Shallow lakes from the Central Plains of Argentina: an overview and worldwide comparative analysis of their basic limnological features

Nadia Diovisalvi, Vanesa Y. Bohn, María Cintia Piccolo, Gerardo M. E. Perillo, Claudio Baigún & Horacio E. Zagarese

Hydrobiologia
The International Journal of Aquatic Sciences

ISSN 0018-8158

Hydrobiologia
DOI 10.1007/s10750-014-1946-x

Springer

Hydrobiologia
DOI 10.1007/s10750-014-1946-x

ARGENTINE PAMPEAN SHALLOW LAKES

Review Paper

Shallow lakes from the Central Plains of Argentina: an overview and worldwide comparative analysis of their basic limnological features

Nadia Diovisalvi · Vanesa Y. Bohn · María Cintia Piccolo · Gerardo M. E. Perillo · Claudio Baigún · Horacio E. Zagarese

Received: 10 April 2014 / Revised: 30 May 2014 / Accepted: 7 June 2014

Abstract The Central Plains of Argentina is a heterogeneous environment, but the lakes there share some fundamental features: they are all shallow and polymictic as being well exposed to wind. First, we provide a synthesis of the climate, geology, and hydrological network. We also discussed shallow lakes origin and their limnological and biological salient features. Second, we focus on Pampean shallow lakes from a global perspective, comparing the limnological variables: total phosphorus concentration (TP), total nitrogen concentration (TN), chlorophyll *a* (Chl *a*) concentrations, and Secchi disk reading (SD) from a compiled database. No significant differences in the Chl *a* vs. TP relationship were found between Pampean and other shallow lakes. Otherwise, the chlorophyll yield per unit of phosphorus of Pampean lakes is similar to the world shallow lakes average. Moreover, the relationship SD vs. Chl *a* differed significantly between Pampean and the remaining world lakes, about 50–60%. When confronted against other lakes worldwide, Pampean shallow lakes depart from most of them as having higher TP, TN, and Chl *a* concentrations and much lower SD transparency, and therefore they stand as extremes of the trophic-state continuum. Despite their highly turbid state, these lakes provide valuable ecosystem services that are highly appreciated and mobilize important economic resources.

Keywords Phosphorus · Chlorophyll · Secchi disk · Comparative limnology

Guest editors: I. Izaguirre, L. A. Miranda, G. M. E. Perillo, M. C. Piccolo & H. E. Zagarese/Shallow Lakes from the Central Plains of Argentina

N. Diovisalvi (✉) · C. Baigún · H. E. Zagarese
Instituto de Investigaciones Biotecnológicas-Instituto Tecnológico de Chascomús (CONICET-UNSAM), Chascomús, Buenos Aires, Argentina
e-mail: nadiadiovisalvi@intech.gov.ar

V. Y. Bohn · M. C. Piccolo
Departamento de Geografía y Turismo, Universidad Nacional del Sur (UNS), Bahía Blanca, Buenos Aires, Argentina

V. Y. Bohn · G. M. E. Perillo
Departamento de Geología, Universidad Nacional del Sur (UNS), Bahía Blanca, Buenos Aires, Argentina

M. C. Piccolo · G. M. E. Perillo
Instituto Argentino de Oceanografía (IADO–CONICET), Bahía Blanca, Buenos Aires, Argentina

Introduction

Shallow lakes have been notably misrepresented in the early limnological literature. Former lake typologies, such as the very influential classification proposed by Hutchinson & Löffler (1956) focused exclusively on lakes deep enough to stratify over seasonal timescales. Shallow lakes and ponds are, however, the most

Published online: 09 July 2014

abundant lake types in the global landscape (Downing et al., 2006). Thus, the initial bias could not resist the reality of numbers for too long. In fact, by the early 1980s Lewis (1983) presented a revised classification, including two new lake categories, continuous cold polymictic and continuous warm polymictic, which encompass most shallow lakes. A more recent landmark in the field was the realization, inspired after May's (1977) classical paper, that shallow lakes may alternate between different alternative stable states (Scheffer et al., 1993), a concept that eventually evolved into what is now known as the shallow lakes theory (Scheffer & van Nes, 2007).

Limnological ideas are strongly influenced by research performed in temperate regions of the Northern Hemisphere (particularly Europe and North America), and those from the *shallow* subfield are not an exception. Therefore, comparisons with lakes from other regions of the world (Rautio et al., 2011; Abell et al., 2012; Kosten et al., 2012) may contribute to broaden the ability of theories to predict and explain the behavior of a wider range of systems (Collins & Sprules, 1983). Previous studies compared Argentine vs. other lakes worldwide, mainly focusing on Patagonian and Pampean regions (Baigún & Marinone, 1995; Quirós et al., 2006; Diaz et al., 2007).

This article is intended to serve as an introduction to the Hydrobiologia special issue devoted to shallow lakes from the central plains of Argentina (hereafter Pampean shallow lakes, for brevity). In the first section, we provide synthesis of the climate and geology of the region and its hydrological network. The geomorphological process that originated most shallow lakes and their most salient limnological features are also discussed. In the second section, we focus on Pampean shallow lakes from a global perspective to investigate how shallow lakes from the Argentine central plains fit within classical limnological models. For this comparison, we have compiled a comprehensive database including 2,727 lakes worldwide. We concentrated on fourth main variables: total phosphorus concentration (TP), total nitrogen concentration (TN), chlorophyll *a* concentration (Chl *a*), and Secchi disk depth (SD). These fourth variables capture a great deal of information about lake trophic state (Carlson, 1977; Kratzer & Brezonik, 1981) and, particularly for shallow lakes, they provide the raw input for the classification of a lake into some of its possible alternative steady states. Roughly speaking, phytoplankton growth in clear lakes is assumed to be limited by nutrient availability, while in turbid ones it is thought to be limited by light availability. Phosphorus, and to a lesser extent nitrogen, are commonly accepted as the most important limiting nutrients in freshwater lake ecosystems (Schindler, 1975, 1977; Vollenweider, 1976; Guildford & Hecky, 2000), while SD readings provide a rough, but robust indicator of water clarity (Preisendorfer, 1986). Chl *a* concentration is perhaps the most widely used proxy for phytoplankton biomass. Conveniently enough, these fourth variables are usually included in lakes surveys or monitoring programs and, therefore, there are a number datasets available for many lakes worldwide.

Salient features of the study area and its shallow lakes

Geology and hydrology

Central region of Argentina includes the Pampas and Espinal subregions, which together cover an extension of about 673,000 km^2 (Viglizzo et al., 2011), and represents one of the largest wetland areas of South America (Quirós, 2005). From a geological and geomorphological point of view, the region is a heterogeneous environment, which includes the large Pampean plains, crossed by rivers and scattered with shallow lakes; extensive inland and marine dune systems; and mountain ranges, such as Tandilia and Ventania systems (Buenos Aires Province) and the Sierras Pampeanas (Córdoba Province). Although the origin of these formations can be traced back to the Precambrian–Paleozoic (mountain ranges) or Cenozoic–late Holocene (plains) eras (Zárate & Rabassa, 2005), the Pampean shallow lakes have a more recent origin. In Argentina, the term *pampa* refers to a system of quaternary geological units, which occurs between latitudes 30°S and 38°S. These units are composed basically of brown silt with variable concentrations of $CaCO_3$ concretions (Iriondo, 1989). The modern geoformations (i.e., dune fields, floodplains and fluvial valleys, lake systems) was originated during the last 10,000 years (Zárate & Rabassa, 2005), under the arid or semi-arid conditions and cold temperatures that prevailed during the last glaciation; and were subsequently modified by the increase in temperature and humidity that occurred during the last 10,000 years.

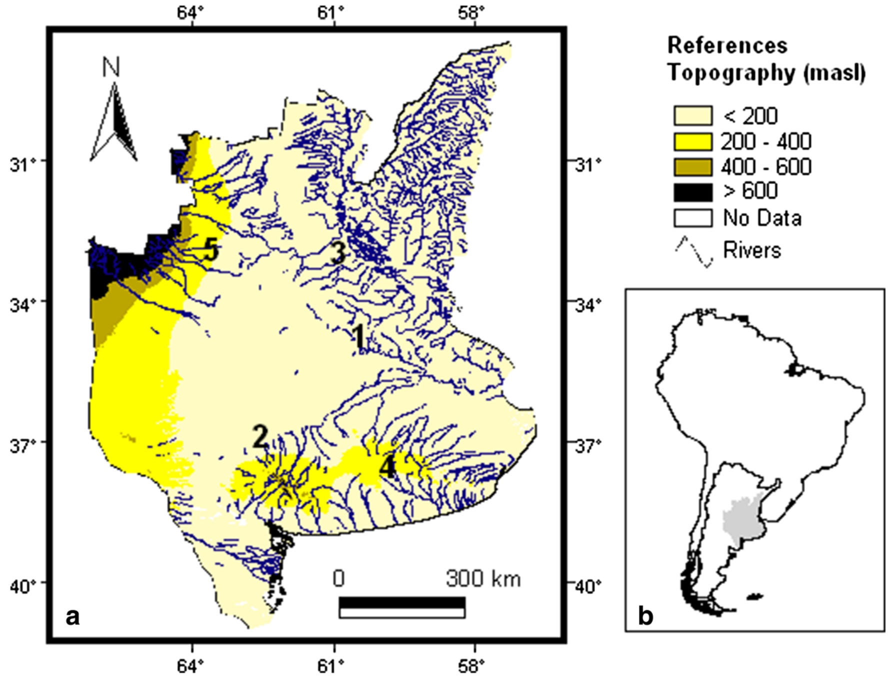

Fig. 1 The Central Region of Argentina, including the Pampas and Espinal subregions, and its main hydrology basins (a), location of this study area in South America (b)

