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The limnological trace of contemporaneous anthropogenic activities in the Pampa Region

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Abstract. Shallow lakes are the most productive freshwater ecosystems in the Argentinian Pampa Region. Only in Buenos Aires province, about 14000 shallow lakes larger than 10 ha exist, which provide important ecosystem services. Since the middle XX century profound changes are occurring in the region as a consequence of the anthropogenic activities, mainly associated to the expansion of agriculture, but also to livestock and urbanization. Different studies strongly suggest that changes in land use, as well as increased eutrophication of lakes, accelerated since 1990's. In this article, we provide a general overview of the main features of the Pampean shallow lakes and a review of published evidences based on paleolimnological and satellite images studies that indicate changes in the state of the lakes related with eutrophication during the last two centuries. On the other hand, we analyzed the historical changes that are occurring in these systems since the 1980's until the present by means of the principal variables associated with trophic status. This analysis, based on a data set of 740 samples from 87 shallow lakes, showed that nutrients (TP and TN) and algal biomass (as chlorophyll a) increased over the time, whereas transparency (Secchi depth) decreased; differences between XX and XXI centuries were significant. We also evaluated the change in the cyanobacteria assemblages (abundance and composition) between both centuries. We found that the biomass of this group increased in the XXI century and the composition of the assemblages changed, which nowadays are frequently represented by potentially toxic, bloom forming species. The shallow lakes of the region play an important role as sentinels of changes and all pieces of evidence are showing the impact of the anthropogenic activities.

[Keywords: shallow lakes, eutrophication, anthropogenic impact, historical analyses, lakes as sentinels]

Resumen. La huella limnológica de las actividades antropogénicas contemporáneas en la Región Pampeana. Las lagunas son los ecosistemas de agua dulce más productivos de la Región Pampeana argentina. Sólo en la provincia de Buenos Aires existen ~14000 lagunas >10 ha, que proveen servicios ecosistémicos importantes. Desde mediados del siglo XX se producen cambios profundos en la región como consecuencia de las actividades antrópicas, principalmente asociadas a la expansión de la agricultura, pero también a la ganadería y a la urbanización. Diferentes estudios evidencian que por estos cambios en el uso de la tierra, la eutroficación en las lagunas se aceleró desde los años noventa. En este trabajo presentamos un panorama general de las principales características de las lagunas pampeanas, y una revisión de las evidencias publicadas basadas en estudios paleolimnológicos e imágenes satelitales que indican cambios en el estado de las lagunas relacionados con la eutroficación en los últimos dos siglos. También analizamos los cambios históricos en estos sistemas a través de las principales variables asociadas al estado trófico desde los ochentas hasta hoy. Este análisis, basado en una serie de datos obtenidos de 740 observaciones en 87 lagunas, mostró que los nutrientes (PT y NT) y la biomasa algal (como clorofila a) aumentaron en el tiempo, mientras que los valores de transparencia (profundidad del Secchi) disminuyeron; las diferencias entre los siglos XX y XXI fueron significativas. Además, analizamos el cambio en los ensambles de cianobacterias (abundancia y composición) entre ambos siglos. Observamos que la biomasa de este grupo aumentó en el siglo XXI y la composición de los ensambles cambió, los que actualmente suelen estar representados en muchas lagunas por especies formadoras de floraciones tóxicas. Las lagunas de la región tienen un rol clave como centinelas de cambios, y todas las evidencias muestran el impacto de las actividades antropogénicas.

[Palabras clave: lagunas, eutroficación, impacto antropogénico, análisis histórico, lagos como centinelas]

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Introduction

The Pampa Region, one of the largest flatlands in the world, extends across the center-east part of Argentina, the best part of Uruguay and the southernmost Brazilian state, Rio Grande do Sul. Its gentle slope is only interrupted by two mountain ranges: Ventania and Tandilia. Buenos Aires province, with an area of 307000 km^2, is located at the core of the Pampa Plain. Its climate is temperate, with warm-temperate summers and mild winters. Precipitation ranges from 1000 mm/year in the Northeast to 400 mm/year in the Southwest (Viglizzo and Frank 2006; Volpedo and Cirelli 2013). The poorly developed drainage of the area results in a large wetland, comprising large numbers of shallow lakes (Iriondo 2004; Volpedo and Cirelli 2013). A flat landscape, combined with a humid climate, results in the accumulation of surface water that gives rise to a variety of water bodies (i.e., ponds, shallow lakes and marshes) (Geraldi et al. 2011) of different geomorphological origin. In recent times, human activities have greatly modified the shallow Pampean lakes by emplacing different hydraulic structures (e.g., embankments, dams and floodgates) or through the construction of channels in an attempt to prevent or alleviate floods. The latter have increased the connectivity between lakes and facilitated the spread of exotic species, such as the common carp (Colautti 1997).

Only in Buenos Aires province, there are roughly 14000 large (>10 ha) and 146000 small (0.05-10 ha) shallow lakes (Geraldi et al. 2011), in addition to about 200000 microbasins (0.01-0.05 ha) (Dangavs 2005). The patterns of abundance and size of Pampean shallow lakes vary spatially depending on local geomorphology, drainage density, soil type, mean annual precipitation and the inter-annual variability in precipitation. For example, in the southern part of the Pampean Region, lakes occurring in the continental plain tend to have circular contours and small surface area (~50 ha). These lakes are also more abundant than those occurring on the coastal plain, where they tend to have larger areas (~100 ha) and elongated shapes. Individual lakes display considerable inter-annual differences in lake area between wet and dry periods (Bohn et al. 2011). Greater abundance of lakes and large total lake area are observed during or after rainy years, while the opposite occurs after dry years.

Shallow lakes are the most important freshwater ecosystems in the Pampa Region. They constitute a very productive wetland system, which provides relevant ecosystem services such as commercial and sport fishing, recreation, water provision, climate regulation, among others (Grosman 2008). Shallow lakes are also key ecosystems from the point of view of biodiversity. There is evidence that these aquatic systems are being deeply affected by the human activities that take place in the region (i.e., agriculture, livestock, urbanization, canalizations), which have most likely promoted ecosystemic regime shifts, from clear with submerged vegetation to turbid with high phytoplankton biomass, in many lakes (Quirós et al. 2006; Kosten et al. 2012). Different studies show increasing occurrence of harmful algal blooms, particularly cyanobacteria, which frequently extend until autumn, in many shallow lakes of the region (Izaguirre et al. 2015; O'Farrell et al. 2021).

An associated impact of agriculture on Pampean freshwater systems is the presence of agrochemicals. In a regional study conducted in 52 Pampean shallow lakes, residues of herbicides (i.e., glyphosate and its main degradation product AMPA) were detected in more than 40% of the samples collected (Castro Berman et al. 2018). In lotic systems, pollution by agrochemicals was suggested as a probable cause of acidification by Hegoburu (2021), who studied the dynamics of the phosphorus in Pampean streams.

In this paper we present an overview of the main features of the shallow lakes from the Argentinian Pampa Region, focusing particularly on the changes that are occurring in these ecosystems as a consequence of anthropogenic activities. We provide a review of the available information based on paleolimnological and satellite image studies that indicate changes in the steady state of the shallow lakes related with eutrophication in the last two centuries. On the other hand, we analyzed the historical changes in the shallow lakes by means of the main variables associated with trophic status: nutrients (N and P), transparency (Secchi depth) and phytoplankton biomass (chlorophyll a) from middle 1980's to the present. This analysis was based on a data set of 740 observations obtained from 87 shallow lakes (including data reported by other authors and by our own). We also analyzed the changes in the structure of the phytoplankton assemblages (particularly Cyanobacteria) between the XX and XXI centuries, evaluating changes in their biomass, dominant species and tendency to the development of blooms.

