Anales de Biología 42: 21-30, 2020
http://dx.doi.org/10.6018/analesbio.42.03

ARTICLE

Dynamics of an autumn phytoplankton bloom in a hypereutrophic urban lake in the semiarid Pampean region (Argentina)

Alberto Pilati, Santiago Andrés Echaniz, Alicia María Vignatti & Graciela Inés Bazán

Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Uruguay 151, 6300, Santa Rosa, La Pampa, Argentina.

Correspondence
A. Pilati
E-mail: apilatiunlpam@gmail.com

Received: 13 May 2019
Accepted: 12 February 2020

Resumen

Dinámica de un florecimiento algal otoñal en un lago hipereutrófico urbano de la región pampeana semiárida (Argentina).

En este trabajo, se reporta un raro florecimiento fitoplanctónico otoñal en un lago somero de la región semiárida pampeana (Argentina). La biomasa fitoplanctónica presentó un solo pico otoñal, seguido dos meses más tarde por un pico en la clorofila. El pico de biomasa coincidió con un débil pastoreo sobre la comunidad fitoplanctónica (dominada por la poco pastoreada *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek) junto con una reducción de la limitación por N en el otoño. El pico de clorofila ocurrió cuando las algas aumentaron su contenido de clorofila probablemente debido a la reducción de la radiación solar y la baja transparencia del agua. Esto indicará que la estacionalidad del fitoplancton en esta área particular depende de múltiples factores bióticos y abióticos.

Palabras clave: Cambios fenológicos; Lago somero hipereutrófico; *Planktothrix agardhii*; Zooplancton; Limitación por N.

Abstract

In this paper we report a rare autumm phytoplankton bloom in a shallow lake of the semiarid Pampean area of Argentina. Phytoplankton biomass peaked only once during the autumn, followed 2 months later by a chlorophyll peak. The biomass peak might have been the result of a weak grazing pressure on the phytoplankton community (dominated by the nongrazeable *Planktothrix agardhii* (Gomont) Anagnostidis & Komárek) coupled with a reduction in the N-limitation towards the autumm. The chlorophyll peak took place when phytoplankton cells increased their chlorophyll content probably due to a reduction of solar irradiance and low water transparency. This findings indicate that phytoplankton seasonality in this particular area may depend on multiple biotic and abiotic factors.

Key words: Phenological shifts; Hypereutrophic shallow lake; *Planktothrix agardhii*; Zooplankton; N-limitation.

Introduction

Succession in freshwater lakes has been extensively studied since the 80’s. The Plankton Ecology Group (PEG) model (Sommer *et al.* 1986) predicted that eutrophic lakes have two phytoplankton blooms, one in spring and a more important one in summer. Those blooms, characterized by low water transparency, are separated by a clear water phase (high water transparency) caused by high zooplankton biomass and grazing. The applicability of the PEG model to shallow lakes or tropical lakes has not been very well documented (Lampert & Sommer 2007). Nevertheless, Moustaka-Gouni *et al.* (2014) recently found that eutrophic Mediterranean lakes have a minimal phytoplankton bloom in spring followed by maximum biomass peak in autumn.

As the PEG model not always apply to all aquatic systems, many attempts have been made to determine the factors that affect phytoplankton peaks and their occurrence. Phytoplankton peaks can be measured as biovolume or chlorophyll as a surrogate of biomass. Biovolume calculation is time consuming and requires the expertise of the researcher in classifying the algae (Hillebrand *et al.* 1999). Chlorophyll measurements, on the other hand, can change with light, nutrient availability and phytoplankton composition, so caution is needed when using this surrogate as a biomass estimator (Kasprzak *et al.* 2008). Regarding occurrence, Winder & Cloern (2010), using chlorophyll as a phytoplankton biomass estimator, described different aquatic systems with regular or irregular cycles which were affected not only by physical and chemical factors, but also by food-web seasonality. They found that most aquatic systems show one peak in spring as a consequence of a temperature increase and water mixing with nutrient inputs. These authors also found that lakes with two peaks (spring and autumn or winter) were present in lakes with high grazing rates and shifts in the phytoplankton community, whereas lakes with irregular blooms generally respond to short-term climatic events which affect the lake’s temperature and mixing dynamics. Other lakes, on the other hand, may show a shift in periodicity between the previous two patterns, or even the absence of a periodic pattern (generally hypertrophic lakes, with cyanobacteria domination all year long, and low grazing pressure by zooplankton) (Winder & Cloern 2010) .

The Pampean region of Argentina, is characterized by the presence of a large number of shallow, eutrophic-hypertrophic, polymictic lakes (Quirós *et al.* 2002, Diovisalvi *et al.* 2015). Their phytoplankton communities are generally dominated by cyanobacteria which generally bloom during the warm season (Quirós *et al.* 2002, Izaguirre *et al.* 2015) as a result of water level fluctuations and eutrophication, or early spring depending on zooplankton grazing and light limitation (Torremorell *et al.* 2007). The western part of this region is located below the 700 mm/year isohyet (Diovisalvi *et al.* 2015) with mainly temporary, shallow, and saline lakes (Vignatti *et al.* 2017), with water level fluctuations depending on precipitation cycles (Viglizzo 2011). Some of these lakes had uncommon fall/winter chlorophyll peaks but no affecting factors were associated to them (Echaniz *et al.* 2013, Echaniz *et al.* 2016). To help understand factors driving the seasonality of phytoplankton in this area, we studied Don Tomás, a shallow urban lake with frequent summer chlorophyll peaks (Echaniz *et al.* 2008) that in 2008-2009 showed only one important chlorophyll and phytoplankton biomass peak (2-months apart) during the fall. Thus, we analyzed how nutrients, zooplankton and phytoplankton nutrient limitation may have triggered this rare phenomenon.