These processes produced fertile, nutrient rich soils, composed mostly by loess (Rodrigues Capítulo et al., 2010). The Pampean region and adjacent areas may be divided into five hydrological systems (Frenguelli, 1956) (Fig. 1): (1) The Salado river and its tributaries, (2) Arroyo Vallimanca system, (3) Paraná and its tributaries, and the estuary of Río de la Plata, (4) direct tributaries to the Atlantic Ocean, and (5) Eastern slope of the Sierras Pampeanas. These systems are characterized by very low regional slope (10^{-3} to 10^{-4}) (Sala et al., 1983 in Kruse & Laurencena, 2005) and drainage densities (<0.16 km km^{-2}) (Kruse & Laurencena, 2005).

Climate

Situated in the Southern Hemisphere temperate belt, the Pampean region is characterized by marked thermal seasonality and the lack of a dry season. The climate has been characterized as temperate humid (Burgos & Vidal, 1951). However, the region can hardly be considered uniform, due to its highly heterogeneous character in geologic history, relief types, hydrology, and climate. In fact, Díaz & Mormeneo (2002) identified six climatic subregions, covering a range from warm humid to cold sub-humid conditions (Fig. 2).

Across the region, from North to South, mean temperatures vary from 20 to 14°C (Viglizzo & Frank, 2006). Precipitation patterns also display large variability, both geographically and inter-annually. From the Northeast to the Southwest of the region mean annual precipitation range from 1,000 to 400 mm (Viglizzo & Frank, 2006). In relation to the inter-annual variation, Scarpati & Capriolo (2011) compared two consecutive time-series (1947–1976 vs. 1977–2006). The first series corresponds to a dry period, with mean annual precipitation ranging from 300 to 1,200 mm y^{-1}, while the second series corresponds to a wet period, with precipitations ranging from 400 to 1,400 mm y^{-1}. The largest inter-annual differences ($\sim$200 mm y^{-1}) occur in the northern and middle areas of the region (Fig. 3). This large inter-annual variability in combination with poorly developed drainage systems results in recurrent and extensive floods, alternating with drought periods. All these processes affect the lake water residence time, the water content of soils, and the depth of the water table. Moreover, many semi-permanent rivers develop during prolonged rainy periods, connecting individual shallow lakes along the palaeo-valleys.

In many depressed areas of Pampean region, soil water surplus is often unable to infiltrate because the water table is too close the surface. Although water

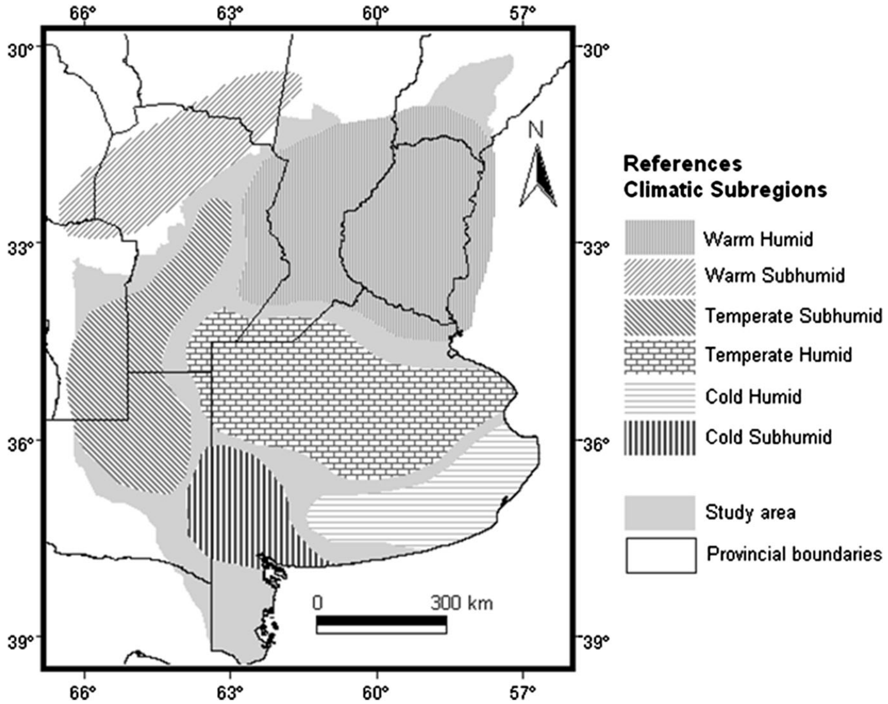

Fig. 2 Climate classification of the Pampas and Espinal subregions modified from Díaz & Mormeneo (2002)

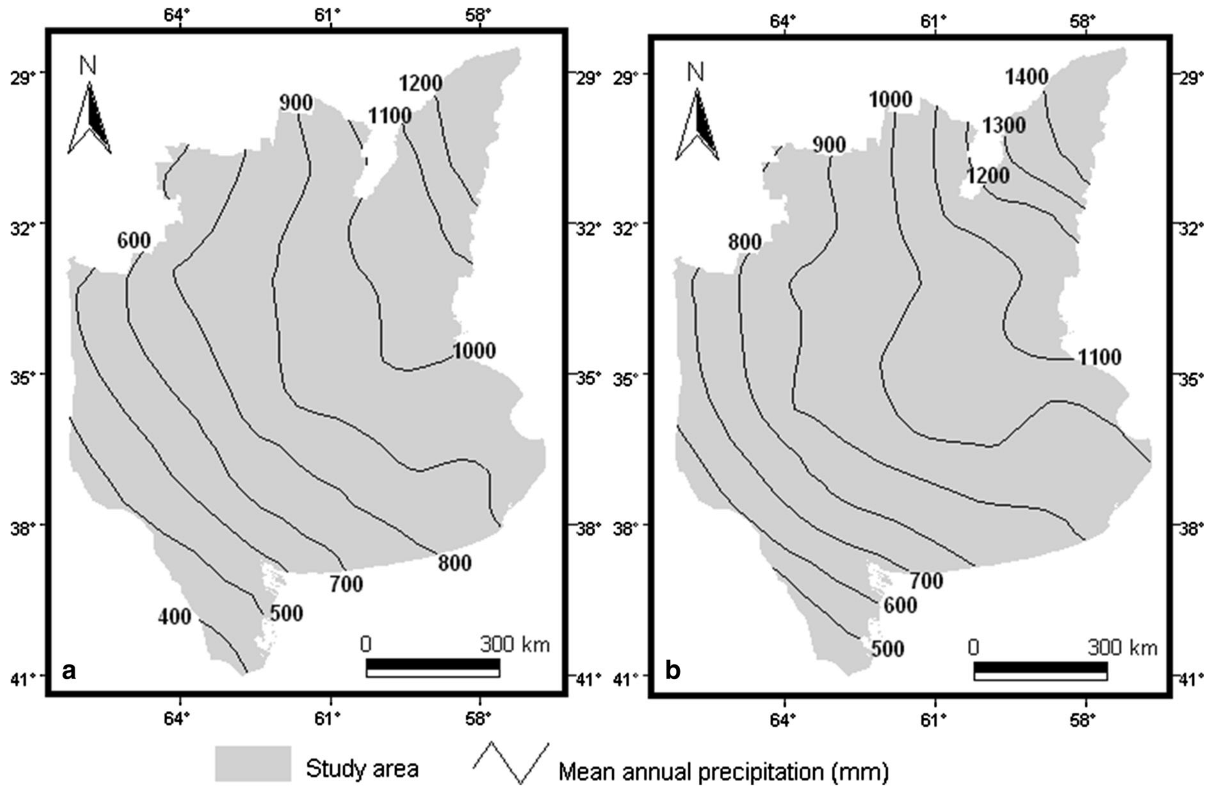

Fig. 3 Precipitation distribution and its inter-annual variation: **a** isohyets for the period 1947–1976 and **b** ídem for the period 1977–2006 (after Scarpati & Capriolo, 2011)

