |
| Bacillariophyceae | | | | | | | | | | |
| <i>Aulacoseira granulata</i> | P | | | | | | | x | | |
| <i>Chaetoceros muellerii</i> | B | | | | | | | | | x |
| <i>Chaetoceros</i> sp. | B | | | | | x | x | | | |
| <i>Cyclotella choctawhatcheeana</i> | B | | | | | | | | | x |
| <i>Cyclotella meneghiniana</i> | C | | x | | | | | x | | |
| <i>Cyclotella</i> sp. | C | | x | | | | | | | |
| <i>Fragilaria construens</i> | P | | x | | | | | | | |
| Chrysophyceae | | | | | | | | | | |
| <i>Ochromonas</i> sp. | X2/X3 | | | | | | | | x | x |

contribution of codon **S_N** (cyanobacteria typical of warm mixed environments tolerant to low light conditions and usually nitrogen deficiency). In LI, a lake with high amount of inorganic suspended matter, dominant functional groups were **P** (diatoms frequently found in higher trophic states), **C** (diatoms described as typical of mixed eutrophic lakes) and **F**. Interestingly, and differing to previously reported in Izaguirre et al. (2012), the composition of lake TR changed drastically, since shifting from clear to turbid state; in the present study, this lake shared the same functional phytoplankton groups as found in the other turbid lakes.

Due to its eutrophic condition, HE also shared a similar composition of dominant functional groups

with the Salado's river basin lakes, but in this water body we also found an important contribution of codon **S1** (shade-adapted cyanobacteria).

In OT, the dominant functional groups were **P**, **C**, **X1** and **S_N**, the latter completely dominant at the end of the study period.

In the saline lake (SA), the more abundant coda were: **B** (diatoms of mesotrophic lakes, with species sensitive to the onset of stratification), and **X2** (represented by a persistent and abundant nanoflagellated chrysophyte).

In all the lakes of the Salado River Basin, the functional diversity (Simpson) was relatively low during summer, with increasing trend observed towards the autumn; extreme values varied between 1.05 and

