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ECOSYSTEMS

Divergent dynamics of microbial components in two temperate shallow lakes with contrasting steady states in the Southern Hemisphere

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Abstract: Factors that affect abundances of organisms in water bodies are influenced by extrinsic and intrinsic drivers that operate from outside and within a system. A high temporal coherence in the dynamics of abiotic parameters and biological communities among neighboring lakes evidences a strong extrinsic control operating similarly across lakes, and allows for prediction of ecosystems evolution in the context of global change and intensive land use. The Pampa region (Argentina) encompasses many shallow lakes submitted to different degrees of anthropic influence and showing contrasting alternative states. We studied an eutrophic clear and a hypertrophic turbid shallow lake during an annual cycle in order to evaluate whether they responded similarly to extrinsic factors or these were overridden by the effects of the steady state of each lake. Physical and chemical variables were highly coherent between both lakes, but accounted little for the large disparities among abundances and dynamics of microorganisms. While communities from the clear lake responded to a combination of extrinsic and intrinsic factors, the turbid lake showed a state less prone to be affected by climatic effects. We hypothesize that clear lakes would perform better as sentinels of climate change in the Pampa wetland.

Key words: Climate change, microorganisms, multiple stable states, pampean lakes, South America, synchronicity.

INTRODUCTION

One of the central issues of ecology is to determine which factors affect the abundance and distribution of organisms (Carpenter et al. 1987, Cohen et al. 2003) and aquatic ecologists define functional ecology as the way to recognize the main factors that act from individual to ecosystem scales (Weisse et al. 2016). Shallow lakes are ecosystems that sustain a high biological diversity and contribute to global biogeochemical cycles, water supply, food production, among other ecosystem services (Malvárez & Bó 2004, Roland et al. 2012). They are particularly susceptible to disturbances because of their modest depth, which results in them being more responsive to variation in water supply and other natural and anthropic environmental changes (Adrian et al. 2009, Beklioğlu et al. 2016).

The drivers that directly or indirectly affect the abundance and diversity of aquatic organisms can be separated into intrinsic and extrinsic factors (Liebhold et al. 2004). The first ones are site-specific controls, such as the food web interactions, lake morphometry and nutrient source (Kent et al. 2007, Caliman et al. 2010, Weisse et al. 2016). On the other hand, extrinsic factors such as climatic drivers operate on natural systems at a regional scale. As nearby shallow lakes experience the same climatic drivers (Kent et al. 2007), this regional influence is often detected as synchronous changes (*i.e.* temporal coherence) on the dynamics of different parameters, such as water temperature (Caliman et al. 2010), bacterioplankton (Crump & Hobbie 2005) and phytoplankton (Andrus et al. 2013) communities.

The Pampa plain of Argentina comprises a mosaic of shallow lakes which are stabilized in either a turbid phytoplankton-dominated state or a clear macrophyte-dominated state (*sensu* Scheffer et al. 1993); while other Pampa lakes recurrently shift between different regimes (Quirós et al. 2002, Allende et al. 2009). Frequently they are cited as examples of regime shifts or multiple stable states (Andersen et al. 2009, Izaguirre et al. 2012), since natural systems suffer permanent slow changes. The two most common states (clear-vegetated and phytoplankton-turbid) represent different outcomes of the interactions between phytoplankton and submerged plants and differ mainly in the food web structure (Scheffer et al. 1993, Scheffer & van Ness 2007). Many researchers have documented complex interactions between internal and external factors that may lead to a shift between states (Scheffer & van Ness 2007, Scheffer & Jeppesen 2007). In this region, external factors such as drought-wet cycles as well human eutrophication can promote shifts from clear to turbid ones (Quirós et al. 2006, Izaguirre et al. 2012), thus modifying the structure of biological communities such as the main autotrophic communities, zooplankton assemblages and fish populations; as well as the stability of aquatic ecosystems (Scheffer & van Ness 2007, Cano et al. 2008, Meerhoff et al. 2012).

Extrinsic environmental factors, such as solar radiation and temperature, can regulate microbial growth (Muylaert et al. 2002, Weisse et al. 2016) and bring forward distinct seasonal abundance patterns (Auer & Arndt 2001, Crump & Hobbie 2005, Simon et al. 2015). Likewise, seasonal variability affecting phytoplankton can also modify the relative importance of the microbial food web (Segovia et al. 2015). Although the influence of intrinsic and extrinsic factors has been investigated previously, studies dealing with highly eutrophic environments (Sommaruga 1995, Jürgens & Jeppesen 2000, Wieltschnig et al. 2001), as well as analysis of temporal patterns throughout the microbial food web among contrasting systems (Yannarell et al. 2003, Crump & Hobbie 2005) are still scarce. Most studies were focused on bacterial communities in lakes of the Northern Hemisphere (Van der Gucht et al. 2001, Yannarell et al. 2003, Kent et al. 2007). As to the Pampa region of South America, some authors noted that dynamics of lakes is governed by climatic and hydrological conditions (Torremorell et al. 2007, Schiaffino et al. 2019), while other works showed that the alternative state played a major role in structuring bacterial (Llames et al. 2013), picoplankton (Silvoso et al. 2011) and phytoplankton (Allende et al. 2009) communities. Despite the importance of heterotrophic protists in aquatic food webs, they have seldom been considered (Caron et al. 2009, Weisse et al. 2016) and little is known about their structure and dynamics, as well as the relationship with other microbial components, particularly in this region.