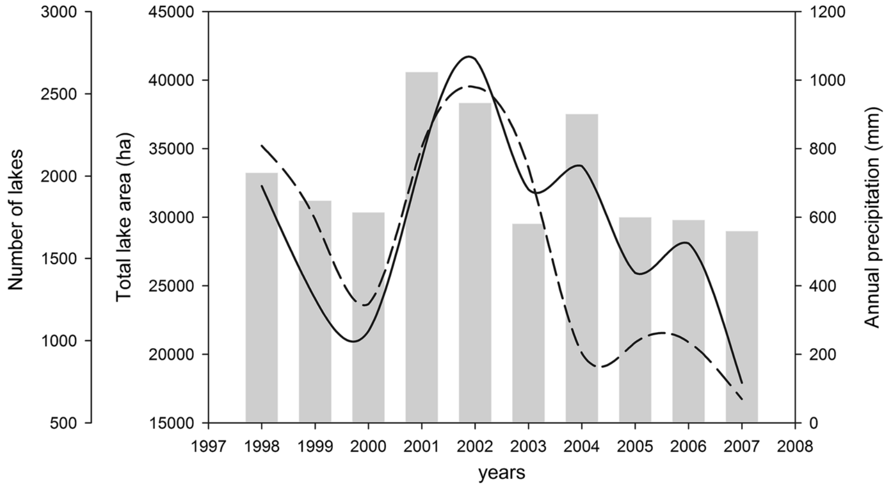

Fig. 4 Inter-annual variation in number of lakes (*dashed line*) and total lake area (*solid line*), in relation the mean annual precipitation (*bar graph*), for Southern Pampean Region

surpluses occur in almost all years, they are particularly marked during the El Niño phase of ENSO (Scarpati et al., 2007). Analyzing the impact of ENSO on monthly changes in evapotranspiration for a region of the Pampas, Texeira Soria et al. (2013) demonstrate that during La Niña (El Niño) events the monthly evapotranspiration rate increase (decrease) in relation to the historical mean. Therefore, ENSO events are important to partly explain the distribution and number of shallow lakes on the Pampas.

In most of the Pampean region, the winds blow predominantly from N and NW directions, as a direct consequence of the quasi-stationary South Atlantic anticyclone position. Although less frequently, other directions are also important, and so they are given vernacular names, such as Pampero (W, SW) and Sudestada (SE). The average wind speeds in the Pampean region are moderate, and increase southward as one approaches the westerlies belt. The average wind speed ranges from 10 to 24 km h^{-1}, depending on the particular characteristics of each site (topography, continentality, etc.). Maximum wind gust speeds range between 150 and 200 km h^{-1} in northern and southern areas, respectively.

Origins, size, and abundance of Pampean shallow lakes

The low morphogenetic energy of a flat landscape combined with the occurrence in humid to sub-humid climates results in the accumulation surface water that forms a variety of water bodies (ponds, shallow lakes, and marshes) (Geraldi et al., 2011). The geomorphology of these water bodies involved different process acting alone or in combination. A large proportion of Pampean shallow lakes were formed during dry quaternary periods by the action of wind (aeolian origin) (Tricart, 1973). These lakes lack effluents and occupy ancient interdune depressions. Other lakes were formed by fluvial action resulting from abandoned meanders or depression located along active rivers and streams. A third group of lakes occupy palaeochannels of presently inactive ancient rivers. Another group of lakes, along the Atlantic Ocean coastline, was formed by damming of coastal dunes (Isla, 2002). These lakes have elongated shapes oriented W–E. The Pampa also hosts lakes originated by tectonic movements, and subsequently modeled by fluvial and aeolian action. As these lakes lay along structural axes (i.e., the lines formed by sunken crustal blocks), they are conveniently named lagunas encadenadas (chained lakes). Still another group of lakes were formed on tidal channels which corresponded to ancient coastal wetlands. More recently, 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).

Table 1 Summary of the world lake sources dataset and main characteristics

Source	Number of lakes and lake type	Period	Country
Lopes et al. (2011)	38 upland Amazonian lakes	2004–2008	Brazil
Jackson (2003)	30 lakes	1998 and 1999 on summers	Canada
Schallenberg & Kelly (2012)	5 lakes	2004 and 2012 on March	New Zealand
Abell et al. (2012)—synthesis on Table 2	1,316 lakes		World
Hessen (personal database)	16 shallow lakes		Norway
Balogh et al. (2009)	30 lakes, reservoirs and ponds	2003, 2004, and 2006 on summers	Hungary
Pedrozo & Rocha (2007)	6 shallow lakes from Coastal Plain of Rio Grande do Sul	1997 on January, May, July, and October	Brazil
Gunn et al. (2001)	21 lakes from Killarney Park	1998	Canada
ECOFRAME—database Version 7	66 European shallow lakes (depth <3 m)	2000 on late summer year	UK, Ireland, Poland, Netherlands, Estonia, Sweden, Germany, Spain, Denmark, and Finland
Kruk et al. (2009)	18 coastal shallow lakes	2003 on summer	Uruguay
NLA (National Lakes Assessment Data)	607 lakes	2007, 2011	USA
Fermani et al. (2014)	40 Pampean shallow lakes	2009–2010 on spring–summer	Argentina
Díaz & Colasurdo (2008)	26 Pampean shallow lakes	2004–2006	Argentina
Quirós (1988)	96 lakes and reservoirs, including 24 Pampean shallow lakes	1984–1986 on summer	Argentina
Izaguirre & Vinocur (1994)	11 Pampean shallow lakes	1987–1989 annual	Argentina
Unpublished data from PhD thesis by Torremorell (2010) and Lagomarsino (2011), plus data from the PAMPA^2 network	15 Pampean and 10 Patagonian shallow lakes	2008–2013, sampled on different seasons	Argentina

Considering only the province of Buenos Aires, Geraldi et al. (2011) estimated that there are 13,824 large (>10 ha) and 146,000 small (0.05–10 ha) shallow lakes and, according to Dangavs (2005), there are about 200,000 microbasins (0.01–0.05 ha). 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 ($\sim$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). At a regional scale, the inter-annual variability can be examined using satellite images (Fig. 4). Greater abundance of lakes (2,539) and large total lake area (41,500 ha) were recorded following a period of two rainy year (2001–2002), while the minimum number of lakes (645) and smaller total lake area (17,900 ha) occurred after a run of three dry years (2005–2007).

Table 2 Descriptive statistic of basic parameters for the four groups of lakes, and statistical comparisons between Pampean lakes and different groupings of lakes worldwide

	TP (µg/l)				TN (µg/l)				Chl *a* (µg/l)				Secchi disk (m)			
	n	Mean	SD	*P* value	*n*	Mean	SD	*P* value	*n*	Mean	SD	*P* value	*n*	Mean	SD	*P* value
All non-Pampean lakes	2,625	87.23	202.21	*	2,507	1139.43	1853.16	*	2,626	22.96	55.38	*	2,067	2.32	2.42	*
All non-Pampean shallow lakes	1,463	125.19	228.22	*	1,422	1491.92	2287.70	*	1,464	34.37	71.09	*	1,128	1.26	1.11	*
All non-Pampean low temperate shallow lakes	872	138.99	239.81	*	872	1568.49	2454.42	*	872	39.70	76.25	*	717	1.12	1.01	*
Pampean lakes	103	708.97	973.60		88	4970.04	3947.61		98	176.79	244.28		101	0.40	0.60	

Number of data (*n*), mean, standard deviation (SD)

*Statistically significant differences ($P < 0.0001$) Mann–Whitney test

Morphology and thermal regime

From a limnological perspective, the most salient and unifying feature of Pampean lakes is their shallowness. They show typical *pfanne* or *wanne* profiles and tend to have rounded shapes (shoreline development ratio <4) (Dangavs, 1976; Quirós, 2004). Most lakes lay within the oligohaline (0.5–5 g l^{-1}) and mesohaline (5–15 g l^{-1}) range, but a few are polyhaline (16–40 g l^{-1}) or hyperhaline (>40 g l^{-1}). Few lakes exceed 3 m in maximum depth (Z_{max}) and mean depth (Z_{mean}) is, on average, 70% of Z_{max}. Owing to their shallowness, the dynamics of Pampean lakes are tightly tied to climate conditions, and the annual precipitation and evaporation volumes are within the same order of magnitude as their hydric volumes (Fernández Cirelli & Miretzky, 2004). Thermally, they behave as warm-polymictic lakes (Lewis, 1983), which seldom stratify for more than a few hours if at all. Upper sediments are sandy silt, silt, and clayey silt, with a predominance of fine sediments (clays and silts) over coarse ones (sands). Typically the calcium carbonate fraction of sediments ranges from 1 to 20%, and organic matter content is lower than 15% (Fernández Cirelli & Miretzky, 2004).The morphology of Pampean shallow lakes and their occurrence in nutrient rich, fertile soils determine their eutrophic state and high biological productivity (Quirós, 1988), which has probably been aggravated by human activities (Quirós et al., 2006). Their shallowness favors the interaction between sediments and the water column through wind-driven turbulence.

Land use

The introduction of livestock (cattle, sheep, and horses) in the sixteenth century, followed by the development of agriculture by the end of the nineteenth century, has deeply modified the original Pampean landscape and caused large losses of grassland habitat (Soriano et al., 1992). Recent technological developments (i.e., transgenic, glyphosate-resistant crops, and no tillage practices) have resulted in the substitution of livestock and cereal production by oilseeds crops (most notably soy), which further, and significantly, increased the land area devoted to agriculture. In addition, drainage modifications, through channeling and damming (Quirós et al., 2006) and invasion of the exotic *Cyprinus carpio* has probably aggravated the process of cultural eutrophication. As a result, many lakes have shifted from a clear-vegetated, and presumably pristine, state to a turbid state.