Materials and methods

Study area

Don Tomás lake is a hypereutrophic shallow lake (146 Ha) located by Santa Rosa, capital city of La Pampa province (Fig. 1) (36º37’ S; 64º19’ W). It is located on the eastern edge of the Thorny Forest ecoregion. The climate is semi-arid, with a temperature range between 8.9 and 23.6 ºC, an annual mean temperature of 15.8 ºC. The average wind speed is around 13 km/h and the annual rainfall is 746 mm (Morello *et al.*, 2012). It is a region with gentle slopes produced by wind action, covered by open deciduous forest dominated by *Prosopis caldenia* Burkart, *Prosopis flexuosa* De Candolle, and *Geoffroea decorticans* (Gill. ex Hook. & Arn.) Burkart (Morello *et al.*, 2012). However, most of the basin has been currently deforested due to the increase in urbanization. Its waters are well oxygenated (>6 mg/L) and its ionic content characterized by the presence of sodium bicarbonate. Total suspended solids averaged 54.6 mg/L

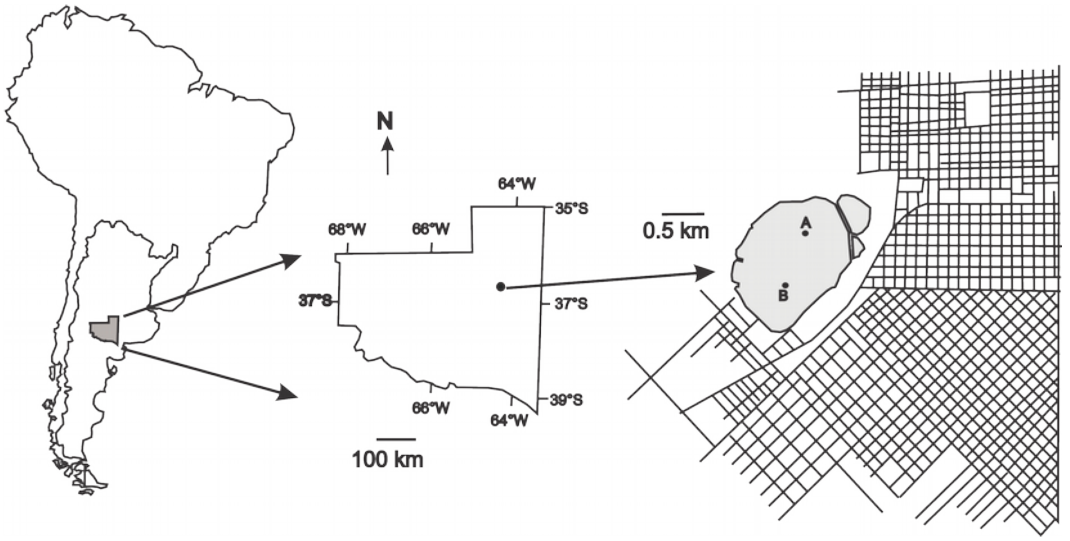

Figura 1. Mapa de la ubicación de la laguna Don Tomás (Provincia de La Pampa, Argentina), posición de los sitios de muestreo (A: 36º37’ 11” S, 64º18’49”O y B: 36º37’29”S, 64º18’56”O) y zona oeste de la ciudad de Santa Rosa.

Figure 1. Map showing the location of Don Tomás Lake (La Pampa province, Argentina), the position of the sampling sites (A: 36º37’11”S, 64º18’49”W and B: 36º37’29”S, 64º18’56”W) and the west side of Santa Rosa city.

and were mostly organic (Echaniz *et al.* 2008). From 1996 to 2006, as the city increased its drainage area, both the lake’s salinity and water transparency decreased from 1.65 to 0.65 g/L and from 0.24 to 0.14 m respectively (Echaniz *et al.* 2012). These authors suggest that water transparency reduction in this lake was associated with a decline in cladoceran grazers due to a zooplanktivorous fish, the silverside, *Odontesthes bonariensis* Valenciennes, 1835. In fact, silverside density has increased from 125.7 ind/Ha (25.5 Kg/Ha) in October 1998 to 220.9 ind/Ha (32.3 Kg/Ha) in June 2008 (O. Del Ponti, pers. comm.). Currently, the lake receives only the city storm drainage as the sewage drainage was diverted to other lake since 1987.

During this study, there was an important drought in the area, consequently Don Tomás Lake reduced its mean depth from 1.7 m at the beginning of the study to 1.5 m at the end. Lake temperatures ranged from 8 ºC in winter (June-July) to 26 ºC in summer, but the lake never stratified. Trophic state indexes based on water transparency, total phosphorus and chlorophyll (Carlson 1977) were always higher than 70 (88.1±1.3; 91.3±1.6 and 75.9±5.4 respectively) indicating the hypereutrophic condition.

Sampling, analytical and statistical procedures

From September 2008 to August 2009, we firstly determine the stratification regime by measuring monthly *in situ* temperature and dissolved oxygen profiles with a YSI oxygen meter (Model 55). These measurements were taken every 0.5 m at midday at two points 500 m-apart in the deepest part of the lake (Fig. 1). As the lake was always well mixed (polymictic), monthly sub-surficial water samples (0.10 m) were considered representative of the water column at those sampling points. The study area, sampling protocols, water transparency and some laboratory analyses (chorophyll, and zooplankton biomass) are described elsewhere (Echaniz *et al.* 2012). Dissolved nutrients were analyzed after filtering the water through a GF/F glass fiber filter. Dissolved inorganic nitrogen (DiN) was considered to be the sum of only ammonia (phenate method; APHA 1992) and nitrate (cadmium reduction; Hach, method #8039) as nitrite was below detection levels. Soluble reactive phosphorus (SRP) was measured with the ascorbic acid method (APHA 1992). Total nitrogen (TN) and phosphorus (TP) were digested with a peroxodisulfate oxidation following Ebina *et al.* (1983) and read with the cadmium reduction and ascorbic acid methods, respectively. All nutrients were measured with a Hach DR/4000 spectrophotometer.