From an ecosystem management perspective, it is vital to analyze the temporal variation of the microbial communities in contrasting environments, and to determine whether shallow lakes with different alternative states respond similarly to extrinsic factors or these are overridden by intrinsic ones in regulating microbial communities. We therefore analyzed two warm-temperate eutrophic Pampean shallow lakes classified under contrasting states (Allende et al. 2009, Pérez et al. 2010) during an annual period. As the two lakes are only 35 km apart, we hypothesized that extrinsic factors will affect the physical-chemical parameters similarly; however, due to the differences in the alternative states, that synchronicity will not be reflected in the biological communities. Specifically, the aims of this work were 1) to detect the occurrence of coherent patterns in abiotic variables among both lakes, 2) to evaluate changes in microorganisms abundances and to determine their main regulating factors and 3) to assess to which extent such patterns of variation are synchronous in these two systems and associated with climatic variables.

MATERIALS AND METHODS

Study area

Pampa Region of Argentina is an extensive plain (800.000 km^2) (Diovisalvi et al. 2015) that encompasses one of the largest wetland systems of South America (Quirós et al. 2002, Castro-Berman et al. 2018). The region is characterized by a warm temperate climate (mean annual temperature: 15.3 °C) and by highly variable rainfall patterns leading to dry and wet periods (mean annual rainfall: 935 mm) (Diovisalvi et al. 2015, Pérez et al. 2015). The Pampa Plain hosts many shallow freshwater systems (mean depth: 2 m), which are naturally eutrophic and without permanent stratification due to persistence and strength of winds (Quirós et al. 2002). Moreover, when confronted with other lakes worldwide, Pampean shallow lakes depart from most of them as they stand as extremes of the trophic-state continuum, due mainly to the high nutrient load (Diovislavi et al. 2015, Fermani et al. 2015).

The study was carried out in two shallow lakes of Pampa Plain located in one of the most productive agricultural areas of Argentina (Quirós et al. 2006) (Fig. 1). Both water bodies are located within the Salado River floodplain but exhibit contrasting limnological characteristics. El Triunfo lake (35° 51'S, 57° 52' W) has a small area (1.5 km^2) and is a clear-vegetated lake (Secchi disk mean depth: 100 cm). At the time of study, it was fully covered by abundant submerged (*Ceratophyllum demersum*) and emergent macrophytes (*Schoenoplectus californicus*) (Allende et al. 2009, Silvoso et al. 2011). On the other hand, Chascomús lake (35° 35´ S, 58° 01´ W) is a large (30.1 km^2) turbid water body (Secchi disk mean depth: 8 cm) with a very high phytoplankton biomass (Allende et al. 2009, Torremorell et al. 2009).

Sampling of lakes

Both El Triunfo and Chascomús lakes were sampled every two weeks from April 2008 to May 2009. Subsurface water samples (depth about 10 cm) at the pelagic zone were taken at the same sampling stations each date. Water Temperature (Temp) (mercury thermometer), pH (Orion pH-meter), conductivity (Cond) (Hach conductimeter) and dissolved oxygen concentration (DO) (YSI 5000 meter) were measured *in situ*. Water depth (Z) was measured at a gaging station. Samples were collected in 10 L polypropylene containers and immediately transported to the laboratory for chemical and biological analysis.

Chemical analyses

At the laboratory, alkalinity (Alk) was determined by titration with H_2SO_4 0.1 N according to the Gran method (Wetzel & Likens 2000). For nutrients analysis, samples were filtered through Whatman GF/F filters. Nitrates ($N\text{-}NO_3^-$) were reduced to nitrites ($N\text{-}NO_2^-$) using a cadmium reduction column; then, nitrites were determined by diazotization. Ammonia ($N\text{-}NH_4^+$) was determined by the indophenol blue method