Biota

The ichthyofauna of the Pampean region belongs to the Paranense province, within the Brasilica subregion (Ringuelet, 1975; López et al., 2001). The Pampean region is the southernmost distributional limit of the parano-platense fish assemblage (López & Miquelarena, 2005). A total of 47 native species have been recorded. *Cyprinus carpio* is the only exotic species, which is presently widely distributed (Colautti, 1997). In turbid shallow lakes, fish abundance may be quite high and dominated by *Odontesthes bonariensis*, highly appreciated by sport fishermen and a very important commercial resource in the past (Baigún & Delfino, 2002), and *Parapimelodus valenciennesi*, whereas in clear lakes the most relevant target species is *Hoplias malabaricus*. *Austrolebias nonoiuliensis* is the only endemic species of the Pampa region (López et al., 2002).

The main features of phytoplankton are similar to the other eutrophic temperate shallow lakes. The phytoplankton of turbid shallow lakes is dominated by Cyanobacteria, Chlorophyceae and Bacillariophyceae. Some lakes display absolute dominance of cyanobacteria, with algal blooms developing during the warm season (Izaguirre et al., 2014). Other turbid lakes present relatively long periods of stable phytoplankton composition (Iachetti & Llames, 2014). In inorganic-turbid shallow lakes, the dominant algal groups are usually Bacillariophyceae and Chlorophyceae, with species well adapted to low light intensities. Clear-vegetated lakes exhibit lower phytoplankton biomass, a higher proportion of nanophytoplankton, and a more balanced representation of algal groups. These lakes usually show high abundance of small flagellates (Cryptophyceae, Chrysophyceae) together with Chlorophyceae and small colonial cyanobacteria (Allende et al., 2009; Izaguirre et al., 2012). The phytoplankton of lakes heavily covered with floating plants is represented by species tolerant to low oxygen concentrations and adapted to very low light conditions (Izaguirre et al., 2004, 2010; O'Farrell et al., 2007).

The zooplankton is typically dominated by a few species. Rotifers are the most diverse taxonomic group. The genera *Brachionus* (*B. caudatus*, *B. havanaensis*, and *B. angularis*) and *Keratella* (*K. tropica*) are often dominant (Olivier, 1965; Rennella, 2007; Ardohain, 2008). Copepods are typically represented by the cyclopoid, *Acanthocyclops robustus*, and the calanoid, *Notodiaptomus incompositus* (Menu Marque, 2000). Among the most frequent genera of cladocera are *Bosmina*, *Ceriodaphnia*, *Daphnia*, *Diaphanosoma*, *Moina*, and Chidoridae. Cladocerans are particularly abundant at places or periods of low planktivore fish abundance (Sosnovsky et al., 2010; Diovisalvi et al., 2014), as well as in lakes densely populated with macrophytes (Ardohain, 2008). Several endemic species of *Dahpnia* and Diaptomids have been reported (Adamowicz et al., 2004; Perbiche-Neves et al., 2014).

How do Pampean lakes compare to lakes worldwide?

We assembled a comprehensive database of 2,727 lakes. Most data corresponds to dataset compiled by other authors or online databases generated by lake monitoring agencies or networks (Table 1). Information on Pampean lakes was obtained from the literature and our own unpublished data (generated within the PAMPA^2 network or in previous work). For the comparative analyses, we made sequential refinements of the dataset. We began by comparing Pampean lakes vs. all other world lakes. In a second step, deep lakes were excluded (i.e., Pampean lakes vs. all other shallow lakes). Following Abell et al. (2012), lakes were considered shallow according their mean depth ($Z_{mean} \leq 3$ m) or, when Z_{mean} was unknown, according to their maximum depth (Z_{max} - ≤ 10). Finally, we compared Pampean lakes vs. shallow lakes occurring within the lower temperate latitudinal range, defined as 23.6 – 44.5° N/S, for comparison with Abell et al. (2012). A number observations corresponding to the oligotrophic end were excluded (=247 outliers) as the values of either Chl *a* or TP were suspected to lay below analytical detection limits.

The Mann–Whitney test of ranks was used for univariate comparisons of TP, TN, Chl *a*, and SD values. Least squares multiple linear regression was used to analyze the relationships between (i) Log Chl *a* vs. Log TP, (ii) Log Chl *a* vs. Log TN, and (iii) Log SD vs. Log Chl *a*. A categorical variable, *Location*,

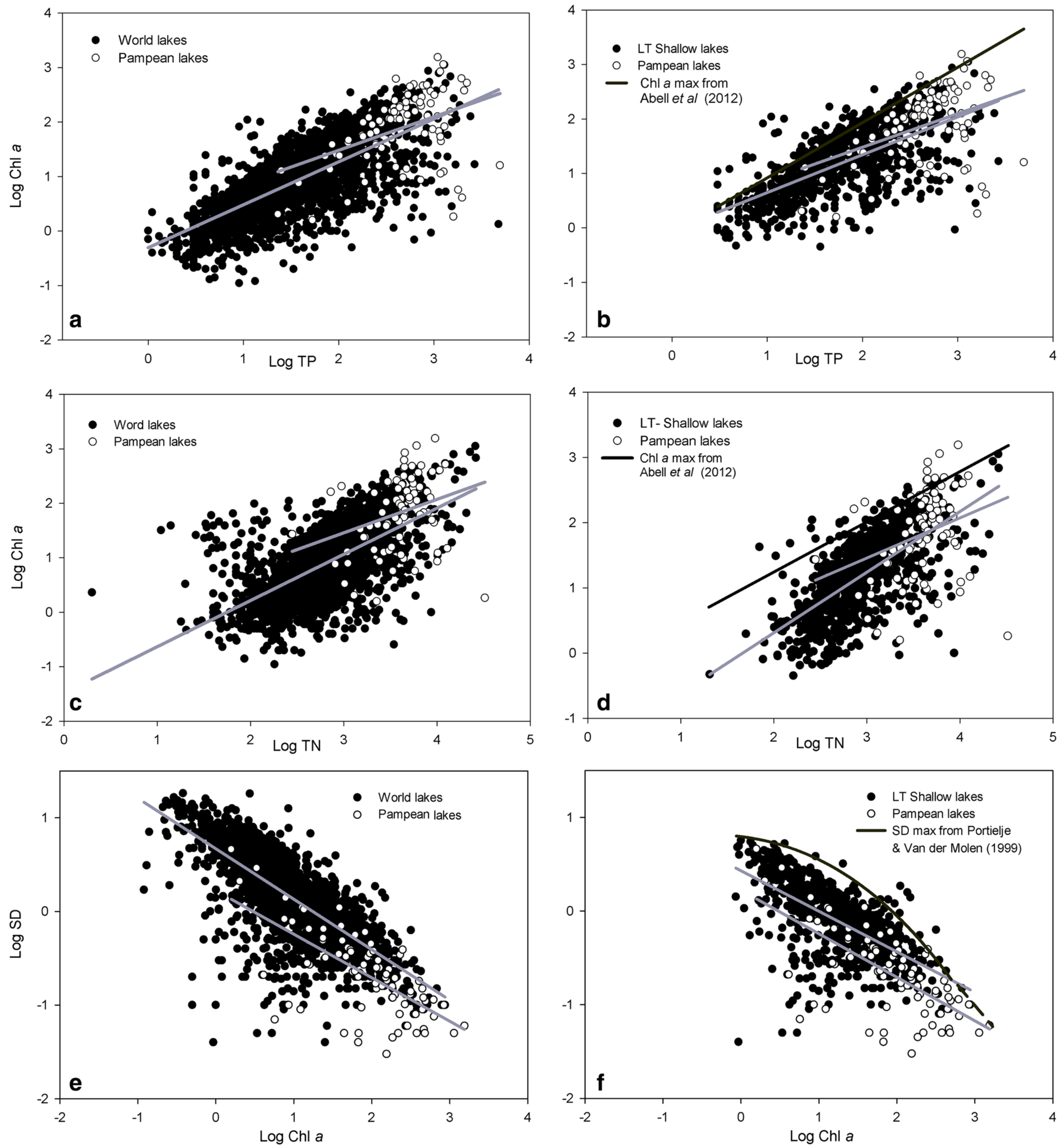

Fig. 5 Relationship between chlorophyll *a* (Chl *a*) vs. total phosphorus (TP) and total nitrogen (TN), and Secchi disk depth (SD) vs. Chl *a* considering all world lakes (**a**, **c**, **e**) or only low temperate (LT) shallow lakes (**b**, **d**, **f**). *Black solid lines* in panels **b**, **d**, and **f** are the upper boundary of Chl *a* concentration conditional on TP (Chl $a_{\max} = 0.87$ TP $-$ 0.42) and TN (Chl $a_{\max} = 0.046$ TN + 4.14) estimated by Abell et al. (2012) and the upper boundary of SD transparency conditional on Chl *a* ($1/\mathrm{SD}_{\max} = 0.16 + 0.01$Chl *a*), estimated by Portielje & Van der Molen (1999), respectively

was set to 1 for Pampean lakes and 0 for all other lakes. Analysis of variance was used to test for the significance of the main effects (i.e., *TP*, *TN* or *Chl a*, and *Location*) and the interaction term (i.e., *TP * Location*, *TN * Location*, or *Chl a * Location*) (Quinn & Keough, 2002, p. 135).