Total suspended solids (TSS) were estimated by filtering lake water onto a pre-weighted Gelman A/E glass fiber filter and drying the filter for 24 hours at 60 ºC. Organic suspended solids (OSS) were calculated by difference between TSS and non-volatile suspended solids (ashing the same filter (TSS) at 550C for 1 hour) (APHA 1992).

Phytoplankton samples were taken from a depth of 0.10 m and preserved with 4% formalin. Identification followed literature by Prescott (1951), Komárek & Anagnostidis (1999, 2007), Komárek (2013), and Bourrelly (1985). Quantification was done using an inverted microscope Iroscope SH-24PH with a 10-mL Utermhöl settling chamber. Two hundred fields were counted. Phytoplankton biovolume was estimated by geometric approximation based on micrometer measurements of 25 randomly selected specimens (Hillebrand *et al.* 1999).

To quantify the severity of phytoplankton nutrient limitation, we took monthly sub-surficial water samples. Water was screened with a 63µm mesh to remove zooplankton and placed into 250 mL flasks (3 per treatment). There were four treatments: Control (no nutrients added), +N (150 µmol/L N added as NH_4NO_3), +P (9.3 µmol/L P added as $Na_2HPO_4*12H_2O$) and +N+P. Flasks were incubated in an environmental chamber at 200 µmol PAR/m^{2}s for 48 h. We considered phytoplankton communities to be N-limited, P-limited, or N+P-limited when the chlorophyll level of the treatment (log-transformed) was significantly higher than the control using an one-way ANOVA followed by a Tukey test for treatment means comparisons. Percent of control responses were calculated following Marcarelli *et al.* (2006). To analyze the effect of light limitation on the chlorophyll content of algal cells, we used the C:Chlorophyll ratio. Although we did not measure C content in phytoplankton directly, we estimated it at 10% of algal biovolume (Peters & Downing 1984).

Spearman's R_s correlation coefficients were calculated to examine relationships among main limnological variables.

Results

In spring (September to December), chlorophyll had the lowest values (~50 µg/L), while by late autumn (May and June) it had a distinctive peak (~191 µg/L) (Fig. 2) almost 4 times higher than the spring values. Mean chlorophyll-a concentration was 115 µg/L (±55.1). Water transparency was low (0.14 m ± 0.01). TSS (100% organic) ranged from 45-60 mg/L. Although water trans-

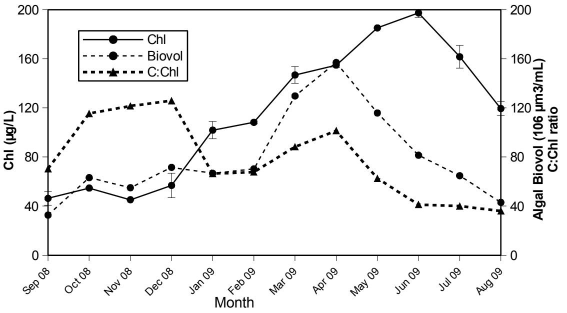

Figura 2. Concentración media mensual de clorofila (círculos. negros), biovolumen algal total (círculos blancos) y relación Carbono:clorofila (cruz) en la laguna Don Tomás, 2008-2009, Santa Rosa, La Pampa, Argentina.

Figure 2. Mean monthly chlorophyll concentrations (black circles), total algal biovolume (white circles) and C:Chl ratios (cross) in Laguna Don Tomás, 2008-2009, Santa Rosa, La Pampa, Argentina.

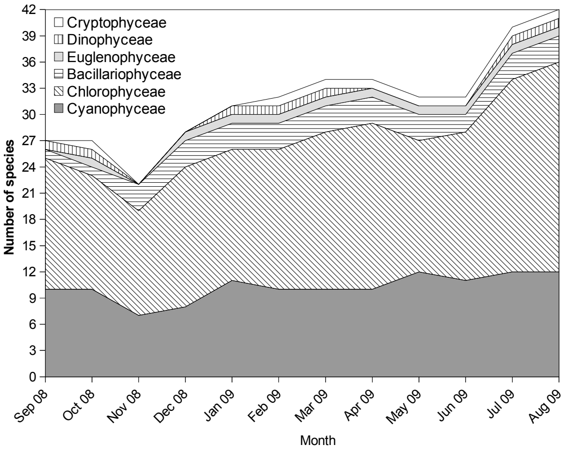

Figura 3. Riqueza de especies de grupos de fitoplancton en la laguna Don Tomás durante 2008-2009. La línea superior indica el número total de especies encontradas.

Figure 3. Species richness of phytoplankton groups in Laguna Don Tomás during 2008-2009. The top line in the figure indicates the total number of species found.

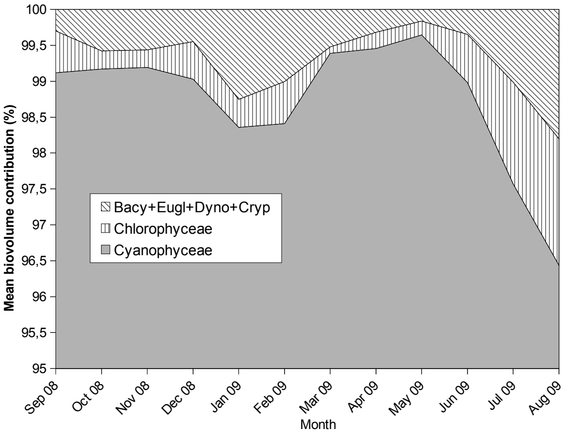

Figura 4. Contribución relativa del biovolumen (%) de los principales grupos algales en la laguna Don Tomás durante 2008-2009.