Regime shifts in Pampean shallow lakes

One of the main paradigms for shallow lakes initially postulated that these ecosystems may alternate between two possible stable states, a clear-vegetated state with dominance of submerged macrophytes and a turbid state characterized by high phytoplankton biomass and the (almost) absence of submerged vegetation (Scheffer et al. 1993; Scheffer 2009). The mechanism involved in the transition from the clear state to the turbid one is assumed to be driven mostly by the concentration of nutrients; at low levels, the clear-water regime would be the only possible stable state; at the opposite, hypertrophic situation, just the turbid regime would be possible, while at intermediate range of nutrients the system could potentially alternate between the two states. Nevertheless, other factors such as climate, lake size and depth, and changes in water level were also associated to shifts in lake regime (e.g., Scheffer and Carpenter 2003; Scheffer and Van Nes 2007; O'Farrell et al. 2011; Izaguirre et al. 2018).

Shallow lakes in the Pampa Region display the two main regimes above described (Quirós et al. 2002; Allende et al. 2009; Izaguirre et al. 2012). In addition, an inorganic turbid state has also been reported in the Pampa Region. This state is found in a few lakes in which turbidity is mainly due to large concentrations of inorganic suspended material (i.e., clay). In such lakes, primary production is severely limited by low light availability caused by absorption and scattering by inorganic particles (Pérez et al. 2013). Table 1 shows examples of two shallow lakes of the region that have contrasting regimes (clear with submerged vegetation and turbid with high phytoplankton biomass), as indicated by Sanchez et al. (2013).

There is a documented evidence on regime shifts for a few Pampean shallow lakes (Cano et al. 2008; Casco et al. 2009; O'Farrell et al. 2011; Sánchez et al. 2015). A sharp decrease in water level was associated with the change from a clear vegetated state to a turbid condition with higher phytoplankton biomass in lake El Triunfo from 2005 to 2013 (Sánchez et al. 2015). Interestingly, this lake shifted back to a clear vegetated state when the hydrometric level was reestablished. In Laguna Grande (the largest lake within the Otamendi Natural Reserve; today, a national park), water level changes have also been linked to changes in lake regime, characterized by sequential periods of floating macrophytes dominance, high phytoplankton biomass and submerged vegetation (O'Farrell et al. 2011; Izaguirre et al. 2019). Nevertheless, beyond the changes associated with variations in water level, in the Pampa Region there has been a clear decreasing tendency in the number of clear vegetated shallow lakes over the time, aspect that is addressed further down in this article.

Table 1. Examples of two Pampean shallow lakes located in the Buenos Aires province, which present contrasting states (clear vegetated and phytoplankton turbid). Some of their main limnological features are shown. Field data were obtained and provided by Dr. M. Laura Sánchez. More information is detailed in Sánchez et al. (2013).

Tabla 1. Ejemplos de dos lagunas pampeanas de la provincia de Buenos Aires, presentando estados contrastantes (clara vegetada y fitoplancton-turbia). Se muestran algunas de sus principales características limnológicas. Los datos de campo fueron obtenidos y provistos por la Dra. M. Laura Sánchez. En el trabajo de Sánchez et al. (2013) se detalla más información.

	Kakel Huincul (clear vegetated)	El Burro (turbid high phytoplankton biomass)
Kd_{PAR} (m^{-1})	3.3	9.6
Euphotic depth (cm)	139.5	48
Turbidity (NTU)	1.45	66.9
TP (µg/L)	20	202
DIN (µg/L)	18.6	30
SRP (µg/L)	6.2	40
Chl a (µg/L)	(3.3-1.9)	(188-93)

Shallow lakes as sentinels

Lakes are increasingly regarded as sentinels of global climate change due to their responsiveness to environmental modifications and their capacity to integrate the variability of the associated watershed (Adrian et al. 2009). They are also very responsive to land-use changes in their watersheds. Lakes, ponds, rivers and streams are being degraded globally through anthropogenic eutrophication as growing human populations increase demands for food, energy and fiber that intensify agriculture and increase sewage and industrial wastewater effluents (Tilman et al. 2001). The global correlation of agricultural fertilizer use and the global distribution of lakes and reservoirs suggest that anthropogenic eutrophication may already dominate some regions and will have major future influences in others (Pacheco et al. 2013).

In industrialized countries of the Northern Hemisphere, eutrophication started to be recognized from the beginning of the 20th century, at first mostly related to point-source pollution from industrial and domestic discharges, which led to public actions demanding the improvement of wastewater treatment between the 1970's and 1990's. Later, a new wave of eutrophication has been spreading, affecting many lakes, reservoirs, rivers and coastal areas around the world due to changes in the land use. Thus, since the turn of the century, public actions have also focused on non-point pollution, mainly from agriculture (Le Moal et al. 2019). Over the last two centuries profound changes occurred in the landscape of the Argentine Pampa Region, involving the reduction of natural grasslands, which were substituted by cultivated grasslands and croplands (Castro Berman et al. 2018). More recent changes in land use within the region become evident by looking at the trend in the cultivated land area (mainly soy), which increased dramatically during the last half of the last century (Supplementary Material 1).

The historical changes observed in the shallow lakes are most likely associated with the aforementioned anthropogenic landscape modifications. As mentioned before, eutrophication of the shallow lakes from the Pampa Region accelerated from the 1990's onwards, most likely as a consequence of the change in the land use (Quirós et al. 2006), provoking the shift in the regime of many lakes from clear vegetated to turbid with high phytoplankton biomass. A study based on satellite image of many Pampean shallow lakes evidenced that about 68% of the water bodies analyzed were clear in 1987 and turbid in 2005, and it was hypothesized that the change in land use would be the main associated cause to the shift in their regime (Kosten et al. 2012).

Paleolimnological studies conducted on Pampean lakes also provide evidence on eutrophication increases due to human activities. In particular, Plastani et al. (2019) analyzed the main forcing factors behind hydrological shifts during the past ca. 200 years in the lake La Barrancosa, located in the southern humid Pampa, between the low mountain systems of Tandilia and Ventania. Changes in sedimentological, geochemical and biological variables indicated that eutrophication accelerated since 1990, probably as a consequence of the increase in sown area around the lake, the massive application of fertilizer and the adoption of pesticide-intensive transgenic soybeans.

In a study of lake Blanca Chica, the responses of multiple proxies corresponding to different trophic levels were assessed over the last 250 years (González Sagrario et al. 2020), and the nature of changes (linear *vs.* non-linear dynamics) was evaluated. The results revealed two transitions: ca. 1860-1900 and 1915-1990. During the second transition, nutrient levels increased, cyanobacteria and diatoms (typical of turbid waters) dominated the primary producer assemblage and rotifer species richness and fish scales increased. All these indicators showed multimodality, non-linear dynamics and an increase in standard deviation prior to the regime shift, which is consistent with a critical transition in response to eutrophication and was coincident with a post-1920 change in land use.

The paleoenvironmental history was also reconstructed in the shallow lake Cabeza de Buey, located at the central Pampa plain. Four periods were identified during the last 600 years of the lake evolution, which were based on changes in macrophytes and algal communities (Sánchez Vuichard et al. 2021). The study showed that the last hundred years of the lake history were characterized by increased eutrophication associated with the increase in agriculture, cattle breeding and urban settlement. Moreover, towards the beginning of the XXI century, the lake turned to an even more eutrophic state, evidenced by the abundance increase in the phytoplankton community.

A historical analysis of changes and trends observed in Pampean lakes in the XX and XXI centuries

Indicators of eutrophication are generally classified into indicators of pressure, chemical status and impact. Pressure indicators involve nutrient emissions and nutrient loads; status indicators are related to the concentrations of P and N in the water bodies, whereas impact indicators use biological responses of living communities (Ibisch et al. 2017). In this section we focus on status indicators of trophism (nutrient concentrations) and impact indicators (phytoplankton abundance and biomass). We analyzed historical information obtained from a large number of shallow lakes over the last four decades, spanning the period of most drastic change in land use, which took place in the 1990's.