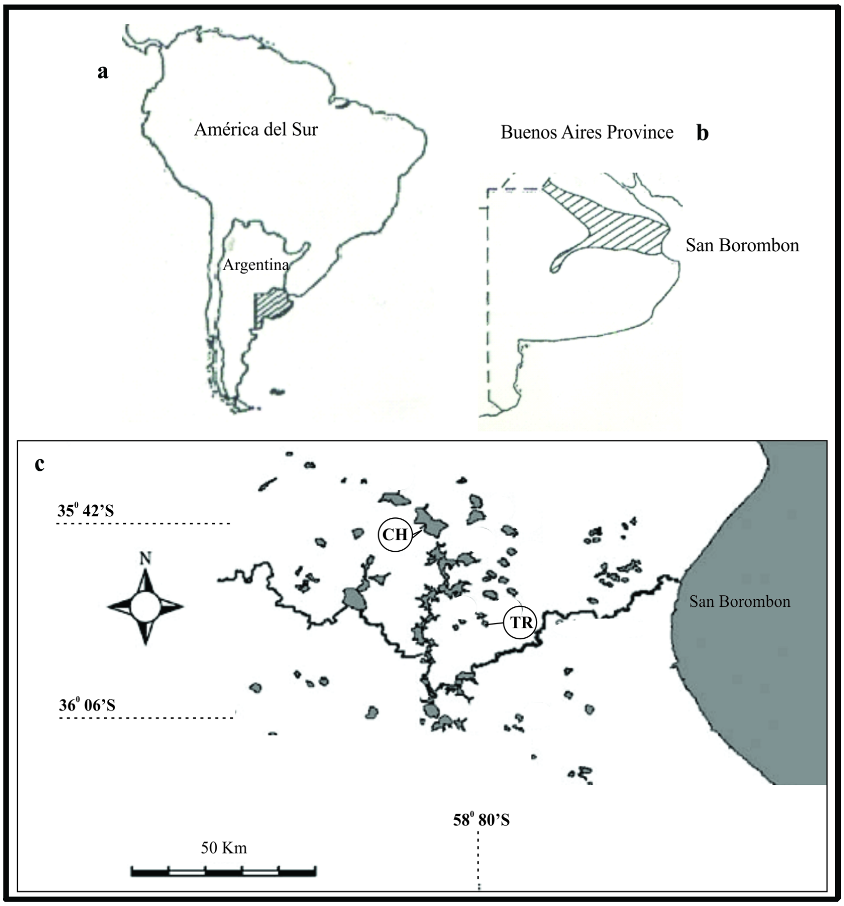

Figure 1. Geographical location of the study sites: (a) South America, Argentina and Buenos Aires Province (representative of Pampa Plain), (b) Buenos Aires Province and Río Salado Basin, (c) Salado River with the two shallow lakes sampling. TR: El Triunfo. CH: Chascomús.

(Perkin Elmer lambda 25 spectrophotometer). Organic nitrogen (Norg) determinations were performed on unfiltered water using the semi-micro-Kjeldahl method. All these analyses were performed following APHA (1998). Total nitrogen (TN) was calculated as the sum of N-NO_3^-, N-NO_2^- and Norg; while dissolved inorganic nutrients (DIN) was defined as the sum of N-NO_3^-, N-NO_2^- and N-NH_4^+.

On the other hand, total phosphorus (TP) was calculated from unfiltered water samples and total dissolved phosphorus (TDP) was determined from GF/F filtered water. Both were converted to soluble reactive phosphorus (SRP) after an acid digestion with potassium persulfate and measured by ascorbic acid method (APHA 1998). Particulate phosphorus (Ppart) was calculated by subtracting TDP from TP (APHA 1998). Chlorophyll *a* concentrations (Chl-*a*) were determined spectrophotometrically (Perkin Elmer lambda 25 spectrophotometer) after filtration of known volumes through GF/F filters and extraction with methanol (24 h) (Lopretto & Tell 1995). Total suspended solid (TSS, also referred as seston) concentrations were determined by weighing the dried residue (60°C) resulting from the filtration of a water sample through precombusted (530°C, 2 h) GF/F filters. The ash content was estimated by reweighing the GF/F filters after combustion at 530°C for 3 h (APHA 1998). The ash-free dry weight (AFDW) was estimated as the difference between TSS and ash content.

Solar radiation, rainfall and optical properties measurements

Incident solar radiation (I_0) was recorded on site every 5 minutes using an IL-1700 radiometer (International Light) equipped with broadband photosynthetic active radiation (PAR: 400-700 nm) to measure incident photosynthetic active irradiance impinging on the water surface (I_0PAR). Mean rainfall for the study area was obtained using a pluviometer located in the "El Espartillar" experimental field near Chascomús City. The vertical diffuse light attenuation coefficient (K_dPAR) was determined using a spectro-radiometer (USB2000, Ocean Optics). Profiles were obtained around 1h from astronomic noon. Nephelometric turbidity (Turb) was measured with a 2100P Hach turbidimeter.

Chromophoric dissolved organic matter (CDOM) was expressed using the absorption coefficient at a reference wavelength 440 nm (Pérez et al. 2013). CDOM was measured from filtered (0.22 µm) water samples in 0.01 m 27 quartz cuvettes and compared against ultrapure water blank using a Lambda 3 (PerkinElmer) spectrophotometer (from 200 to 800 nm, at 1 nm intervals). The absorbance at 440 nm (aCDOM$_{440}$) was used as a proxy of the water colour (Rasmussen et al. 1989).