Figure 4. Relative biovolume contribution (%) of main phytoplankton groups in Laguna Don Tomás during 2008-2009.

parency and TSS did not show any particular seasonal pattern, both were significantly and negatively correlated (R_s=-0.952; p≤0.0001). Chlorophyll, on the other hand, was not correlated with water transparency (R_s=0.322; p=0.291).

Mean algal biovolume during the study was 0.78 mm3/mL (±0.38), but in contrast to chlorophyll-a, it had a peak in mid-autumn (April) (Fig. 2). C:Chl ratios had a mean value of 78, showing a minimum value of 36 in winter and a maximum value of 126 in spring (Fig. 2). Chlorophyll-a and algal biomass were significantly correlated (R_s= 0.664; p=0.018).

Phytoplankton richness increased from 27 species at the beginning of spring (September 2008) to 42 species by the end of the winter (August 2009) (Fig. 3, Table 1). Chlorophyceae was the most diverse group (Fig. 3, Table 1). Nevertheless, Chlorophyceae had the lowest contribution to biomass in the phytoplankton community (Fig. 4). Cyanobacteria, on the other hand, never had more than 12 species but contributed more than 96% of total phytoplankton biomass (Fig. 4) with *Planktothrix agardhii* as the dominant species (Table 1). The dominant species during the biomass (April 2009) and chlorophyll (June 2009) peaks were *Plankthotrix agardii* followed by *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault (Table 1).

Zooplankton richness ranged between 8 and 14 species in winter and spring respectively (Table 2). Rotifers were the most diverse group, and dominated the zooplankton biomass (Fig. 5) (mainly *Brachionus angularis* Gosse, 1851, *Brachionus havanaensis* Rousselet, 1911, *Keratella tropica* Apstein, 1907, *Pompholyx complanata* Gosse, 1851) and copepods (*Microcyclops anceps* Richard, 1897). Biomass peaked twice during the study, with the most important peak during the summer (February-March). Total zooplankton biomass was not correlated to any other variable.

Mean total phosphorus (TP) and total nitrogen (TN) were high (0.42 mgP/L±0.05 and 5.7 mgN/L±1.1, respectively). SRP and N-NO$_3$ did not show any particular trend, averaging 19.4 g P-PO$_4$ /L (±3.7) and 127 g N-NO$_3$ /L (±47), respectively. On the other hand, N-NH$_4$ levels ranged from 48-830 gN/L throughout the study and increased by more than 13 times towards the winter. This fact resulted in a slight increase of TN:TP molar ratios and an important increase in DiN:TP molar ratios

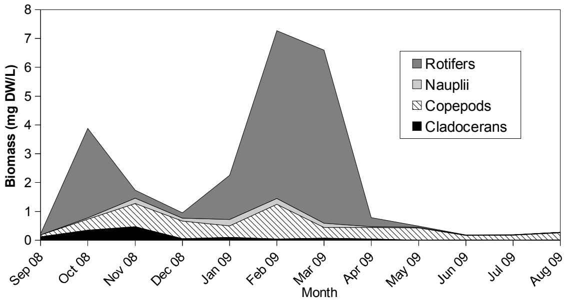

Figura 5. Biomasa (peso seco) de los principales grupos de zooplancton de la laguna Don Tomás, 2008-2009. Redibujado de Echaniz *et al.* (2012).

Figure 5. Biomass (dry weight) of the main zooplankton groups of Laguna Don Tomás, 2008-2009. Re-drawn from Echaniz *et al.* (2012).

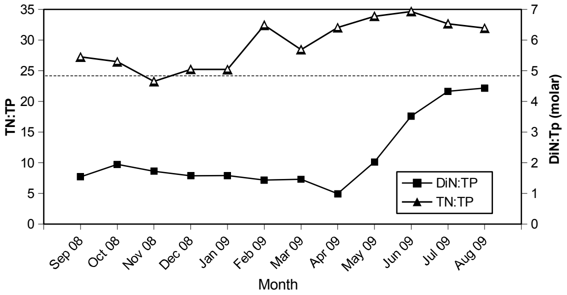

Figura 6. Relaciones molares de N inorgánico disuelto a P total (DiN:TP) y N total a P total (TN:TP) encontrados en la laguna Don Tomás, 2008-2009. La línea punteada indica el límite teórico entre limitación por N y P según Bergstørm (2010).

Figure 6. DiN:TP (black squares) and TN:TP (white triangles) molar ratios found in Laguna Don Tomás, 2008-2009. The dotted line show the theoretical breakpoint between estimated N limitation and P limitation using DiN:TP ratios according to Bergstørm (2010).

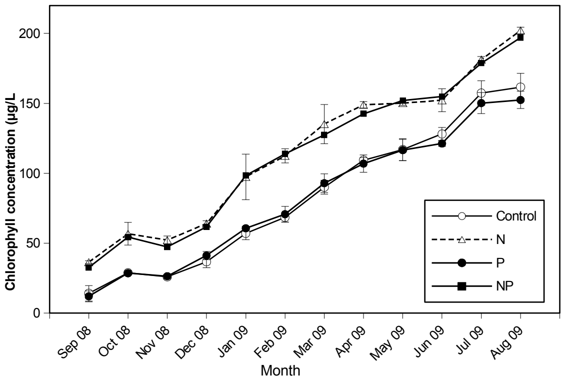

Figura 7. Concentración media final mensual de clorofila (µg/L) en bioensayos de limitación por nutrientes en la comunidad algal de la laguna Don Tomás. Las barras de error indican la desviación estándar. Para todos los meses, las concentraciones de clorofila encontradas con la adición de N (solo o combinado con P) fueron significativamente más altas que las adiciones de P solo y el control (Tukey, p<0.0001).

Figure 7. Mean final chlorophyll concentrations (µg/L) in monthly nutrient limitation bioassays for the phytoplankton community in Don Tomás Lake. Error bars indicate the standard deviation. For all months, chlorophyll concentrations due to N additions (alone or combined with P) were significantly higher than P additions alone and the control (Tukey, p<0.0001).