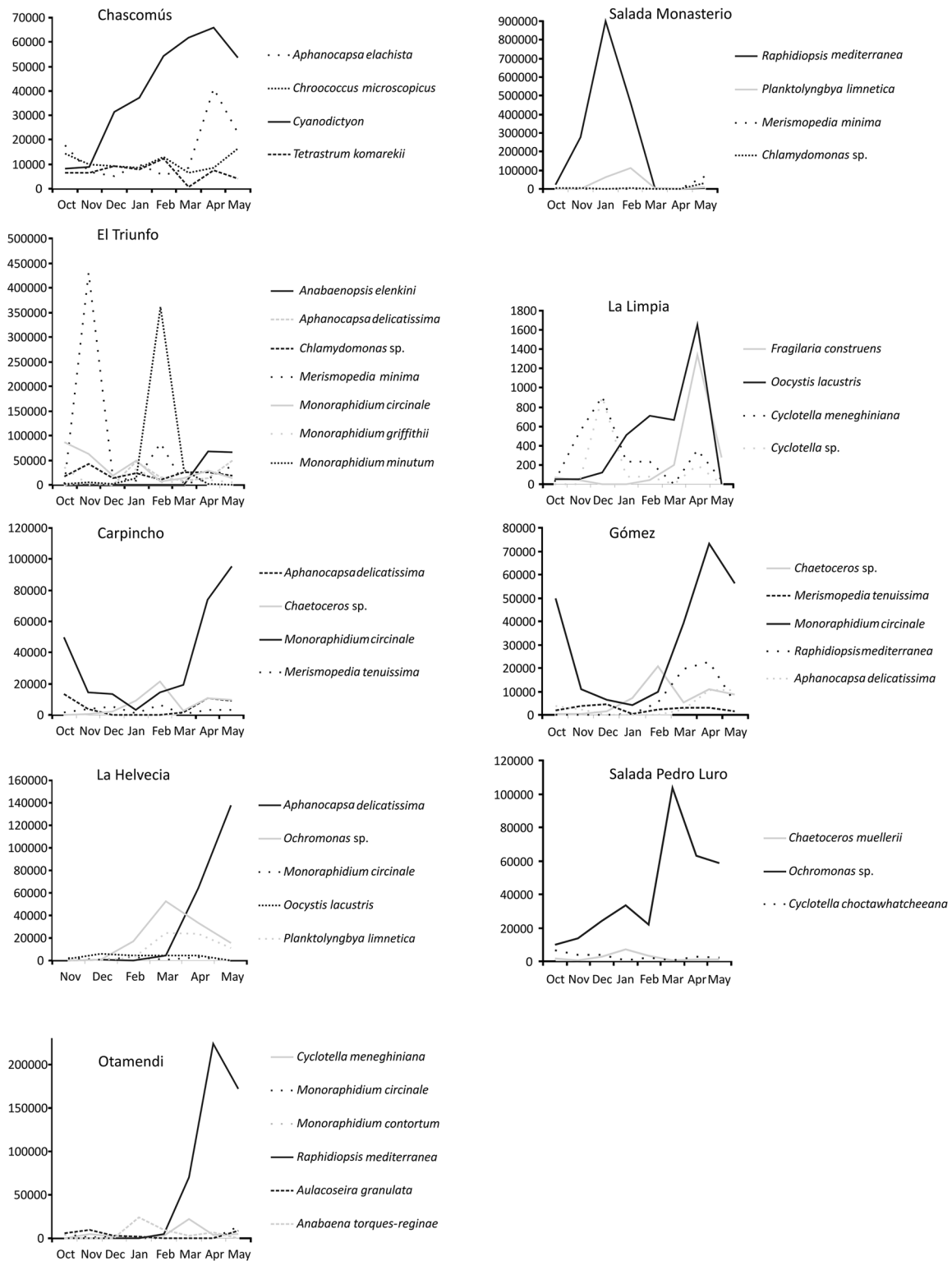


Fig. 6 Temporal variation of the dominant species in the shallow lakes

6.93. In OT, a fluctuating pattern was observed, with the highest functional diversity in spring (2.88) and the lowest one in autumn concomitantly with the cyanobacteria bloom (1.09). HE also presented a variable pattern, with a maximum in December (3.18) and a minimum in May (1.61). A low functional diversity was always recorded in the saline lake SA, ranging from 1.02 to 1.54. Figure 7 shows the temporal fluctuation of the functional diversity in all lakes.

Canonical correspondence analysis (CCA)

The ordination of the lakes obtained in the CCA based on the abundance of the phytoplankton functional groups and the environmental variables reflected their geographical location along the gradient, as well as their trophic state (Fig. 8a, b). The first two axes accounted for 68.4% of the variance (axis 1 43.7%; axis 2 24.7%). According to the Monte Carlo test, the environmental variables were significantly correlated with the first axis ($P = 0.002$), and the test of all canonical axes was also significant ($P = 0.002$). The significant variables according to forward selection were: temperature, pH, conductivity, TP, and TN. The first axis was mainly defined by variables related with the trophic state of the lakes, being correlated with TP, pH and TN (intra-set correlation coefficients: 0.67, -0.37 and 0.36 respectively). The second axis was principally associated with conductivity and transparency, and reflected the geographical position of the lakes; it showed higher correlation with conductivity, Secchi depth, and TP (intra-set correlation coefficients: 0.70 , 0.57 and -0.53 , respectively). The samples from the saline lake SA were positioned towards the upper part of the figure, at higher values of conductivity and transparency, and lower temperatures, where species of the codon **X2** attained higher abundances. The samples from the westernmost lake HE were positioned intermediately in relation to this conductivity gradient (axis 2). Several samples of OT and some from SM, located at the left part of the figure, were related to high pH values, corresponding with a dominance of the coda **S1** and **S_N**. The ordination of most samples of LI, and many of GO, CA and TR, towards higher TP, reflects the high trophic state of these lakes, where the coda **L0** and **X1** were very abundant. The samples from CH were situated in a middle position, near the center of the graph, with dominance of coda **J** and **K**.