Picoplankton and heterotrophic flagellates abundances

Quantitative samples for picoplankton (PP) (Heterotrophic Bacteria: HB, Picocyanobacteria: Pcy and Picoeukayotes: Peuk) and heterotrophic flagellates (HF) were preserved in 45 mL Falcon flasks with ice-cold filtered glutaraldehyde (1% final concentration), as in previous studies (Fermani et al. 2015, Huber et al. 2017). Subsamples of each lake were filtered through 0.2 µm (for PP) and 0.8 µm (for HF) black polycarbonate filters (Osmonics Inc.) following the protocols of Porter & Feig (1980). For El Triunfo lake we filtered between 0.5 and 3 mL for counting PP and HF, respectively; whereas samples of Chascomús lake were diluted before filtration (1:30), due to high amounts of particulate matter. For PP and HF quantification, 1.2 mL and 3 mL, respectively, of the dilution (*i.e.* 40 µL and 100 µL of the original lake water sample) were brought to 5 ml with distilled water and stained with 50 µL of DAPI (4´, 6´-diamidino-2-phenylindole, 0.5 mg mL^{-1}). All filters were mounted onto a microscope slide with immersion oil for fluorescence (Immersol 518F) and stored at -20°C. Samples were observed using a Nikon Eclipse 600 microscope equipped with a HBO 50W lamp, and a filter set for blue, green and UV light excitation. Single-cell HB and filamentous bacteria (FB) were counted under UV light excitation. Pcy and Peuk (Picophytoplankton: PPP) were enumerated under blue and green light excitation (Callieri & Pinolini 1995). In some cases, we observed between 4 and 40 Pcy cells loosely attached within inconspicuous mucilage that we called Pcy aggregates (Pcy-ag). On the other hand, HF were counted under blue and UV light excitation and sorted into four size categories: <2 µm, 2-5 µm, 5-10 µm and >10 µm. For PP enumeration a minimum of 40 fields were inspected a 1000x magnification (corresponding to at least 400 cells of HB and 200 of Pcy); while at least 100 fields were inspected for Peuk (corresponding to 20 cells). For HF, at least 200 fields were inspected and 50 cells were counted.

Ciliate abundances

Ciliates are usually counted using the Utermöhl method (Jürgens & Jeppessen 2000, Küppers & Claps 2012), however the high density of particulate matter rendered this procedure unfeasible. Therefore, quantitative samples for ciliate counting were collected in PVC flasks and preserved with 1 % acid Lugol's iodine solution. Then, subsamples were bleached with a few drops of thiosulphate and fixed with 2 % formalin according to Macek et al. (2008). Next, either 1 or 5 mL for Chascomús and El Triunfo, respectively, were stained with 50 µL of DAPI (0.5 mg mL^{-1}) and gently filtered through a 2 µm pore-size black polycarbonate filter (Sherr & Sherr 1993). Filters were mounted onto microscope slides with immersion oil for fluorescence and stored at -20°C until counting. As small bacterivorous ciliates prevail in eutrophic systems (Beaver & Crisman 1989), the probability of finding large ciliates is low; in any case, before counting cells, we inspected the entire field with a lower magnification of the microscope looking for large organisms. Then, ciliates were enumerated by epifluorescence microscopy at 1000x magnification under blue and UV light excitation and also sorted into three size categories: <10 µm, 10-20 µm and > 20 µm. A minimum of 400 fields and 25 cells were counted.

Data analysis

As the distributions of most variables were non-normal we performed nonparametric Mann-Whitney tests to compare both abiotic and biotic parameters between lakes, and we used Spearman rank correlations to evaluate possible relationships among them both within and between lakes. We used the statistical software Sigmaplot 12.0 (Systat inc.).

In order to detect seasonal differences in the microbial community structure we grouped the samples of each lake by season (Autumn: April, May, June; Winter: July, August, September; Spring: October, November, December; Summer: January, February, March) and we performed the analysis of similarities (ANOSIM) test (Clarke 1993), based on Bray Curtis dissimilarities, with Bonferroni method for a *posteriori* contrasts, using PAST 2.0 program (Hammer et al. 2001). ANOSIM is a nonparametric test of significant difference between two or more groups and generates a test statistic, R. The magnitude of R indicates the degree of separation between groups, with a score of 1 indicating complete separation and 0 indicating no separation. Moreover, to test synchronicity between the microbial communities of both lakes we first calculated matrices of dissimilarity on the Bray-Curtis dissimilarity index through XLSTAT program for each community (HB, Pcy, Peuk, HF and ciliates), in order to estimate the degree of similarity (1-dissimilarity) among different communities. Then, to test coherence in temporal changes for each component between lakes, we correlated the microbial component similarity matrices (Bray–Curtis) using the Mantel non-parametric statistical test. This method compares the two matrices based on Spearman's rank correlation rho, with 999 permutations (Mantel 1967).