The current analysis is based on data of shallow Pampean lakes obtained by us and by other limnologists, which covers the period from the beginning of the 1980´s until 2021. The data set includes information from 740 samples collected from 87 shallow lakes scattered over the Buenos Aires Province (34°29′ - 38°57′ S; 56°58′- 63°06′ W), which were sampled one or more times (Figure 1). In almost all cases (except when very few data were available), we selected only data corresponding to the spring and summer seasons. The information was gathered from published papers (Quirós et al. 1988; Boltovskoy et al. 1990; Izaguirre and Vinocur 1994; Conzonno 1996; Miretzky et al. 2002; Torremorell et al. 2007, 2009; Weigand and Escalante 2008; Allende et al. 2009; Benitez and Claps 2009; Mac Donagh et al. 2009; Cano et al. 2012; Izaguirre et al. 2012; Sánchez 2012; Ardohain et al. 2014; Fermani et al. 2015; Gabellone et al. 2017; Castro Berman et al. 2018), unpublished data gently provided by colleagues and our own unpublished data. The full data table with the corresponding sources is presented in Supplementary Material 2.

We analyzed the long-term changes in the concentration of total phosphorus (TP), total nitrogen (TN), chlorophyll a (Chla) and in the Secchi depth. Differences in the median of these variables between the XX and XXI centuries were analyzed by the non-parametric test Wilcoxon. It is important to point out that the number of data available for the XX century is lower than that of the XXI century, since many more limnological studies are currently being conducted in the lakes of the region. Changes in the variables analyzed are illustrated in Figure 2 a-d.

The analysis showed that nutrient concentrations increased significantly in the XXI century. TP increased from a mean value of 0.273 mg/L (median 0.22 mg/L) in the XX century to a mean of 0.612 mg/L (median 0.53 mg/L) in the XXI century. Mean TN concentration doubled its value, increasing from 2.418 mg/L (median 2.53 mg/L) in the XX century to 4.833 mg/L (median 4.395 mg/L) in

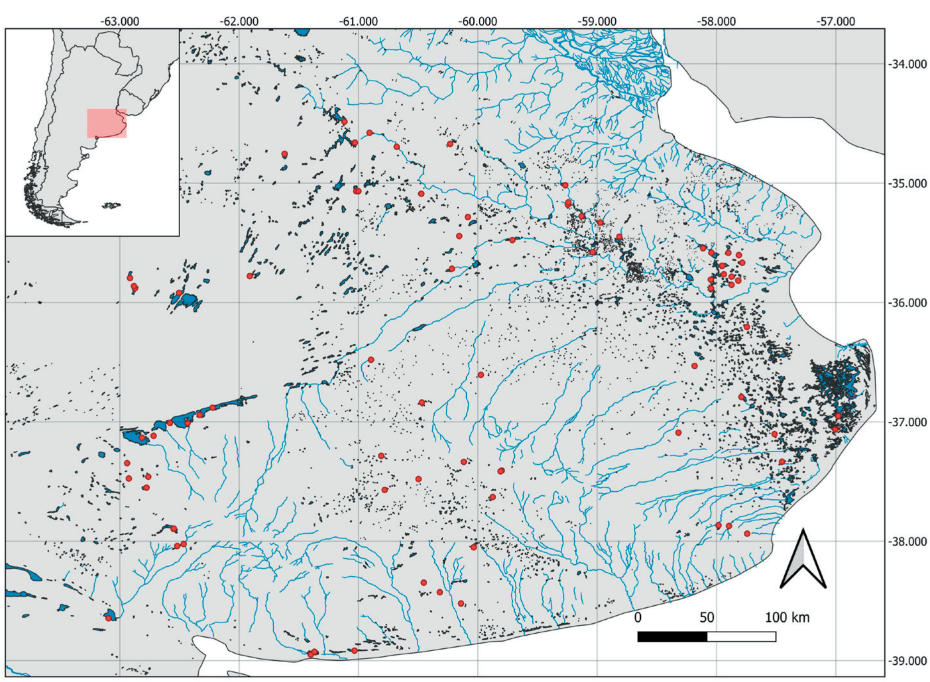

Figure 1. Map showing the geographic position of the shallow lakes (in red circles) included in the historical analysis.

Figura 1. Mapa que muestra la posición geográfica de las lagunas (en círculos rojos) incluidas en el análisis histórico.

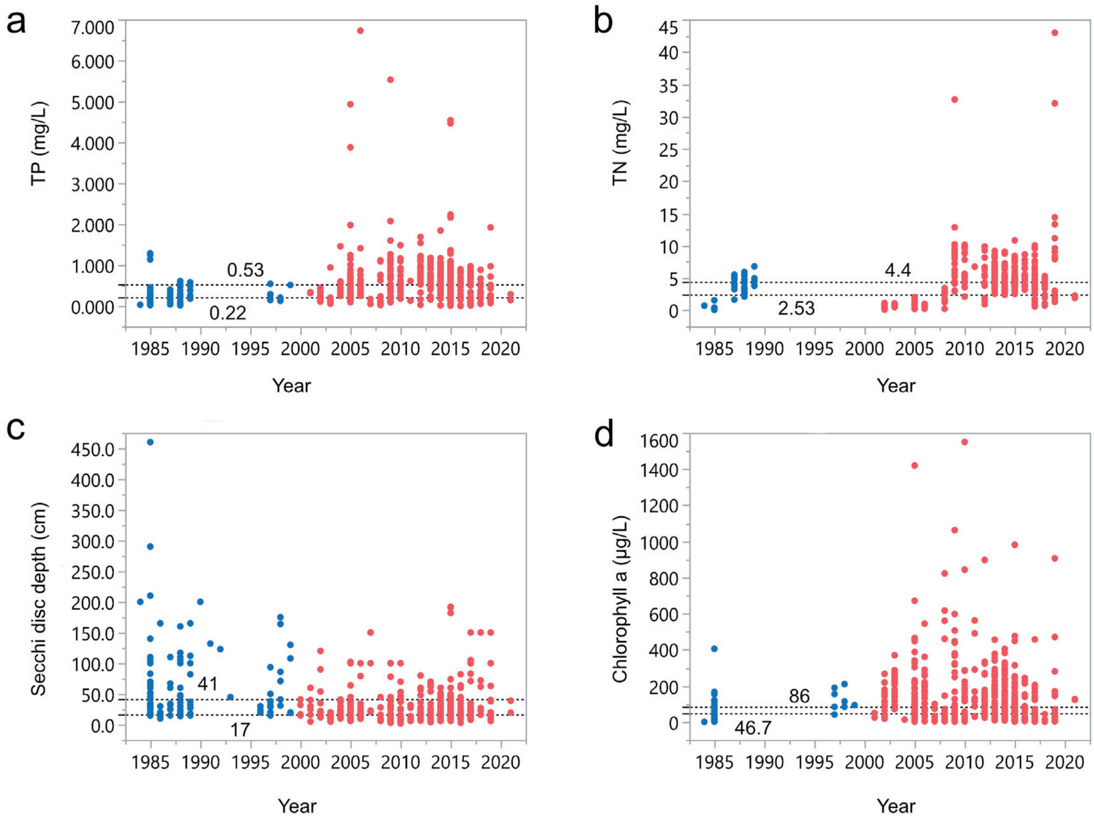

Figure 2. a-d) Historical changes in TP, TN, Secchi depth and chlorophyll a in Pampean shallow lakes from 1985 to 2021. Data set includes 87 shallow lakes. Blue and red circles represent XX and XXI centuries, respectively. Lines in blue and red are the median for the XX and XXI centuries, respectively, compared using the non-parametric Wilcoxon test.