Especies	**Sep-08**	**Oct-08**	**Nov-08**	**Dec-08**	**Jan-09**	**Feb-09**	**Mar-09**	**Apr-09**	**May-09**	**Jun-09**	**Jul-09**	**Aug-09**
Cyanobacteria												
Anabaena aphanizomenoides Forti	747	267	587	2613	160	373	1600	1173	213	213	267	267
Anabaena sp.	107	160	107	640	1333	533	1653	2293	2667	1867	1013	960
Anabaenopsis arnoldii Aptekar					53	640		53	587	107	213	107
Aphanizomenon flos-aquae Ralfs ex Bornet & Flahault	587	1600			693	5920	24373	40000	64747	39307	18400	4000
Merismopedia tenuissima Lemmermann									107			
Microcystis pulverea (H.C.Wood) Forti	107	107		107	53		53	213	53	107	320	53
Oscillatoria proboscidea Gomont	1973	9173	10827	14347	12320	16373	32000	37280	9920	2027	1333	1707
Oscillatoria pseudogeminata (G.S.Schmid)	373	907	533	800	1147	427	3627	3840	4213	747	747	1387
Oscillatoria subbrevis Schmidle	907	3040	1387		213	267					5600	6667
Phormidium tenue Gomont	2293	3253	2613	3413	2507	4373	25280	26880	14667	9333	9387	5280
Planktothrix agardhii (Gomont) Anagnostidis & Komárek	34080	78827	57973	73707	52000	49227	60373	60907	63467	79467	83947	64853
Spirulina laxissima G.S.West	373	53					107		267	373	640	1440
Spirulina subsalsa Ørsted ex Gomont				53								
Synechococcus sp.					1067	907	3040	2613	1013	480	427	267
Chlorophyta												
Actinastrum raphidoides (Reinsch) Brunnthaler	53					53	53	267	53	107	160	160
Chlamydomonas sp.	320	160	213	587	160	533	53	320		747	1600	1013
Closteriopsis acicularis (Chodat) J.H.Belcher & Swale		107	53	53	267	1547	533	213	107	53	160	53
Dictyosphaerium elegans Bachmann		213		160			107		107	160	267	160
Golenkinia radiata Chodat			53	213	107	53	53	320		107	160	320
Kirchneriella contorta var. *contorta* (Schmidle) Bohlin	320	1440	320	107	693	107		267		960	1280	1973
Kirchneriella obesa (West) West & G.S.West	373	960	587	427	107	53	53	267	320	1013	1067	1760
Monoraphidium arcuatum (Korshikov) Hindk	160	213		160	107	53	53	373	267	160	160	1173
Monoraphidium contortum (Thuret) Komrkov-Legnerov						160	53	107				373
Monoraphidium griffithii (Berkeley) Komrkov-Legnerov	160	53	160	267	1653	1440	747	213	800	587	640	1067
Monoraphidium indicum Hindak						213	107		53		213	213
Monoraphidium irregulare (G.M. Smith) Komrkov Legenerova	53	53					427	160			53	587
Oocystis lacustris Chodat	53	53	53	107					107		107	107
Oocystis solitaria Wittrock in Wittrock & Nordstedt	53		53	213	53			107	267	747	747	853
Pediastrum boryanum (Turpin) Meneghini								107	160	107		
Scenedesmus acuminatus (Lagerheim) Chodat	267	587		160	267	373	53	160	373	480	533	427
Scenedesmus arcuatus (Lemmermann) Lemmermann				53	53	107					53	53
Scenedesmus ecornis (Ehrenber) Chodat	53				320		53	320			107	160
Scenedesmus opoliensis P.G. Richter	53		160				160	107	160	53	160	160
Scenedesmus quadricauda Chodat	53	53	213	107		53			53	53	213	267
Schroederia setigera (Schrder) Lemmermann	160	107	160	213	373	320	213	480	427	427	587	907
Tetradron caudatum (Corda) Hansgirg							53	53				53
Tetradron minimum (A. Braun) Hansgirg	53	107	53	320	267		107	267		107	107	213
Tetradron triangulare Korshikov				53	53			53	53			
Tetrastrum peterfii Hortobgyi						53					160	160
Tetrastrum staurogeniaeforme (Schrder) Lemmermann				107	53		53			53	53	107
Charophyta												
Staurastrum sp.						53						
Bacillariophyta												
Aulacoseira granulata (Ehrenberg) Simonsen		107	533	160	1067	747	693	320	107		213	533
Cyclotella meneghiniana Ktzing			267	267	480	533	533	693	213	267	480	800
Fragilaria sp.	107		320	747	1333	533	1760	693	1440	373	213	427
Euglenozoa												
Euglena variabilis G.A.Klebs		427		267	107	480	480	160	53	1280	1173	640
Miozoa												
Peridinium sp.	107	320		107	107	160	107				267	107
Cryptophyta												
Cryptomonas ovata Skuja		107				53	107	53	53	267	53	267

Tabla 1. Abundancia de especies de fitoplancton (organismos por mililitro) encontradas en la laguna Don Tomás durante el estudio.

Table 1. Phytoplankton species abundance (organisms per mL) found in Don Tomás lake during the study.