To detect the main factors driving microorganisms abundances we performed a variation partitioning to evaluate the possible segregation of intrinsic and extrinsic factors that could explain the community structure in each lake followed by a redundancy analysis (RDA). For this, we generated a minimal set of significantly explanatory variables for each community of each lake (PPP, HF and ciliates), excluding those that were highly correlated and with inflation factor > 20. Automatic forward selection was used to determine the most important variables. The extrinsic factors that significantly explained the model were IoPAR and rainfall for all communities; while a set of different intrinsic parameters were selected, depending on community and lake. For PP in Chascomús these were Temp, pH, Cond, DO, Chl-*a*, TN and SRP. For PP in El Triunfo the intrinsic variables used were Temp, pH, Alk, Chl-*a* and SRP. The intrinsic factors for HF in Chascomús were Chl-*a*, Cond and SRP; while in El Triunfo were Temp, pH, Alk, Chl-*a* and SRP. Finally, the intrinsic variables used for explained the ciliates abundances in Chascomús were Alk and OM; and in El Triunfo, Alk, TSS and TP. Prior to the analyses, both environmental and microbial matrices were transformed. Variables of the environmental matrix were transformed to their standardized equivalents [(x-mean)/SD] to fix the different units of the different variables (Legendre & Birks 2012). The microbial matrices were transformed using a Napierian transformation [$y' = \ln (y + 1)$] in order to reduce the weight of the most abundant organisms in each sample, improve homoscedasticity and allow the use of linear ordination methods (ter Braak 1987). The preliminary detrended correspondence analyses (DCA) revealed a short gradient length (< 2 units long), thereby we performed a redundancy analysis (RDA), a linear response model, for subsequent ordination analyses (ter Braak 1987). Calculations were performed using the software CANOCO 5 (ter Braak 1986) and the statistical significance of the first axis and of all axes were tested by a Monte Carlo permutation test with 999 permutations. A probability level of $p < 0.05$ was considered significant in all analyses.

RESULTS

In general, nutrients and Chl-*a* concentrations were very high and the turbid lake displayed much higher values than the clear one (Mann-Whitney U, $n = 29$, $p < 0.01$) (Tables I and II).

In particular, Turb, TSS, AFDW, TP, K_dPAR and Chl-*a* concentrations were between one and two orders of magnitude higher in Chascomús lake. Also, dissolved inorganic nutrients (DIN and SRP) were significantly higher in this lake (Mann-Whitney U, $n = 29$ $p < 0.01$). In addition, in Chascomús, only 37.7 % of TSS corresponded to suspended organic matter; whereas in El Triunfo this share was more than double (89.8 %). Most abiotic parameters were significantly correlated with each other in both water bodies (Figs. 2a, b).

Both lakes evidenced temporal coherence in their physical-chemical parameters dynamics

In the region, the average annual accumulated rainfall during the last three previous years was 978 mm; and, in the course of this study that level fell to 536 mm, with large seasonal fluctuation (Fig. 3).

Mean daily solar radiation (I_0PAR) varied seasonally between 14.2 W m^{-2} and 164.5 W m^{-2}. Accordingly, water temperature in both lakes followed the same trend of incident irradiance (Fig. 4a). Several environmental parameters (Alk, Cond, water depth, Turb, TSS, TP, TN and KdPAR) evidenced synchronicity between lakes (Table III, Fig. 4), and some as Alk, Turb, TN and TP increased notably from the middle of spring onwards, which concurred with a regional drought (Figs. 4b-e). Precipitations remained low until the end of the study, when El Triunfo lake dried out as reflected in water depth (Fig. 4f) and affected both Alk and Cond in the two lakes, also enhancing turbidity and related variables.

Microbial communities from the two lakes did not evidence temporal coherence in their dynamics

Both lakes showed high microorganisms abundances, with communities from Chascomús exhibiting values one to three orders of magnitude higher than those from El Triunfo (Mann-Whitney U, $n = 29$, $p < 0.001$) (Table II, Fig. 5).

In El Triunfo lake, HB abundance averaged 5.3×10^6 cells mL^{-1} and showed high positive correlations with extrinsic I_0PAR, as well as intrinsic water temperature and precipitation-dependent water depth, followed by AFDW (Fig. 2a) . Moreover, HB numbers were positively

Table I. Chemical and physical parameters of El Triunfo and Chascomús lakes during the sampling period.