Figura 2. a-d) Cambios históricos en el PT, el NT, la profundidad del Secchi y la clorofila a en lagunas pampeanas desde 1985 hasta 2021. El set de datos incluye 87 lagunas. Los círculos azules y rojos representan los siglos XX y XXI, respectivamente. Las líneas azules y rojas son las medianas para los siglos XX y XXI, respectivamente, comparados usando la prueba no paramétrica de Wilcoxon.

the XXI century. For both nutrients, differences between centuries were statistically significant ($P<0.0001$).

The increase in nutrients was coincident with the increase in phytoplankton biomass as estimated by Chla. Mean value in the XX century was 74.3 µg/L (median 46.7 µg/L) and increased to an average value of 133.7 µg/L (median 86 µg/L) in the XXI century, being differences statistically significant ($P=0.0093$).

Due to the phytoplankton biomass increase, many shallow lakes shifted from a clear state to a turbid one, thus values of Secchi depth markedly decreased. Our data set showed that mean Secchi depth was 67 cm (median 41 cm) in the XX century, decreasing to a mean of 25 cm (median 17 cm) in the XXI century, and differences were also statistically significant ($P<0.0001$).

On the other hand, we also performed a temporal analysis including a subset of 30 shallow lakes that were sampled in both centuries, and we found clear increasing trends in TP ($R^2=0.22$) and TN ($R^2=0.16$), as well as a decreasing tendency in Secchi depth ($R^2=0.16$) over the time (Supplementary Material 3). For this subset of shallow lakes, sampled in both centuries more than 50% shifted their regimes from clear vegetated to phytoplankton turbid.

Regime shift in lake El Burro. A case study

Lake El Burro (35.69° S - 57.95° W), which belongs to the river Salado chained lake-system, was sampled periodically by us from 1984 to 2021 within the framework of different research projects and also as part of the field work performed by the Limnology course students at the University of Buenos Aires. A remarkable shift in the state of the lake becomes apparent in this time series, showing a strong decrease (R^2=0.905) in water transparency, measured as Secchi depth, over time (Figure 3). In 1984 the depth of Secchi disc disappearance (SD) was about 200 cm. Since then, SD decreased steadily until the year 2000, reaching a value of ~20 cm (range: 0.17-0.35 cm), which has remained relatively unchanged thereinafter. In the former years, and until about 1992, when SD dropped below 120 cm, the lake remained almost entirely colonized by submerged macrophytes. During the 1990´s, water transparency decreased sharply as phytoplankton abundance increased.

Phytoplankton abundance was in general lower than 2000 ind./mL in the 1980´s, increasing up to 85000 ind./mL in 2005. Indeed, during the two first decades of the XXI century, algae counts remained remarkably high, ranging from 10760 to 92950 ind./mL. The huge difference in phytoplankton abundance between the two centuries is illustrated in Figure 3. Moreover, data obtained from the literature indicate that Chla was 0.5 µg/L in 1985 (Conzonno 1996) and increased from 40 to 167 µg/L during the present century (Allende et al. 2009; Sánchez 2012; Baliña unpublished data). Concomitantly with the phytoplankton increase, a sharp decline in the submerged macrophytes occurred in the lake.

Comparing data of nutrients (TP and TN) reported by different authors, an increase in the XXI century is also evident. In 1985, Conzonno (1996) measured concentrations of 0.031 mg/L and 0.73 mg/L for TP and TN, respectively. In 2005, data obtained by Allende et al. (2009) were considerably higher (0.202 and 1.179 mg/L for TP and TN, respectively); between 2009 and 2015, even much higher values were reported (Fermani et al. 2015; Castro Berman et al. 2018), with maximum concentrations reaching 0.513 mg/L and 6.16 mg/L for TP and TN, respectively.

The changes in the lake and its surroundings can also be evidenced with a quite simple analysis of the satellite images. Particularly, the change in the land use in the surrounding area of lake El Burro from XX to XXI centuries becomes apparent by comparing 1986 and 2021 summer satellite images, which were downloaded from the US Geological Service Site in level 2 (with atmospheric correction) (Figure 4). The 1986 image shows a greater vegetation cover compared to the 2021 image, probably also including some natural grasslands. The 2021 image shows a higher proportion of cultivated land and bare soil areas. The difference in the band reflectance corresponding to the lake is also evident, increasing the reflectance of band 2 (green) in 2021 (Figure 4).

Cyanobacterial harmful algal blooms

A first record of cyanobacterial blooms in Pampean shallow lakes is known for the mid XX century. This report corresponds to Laguna San Miguel del Monte in 1949, when summer phytoplankton was initially dominated by *Microcystis aeruginosa* and then replaced by *Dolichospermum circinalis*, *D. inaequalis*, *D. sphaerica* and *D. spiroides* (Guarrera 1962). Interestingly, though *Microcystis aeruginosa* was the first species

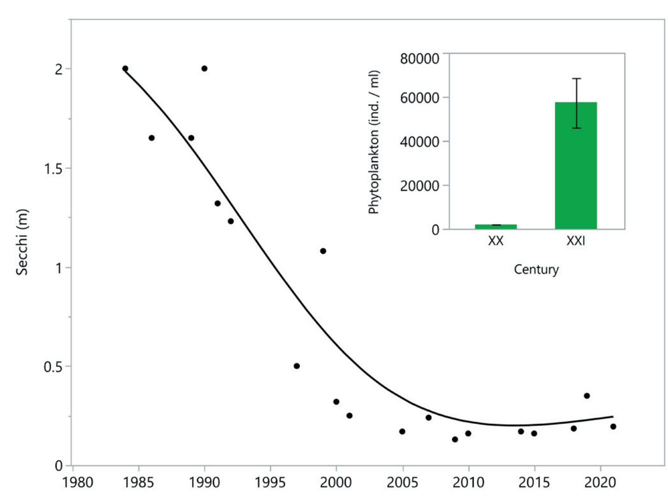

Figure 3. Variation in Secchi depth from 1984 to 2021 in El Burro shallow lake (adjustment: Gaussian Kernel smoother). The bar graph shows the change in phytoplankton abundance between the XX and XXI centuries.

Figura 3. Variación en la profundidad del Secchi desde 1984 hasta 2021 en la laguna El Burro (ajuste: método suavizante Kernel Gaussiano). El gráfico de barras muestra el cambio en la abundancia de fitoplancton entre los siglos XX y XXI.

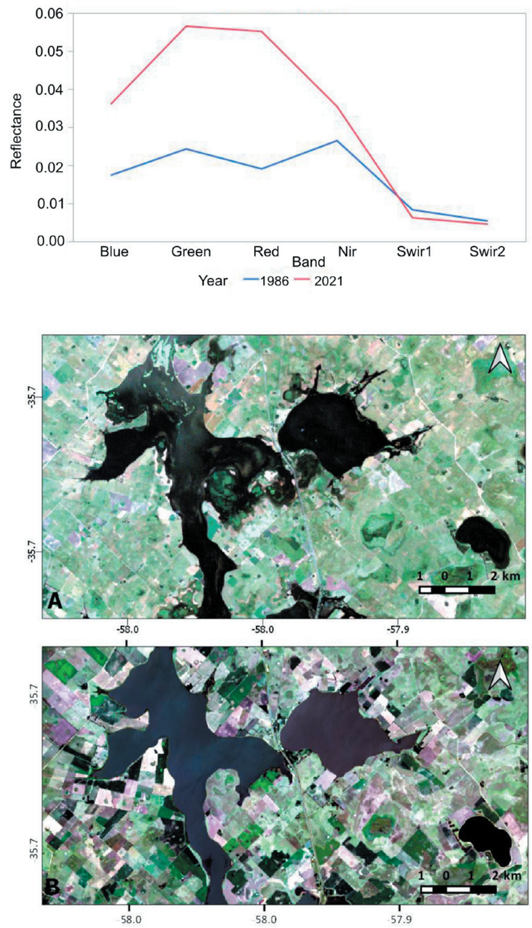

Figure 4. Satellite images of the shallow lake El Burro. A) Image Landsat 5TM- Natural Colour. Date: 13 January 1986. B) Image Landsat 8 OLI- Natural Colour. Date: 13 January 2021. Path-Row: 224-085. The upper figure shows the surface reflectance of the bands for each year. Images were downloaded from the United States Geological Service Site in level 2, with atmospheric correction (earthexplorer.usgs.gov).