Discussion

The results of our investigation provided important evidences for algal biomass dynamics, dominant phytoplankton species and functional groups during the warm season for a set of Pampean shallow lakes located along an environmental moisture gradient. We observed that in most lakes of the region, a high algal proliferation (in density and biomass) occurred during the entire warm season, persisting in some cases until autumn. In some lakes, conspicuous bloom-forming Cyanobacteria could be detected for 3–4 months.

The most obvious differences among the lakes investigated were related to their geographical position along the moisture gradient. The saline shallow lake La Salada (SA) was remarkably different from the others, due to its high salinity (evaluated by conductivity). Judging by its high TN level, this water body could be classified as eutrophic together with the others in this gradient, but its phytoplankton composition and biomass were noticeably different, and it exhibited the lowest species and functional diversity. These results are in line with those obtained by Borics et al. (2012) for a set of Hungarian lakes, where they found the lowest values of both functional and species diversity in astatic saline lakes. In SA, the high salinity is the main stressor for phytoplankton, selecting for a dominance of halotolerant species, such as *Cyclotella choctawhatcheeana* that has been reported as typical of marine and brackish waters, and was previously recorded in other hypersaline shallow lake from Argentina (Maidana & Romero, 1995). An unidentified Chrysophyceae (cf. *Ochromonas* sp.) was also found to be very abundant in this shallow lake, with a peak in late summer; although this algal group was mostly described from freshwater systems, few species are found in brackish or marine waters (Nicholls, 2003) and further molecular analysis is needed to elucidate the correct identification of this species.

All the shallow lakes studied from the Salado River basin showed a phytoplankton composition well adapted to turbid and enriched environments. Nevertheless, the species that became dominant in the warm period differed among systems. As was discussed in previous papers, light-limiting conditions prevail in most lakes of the more impacted zone of the Pampa (e.g. Allende et al., 2009; Llames et al., 2009; Izaguirre et al., 2012). Torremorell et al. (2007) previously reported that one of the deepest studied