Lakes	El Triunfo			Chascomús		
	AVG ± SD	**Max**	**Min**	**AVG ± SD**	**Max**	**Min**
Temp (°C)	15.5 ± 5.7	24.0	5.5	15.7 ± 5.4	24.0	6.0
pH	9.2 ± 0.4	9.9	8.4	9.2 ± 0.1	9.5	8.9
Cond (mS cm^{-1})***	1.8 ± 0.3	2.7	1.4	2.7 ± 0.5	3.7	2.2
Alk (mEq L^{-1})***	9.08 ± 2.9	14.4	6.2	11.22 ± 3.2	16.6	7.9
DO (mg L^{-1})	8.8 ± 2.7	12.8	4.0	9.2 ± 1.5	11.8	6.0
Turb (NTU)***	3.2 ± 2.3	9.4	0.8	221.1 ± 133.4	529.0	62.4
K_d PAR (m^{-1})***	4.5 ± 2.3	8.4	2.1	19.8 ± 7.1	33.8	10.1
aCDOM$_{440}$ **	5.2 ± 1.0	7.2	2.7	3.6 ± 1.4	7.3	2.2
N-NO$_3^-$ (µg L^{-1})	9.2 ± 8.4	26.3	1.0ɣ	9.9 ± 12.9	45.4	1.0ɣ
N-NO$_2^-$ (µg L^{-1})	2.5 ± 2.1	8.1	1.0ɣ	3.1 ± 1.9	9.3	1.0ɣ
N-NH$_4^+$ (µg L^{-1})**	3.3 ± 5.0	23.3	2.0ɣ	8.2 ± 7.2	28.0	2.0ɣ
TN (mg L^{-1})***	0.6 ± 0.4	2.0	0.2	4.1 ± 3.3	18.8	1.3
TP (µg L^{-1})***	89.5 ± 55.6	220.3	6.1	811.6 ± 257.0	1251.2	378.4
SRP (µg L^{-1})***	4.3 ± 8.1	42.9	2.0ɣ	14.7 ± 9.1	41.4	4.5
Ppart (µg L^{-1})***	39 ± 33.5	144.0	2.1	700.6 ± 232.4	1147.0	366.3
AFDW (mg L^{-1})***	4.4 ± 3.6	15.5	0.4	96.1 ± 40.9	193.4	46.0
TSS (mg L^{-1})***	4.9 ± 4.1	16.6	0.4	254.7 ± 142.5	591.7	87.0
% AFDW/TSS***	89.8 ± 8.2	100.0	70.6	37.7 ± 7.6	54.4	30.5
Z (m)***	0.75 ± 0.30	1.15	0.20	1.60 ± 0.30	1.95	1.07

(AVG: average values. SD: standard deviation. Max: maximum. Min: minimum. Temp: water temperature. Cond: conductivity. Alk: alkalinity. DO: dissolved oxygen. Turb: turbidity. K_d PAR: attenuation coefficient of photosynthetic active radiation. aCDOM$_{440}$: absorbance of chromophoric dissolved organic matter. TN: total nitrogen. TP: total phosphorous. SRP: soluble reactive phosphorus. Ppart: particulate total phosphorous. TSS: total suspended solid. AFDW: ash-free dry weight). ɣ: detection limit. Statistically significant differences between lakes (Mann-Whitney test): ** $p < 0.01$, *** $p < 0.001$).

correlated with Chl-*a* and Peuk abundance ($r = 0.69$ and 0.60 respectively, $p < 0.001$). Pcy abundance was two orders of magnitude lower than that of HB (mean 7×10^4 cells mL^{-1}) (Table II) and correlated positively with Turb ($r = 0.70$, $p < 0.001$), AFDW ($r = 0.65$, $p < 0.001$) and TSS ($r = 0.64$, $p < 0.001$). In turn, Peuk abundance was even lower and only had a significant positive correlation with Z ($r = 0.82$, $p < 0.001$). Abundance of HF 5-10 µm was positively associated with Turb ($r = 0.73$, $p < 0.001$) and that of ciliates 10-20 µm with I_0PAR ($r = 0.75$, $p < 0.001$). Interestingly, both communities were also positively correlated with Pcy ($r = 0.64$ and 0.68 respectively, $p < 0.001$).

In Chascomús, HB abundance also were positively correlated with I_0PAR and water temperature, but equally responded strongly to a set of turbidity-related intrinsic variables

Table II. Biological parameters of El Triunfo and Chascomús lakes measured during sampling period.