Figura 4. Imágenes satelitales de la laguna El Burro. A) Imagen Landsat 5TM- Color Natural. Fecha: 13 de enero de 1986. B) Imagen Landsat 8 OLI- Color Natural. Fecha: 13 de enero de 2021. Path-Row: 224-085. La figura superior muestra la reflectancia en superficie de las bandas para cada año. Las imágenes fueron descargadas de la página del Servicio Geológico de los Estados Unidos en nivel 2, con corrección atmosférica.

reported to form a bloom (named at that time as an "aquatic fluorescence"), this species is neither the most frequent nor the most abundant in Pampean shallow lakes (O'Farrell et al. 2019). This species is reported in worldwide blooms because its ability to regulate flotation provides a high ecological fitness in stratified water columns. In contrast, the dispersive strategy assigned to straight filaments provides high ecological fitness in the mixed and turbid layers characteristic of shallow polymictic Pampean lakes, thanks to the antenna morphology which enhances light uptake.

A detailed analysis of the information included in papers and thesis published up to day and in databases of ongoing studies revealed that there is a clear difference in the cyanobacterial assemblages of clear and turbid shallow lakes, as defined in the previous sections. Moreover, those lakes shifting to an alternative regime, either from clear to turbid or even in a state transition, evidenced a species replacement that involves both strong cyanobacterial abundance and biomass enhancements. In the period before the implementation of modern agricultural techniques (XX century), seven out of twelve lakes for which detailed standardized phytoplankton information exists (Adela, Chis Chis, La Tablilla, Las Barrancas, Kakel Huincul, El Triunfo and Colis) were in a clear state and their cyanobacterial assemblages were constituted by numerous small-sized cells chroococcalean species, most of which belong to the genera *Aphanocapsa*, *Chroococcus*, *Merismopedia* and *Eucapsis* (Supplementary Material 4), and whose populations did not exceed some hundred colonies/mL. According to this survey, nearly all shallow lakes characterized by a turbid regime were at that time dominated by nostocalean species usually exceeding 1000 filaments/mL, value that surely corresponded to more than 20000 cells/mL (WHO Guide level 1 for recreation and Alert level 1 drinking water). The species representative of this period belong to the genera *Anabaenopsis*, *Aphanizomenon*, *Raphidiopsis*, *Sphaerospermopsis* and *Dolichospermum* (Supplementary Material 4). Only five lakes were assigned to a turbid regime, namely Lobos, San Miguel del Monte, Chascomús, Todos los Santos and La Salada. Izaguirre and Vinocur (1994) mentioned that these turbid lakes were periodically cleared mechanically of macrophytes and their watersheds were associated either to relatively small cities, with limited or deficient effluent treatments, or to camping and fishing resorts. On the other hand, lake La Salada is actually a widening of the Salado river; thus, its turbidity and phytoplankton flora were highly influenced by the river.

Since the XXI century, when agriculture intensification took place, a larger and consistent data base allowed a more comprehensive characterization of the planktonic cyanobacteria of Pampean shallow lakes. As previously stated, nearly 90% of the shallow lakes are presently in a turbid state and present cyanobacterial assemblages are mostly dominated or co-dominated by one or two of the following filamentous species: *Raphidiopsis mediterranea*, *R. contorta*, *R. raciborskii*, *Sphaerospermopsis aphanizomenoides*, *Planktothrix agardhii*, *Cuspidothrix issastchenkoi* and several species of *Anabaenopsis* (Figure 5, Supplementary Material 4). *Nodularia spumigena* deserves a special mention as it forms blooms exclusively in saline lakes (Chasicó or El Paraíso), or in less salty lakes (Carpincho, Gómez, Mar Chiquita de Junín) during drought periods, when conductivity often exceeds the levels of more typical conditions (Figure 5, Supplementary Material 4). Filament densities of each one of these species achieve numbers two orders of magnitude higher than those recorded during the previous century, and thus, cell densities presently exceed largely WHO Guide level 2 for recreation and Alert level 2 drinking water (105 cells/mL). The highest density of *R. mediterranea* registered by us corresponds to Salada de Monasterio, where this species exceeded 10^6 cells/mL for several consecutive months, from spring to autumn, and was accompanied by *Planktothrix agardhii* (maximum 2.4×10^5 cells/mL), *Cuspidothrix issastchenkoi*, *Anabaenopsis cunningtoni* and *A. circularis*, each one with ca. 10^4 cells/mL (Cocciolo et al. 2021). Though the mentioned filamentous species contribute to the bulk of cyanobacterial biomass in Pampean lakes, there are several small cell Oscillatoriales and Chroococcales species that add significantly to plankton abundance. The most abundant are *Planktolyngbya contorta*, *P. limnetica*, *Aphanocapsa delicatissima*, *A. elachista*, *A. incerta*, *Coelosphaerium minutissimum*, *Merismopedia tenuissima*, *M. minima* and *Cyanodyction* sp. (Figure 5, Supplementary Material 4). The few lakes that during the XXI century were assigned to a clear state (Colis, Los Toldos, Samboy) showed poorly developed populations of small cell colonial or filamentous species such as *A. delicatissima*, *A. elachista*, *Chroococcus minor*, *Merismopedia* spp., *P. limnetica* and *P. contorta* (Figure 5, Supplementary Material 4). These same species were more abundant in those lakes in transition from clear to turbid (e.g., Kakel Huincul and Monte). Contrary to the findings of the XX century, many of the turbid lakes affected by cyanobacterial blooms are not impacted by urban effluents, macrophyte drawal or fisheries, but they are immersed in agricultural landscapes. Castro Berman et al. (2018) classified many of the Pampean lakes included in this analysis and reported that most of them have a high percentage of

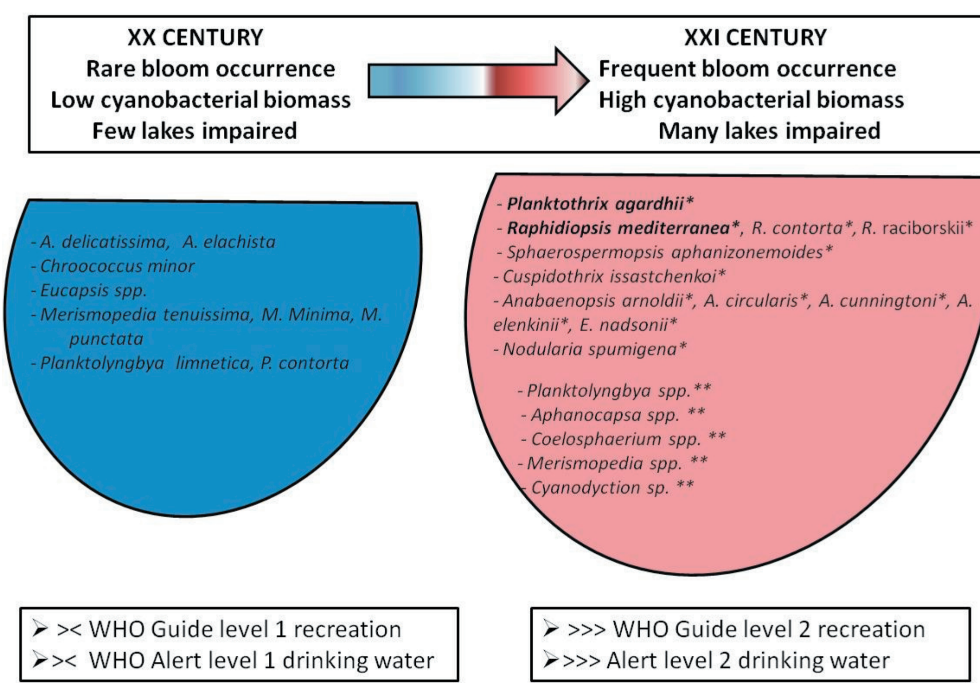

Figure 5. Characterization of cyanobacterial assemblages in clear and turbid Pampean lakes. Notes: *Species contributing with low biomass. **Species contributing with high biomass.