Especies	**Sep-08**	**Oct-08**	**Nov-08**	**Dec-08**	**Jan-09**	**Feb-09**	**Mar-09**	**Apr-09**	**May-09**	**Jun-09**	**Jul-09**	**Aug-09**
Cladocerans												
Bosmina huaronensis Delachaux, 1918	138	605	817	107	257	117	15	110	10	8	6	10
Diaphanosoma birgei Korinek, 1981						22	18					
Copepods												
Acanthocyclops robustus (G.O. Sars, 1863)*									1	6		
Microcyclops anceps (Richard, 1897)*	15	180	361	393	412	733	445	370	157	39	72	66
Nauplii	35	289	1612	627	1467	1193	802	213	97	12	84	54
Rotifers												
Anuraeopsis fissa (Gosse, 1851)		30					20					6
Brachionus plicatilis Mller, 1786	9	11				7		17				
Brachionus angularis Gosse, 1851		255	3		77	213	3500		1	4		
Brachionus havanaensis Rousselet, 1913		45	1087	13	157	8440	7200	7	2	7	6	
Brachionus dimidiatus Bryce, 1931		10						3				
Brachionus calyciflorus (Pallas, 1766)	2			4	57	80	165					
Colurella sp.		5										
Filinia longiseta (Ehrenberg, 1834)		5										
Hexarthra intermedia (Wiszniewski, 1929)				103	733	477	205					
Keratella cochlearis (Gosse, 1851)	158	1370	813									
Keratella tropica (Apstein, 1907)	38	11520	760	517	1913	5020	2750	2377	520	20	10	4
Lecane sp.	3											
Polyarthra dolichoptera Idelson, 1925	78	35	83	17	197	187	170	107	17	4	24	50
Pompholyx complanata Gosse, 1851	93	6600	97	37	647	67	800	1397	3	44	38	4
Synchaeta sp.						10	20				10	2

Tabla 2. Abundancia de especies de zooplancton (individuos por mililitro) encontradas en la laguna Don Tomás durante el estudio. Los asteriscos indican que el número incluye adultos y estadios copepoditos.

Table 2. Zooplankton species abundance (individuals per liter) found in Don Tomás lake during the study. The asterisk indicate that the number comprises adults and copepodite stages.

(Fig. 6). DiN:TP molar ratios were always less than 4.5 during the study.

The phytoplankton community was N-limited all year long (Fig. 7). Bioassays with N additions (N or N plus P) always had a higher chlorophyll response than the control or P treatments (ANOVA: $F_{2,33}$=91.35; p<0.0001). N treatments averaged 64% of controls, and N+P treatments were 58% of controls whereas P treatments averaged -1% of controls.

Discussion

Don Tomás lake frequently had summer chlorophyll peaks (Echaniz *et al.* 2008). The existence of an important, non-frequent, autumn chlorophyll peak (Fig. 2) in 2009 gave us the chance to analyze the factors that may have induced this phenomenon. There are two main factors that could have influenced this late in the season peak: reduced zooplankton grazing pressure (Top-Down effect) and nutrient/light stimulus (Bottom-Up effect).

Regarding the first factor, it is important to note that Don Tomás zooplankton taxonomic composition has dramatically changed in the last 13 years due to predation on large zooplankton by silversides (*Odontesthes bonariensis*). When the current zooplankton richness was compared to that from more than a decade ago (Echaniz *et al.* 2012), we observed that 7 cladocerans and 2 copepod species were lost (with *Daphnia obtusa* Kurz, 1874 and *Daphnia spinulata* Biraben, 1917, among the largest) and 8 small-sized new rotifer species were found by 2008-9 (*B. dimidiatus*, *B. calyciflorus*, *K. tropica*, *H. intermedia*, *P. complanata*, *Lecane* sp. Nitzsch, 1827, *A. fissa*, *Synchaeta* sp. Ehrenberg, 1832). Since microzooplankton have lower grazing efficiencies than macrozooplankton, a reduction in mean water transparency was consequently observed (0.24 m in 1995-96 to 0.15 m in 2006) (Echaniz *et al.* 2008). During the present study, Don Tomás zooplankton biomass was dominated by rotifers and small-sized copepods (Fig. 5) which have low grazing efficiencies. Particularly, during May and June (fall/winter) when the chlorophyll peak was observed, there was a notorious lack of grazers (Fig. 5) (0.2-0.5 mgDW/L) that could have released the grazing pressure on the algal community even more. At this very same time, the phytoplankton community was dominated by cyanobacteria (94.3-96.9% of the whole algal community biovolume) (Fig. 4). Cyanobacteria is considered a low quality food resource group for zooplankton and produces a variety of toxins which induce limitations to the survival, growth and reproduction of zooplanktonic organisms (Lampert 1987, Ghadouani *et al.* 2003). Thus, we assumed that the zooplankton groups present when chlorophyll peaked, did not exert a strong grazing pressure on the algal community in order to control its biomass as was already observed for another hypereutrophic Pampean shallow lake by Diovisalvi *et al.* (2010).

The second factor that could have affected this late in the season chlorophyll peak in 2008-2009 is a direct response to a nutrient/light stimulus. Don Tomás nutrient concentrations were high, and consequently affected the phytoplankton community nutrient limitation. As predicted by Bergström (2010), and corroborated by our bioassays, Don Tomás's phytoplankton community was always N-limited, as DiN:TP molar ratios were always lower than 4.9 (Fig. 7). This corroborates the findings by Halstvedt *et al.* (2007) who reported N-limitation in *Planktothrix rubescens* (De Candolle ex Gomont) Anagnostidis & Komárek and *P. agardhii* populations in enrichment experiments, and that Don Tomás Lake cyanobacteria community was dominated by *P. agardhii*. In Don Tomás, we also observed that the response to N additions was significantly inversely correlated to DiN (R_s= -0.602; p=0.038). Nevertheless, chlorophyll concentrations were not correlated to DiN (R_s= 0.347; p=0.270) indicating that nitrogen availability would not be enough to regulate the chlorophyll increase during the autumn.