Table 3 Equations for Chl *a* vs. PT, Chl *a* vs. NT, and SD vs. Chl *a* for contrasting all lakes, shallow lakes, and low temperate shallow lakes take in or not Pampean shallow lakes

Lakes	Equations	R^2	Log *X*	Location (Pampa vs. others)	Interaction
Chl *a* vs. TP					
Pampean lakes	Log Chl $a = 0.248 + 0.617$ Log TP	0.55	<0.0001*	0.0236*	0.1155
All non-Pampean lakes	Log Chl $a = -0.306 + 0.788$ Log TP				
Pampean lakes	Log Chl $a = 0.230 + 0.623$ Log TP	0.49	<0.0001*	0.0818	0.2210
All non-Pampean shallow lakes	Log Chl $a = -0.242 + 0.772$ Log TP				
Pampean lakes	Log Chl $a = 0.230 + 0.623$ Log TP	0.45	<0.0001*	0.1924	0.5526
All non-Pampean low temperate shallow lakes	Log Chl $a = -0.046 + 0.695$ Log TP				
Chl *a* vs. TN					
Pampean lakes	Log Chl $a = -0.382 + 0.614$ Log TN	0.42	<0.0001*	0.0029*	0.1828
All non-Pampean lakes	Log Chl $a = -1.481 + 0.848$ Log TN				
Pampean lakes	Log Chl $a = -1.392 + 0.85$ Log TN	0.40	<0.0001*	0.0191*	0.2032
All non-Pampean shallow lakes	Log Chl $a = -0.384 + 0.614$ Log TN				
Pampean lakes	Log Chl $a = -1.548 + 0.93$ Log TN	0.46	<0.0001*	0.0549	0.0629
All non-Pampean low temperate shallow lakes	Log Chl $a = -0.381 + 0.614$ Log TN				
SD vs. Chl *a*					
Pampean lakes	Log SD $= 0.670 - 0.540$ Log Chl *a*	0.59	<0.0001*	<0.0001*	0.1682
All non-Pampean lakes	Log SD $= 0.223 - 0.465$ Log Chl *a*				
Pampean lakes	Log SD $= 0.205 - 0.459$ Log Chl *a*	0.45	<0.0001*	<0.0001*	0.3109
All non-Pampean shallow lakes	Log SD $= 0.483 - 0.402$ Log Chl *a*				
Pampean lakes	Log SD $= 0.205 - 0.459$ Log Chl *a*	0.50	<0.0001*	<0.0001*	0.6316
All non-Pampean low temperate shallow lakes	Log SD $= 0.430 - 0.433$ Log Chl *a*				

*Statistically significant differences

On average, Pampean lakes are more eutrophic than any other grouping of lakes considered in this study. They tend to display higher nutrients (*TP*, *TN*[1]) and Chl *a* concentrations, and smaller SD. All the previous parameters were significantly different for Pampean lakes when compared to the other groups of lakes ($P < 0.0001$). Basic descriptive statistics for TP, TN, Chl *a*, and SD are provided in Table 2.

Although chlorophyll and nutrients concentrations observed in Pampean lakes lay within the range of values reported for lakes worldwide, they are strongly biased toward the eutrophic end (i.e., they tend to fill the upper right side of the scatter plots in Fig. 5a–d). Multiple regression analysis showed significant differences between Pampean lakes and all other lakes for TP and TN. Pampean lakes differed from the whole set of shallow lakes in the relationship of Chl *a* vs. TN, but not in the relationship of Chl *a* vs. TP. No significant differences were observed when comparing Pampean lakes vs. lower temperate shallow lakes for both Chl *a* vs. TN and Chl *a* vs. TP (Fig. 5a–d and Table 3). In other words, the chlorophyll yield per unit of phosphorus of Pampean lakes is significantly lower than the world lakes average (although the magnitude of this difference is small), but it is essentially

[1] TN concentration in Pampean lakes is higher than for other grouping of lakes even though it is underestimated in part of our Pampean lakes dataset, as for a number of lakes only Kjeldahl estimates were available.

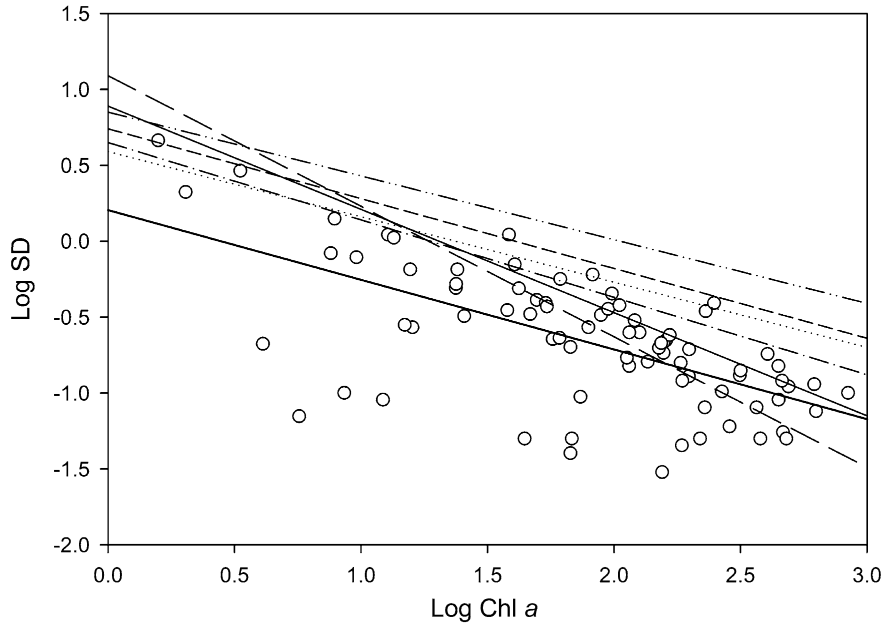

Fig. 6 Scatter plot of SD vs. Chl *a* for Pampean shallow lakes and the fitted regression equation, several published regression estimates for different lakes and ponds are shown for comparison. (*open circle*) Pampean lakes data, (*solid thick line*) Pampean lakes: Log SD = 0.205 – 0.459 Log Chl *a*, (*thick line*) Carlson (1977): Ln SD = 2.04 – 0.68 Ln Chl *a*, (*dotted line*) Mazumder & Havens (1998) for subtropical lakes SH: Log SD = 0.59 – 0.43 Log Chl *a*, (*dashed line*) Mazumder & Havens (1998) for template North American & European-SH lakes: Log SD = 0.74 – 0.46 Log Chl *a*, (*dashed-double dot line*) Mazumder & Havens (1998) for template North American & European-LH lakes: Log SD = 0.85 – 0.42 Log Chl *a*, (*long-dashed line*) Lambou et al. (1983) for EEUU lakes: Ln SD = 2.51 – 0.86 Ln Chl *a*, (*dashed-single dot line*) Almazan & Boyd (1978) for aquaculture: Log SD = 9.69 – 0.51 Log Chl *a*

identical to that of other shallow lakes, irrespective of their geographical location. In contrast, geographic gradients appear to affect the chlorophyll a yield per unit of nitrogen, as observed by Abell et al. (2012).

Resource limitation theory states that the yield of phytoplankton biomass is controlled by the availability of the factor most deficient in relation to algal growth requirements. Here, as well as in most comparative studies, phytoplankton biomass is inferred from Chl *a* concentration. Researchers typically focus on the mean response of Chl *a*. However, as pointed out by Abell et al. (2012), what the law of limiting factors actually imposes is not a mean response, but rather a "factor ceiling" to data distributions. It is therefore useful to examine the edge of the Chl *a*–PT relationship. Figure 5b shows the upper boundary of Chl *a* concentration conditional on TP concentration estimated by Abell et al. (2012) using quantile regression ($\tau = 0.95$). The 98% out of 94 observations in Pampean lakes are lower than this conditional maximum. Similarly, the equation for the upper boundary of Chl *a* concentration in function of TN is plotted in Fig. 5d. In this case, the 89% of Pampean lakes ($n = 88$) falls below this maximum. These analyses also confirm that the phosphorus requirement of phytoplankton in Pampean lakes is comparable to other shallow lakes. Phosphorus limitation of phytoplankton seems more common in lakes than nitrogen limitation, but with certain differences in the latitudinal gradient (Abell et al., 2012).