Lakes	El Triunfo			Chascomús		
	AVG ± SD	**Max**	**Min**	**AVG ± SD**	**Max**	**Min**
HB (cells mL^{-1})***	5.3x10^{6} ± 2.6x10^{6}	1.0x10^{7}	1.5x10^{6}	7.1x10^{7} ± 2.3x10^{7}	1.1x10^{8}	2.4x10^{7}
Pcy (cells mL^{-1})***	7.0x10^{4} ± 3.7x10^{3}	1.9x10^{5}	1.5x10^{4}	1.7x10^{7} ± 3.6x10^{5}	2.5x10^{7}	9.8x10^{6}
Peuk (cells mL^{-1})***	3.3x10^{3} ± 1.6x10^{3}	8.8x10^{3}	7.3x10^{2}	2.5x10^{5} ± 1.6x10^{5}	6.6x10^{5}	2.7x10^{4}
FB (fil mL^{-1})***	1.7x10^{4} ± 1.6x10^{4}	5.4x10^{4}	1.4x10^{3}	5.6x10^{6} ± 3.1x10^{5}	1.2x10^{6}	1.2x10^{5}
Pcy-ag (col mL^{-1})***	0.0	0.0	0.0	4.9x10^{5} ± 2.7x10^{5}	1.1x10^{6}	9.6x10^{4}
Chl-***a*** (µg L^{-1})***	15.9 ± 14.4	57.5	3.6	415.1 ± 190.8	589.7	96.1
Total HF (cells mL^{-1})***	2.1x10^{3} ± 1.2x10^{3}	5.3x10^{3}	3.9x10^{2}	3.3x10^{4} ± 1.8x10^{4}	9.2x10^{4}	9.4x10^{3}
HF < 2 µm (cells mL^{-1})***	2.9x10^{2} ± 2.6x10^{2}	1.0x10^{3}	0.0	2.1x10^{3} ± 2.0x10^{3}	8.8x10^{3}	0.0
HF 2-5 µm (cells mL^{-1})***	1.8x10^{3} ± 1.2x10^{3}	4.9x10^{3}	2.2x10^{2}	2.2x10^{4} ± 1.2x10^{4}	6.0x10^{4}	5.2x10^{3}
HF 5-10 µm (cells mL^{-1})***	3.3x10^{2} ± 2.4x10^{2}	9.2x10^{2}	0.0	7.9x10^{3} ± 4.8x10^{3}	2.3x10^{4}	7.4x10^{2}
HF > 10 µm (cells mL^{-1})**	2.3x10^{1} ± 4.4x10^{1}	1.8x10^{2}	0.0	957.2 ± 1.4x10^{3}	6.6x10^{3}	0.0
Total Cil (cells mL^{-1})***	27.8 ± 30.8	116.7	2.3	401.3 ± 275.4	1207.2	0.0
Cil < 10 µm (cells mL^{-1})***	1.3 ± 2.7	9.3	0.0	107.2 ± 96.3	426.1	0.0
Cil 10-20 µm (cells mL^{-1})***	7.8 ± 10.2	46.7	0.0	200.4 ± 154.9	523.1	0.0
Cil > 20 µm (cells mL^{-1})**	18.7 ± 23.4	102.7	2.3	93.7 ± 109.2	497.1	0.0

(AVG: average values. SD: standard deviation. Max: maximum. Min: minimum. HB: heterotrophic bacteria. Pcy: picocyanobacteria. Peuk: picoeukaryotes. FB: filamentous bacteria. Pcy-ag: Picocyanobacteria aggregates. Chl-*a*: chlorophyll *a*. HF: heterotrophic flagellates. Cil: ciliates). Statistically significant differences between lakes (Mann-Whitney test): ** *p* < 0.01, * *p* < 0.001).**

(Turb, K$_{d}$PAR, AFDW, TSS) (Fig. 2b). Furthermore, like in El Triunfo, it was positively correlated with Chl-*a* and Peuk with even higher *r* values (*r* = 0.85 and 0.77 respectively, *p* < 0.001). In turn, Pcy abundances were as high as HB (mean 1.7x10^{7} and 7.1x10^{7} cells mL^{-1}, respectively). Also large densities of bacterial filaments (BF) and Pcy aggregates (Pcy-ag) were found, mainly during the warm period (Table II). Despite their high abundances, Pcy were not significantly correlated to any studied parameter (Fig. 2b). On the contrary, Peuk densities were highly positively correlated with HB and Chl-*a* and hence with Temp, Turb and K$_{d}$PAR, but also with extrinsic I$_{0}$PAR.

Regarding heterotrophic microorganisms, abundances of both HF and ciliates were one order of magnitude higher in turbid Chascomús

a) El Triunfo	Chemical-Physical parameters											Biological parameters								
	Temp	Cond	N-NO$_2^-$	TP	TSS	AFDW	$_a$CDOM$_{440}$	Alk	Z	K$_d$ PAR	I$_0$ PAR	HB	Pcy	Peuk	Chl-*a*	HF 2-5	HF 5-10	t HF	Cil 10-20	t Cil
Turb	0.69 ***	0.67 ***	0.64 *	0.72 ***	0.78 ***	0.79 ***		0.70 ***			0.75 ***		0.70 ***		0.75 ***		0.73 ***		0.60 ***	
Temp					0.81 ***	0.81 ***		0.68 ***	0.81 *		0.74 ***	0.74 ***			0.79 ***					
Cond			0.79 ***	0.67 ***				0.78 ***	-0.64 *	0.69 *										0.60 ***
N-NO$_2^-$							0.78 ***				0.67 **						0.71 ***			
TP					0.66 ***	0.66 ***		0.73 ***							0.64 ***		0.60 ***			0.61 ***
TSS						0.99 ***		0.69 ***		0.75 ***	0.78 ***		0.64 ***							
AFDW								0.69 ***		0.67 **	0.79 ***	0.62 ***	0.65 ***						0.61 ***	
$_a$CDOM$_{440}$																				
Alk									-0.99 ***	0.65 *					0.60 **					
Z											0.86 ***	0.71 ***		0.82 ***		0.63 *		0.60 *		
K$_d$ PAR																				
I$_0$ PAR												0.70 ***			0.79 ***				0.75 ***	
HB														0.60 ***	0.69 ***					
Pcy															0.62 ***		0.64 ***		0.68 ***	
Peuk																				
Chl-*a*																				
HF 2-5																				
HF 5-10																				
t HF																				
Cil 10-20																				
t Cil																				