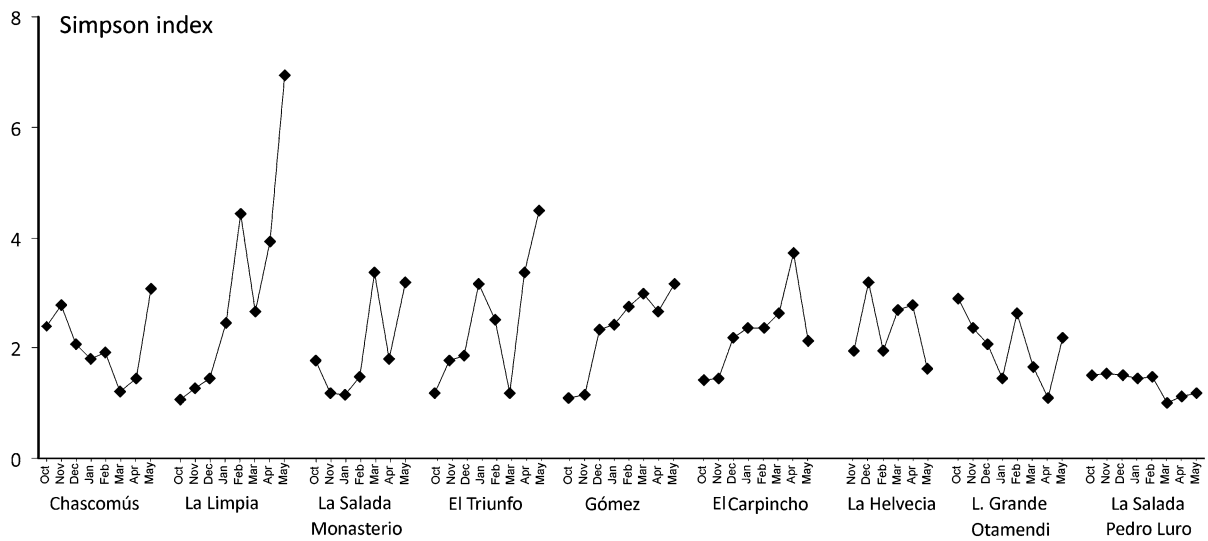


Fig. 7 Temporal variation of functional diversity (Simpson) as reciprocal ($1/D$) in the studied lakes

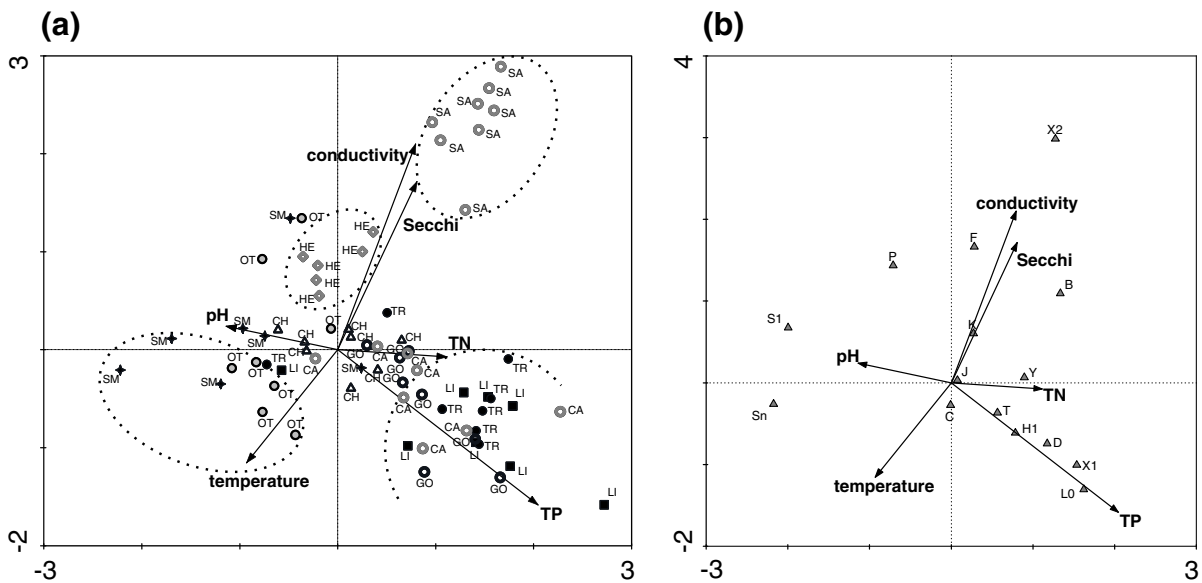


Fig. 8 Biplots of the CCA based on the abundance of the phytoplankton functional groups. **a** Ordination of the samples and environmental variables; **b** functional groups and environmental variables. Chascomús (CH); El Triunfo (ET); La Limpia

(LI); Salada de Monasterio (SM); Gómez (GO); El Carpincho (CA); Laguna Grande Otamendi (OT); La Helvecia (HE); Salada, Pedro Luro (SA)

shallow lakes from this region, Chascomús (CH), has stabilized in a turbid state, with a relatively constant algal assemblage persisting through the annual cycle. We confirmed these observations, since in this water body the entire warm season was characterised by an absolute preponderance of small colonial