On the other hand, the relationship between SD depth and Chl *a* differed significantly between Pampean lakes and the remaining world lakes. The effect of Location (Pampean vs. other places) resulted significant, but there were no significant differences due to the interaction between Chl *a* * Location. The statistical significance of these comparisons remained qualitatively identical after (i) excluding lakes considered deep and, subsequently (ii) shallow lakes located outside the lower temperate latitudinal range (North and South) (Fig. 5e, f, Table 3). The estimated upper boundary of SD transparency conditional on

Chl *a* abundance for 231 sites (lakes and ponds) of Netherlands (Portielje & Van der Molen, 1999) is also presented in Fig. 5f. The lower SD values of Pampean shallow lakes are also evident when plotting SD vs. Chl *a* observations for Pampean lakes along with published relationships for other sets of lakes (Fig. 6). These analyses indicate that, at comparable Chl *a* concentrations, Pampean lakes have, on average, lower SD than the other groupings of lakes considered here. This result is in agreement with the findings reported by Quirós et al. (2006) for an unidentified set of Pampean lakes. The magnitude of this difference is quite considerable: over a wide range of Chl *a* concentration (1–1,000 μg l^{-1}), SD readings of Pampean lakes are on average, only 60–50% of the expected values for other shallow lakes.

Absorbance and scattering due to non-algal components contribute reduce the depth of disappearance of the disk. This is particularly noticeable in two Pampean lakes: La Limpia and Yalca (Allende et al., 2009; Pérez et al., 2010). In La Limpia, for example, light absorption is dominated by unpigmented particulates and CDOM (Pérez et al., 2013). Under conditions of light limitation, theoretical (Scheffer, 1998), and experimental (Huisman et al., 2002) developments predict that an increase in background turbidity[2] should result in a proportional decrease in algae density. In agreement with such prediction, La Limpia and Yalca have relatively low Chl *a* concentrations (Allende et al., 2009; Pérez et al., 2013). It would be tempting to extrapolate these results to the whole set of Pampean shallow lakes to conclude that the lower SD values of Pampean are due to higher background turbidity (i.e., light absorption by all non-phytoplankton components, sensu Huisman et al., 2002), as suggested by Quirós et al. (2006). However, this would also lead to the prediction that Pampean lakes should have lower Chl *a* concentrations, on average, than other shallow lakes, while in practice we have found exactly the opposite result (Table 2).

The conditional maximum SD (dark gray line in Fig. 5c) presumably corresponds to plankton assemblages with low Chl *a*-specific absorption and/or scattering coefficients. An increase in the Chl *a*-specific light absorption coefficient (e.g., smaller package effect) would tend to decrease SD. In Laguna Chascomús for instance, changes in package effect account for up to 63% of the seasonal variation in light absorption coefficients (Pérez et al., 2011). The plankton size distribution would also affect SD readings. The effectiveness of particulates to scatter light per unit of mass is maximum at particle sizes similar to the light wavelengths (0.4–0.7 μm) (Kirk, 1983). Therefore, the pico-plankton fraction (<2 μm) is more effective at scattering light than the nano- (2–20 μm) or micro- (>2 μm) plankton fractions. It is suggestive that the abundance of bacterioplankton in Pampean lakes is roughly an order of magnitude higher than in most other aquatic systems (Fermani et al., 2014). Therefore, smaller SD readings do not automatically indicate the presence of inorganic background turbidity, as they may also be indicative of higher chlorophyll *a*-specific absorption or scattering coefficients, among other factors.

Summarizing, when confronted against other lakes worldwide, Pampean shallow lakes limnological characteristics depart from most of those located in temperate regions as having higher TP, TN, and Chl *a* concentrations and much lower SD transparency, and therefore they stand as extremes of the trophic-state continuum. These highly productive environments support a number of valuable ecosystem services that are highly appreciated providing recreation opportunities. Sport fisheries is the most relevant activity collectively mobilizing high economic resources (Baigún & Delfino, 2003), although they can strongly fluctuate due to lakes variability related to climatic events (Colautti et al., 2014).

[2] There is some ambiguity in the use of turbidity in the limnological literature. In water optics studies, the word "turbidity" has been used in general terms to indicate the extent to which a liquid lacks clarity, i.e., scatters light as perceived by the human eye (Kirk, 1983). Within this context "turbidity" is commonly measured in nephelometric turbidity units (NTU), which for moderate to high turbidity waters has, rather conveniently, the same numerical value than the scattering coefficient (m^{-1}) (Kirk, 1983). On the other hand, phytoplankton ecologists sometimes assimilate "turbidity" with light absorption. For example, Huisman et al. (2002) refer to light absorption by all non-phytoplankton components as background turbidity. There is an important distinction between scattering and absorption. Pure non-phytoplankton scattering does not decrease the amount of light available to the algae; it only increases the pathway of photons before they are ultimately absorbed. In contrasts, absorption by non-phytoplankton components effectively reduced the total amount of light available to algae. Therefore, the context within which the word "turbidity" is used is critical to understand what an author meant to say.

Acknowledgments We thank the PAMPA[2] team for providing the impetus for this study, and particularly Irina Izaguirre for her useful comments on an earlier draft. Several colleagues help us to compile the dataset of world lakes: Alberto Pilatti, Fabián Grosman, Pablo Sanzano, Dag Hessen, Alo Laas, Medina Kadiri, and especially Jonathan M. Abell, Deniz Özkundakci, David P. Hamilton, and John R. Jones who contributed their database including 1,316 lakes. This study was supported by the Argentine network for the assessment and monitoring of Pampean shallow lakes (PAMPA[2]—CONICET), ANPCyT PICT-2011-1029, CONICET PIP 00700; and supported partially for VYB, MCP, and GMEP provided by grants from Universidad Nacional del Sur PGI 24/G059 and by the Inter-American Institute for Global Change Research (IAI) CRN3038 (under US NSF Award GEO-1128040).

References

Abell, J. M., D. Özkundakci, D. P. Hamilton & J. R. Jones, 2012. Latitudinal variation in nutrient stoichiometry and chlorophyll–nutrient relationships in lakes: a global study. Fundamental and Applied Limnology/Archiv für Hydrobiologie 181: 1–14. http://openurl.ingenta.com/content/xref?genre=article&issn=1863-9135&volume=181&issue=1&spage=1.

Adamowicz, S., P. D. N. Hebert & M. C. Marinone, 2004. Species diversity and endemism in the *Daphnia* of Argentina: a genetic investigation. Zoological Journal of the Linnean Society 140: 171–205. http://onlinelibrary.wiley.com/doi/10.1111/j.1096-3642.2003.00089.x/full.

Allende, L., G. Tell, H. Zagarese, A. Torremorell, G. Pérez, J. Bustingorry, R. Escaray & 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. http://www.springerlink.com/index/10.1007/s10750-008-9665-9.

Almazan, G. & C. Boyd, 1978. An evaluation of Secchi disk visibility for estimating plankton density in fish ponds. Hydrobiologia 61: 205–208.

Ardohain, D. M., 2008. Respuesta del zooplancton en su estructura y dinámica a factores clave en una laguna arreica (pcia de Buenos Aires). PhD thesis, Universidad Nacional de La Plata, Buenos Aires, Argentina: 266 pp.

Baigún, C. & R. Delfino, 2002. Sobre ferrocarriles, lagunas y lluvias: características de las pesquerías comerciales de pejerrey en la cuenca del río Salado (Prov. Buenos Aires). Biología Acuática 20: 12–18.

Baigún, C. & R. Delfino, 2003. Assessment of social and economic issues as management tools for summer pejerrey recreational fisheries in Pampean Lakes (Argentina). Journal of Lakes and Reservoir Management 19: 242–250.

Baigún, C. & M. C. Marinone, 1995. Cold-temperate lakes of South America: do they fit northern hemisphere models? Archiv für Hydrobiologie 135: 23–51.

Balogh, V. K., B. Németh & L. Vörös, 2009. Specific attenuation coefficients of optically active substances and their contribution to the underwater ultraviolet and visible light climate in shallow lakes and ponds. Hydrobiologia 632: 91–105. http://link.springer.com/10.1007/s10750-009-9830-9.

Bohn, V. Y., G. M. E. Perillo & M. C. Piccolo, 2011. Distribution and morphometry of shallow lakes in a temperate zone (Buenos Aires Province, Argentina). Limnetica 30: 89–102.

Burgos, J. J. & A. L. Vidal, 1951. The climates of the Argentine Republic according to the new Thornthwaite classification. Annals of the Association of American Geographers 41: 237–263.

Carlson, R. E., 1977. A trophic state index for lakes. Limnology & Oceanography 22: 361–369.

Colautti, D. C., 1997. Ecología de la carpa *Cyprinus carpio* en la cuenca del río Salado, provincia de Buenos Aires. Tesis no. 685, Facultad de ciencias Naturales y Museo (UNLP), 215 pp.

Colautti, D. C., C. Baigún, F. Llompart, T. Maiztegui, J. Garcia de Souza, P. Solimano, L. Balboni & G. E. Berasain, 2014. Fish assemblage of a Pampean shallow lake, a story of instability, Hydrobiologia (this issue).