In Don Tomás, phytoplankton biomass and chlorophyll-a concentration peaked in autumn (Fig. 2), but these two peaks were approximately 2-months apart. When reviewing this phenomenon elsewhere, Kasprzak *et al.* (2008) indicated that this decoupling was mainly affected by seasonal changes in the algal community or changes in the trophic status. In Don Tomás, these two factors can be discarded as the phytoplankton community was always dominated by the cyanobacteria (Fig. 4) and nutrient levels were high enough (Fig. 6) to classify this lake as permanently hypereutrophic. On the other hand, Felip & Catalán (2000) found that a Spanish oligotrophic lake had a biovolume peak a month earlier than chlorophyll-a concentration. These authors suggested that a change in the per-unit cell chlorophyll concentration as a response to winter light-limitation was the main factor affecting this decoupling. This situation is the most compatible one with Don Tomás' as we found that Don Tomás lake has a mean transparency of 0.14 m, meaning an estimated euphotic depth of 0.46 m (Kalff 2003), approximately of the mean depth registered at the beginning of the study. Thus, approximately of the water column within Don Tomás Lake might be under strong light limitation (which could have been alleviated by the polymictic nature of this lake). Light limitation is common in turbid, shallow lakes of Argentinas' pampas (Quirós & Drago 1999, Torremorell *et al.* 2007, 2009, Diovisalvi *et al.* 2015). In addition to the low water transparency, it is necessary to consider the natural light availability reduction during autumn and winter. In order to cope with light limitation, algal cells might increase their pigment concentration as a physiological adaptation to low irradiance, consequently reducing the C:Chl ratio (Cullen 1982). If this is the case here, some changes in C:Chl ratios would be expected in Don Tomás. Although we did not measure C content in phytoplankton directly, we estimated it at 10% of algal biovolume (Peters and Downing 1984). The mean C:Chl ratio of 78 indicated a cyanobacteria dominated lake as suggested by Yacobi & Zohari (2010). This ratio also had lower values during autumn and winter (Fig. 2). According to Cullen (1982) these low values indicate higher chlorophyll concentrations in phytoplankton, typical of periods with low solar radiation (typical of fall/winter months) and high nutrient concentrations (Taylor *et al.* 1997) as observed in figure 6.

As mentioned previously, Don Tomás lake has shown both, phytoplankton successions with typical summer chlorophyll peaks (Echaniz *et al.* 2008) as well as autumn-winter peaks (Echaniz *et al.* 2012; this study). Winder & Cloern (2010) found that phytoplankton biomass peaks may happen regularly (every 6 or 12 months) or irregularly. Irregular occurrence was common in hypereutrophic systems dominated by cyanobacteria, low grazing pressure and short-term climatic variations where Don Tomás Lake would easily fit. Nevertheless, in order to understand the true dynamics of this shallow, urban lake, it will be necessary to include climatic variables in future long-term monitoring since precipitation variability on the west side of the Pampa's plains (Viglizzo 2011) seems to cause important variations in some of the lake's parameters (e.g., depth, salinity, light and nutrient availability).

Conclusion

Don Tomás Lake had an important 2009 fall chlorophyll peak due to the lack of large grazers, which together with the dominance of the non-grazeable *P. agardhii*, probably weakened top-down processes. On the other hand, the presence of bottom-up processes fueled by high nutrients in this system might have stimulated algal growth. The chlorophyll peak occurred later than the biomass peak as phytoplankton cells increased their chlorophyll content in spite of algal biomass (biovolume) probably due to a reduction of solar irradiance and low water transparency. A long-term monitoring would be needed in order to analyze if unusual blooms are affected by climatic variations.

Acknowledegments

This research was funded by Universidad Nacional de La Pampa, project 202 and Préstamo BID PRH-PICT 00301. Daniel Sierra, Claudia Monteira, and "Quito" Baumgaertner (Municipal Canoeing School personnel) helped us with field logistics.

References

APHA (American Public Health Association). 1992. Standard Methods for the Examination of Water and Wastewater. Washington DC, USA: American Public Health Association, American Water Works Association, and Water Environment Federation.

Bergström AK. 2010. The use of TN:TP and DiN:TP as indicators for phytoplankton nutrient limitation in oligotrophic lakes affected by N deposition. Aquatic Sciences 72: 277-281.

Bourrely P. 1985. Les algue d'eau douce. Initiation à la systématique. Tome III: Les Algues bleues et rouges. Les Eugléniens, Peridiniens et Cryptomonadines. París: Société Nouvelle des Éditions Boubée..

Carlson RE. 1977. A trophic state index for lakes. Limnology and Oceanography 22 (2): 361-369.

Cullen JJ. 1982. The deep chlorophyll maximum: comparing vertical profiles of chlorophyll a. Canadian Journal of Fisheries and Aquatic Sciences 39: 291-803.

Diovisalvi N, Berasain G, Unrein F, Colauti D, Fermani P, Llames ME, … & Zagarese H. 2010. Chascomús: estructura y funcionamiento de una laguna pampeana turbia. Ecología Austral 20 (2): 115-127.

Diovisalvi N, Bohn VY, Piccolo MC, Perillo GME, Baigún C & Zagarese H. 2015. Shallow lakes from the Central Plains of Argentina: an overview and worldwide comparative analysis of their basic limnological features. Hydrobiologia 752: 5-20.

Ebina J, Tsuyoshi T & Totoso S. 1983. Simultaneous determination of total nitrogen and total phosphorus in water using peroxodisulfate oxidation. Water Research 17 (12): 1721-1726.

Echaniz SA, Vignatti MA & Bunino PC. 2008. El zooplancton de un lago somero hipereutrófico de la región central de Argentina: cambios después de una década. Biota Neotrópica 8 (4): 63-71.

Echaniz SA, Vignatti MA, Pilati A & Kissner S. 2012. Cambios en la diversidad y variación interanual de la abundancia del zooplancton de un lago somero urbano de La Pampa. Biología Acuática 27: 97-112.

Echaniz SA, Cabrera GC, Aliaga PL, & Vignatti AM. 2013. Variations in zooplankton and limnological parameters in a saline lake of La Pampa, central Argentina, during an annual cycle. International Journal of Ecosystem 3 (4): 72-81.