Cyanobacteria (*A. elachista*, *Cyanodictyon* sp. *C. microscopicus*), that together constituted more than 80% of the total biomass, which is considered a steady state. As has long been recognized, the ecology of turbid systems is controlled by physical interactions, including a high quantity of suspended material which

exerts a profound effect upon the underwater light attenuation, with the consequent selection of “light-antenna” species having a high surface area/volume (SA/V) ratios (Reynolds, 1994). Small chroococcalean Cyanobacteria species are clearly well adapted to these conditions due to their high SA/V. Interestingly, the three dominant species of chroococcaleans in CH have mucilage; in a review of the potential functions of mucilage in phytoplankton, Reynolds (2007) concluded that there is no single and unambiguous function of mucilage, although the buoyant properties, the reducing microenvironment, the selective permeability and the grazing deterrence are among the most credible and authenticable functions. Fermani et al. (2013) demonstrated an extraordinary high abundance of picocyanobacteria in CH, thus intriguing and a challenge for future research will be the elucidation of the relationship between single cells and colonial forms in this extremely turbid ecosystem.

The co-dominance of diatoms and chlorococcaleans in the inorganic turbid shallow lake La Limpia (LI), with species well adapted to turbid and enriched conditions, coincides with our previous report (Izaguirre et al., 2012). The period studied showed the temporal replacement of four main populations, with peaks of two *Cyclotella* species in late spring and peaks of *Fragilaria construens* and *Oocystis lacustris* in early autumn. This shallow lake is also severely light limited by inorganic particulate matter, as has been stated by Pérez et al. (2013). These authors showed that both CH and LI are among the most turbid systems of the Pampean region, with extremely light attenuation coefficients and concentrations of optically active substances comparable with those reported for turbid estuaries. Nevertheless, these lakes show differences between unpigmented particulate material and phytoplankton absorption: in LI much of the light energy is removed by unpigmented particulate absorption, whereas in CH the variation in specific phytoplankton absorption was found to be closely related to changes in the cell pigment content, in response to the seasonal variation of incident light (Pérez et al., *op. cit.*).

The two shallow lakes located at the upper Salado River Basin, Gómez (GO) and El Carpincho (CA), were also characterized by high turbidity and are among the most enriched systems of the gradient, with very high TP concentrations and relatively high TN. Small chlorococcaleans, such as *Monoraphidium*

circinale, were among the most successful species in such lakes; these are typical C-strategists, fast-growing species commonly favoured by high levels of P and N (Reynolds, 2006). These taxa are included in codon X1, a functional group that comprises many small chlorophytes typical of shallow eutrophic and hypertrophic systems (e.g. O’Farrell et al., 2003; Fonseca & Bicudo, 2008; Sinistro et al., 2013). Small colonial Cyanobacteria (e.g. *Aphanocapsa delicatissima*) shared the habitat with those small green algae, and in addition in GO, we found a remarkable peak of *R. mediterranea* in early autumn.

El Triunfo (TR) deserves a special attention. This water body was previously described as a clear lake with high biomass of submerged macrophytes (Allende et al., 2009; Izaguirre et al., 2012), relatively low algal biomass in comparison with other Pampean lakes, and a high abundance of nanoflagellates (mainly cryptophytes). Moreover, prior to the present study, algal blooms were never observed in this lake. Currently, it is much more turbid and displays extremely high values of TP, TN and Chl *a*. The reasons associated with this shift in state seem to be correlated with a drastic reduction in water level, although we cannot discard modifications in the land use in the surroundings basin. The changes that took place in this lake are specifically addressed in Sanchez et al. (this special volume). Throughout the warm season studied, we found several conspicuous peaks of different algal populations; *Anabaenopsis elenkinii* was one of the most abundant species in mid-spring. Wiedner et al. (2002) reported the dominance of several species of Nostocales (among them, *Anabaenopsis* species) in early summer in shallow polymictic lakes. This genus was mentioned as one of the potential toxigenic cyanobacteria by Codd et al. (2005). By mid-summer, the community was dominated by small chlorococcaleans (*Monoraphidium* spp.), which as discussed, are well represented in highly enriched environments.