Collins, N. C. & G. Sprules, 1983. Introduction to large-scale comparative studies of lakes. Canadian Journal of Fisheries and Aquatic Sciences 40: 1750–1751.

Dangavs, N. V., 1976. Descripción sistemática de los parámetros morfométricos considerados en las lagunas pampásicas. Limnobios 1: 35–59.

Dangavs, N. V., 2005. Los ambientes acuáticos de la provincia de Buenos Aires. In de Barrio, R. E., R. O. Etcheverry, M. F. Caballé & E. Llambías (eds), Geología y recursos minerales de la provincia de Buenos Aires. Relatorio XVI Congreso Geológico Argentino: 219–236.

Díaz, O. & V. Colasurdo, 2008. El agua revela sus secretos. Química de las lagunas pampeanas en Espejos en la llanura: Nuestras lagunas de la región pampeana, Grosman F. compilador UNdC, Tandil: 47–65. ISBN/ISSN/DL: 978-950-658-213-5.

Díaz, R. A. & I. Mormeneo, 2002. Zonificación del clima de la región pampeana mediante análisis de conglomerados por consenso. Revista Argentina de Agrometeorología 2: 125–131.

Diaz, M., F. Pedrozo, C. Reynolds & P. Temporetti, 2007. Chemical composition and the nitrogen-regulated trophic state of Patagonian lakes. Limnologica 37: 17–27.

Diovisalvi, N., G. E. Salcedo Echeverry, L. Lagomarsino & H. E. Zagarese, 2014. Seasonal patterns and responses to an extreme climate event of rotifers community in a shallow eutrophic pampean lake. doi: 10.1007/s10750-014-1909-2.

Downing, J. A., Y. T. Prairie, J. J. Cole, C. M. Duarte, L. J. Tranvik, R. G. Striegl, W. H. McDowell, P. Kortelainen, N. F. Caraco & J. M. Melack, 2006. The global abundance and size distribution of lakes, ponds, and impoundments. Limnology and Oceanography 51: 2388–2397. http://www.aslo.org/lo/toc/vol_51/issue_5/2388.html.

Fermani, P., A. Torremorell, L. Lagomarsino, R. Escaray, F. Unrein & G. Pérez, 2014. Microbial abundance patterns along a transparency gradient in Pampean shallow lakes, Hydrobiologia (this issue).

Fernández Cirelli, A. & P. Miretzky, 2004. Ionic relations: a tool for studying hydrogeochemical processes in Pampean shallow lakes (Buenos Aires, Argentina). Quaternary International 114: 113–121.

Frenguelli, J., 1956. Rasgos generales de la hidrografía de la Provincia de Buenos Aires. Ministerio de Obras Públicas de la provincia de Buenos Aires – LEMIT 62: 19 pp.

Geraldi, A. M., M. C. Piccolo & G. M. E. Perillo, 2011. El rol de las lagunas bonaerenses en el paisaje pampeano. Ciencia Hoy 21: 9–14.

Guildford, S. J. & R. E. Hecky, 2000. Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: is there a common relationship? Limnology and Oceanography 45: 1213–1223. http://www.aslo.org/lo/toc/vol_45/issue_6/1213.html.

Gunn, J. M., E. Snucins, N. D. Yan & M. T. Arts, 2001. Use of water clarity to monitor the effects of climate change and other stressors on oligotrophic lakes. Environmental Monitoring and Assessment 67: 69–88. http://www.ncbi.nlm.nih.gov/pubmed/11339706.

Huisman, J., H. C. P. Matthijs, P. M. Visser, H. Balke, C. A. M. Sigon, J. Passarge, F. J. Weissing & L. R. Mur, 2002. Principles of the light-limited chemostat: theory and ecological applications. Antonie Van Leeuwenhoek, International Journal of General and Molecular Microbiology 81: 117–133.

Hutchinson, G. E. & H. Löffler, 1956. The thermal classification of lakes. Proceedings of the National Academy of Sciences 42: 84–86.

Iachetti, C. M. & M. E. Llames, 2014. Light limitation helps stabilize the phytoplankton assemblage steady-state in a temperate and highly turbid hypertrophic shallow lake (Laguna Chascomús, Argentina), Hydrobiologia (this issue).

Iriondo, M. H., 1989. Quaternary lakes of Argentina. Palaeogeography, Palaeoclimatology, Palaeoecology 70: 81–88. doi:10.1016/0031-0182(89)90081-3.

Isla, F. I., 2002. Descripción geológica de la zona costera de Buenos Aires. In Martins, L. R. S., E. Toldo & S. R. Dillenburg (eds), Erosao Costeira: Causas, Analise ee Risco e Sua Relacao com a Genese de Depósitos Minerais. Organización de Estados Americanos, editado en CD-Rom, Porto Alegre.

Izaguirre, I. & A. Vinocur, 1994. Typology of shallow lakes of the Salado River basin (Argentina), based on phytoplankton communities. Hydrobiologia 277: 49–62.

Izaguirre, I., I. O'Farrell, F. Unrein, R. Sinistro, M. dos Santos Afonso & G. Tell, 2004. Algal assemblages across a wetland, from a shallow lake to relictual oxbow lakes (Lower Paraná River, South America). Hydrobiologia 511: 25–36.

Izaguirre, I., H. Pizarro, P. de Tezanos Pinto, P. Rodríguez, I. O'Farrell, F. Unrein & J. M. Gasol, 2010. Macrophyte influence on the structure and productivity of photosynthetic picoplankton in wetlands. Journal of Plankton Research 32: 221–238.

Izaguirre, I., L. Allende, R. Escaray, J. Bustingorry, G. Pérez & G. Tell, 2012. Comparison of morpho-functional phytoplankton classifications in human-impacted shallow lakes with different stable states. Hydrobiologia 698: 203–216. http://link.springer.com/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 & M. Mancini, 2014. Environmental factors associated with the dominant phytoplankton species during a warm season in a gradient of Pampean shallow lakes, Hydrobiologia (this issue).

Jackson, L. J., 2003. Macrophyte-dominated and turbid states of shallow lakes: evidence from Alberta Lakes. Ecosystems 6: 213–223. http://link.springer.com/10.1007/s10021-002-0001-3.

Lewis, Jr., W. M., 1983. A revised classification of lakes based on mixing. Canadian Journal of Fisheries and Aquatic Sciences NRC Research Press 40: 1779–1787. http://www.nrcresearchpress.com/doi/abs/10.1139/f83-207.

Kirk, J. T. O., 1983. Light and Photosynthesis in Aquatic Ecosystems. Cambridge University Press, New York: 401 pp.

Kosten, S., M. Vernooij, E. H. van Nes, M. D. L. Á. Gonzales Sagrario, J. G. P. W. Clevers & M. Scheffer, 2012. Bimodal transparency as an indicator for alternative states in South American lakes. Freshwater Biology 57: 1191–1201. http://doi.wiley.com/10.1111/j.1365-2427.2012.02785.x.

Kratzer, C. R. & P. L. Brezonik, 1981. A Carlson-type trophic state index for nitrogen in Florida lakes. Journal of the American Water Resources Association 17: 713–715.

Kruk, C., L. Rodríguez-Gallego, M. Meerhoff, F. Quintans, G. Lacerot, N. Mazzeo, F. Scasso, J. C. Paggi, E. T. H. M. Peeters & S. Marten, 2009. Determinants of biodiversity in subtropical shallow lakes (Atlantic coast, Uruguay). Freshwater Biology 54: 2628–2641. http://doi.wiley.com/10.1111/j.1365-2427.2009.02274.x.

Kruse, E. & P. Laurencena, 2005. Aguas superficiales, relación con el régimen subterraneo y fenómenos de anegamiento. In de Barrio, R. E., R. O. Etcheverry, M. F. Caballé & E. Llambías (eds), Geología y recursos minerales de la provincia de Buenos Aires. Relatorio XVI Congreso Geológico Argentino: 313–326.

Lagomarsino, L., 2011. Estudios sobre la dinámica de nutrientes en lagunas pampeanas, con énfasis en la dinámica del fósforo de una laguna turbia (Chascomús). PhD thesis, Universidad Nacional de La Plata, Buenos Aires, Argentina: 190 pp.

Lambou, V. W., S. C. Hern, W. D. Taylor & L. R. Williams, 1983. Chlorophyll, phosphorus, Secchi disk, and trophic state. Water Resources Bulletin, American Water Resources Association 18: 807–813.

Lopes, P. M., A. Caliman, L. S. Carneiro, L. M. Bini, F. A. Esteves, V. Farjalla & R. L. Bozelli, 2011. Concordance among assemblages of upland Amazonian lakes and the structuring role of spatial and environmental factors. Ecological Indicators 11: 1171–1176. http://linkinghub.elsevier.com/retrieve/pii/S1470160X10002220.

López, H. L. & A. M. Miquelarena, 2005. Biogeografía de los peces continentales de la Argentina. In Llorente Bousquets, J. & J. J. Morrone (eds), Regionalización biogeográfica de Iberoamérica y tópicos afines: Primeras Jornadas Biogeográficas de la Red Biogeográfica Iberoamericana de Biogeografía y Entomología Sistemática. CYTED, México: 509–550.