Figura 5. Caracterización de los ensambles de cianobacterias en lagunas pampeanas claras y turbias. Notas: *Especies que contribuyen con baja biomasa. **Especies que contribuyen con alta biomasa.

their surrounding area occupied by croplands or pastures (e.g., El Burro, Norte de Lincoln, Cuero de Zorro and La Brava), whereas a low percentage are associated to urban or residential areas (e.g., Carpincho, Los Padres, Chascomús).

The poor ecological status of Pampean shallow lakes is evidenced by the intense cyanobacteria harmful blooms impairing many of these nutrient enriched, turbid and polymictic water bodies (O'Farrell et al. 2021). A 3-year study of ten lakes located across a climatic gradient was aimed at exploring which factors drive the dynamics of cyanobacterial assemblages leading to bloom prevalence in many of these Pampean water bodies. This study concluded that the effect of seasonal annual temperature variation on cyanobacteria was subordinated to the light environment of the water column —which was, on turn, highly affected by water level conditions— and to nutrient concentrations. In this sense, *Raphidiopsis* and *Sphaerospermopsis* blooms were restricted to periods of decreasing turbidity and shallow depths in coincidence with TN pulses, while pico-sized cell colonies of *Aphanocapsa*, *Aphanothece*, *Cyanodictyon* and *Merismopedia* did well even under deeper depth and higher turbidity levels, evidencing their good performance in more turbid and deeper water columns due to a more efficient light utilization and nutrient uptake. The known preference of *P. agardhii* and *Anabaenopsis* for high P lakes was also observed in these Pampean water bodies. Assemblages were composed by more than 35 filamentous and colonial species, where nostocaleans and chroococcaleans abundances mirrored one another along temporal patterns.

Recently, and in coincidence with above mentioned studies, Castro Berman et al. (2022) assessed the environmental implications and the ecological consequences of agricultural land use and glyphosate contamination on spring phytoplankton from 52 shallow lakes in the Pampa Region and concluded that nano- and micro-cyanobacteria relative abundance increased with the trophic status of the lakes and declined with increasing transparency. In hypereutrophic lakes located in highly productive agricultural basins, which were associated to land use that heavily rely on glyphosate use (i.e., summer and double crops) and also to a lower agriculture pressure (i.e., pastures, other crops and urban development), the relative abundance of cyanobacteria was particularly high.

Finally, it is of paramount importance to mention the toxic nature of bloom forming cyanobacteria, as most species involved in the massive growth events in Pampean shallow lakes may produce either microcystin, saxitoxin or anatoxin. Anyhow, there are few cyanotoxin reports, all corresponding to microcystins: Laguna de los Padres (Amé et al. 2010), Salada de Monasterio (Cocciolo et al. 2021), Carpincho, Gómez, Chascomús, El Triunfo (O'Farrell et al. 2018). Aguilera et al. (2017) reviewed cyanotoxin occurrence in Argentina and, in face of the few toxin data, concluded that the limited literature on toxin concentration could be attributed to the fact that most studies are focused on phytoplankton dynamics because the costs of testing methods entailed in cyanotoxin analytical standards, equipment and trained personnel are very high. Harm to livestock, fish and bird mortality has been associated with cyanobacterial blooms but have not been evaluated for toxins (Odriozola et al. 1984; Grosman and Sanzano 2002).

Conclusions

In this paper we summarized the available evidence either on the status indicators and impacts of the anthropogenic activities on the shallow Argentinian Pampean lakes. Paleolimnological and satellite-based studies, as well as our analysis of historical data from lakes within the Pampa Region show increased eutrophication towards the second half of the last century, which is coincident in time with a marked change in land use, which accelerated since 1990's.

The historical analysis based on a large data set assembled from different sources (published data and unpublished data either shared by colleagues or collected by us) showed significant differences in the median values of nutrients (TP and TN), transparency and phytoplankton biomass (as Chla) between XX and XXI centuries. Nutrients and Chla increased and transparency decreased over the time. In one particular shallow lake that has been sampled since 1980's until present, a marked decreasing tendency in Secchi depth was observed, with a concurrent increase in phytoplankton abundance, which led to the loss of submerged macrophytes.

Several shallow lakes that were in a clear vegetated state in the XX century are nowadays turbid with high algal biomass. Moreover, an examination of phytoplankton structure also shows important changes between both centuries. Regarding the cyanobacterial assemblage, during the XX century, most lakes presented lower biomass and the group was mainly represented by small colonial and thin filamentous species, while the occurrence of algal blooms was much less frequent. In the XXI century, higher cyanobacteria biomass is being reported in many lakes, with persistence until autumn, and frequently represented by bloom forming filamentous of potentially toxic strains of cyanobacteria. Thus, many lakes are nowadays impaired.

Shallow lakes are excellent sentinels of the changes that are taking place in the region. The conservation of these ecosystems in a good condition is crucial, not only because of their biodiversity, but also because of the multiple ecosystem services that they provide. The deterioration of the shallow lakes also promotes the proliferation of cyanobacterial blooms, which implies a real danger for the aquatic biota, livestock and human beings.

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References

Adrian, R., C. M. O'Reilly, H. Zagarese, S. B. Baines, D. O. Hessen, W. Keller, D. M. Livingstone, R. Sommaruga, D. Straile, E. V. Donk, G. A. Weyhenmeyer, and M. Winder. 2009. Lakes as sentinels of climate change. Limnology and Oceanography 54:2283-2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283.

Aguilera, A., S. Haakonsson, M. V. Martin, G. L. Salerno, and R. O. Echenique. 2017. Bloom-forming cyanobacteria and cyanotoxins in Argentina: A growing health and environmental concern. Limnologica 69:103-114. https://doi.org/10.1016/j.limno.2017.10.006.

Allende, L., G. Tell, H. Zagarese, A. Torremorell, G. Pérez, J. Bustingorry, R. Escaray, and I. Izaguirre. 2009. Phytoplankton and primary production in clear-vegetated, inorganic-turbid and algal-turbid shallow lakes from the Pampa plain (Argentina). Hydrobiologia 624:45-60. https://doi.org/10.1007/s10750-008-9665-9.

Amé, M. V., L. N. Galanti, M. L. Menone, M. S. Gerpe, V. J. Moreno, and D. A. Wunderlin. 2010. Microcystin-LR, -RR, -YR and -LA in water samples and fishes from a shallow lake in Argentina. Harmful Algae 9:66-73. https://doi.org/10.1016/j.hal.2009.08.001.

Ardohain, D. M., H. H. Benítez, N. A. Gabellone, and M. C. Claps. 2014. Respuesta de la estructura zooplanctónica a cambios físicos y biológicos en una laguna pampásica (Laguna Lacombe). Biología Acuática 30:17-26.

Benítez, H. H., and M. C. Claps. 2009. Distribución horizontal y vertical del zooplancton en un ciclo diario en el litoral de una laguna pampásica. Biología Acuática 26:19-31.

Bohn, V. Y., G. M Perillo, and M. Piccolo. 2011. Distribution and morphometry of shallow lakes in a temperate zone (Buenos Aires Province, Argentina). Limnetica 30:89-102. https://doi.org/10.23818/limn.30.08.