The shallow lake located in the Otamendi (OT) wetland showed some important differences from the other lakes, probably related to its location in the wettest part of the moisture gradient. It is very influenced by the Paraná River regime, the tides of the estuary of the Río de la Plata and the “sudestadas”—a local southeastern wind that is usually associated with rainy weather- (Atlas Ambiental de Buenos Aires, 2008). Studies conducted during the last decade in the main shallow lake of this wetland (Laguna Grande) indicated important

hydrological changes and a shift between a free-floating plant regime and a phytoplankton regime (O'Farrell et al., 2011). The period of our study coincided with a relatively high water level in the lake, which as shown by historical records, is inversely related to salinity, and thus the conductivity of OT was the lowest among the lakes studied. However, this ecosystem is subjected to important fluctuations in water level, and has experienced marked droughts in the past with very high conductivity values and cyanobacteria blooms (Chaparro et al., 2011). The high water level fluctuations contribute to environmental heterogeneity, represented by patches of open waters and macrophytes (Chaparro et al., 2013). A similar spatial pattern was documented for other vegetated systems by Krasznai et al. (2010), who reported that vegetated oxbow lakes may show dense algal populations among the macrophytes.

Despite the relatively high waters during our study, the warm season was marked by a conspicuous bloom of *R. mediterranea* that started in mid-summer and remained very high until mid-autumn. This species is included in codon S_N, typical of warm mixed lakes, and comprises cyanobacteria tolerant to low light conditions and usually nitrogen deficiency (Reynolds et al., 2002; Padisák et al., 2009), and its potential toxicity was reported by Codd et al. (2005). In this sense, it is important to mention that the concentrations of dissolved nitrogen are usually low in OT, and can be limiting for phytoplankton, condition that favours the development of N₂-fixing heterocystous cyanobacteria during certain periods (Unrein et al., 2010).

Finally, our investigation revealed the eutrophic condition of the shallow lake La Helvecia (HE). Nutrient levels, algal biomass and phytoplankton composition were typical of highly enriched systems. Although HE is located in another province (Córdoba), the surrounding zone is also very impacted by human activities. This lake exhibited very important enhancement of several species in late summer: *Aphanocapsa delicatissima*, which rose exponentially until late autumn, attaining a very high biomass, and *Planktolyngbya limnetica*, well represented from late summer to early autumn. Blooms of the several species of the genus *Planktolyngbya* (Syn: *Lyngbya*) were reported as increasingly common in enriched waters, including those that have experienced human disturbance such as dredging, inputs of treated municipal waste, and the discharge of nutrient-laden freshwater through coastal canals (Paerl & Fulton,

2006). In accordance with these observations, the shallow lake HE was subjected to an important anthropogenic disturbance. In order to maintain the agricultural activities in the zone, from February to March 2013, the water entrance to the lake was artificially closed, decreasing its water level about 0.50 m (Mancini, personal observation). This shallow lake constitutes another example of a shallow lake in this region that has shifted from a clear regime with submerged macrophytes for several decades, to the current turbid regime (Mancini et al., 2013).

The results of our investigation provide evidence showing the vulnerability of most shallow lakes in the region to water level fluctuations, eutrophication and canalization. We provide key information about the dominant algal species during the warm period in the different systems along a moisture gradient and identify the persistence of algal blooms (some of which were formed by harmful species) beyond summer in several lakes. The low algal biomass observed in other shallow lakes, despite their high nutrient levels, appeared to be correlated with their extreme environmental factors, such as high salinity or a very high inorganic turbidity. Independent of the moisture gradient, some lakes showed prolonged phases of steady state, correlating with particular characteristics, such as high turbidity or salinity, conditions that select for a few species well adapted to extreme conditions.

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