López, H. L., C. Baigún, J. M. Iwaszkiw, R. L. Delfino & O. Padin, 2001. La cuenca del Salado: uso y posibilidades de sus recursos pesqueros. Univ. Nac. La Plata (ed.): 60 pp.

López, H. L., C. Morgan & M. Montenegro, 2002. Icthyological ecoregions of Argentina. Documentos no. 1, Serie ProBiota, La Plata.

May, R. M., 1977. Thresholds and breakpoints in ecosystems with a multiplicity of stable states. Nature 269: 471–477.

Mazumder, A. & K. E. Havens, 1998. Nutrient–chlorophyll–Secchi relationships under contrasting grazer communities of temperate versus subtropical lakes. Canadian Journal of Fisheries and Aquatic Sciences 55: 1652–1662.

Menu Marque, S., 2000. Datos biogeográficos y nuevas localidades de copépodos de la familia Cyclopidae (Copepoda, Cyclopoida) de la Argentina. Physis 58: 37–41.

O'Farrell, I., P. de Tezanos Pinto & I. Izaguirre, 2007. Phytoplankton morphological response to the underwater light conditions in a vegetated wetland. Hydrobiologia 578: 65–77.

Olivier, S. R., 1965. Rotíferos Planctónicos De Argentina Con Claves De Las Principales Especies, Datos Biológicos Y Distribución Geográfica. Revista del Museo de La Plata Zoologia 8: 177–260.

Pedrozo, S. & O. Rocha, 2007. Environmental quality evaluation of lakes in the Rio Grande do Sul coastal plain. Brazilian Archives of Biology and Technology 50: 673–685.

Perbiche-Neves, G., D. Previattelli, M. R. Pie, A. Duran, E. Suárez-Morales, G. A. Boxshall, M. G. Nogueira & C. E. da Rocha, 2014. Historical biogeography of the neotropical Diaptomidae (Crustacea: Copepoda). Frontiers in Zoology 11: 1–8. http://www.frontiersinzoology.com/content/11/1/36.

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

Pérez, G. L., E. Llames, L. Lagomarsino & H. Zagarese, 2011. Seasonal variability of optical properties in a highly turbid Lake (Laguna Chascomús, Argentina). Photochemistry and Photobiology 87(3): 659–670.

Pérez, G. L., L. Lagomarsino & H. E. 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. http://www.ncbi.nlm.nih.gov/pubmed/24080330.

Portielje, R. & D. T. Van der Molen, 1999. Relationships between eutrophication variables: from nutrient loading to transparency. In Shallow Lakes' 98. Springer, Netherlands: 375–387.

Preisendorfer, W., 1986. Secchi disk science: visual optics of natural waters. Limnology & Oceanography 3: 909–926.

Quinn, G. P. & M. J. Keough, 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, Cambridge: 537 pp.

Quirós, R., 1988. Relationships between air temperature, depth, nutrients and chlorophyll in 103 Argentinian lakes. Verhandlungen des Internationalen Verein Limnologie 23: 647–658.

Quirós, R., 2004. Sobre La Morfología De Las Lagunas Pampeanas. Documento De Trabajo Del Area De: 1–16. http://www.agro.uba.ar/users/quiros/Working/LaMorfologia.pdf.

Quirós, R., 2005. La Ecología De Las Lagunas De Las Pampas. Investigación Y Ciencia. Madrid, España: 13 pp. http://www.produccionovina.com.ar/produccion_peces/piscicultura/11-ecologia_lagunas_pampas.pdf.

Quirós, R., M. B. Boveri, C. A. Petracchi, A. M. Rennella, J. J. Rosso, A. Sosnovsky & H. T. Von Bernard, 2006. Los Efectos De La Agriculturización Del Humedal Pampeano Sobre La Eutrofización De Sus Lagunas. In Tundisi, J. G., T. Matsumura-Tundisi & C. S. Galli (eds), Eutrofizaçao Na América Do Sul: Causas, Conseqüências E Tecnologias De Gerenciamento E Controle. The International Institute of Ecology, Sao Carlos: 1–16.

Rautio, M., F. Dufresne, I. Laurion, S. Bonilla, W. F. Vincent & K. S. Christoffersen, 2011. Shallow freshwater ecosystems of the circumpolar Arctic. Ecoscience 18: 204–222. http://www.bioone.org/doi/abs/10.2980/18-3-3463.

Rennella, A., 2007. Relevancia de las interacciones tróficas en la determinación de la estructura del zooplancton en grandes lagunas pampeanas. PhD thesis, Universidad de Buenos Aires, Buenos Aires: 126 pp.

Ringuelet, R. A., 1975. Zoogeografía y ecología de los peces de agua dulce de aguas continentales de la Argentina y consideraciones sobre las áreas ictiológicas de América del Sur. Ecosur 2: 1–122.

Rodrigues Capítulo, A., N. Gómez, A. Giorgi & C. Feijoó, 2010. Global changes in Pampean lowland streams (Argentina): implications for biodiversity and functioning. Hydrobiologia 657: 53–70.

Sala, J. M., N. Gonzalez & E. Kruse, 1983. Generalización hidrológica de la provincia de Buenos Aires. Hidrología de grandes llanuras. Actas del Coloquio de Olavarría UNESCO-CONAPHI 2: 973–1009.

Scarpati, O. E. & A. D. Capriolo, 2011. Monitoring extreme hydrological events to maintain agricultural sustainability in Pampean flatlands, Argentina. In 1st World Sustainability Forum. Sciforum Electronic Conferences Series.

Scarpati, O., J. Forte Lay & A. Capriolo, 2007. Impacts of ENSO events in soil water moisture in Pampean region (Argentina). Revista Geográfica 141: 39–51.

Schallenberg, M., & D. Kelly, 2012. Ecological condition of six shallow southland lakes. MSI Envirolink Report prepared for Environment Southland. Cawthron Report No. 2198, 43 pp.

Scheffer, M., 1998. Ecology of Shallow Lakes. Chapman & Hall, London: 357 pp.

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

Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss & E. Jeppesen, 1993. Alternative equilibria in shallow lakes. Trends in Ecology and Evolution 8: 275–279.

Schindler, D. W., 1975. Whole-lake eutrophication experiments with phosphorus, nitrogen and carbon. Verhandlungen des Internationalen Verein Limnologie 19: 3221–3231.

Schindler, D. W., 1977. Evolution of phosphorus limitation in lakes: natural mechanisms compensate for deficiencies of nitrogen and carbon in eutrophied lakes. Science 195: 260–262.

Soriano, A., R. J. C. León, O. E. Sala, R. S. Lavado, V. A. Deregibus, M. A. Cahuepé, O. A. Scaglia, C. A. Velázquez & J. H. Lemcoff, 1992. Rio de La Plata grasslands. In Coupland, R. T. (ed) Ecosystems of the world 8A. Natural Grasslands. Introduction and western hemisphere. Elsevier, New York: 367–407.

Sosnovsky, A., J. J. Rosso & R. Quirós, 2010. Trophic interactions in shallow lakes of the Pampa plain (Argentina) and their effects on water transparency during two cold seasons of contrasting fish abundance. Limnetica 29: 233–246.

Texeira Soria, P., A. Pannunzio & L. Borello, 2013. Impacto del fenómeno "El Niño – Oscilación del Sur" sobre la evapotranspiración de la localidad de San Pedro, Buenos Aires, Argentina, para el periodo 2005–2011. Revista de Climatologia 13: 27–34.

Torremorell, A., 2010. Producción primaria fitoplanctónica en lagos someros: el papel de la disponibilidad de luz y los nutrientes. PhD thesis, Universidad Nacional de Comahue, Bariloche, Argentina: 265 pp.

Tricart, J. L., 1973. Geomorlología de la Pampa Deprimida. Base para los estudios edalológicos y agronómicos. INTA, XII Colección Científica 202 pp.

Viglizzo, E. F. & F. C. Frank, 2006. Ecological interactions, feedbacks, thresholds and collapses in the Argentine Pampas in response to climate and farming during the last century. Quaternary International 158(1): 122–126. doi:10.1016/j.quaint.2006.05.022.

Viglizzo, E. F., F. C. Frank, L. V. Carreño, E. G. Jobbágy, H. Pereyra, J. Clatt, D. Pincén & M. F. Ricard, 2011. Ecological and environmental footprint of 50 years of agricultural expansion in Argentina. Global Change Biology 17: 959–973.

Vollenweider, R. A., 1976. Advances in defining critical loading levels for phosphorus in lake eutrophication. Memorie dell'Istituto Italiano Di Idrobiologia Dott. Marco De Marchi Verbania Pallanza 33: 53–83.

Zárate, M. A. & J. Rabassa, 2005. Geomorfología de la provincia de Buenos Aires. In de Barrio, R. E., R. O. Etcheverry, M. F. Caballé & E. Llambías (eds), Geología y recursos minerales de la provincia de Buenos Aires. Relatorio XVI Congreso Geológico Argentino: 119–136.