Boltovskoy, A., A. Dippolito, M. Foggetta, and N. Gómez. 1990. La laguna de Lobos y su afluente: limnología descriptiva, con especial referencia al plancton. Biología Acuática 14:1-43.

Cano, M. G., M. A. Casco, L. C. Solari, M. E. Mac Donagh, N. A. Gabellone, and M. C. Claps. 2008. Implications of rapid changes in chlorophyll-a of plankton, epipelon and epiphyton in a Pampean shallow lake: an interpretation in terms of a conceptual model. Hydrobiologia 614:33-45. https://doi.org/10.1007/s10750-008-9534-6.

Cano, M. G., M. A. Casco, and M. C. Claps. 2012. Effect of environmental variables on epiphyton in a pampean lake with stable turbid- and clear-water states. Aquatic Biology 15:47-59. https://doi.org/10.3354/ab00409.

Casco, M. A., M. E. Mac Donagh, M. G. Cano, L. C. Solari, M. C. Claps, M. C., and N. A. Gabellone. 2009. Phytoplankton and epipelon responses to clear and turbid phases in a seepage lake (Buenos Aires, Argentina). International Review of Hydrobiology 94:153-168. https://doi.org/10.1002/iroh.200711036.

Castro Berman, M., D. J. G. Marino, M. V Quiroga, and H. Zagarese. 2018. Occurrence and levels of glyphosate and AMPA in shallow lakes from the Pampean and Patagonian regions of Argentina. Chemosphere 200:513-522. https://doi.org/10.1016/j.chemosphere.2018.02.103.

Castro Berman, M., I. O'Farrell, P. Huber, D. Marino, and H. Zagarese. 2022. A large-scale geographical coverage survey reveals a pervasive impact of agricultural practices on plankton primary producers. Agriculture, Ecosystems and Environment 325:107740. https://doi.org/10.1016/j.agee.2021.107740.

Cocciolo, F. T., L. Yema, M. L. Sánchez, C. González, and I. O'Farrell. 2021. Floraciones tóxicas de cianobacterias en una laguna pampeana: una aproximación a su ecología desde los rasgos morfo-fisiológicos. Ecología Austral 31:505-519.

https://doi.org/10.25260/EA.21.31.3.0.1514.

Colautti, D. C. 1997. Ecología de la carpa *Cyprinus carpio*, en la cuenca del Río Salado, Provincia de Buenos Aires. Tesis Doctoral, Universidad Nacional de La Plata, La Plata, Argentina.

Conzonno, V. H. 1996. Sustancias húmicas solubles presentes en ambientes acuáticos. Tesis Doctoral, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. Buenos Aires, Argentina.

Dangavs, N. V. 2005. Los ambientes acuáticos de la provincia de Buenos Aires. Pp. 219-236 *in* R. E. de Barrio, R. O. Etcheverry, M. F. Caballé and E. Llambías (eds.). Geología y recursos minerales de la provincia de Buenos Aires. Relatorio XVI Congreso Geológico Argentino, Argentina.

Fermani, P., A. Torremorell, L. Lagomarsino, R. Escaray, F. Unrein, and G. Pérez. 2015. Microbial abundance patterns along a transparency gradient suggest a weak coupling between heterotrophic bacteria and flagellates in eutrophic shallow Pampean lakes. Hydrobiologia 752:103-123. https://doi.org/10.1007/s10750-014-2019-x.

Gabellone, N. A., L. C. Solari, and D. M. Ardohain. 2017. Changes of the trophic status of a pampean shallow lake: causes and consequence. Verhandlungen des Internationalen Verein Limnologie 28:1626-1629. https://doi.org/10.1080/03680770.2001.11902732.

Geraldi, A., M. Piccolo, and G. Perillo. 2011. Lagunas bonaerenses en el paisaje pampeano. Ciencia Hoy 123:16-22.

González Sagrario, M. D. L. A, S. Musazzi, F. E. Córdoba, M. Mendiolar, and A. Lami. 2020. Inferring the occurrence of regime shifts in a shallow lake during the last 250 years based on multiple indicators. Ecological Indicators 117: 106536. https://doi.org/10.1016/j.ecolind.2020.106536.

Grosman, F. 2008. Una invitacioìn a conocer nuestras lagunas pampeanas. Pp. 19-38 *in* F. Grosman (comp.). Espejos en la llanura: Nuestras lagunas de la regioìn pampeana. Universidad Nacional del Centro de la Provincia de Buenos Aires. Tandil.

Grosman, F., and P. Sanzano.2002. Mortandades de Pejerrey Odontesthes bonariensis originadas por floraciones de cianobacterias en dos ambientes de Argentina. Aquatic 17:1-7.

Guarrera, S. A. 1962. Estudios limnológicos en la laguna de San Miguel del Monte (Provincia de Buenos Aires, República Argentina) con especial referencia al fitoplancton. Revista del Museo de la Plata (Nueva Serie). Sección Botánica, Tomo IX:125-174.

Hegoburu, C. 2021. Dinámica del fósforo en arroyos pampeanos: patrones espaciales y temporales e implicancias del cambio climático. Tesis Doctoral, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina.

Ibisch, R., K. Austnes, D. Borchardt, B. Boteler, W. Leujak, E. Lukat, J. Rouillard, U. Schmedtje, A. L. Solheim, and K. Westphal. 2017. European assessment of eutrophication abatement measures across land-based sources, inland, coastal and marine waters. European Topic Centre on Inland, Coastal and Marine Waters, Helmholtz Centre for Environmental Research GmbH-UFZ, Germany, ETC/ICM Technical Report. Pp. 95.

Iriondo, M. 2004. Large wetlands of South America: a model for Quaternary humid environments. Quaternary International 114:3-9. https://doi.org/10.1016/s1040-6182(03)00037-5.

Izaguirre, I., and A. Vinocur. 1994. Typology of shallow lakes of the Salado River basin (Argentina), based on phytoplankton communities. Hydrobiologia 277:49-62. https://doi.org/10.1007/BF00023985.

Izaguirre, I., L. Allende, R. Escaray, J. Bustingorry, G. Pérez, and G. Tell. 2012. Comparison of morpho-functional phytoplankton classifications in human-impacted shallow lakes with different stable states. Hydrobiologia 221:203-216. https://doi.org/10.1007/s10750-012-1069-1.

Izaguirre, I., M. L. Sánchez, M. R. Schiaffino, I. O'Farrell, P. Huber, N. Ferrer, J. Zunino, L. Lagomarsino, and M. Mancini. 2015. Which environmental factors trigger the dominance of phytoplankton species across a moisture gradient of shallow lakes? Hydrobiologia 752:47-64. https://doi.org/10.1007/s10750-014-2007-1. https://doi.org/10.1007/s10750-016-2951-z.

Izaguirre, I., J. Lancelotti, J. F. Saad, S. Porcel, M. C Marinone, I. Roesler, and M. C. Diéguez. 2018. Influence of fish introduction and water level decrease on lakes of the arid Patagonian plateaus with importance for biodiversity conservation. Global Ecology and Conservation 14:e00391. https://doi.org/10.1016/j.gecco.2018.e00391.

Izaguirre, I., I. O'Farrell, and M. L. Sánchez. 2019. A monitoring project in Pampean shallow lakes (Argentina) reveals a joint effect of cultural eutrophication and hydrological variability on phytoplankton communities. SIL News 74: 9-11.

Kosten, S., M. Vernooij, E. H. Van Nes, M. D. L. A. Sagrario, J. G. Clevers, and M. Scheffer. 2012. Bimodal transparency as an indicator for alternative states in South American lakes. Freshwater Biology 57:1191-1201. https://doi.org/10.1111/j.1365-2427.2012.02785.x.