Echaniz SA, Vignatti MA, Cabrera GC, Capecce C & Treffinger-Cienfuegos MS. 2016. Comparación de los parámetros limnológicos y el zooplancton de un lago somero salino de La Pampa (Argentina) durante dos ciclos anuales de condiciones diferentes. Biología Acuática 31: 28-39.

Felip M & Catalán J. 2000. The relationship between phytoplankton biovolume and chlorophyll in a deep oligotrophic lake: decoupling in their spatial and temporal maxima. Journal of Plankton Research 22 (1): 91-105.

Ghadouani A, Pinel-Alloul B & Prepas EE. 2003. Effects of experimentally induced cyanobacterial blooms on crustacean zooplankton communities. Freshwater Biology 48: 363-381.

Halstvedt CB, Rohrlack T, Andersen T, Skilberg O & Edvarsen B. 2007. Seasonal dynamics and depth distribution of Planktothrix spp. in Lake Steinsfjorden (Norway) related to environmental factors. Journal of Plankton Research 29 (5): 471-482.

Hillebrand H, Dürselen CD, Kirschtel D, Pollingher U & Zohary T. 1999. Biovolume calculation for pelagic and benthic microalgae. Journal of Phycology 35: 403-424.

Izaguirre I, Sánchez ML, Schiaffino MR, O'Farrel I, Huber P, Ferrer N, … & Mancini M. 2015. Which environmental factors trigger the dominance of phytoplankton species across a moisture gradient of shallow lakes? Hydrobiologia 752: 47-64.

Kalff J. 2003. Limnology: inland water ecosystems. New Jersey: Prentice Hall.

Kasprzak P, Padisák J, Koschela R, Krientiza L & Gervaisa F. 2008. Chlorophyll a concentration across a trophic gradient of lakes: An estimator of phytoplankton biomass? Limnologica 38: 327-338.

Komárek J & Anagnostidis K. 1999. Cyanoprokaryota part I: Chroococcales. Süßwasserflora von Mitteleuropa 19/1. Heidelberg: Spektrum Akademischer Verlag.

Komárek J & Anagnostidis K. 2007. Cyanoprokaryota part 2: Oscillatoriales. Süßwasserflora von Mitteleuropa 19/2. Heidelberg: Spektrum Akademischer Verlag.

Komárek J. 2013. Cyanoprokaryota. 3. Heterocytous genera. Süswasserflora von Mitteleuropa/Freshwater flora of Central Europe. Heidelberg: Springer

Spektrum Berlin.

Lampert W. 1987. Laboratory studies on zooplankton-cyanobacteria interactions. New Zealand Journal of Marine and Freshwater Research 21 (3): 483-490.

Lampert W & Sommer U. 2007. Limnoecology. 2nd Edition. New York: Oxford University Press.

Marcarelli AM, Wurtsbaugh WA & Griset O. 2006. Salinity controls phytoplankton response to nutrient enrichment in the Great Salt Lake, Utah, USA. Canadian Journal of Fisheries and Aquatic Sciences. 63: 2236-2248.

Morello J, Matteucci S, Rodríguez A & Silva M. 2012. Ecorregiones y complejos ecosistémicos argentinos. Buenos Aires: Orientación Gráfica Editores.

Moustaka-Gouni M, Michaloudi E & Sommer U. 2014. Modifying the PEG model for Mediterranean lakes - no biological winter and strong fish predation. Freshwater Biology 59: 1136-1144.

Peters RH & Downing JA. 1984. Empirical analysis of zooplankton filtering and feeding rates. Limnology and Oceanography 29 (4): 763-784.

Prescott GW. 1951. Algae of the Western Great Lakes Area: Exclusive of desmids and diatoms. Bulletin 31. Bloomfield Hills MI, USA: Cranbrook Institute of Science.

Quirós R & Drago E. 1999. The environmental state of Argentinean lakes: an overview. Lakes & reservoirs: Research and Management 4: 55-64.

Quirós R, Rennella AM, Boveri MV, Rosso JJ & Sosnovsky A. 2002. Factores que afectan la estructura y funcionamiento de las lagunas pampeanas. Ecología Austral 12: 175-185.

Sommer U, Gliwicz ZM, Lampert W & Duncan A. 1986. The PEG-model of seasonal sucesión of planktonic events in fresh waters. Archiv für Hydrobiologie 106: 433-471.

Taylor AH, Geider JR & Gilbert FJH. 1997. Seasonal and latitudinal dependencies of phytoplankton carbon-to-chlorophyll a ratios: results of a modelling study. Marine Ecology Progress Series 152: 51-66.

Torremorell A, Bustingorry J, Escaray R, & Zagarese HE. 2007. Seasonal dynamics of a large, shallow lake, laguna Chascomús: the role of light limitation and other physical variables. Limnologica 37: 100-108.

Torremorell A, Llames ME, Pérez GL, Escaray R, Bustingorry J & Zagarese H. 2009. Annual patterns of phytoplankton density and primary production in a large, shallow lake: the central role of light. Freshwater Biology 54: 437-449.

Viglizzo EF. 2011. El agro, el clima y el agua en La Pampa semiárida: revisando paradigmas. Tomo LXIV. Jornada "Condiciones para el Desarrollo de Producciones Agrícola-Ganaderas en el S.O. Bonaerense". Bahía Blanca, Argentina: Academia Nacional de Agronomía y Veterinaria, pp 251-267.

Vignatti AM, Cabrera GC, Canosa M & Echaniz SA. 2017. Environmental and zooplankton parameter changes during the drying of a saline shallow temporary lake in central Argentina. Universitas Scientarium 22 (3): 177-200.

Winder M & Cloern JE. 2010. The annual cycles of phytoplankton biomass. Philosophical Transaction of the Royal Society B. 365: 3215-3226.

Yacobi YZ & Zohary T. 2010. Carbon:chlorophyll a ratio, assimilation numbers and turnover times of Lake Kinneret phytoplankton. Hydrobiologia 639: 185-196.