Le Moal, M., C. Gascuel-Odoux, A. Ménesguen, Y. Souchon, C. Étrillard, A. Levain, F. Moatar, A. Pannard, P. Souchu, A. Lefebvre, and G. Pinay. 2019. Eutrophication: A new wine in an old bottle? Science of the Total Environment 651: 1-11. https://doi.org/10.1016/j.scitotenv.2018.09.139.

Mac Donagh, M. E., M. A Casco, M. G. Cano, L. C. Solari, M. C. Claps, and N. A. Gabellone. 2009. Fitoplancton, epipelon, materia orgánica y fósforo de una laguna arreica en relación con fases claras y turbias. Biología Acuática 26:133-142.

Miretzky, P., N. I. Maidana, and A. F. Cirelli. 2002. Stability of diatom composition in a variable lake environment: Lake Chascomús, Argentina. Limnology 3:77-85. https://doi.org/10.1007/s102010200009.

Odriozola, E., N. Ballabene, and A. Salamanco. 1984. Intoxicación en ganado bovino por algas verde-azuladas. Revista Argentina de Microbiología 16:219-224.

O'Farrell, I., I. Izaguirre, G. Chaparro, F. Unrein, R. Sinistro, H Pizarro, P. Rodríguez, P. de Tezanos Pinto, R. Lombardo, and G. Tell. 2011. Water level as the main driver of the alternation between a free-floating plant and a phytoplankton dominated state: a long-term study in a floodplain lake. Aquatic Sciences 73:275-287. https://doi.org/10.1007/s00027-

010-0175-2.

O'Farrell, I., L. Yema, M. R. Schiaffino, M. L. Sánchez, P. Huber, C. González, F. T. Cocciolo, M. Mancini, L. Lagomarsino, and I. Izaguirre. 2018. Caracterización ecológica de los ensambles de cianobacterias potencialmente formadoras de floraciones en lagunas pampeanas. VIII Congreso Argentino de Limnología, Luján, Argentina.

O'Farrell, I., C. Motta, M. Forastier, W. Polla, S. Otaño, N. Meichtry, M. Devercelli, and R. Lombardo. 2019. Ecological meta-analysis of the bloom-forming planktonic Cyanobacteria in Argentina. Harmful Algae 83:1-13. https://doi.org/10.1016/j.hal.2019.01.004.

O'Farrell I., M. L. Sánchez, M. R. Schiaffino, I. Izaguirre, P. Huber, L. Lagomarsino, and L. Yema. 2021. Human impacted Pampean shallow lakes are ideal hosts for cyanobacterial harmful blooms. Environmental Pollution 288:117747. https://doi.org/10.1016/j.envpol.2021.117747.

Pacheco, F. S., F. Roland, and J. A. Downing. 2013. Eutrophication reverses whole-lake carbon budgets. Inland Waters 4:41-48. https://doi.org/10.5268/iw-4.1.614.

Pérez, G. L., L. Lagomarsino, and H. Zagarese. 2013. Optical properties of highly turbid shallow lakes with contrasting turbidity origins: The ecological and water management implications. Journal of Environmental Management 130: 207-220. https://doi.org/10.1016/j.jenvman.2013.09.001.

Plastani, M. S., C. Laprida, F. Montes de Oca, J. Massaferro, H. O. Panarello, J. Ramón Mercau, and A. Lami. 2019. Recent environmental changes inferred from sediments in a shallow lake of the Argentinian pampas. Journal of Paleolimnology 61:37-52. https://doi.org/10.1007/s10933-018-0043-y.

Quirós, R., C. R. M. Baigún, S. Cuch, R. Delfino, A. DeNichilo, C. Guerrero, M. C. Marinone, S. Menu Marque, and M. C. Scapini. 1988. Evaluación del Rendimiento Pesquero Potencial de la República Argentina: I. Datos 1. Informe 7. Instituto Nacional de Desarrollo Pesquero, Informes Técnicos del Departamento de Aguas Continentales. Pp. 56.

Quirós, R., A. M. Renella, M. B. Boveri, J. J. Rosso, and A. Sosnovsky. 2002. Factores que afectan la estructura y el funcionamiento de las lagunas pampeanas. Ecología Austral 12:175-185.

Quirós, R., M. B. Boveri, C. A. Petrachi, A. M. Renella, J. J. Rosso, A. Sosnovsky, and H. T. von Bernard. 2006. Los efectos de la agriculturización del humedal pampeano sobre la eutrofización de sus lagunas. Pp. 1-6 *in* Tundizi, J. G., T. Matsumura-Tundisi and C. Sidagis Galli (eds.). Eutrofizaçaõ na América do Sul: Causas, conseqüèncias e tecnologias de gerenciamento e controle. Instituto Internacional de Ecologia, Instituto Internacional de Ecologia e Gerenciamento Ambiental, Academia Brasileira de Ciências, Conselho Nacional de Desenvolvimento Científico e Tecnológico (Publ.).

Sánchez, M. L. 2012. Estructura de la comunidad perifítica y sus interacciones con la comunidad fitoplanctónica en lagunas turbias y claras de la llanura Pampeana (Provincia de Buenos Aires, Argentina). Tesis Doctoral, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina.

Sánchez, M. L., G. L. Pérez, I. Izaguirre, and H. N. Pizarro. 2013. Influence of underwater light climate on periphyton and phytoplankton communities in shallow lakes from the Pampa plain (Argentina) with contrasting steady states. Journal of Limnology 72:62-78. https://doi.org/10.4081/jlimnol.2013.e6.

Sánchez, M. L., L. Lagomarsino, L. Allende, and I. Izaguirre.2015. Changes in the phytoplankton structure in a Pampean shallow lake in the transition from a clear to a turbid regime. Hydrobiologia 752:65-76. https://doi.org/10.1007/s10750-014-2010-6.

Sánchez Vuichard, G., S. Stutz, M. S. Tonello, D. Navarro, M. Schmelz, and S. L. Fontana. 2021. Structure and dynamics of a Pampa plain, (Argentina) shallow lake over the last 600 years. Journal of Paleolimnology 66:141-155. https://doi.org/10.1007/s10933-021-00194-w.

Scheffer, M. 2009. Critical Transitions in Nature and Society. Princeton University Press, Princeton/Oxford. https://doi.org/10.1515/9781400833276.

Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8:275-279. https://doi.org/10.1016/0169-5347(93)90254-M.

Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution 18:648-656. https://doi.org/10.1016/j.tree.2003.09.002.

Scheffer, M., and E. van Nes. 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. Hydrobiologia 584:455-466. https://doi.org/10.1007/s10750-007-0616-7.

Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. W. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. Science 292:281-284. https://doi.org/10.1126/science.1057544.

Torremorell, A., J. Bustigorry, R. Escaray, and H. Zagarese. 2007. Seasonal dynamics of a large, shallow lake, laguna Chascomús: The role of light limitation and other physical variables. Limnologica 37:100-108. https://doi.org/10.1016/j.limno.2006.09.002.

Torremorell, A., M. E. Llames, G. L. Pérez, R. Escaray, J. Bustingorry, and H. Zagarese. 2009. Annual patterns of phytoplankton density and primary production in a large, shallow lake: the central role of light. Freshwater Biology 54:437-449. https://doi.org/10.1111/j.1365-2427.2008.02119.x.

Viglizzo, E. F., and F. C. Frank. 2006. Land-use options for Del Plata Basin in South America: Tradeoffs analysis based on ecosystem service provision. Ecological Economics 57:140-151. https://doi.org/10.1016/j.ecolecon.2005.03.025.

Volpedo, A., and A. F. Cirelli. 2013. El Lago Chasicó: similitudes y diferencias con las lagunas pampásicas. Augm Domus 5(1):1-18.

Weigand, P. V., and A. H. Escalante. 2008. ¿Existen migraciones verticals en el zooplancton de la Laguna de los Padres? Biología Acuática 24:165-172.