b) Chascomús	Chemical-Physical parameters															Biological parameters				
	DO	Temp	Cond	N-NO$_3^-$	N-NO$_2^-$	TN	SRP	TP	TSS	AFDW	$_a$CDOM$_{440}$	Alk	Z	K$_d$ PAR	I$_0$ PAR	HB	Peuk	Chl-*a*	HF > 10	Cil 10-20
Turb			0.66 ***					0.94 ***	0.96 ***	0.92 ***		0.75 ***	-0.70 ***	0.96 ***	0.83 ***	0.76 ***	0.60 ***	0.95 ***		
DO		-0.63 ***									-0.61 **									
Temp						0.60 **									0.73 ***	0.62 ***	0.60 **			
Cond								0.65 ***		0.61 ***	0.66 ***	0.77 ***		0.69 ***	0.73 ***	0.64 ***	0.60 ***	0.69 ***		
N-NO$_3^-$										0.60 **	0.64 ***							0.70 ***		-0.60 **
N-NO$_2^-$									0.60 **											
TN													-0.60 ***		0.60 **					
SRP									0.61 ***		0.78 ***									
TP									0.83 **	0.82 ***		0.74 ***	-0.73 ***	0.84 ***	0.81 ***	0.61 ***		0.85 ***		
TSS										0.97 ***		0.70 ***	-0.70 ***	0.93 ***	0.68 **	0.70 ***		0.92 ***		
AFDW												0.73 ***	-0.74 ***	0.94 ***	0.68 ***	0.71 ***		0.94 ***		
$_a$CDOM$_{440}$												0.72 ***	-0.70 ***				0.63 ***		0.60 *	
Alk													-0.94 ***	0.78 ***	0.60 **	0.68 ***		0.79 ***		
Z														-0.75 ***	-0.62 ***	-0.70 ***				
K$_d$ PAR															0.79 ***	0.76 ***	0.61 ***	0.93 ***		
I$_0$ PAR																0.71 ***	0.64 **	0.79 ***		
HB																	0.77 ***	0.85 ***		
Peuk																		0.62 ***		
Chl-*a*																				
HF > 10																				
Cil 10-20																				

Figure 2. Main Spearman rank correlations ($r > 0.60$) in: (a) clear El Triunfo lake and (b) turbid Chascomús lake (Turb: turbidity, DO: dissolved oxygen, Temp: water temperature, Cond: conductivity, N_NO$_3^-$: nitrate, N_NO$_2^-$: nitrite, TN: total nitrogen, TP: total phosphorus, TSS: total suspended solid, AFDW: ash free dry weigh, $_a$CDOM$_{440}$: absorbance of chromophoric dissolved organic matter at 440 nm, Alk: alkalinity, Z: water depth, Kd: light attenuation coefficient, PAR: photosynthetically active radiation, I$_0$: incident irradiance, HB: heterotrophic bacteria, Pcy: picocyanobacteria, Peuk: picoeukaryotes, Chl-*a*: chlorophyll-a, HF: heterotrophic flagellates (2-5 µm, 5-10 µm, > 10 µm), t HF: total HF, Cil: ciliates (10-20 µm), t Cil: total Cil. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

lake (Table II, Figs. 5d, e), though no correlation between water bodies was observed. Surprisingly, neither their total abundances nor their different size fractions correlated with any other microbial community analyzed in this turbid lake; while in clear El Triunfo, heterotrophic protist abundances correlated positively and significantly with some parameters relating light climate. In particular, HF 5-10 µm was positively associated with Turb ($r = 0.73$, $p < 0.001$) and ciliates 10-20 µm with incident radiation ($r = 0.75$, $p < 0.001$).

Among all microbial components analyzed here, only the abundances of HB correlated positively between both lakes ($r = 0.50$, $p < 0.01$) (Fig. 5a), as the corresponding Mantel test revealed a weak but significant positive value ($r = 0.12$, $p = 0.022$). On the other hand, Mantel test of Pcy showed a negative correlation ($r = -0.13$, $p < 0.001$), suggesting that these communities are the most dissimilar among lakes. In turn, Peuk, HF and ciliates did not show any significant correlation, suggesting that they behave independently (Peuk: $r = 0.005$, $p = 0.92$; HF: $r = 0.12$, $p = 0.96$; Ciliates: $r = 0.08$, p

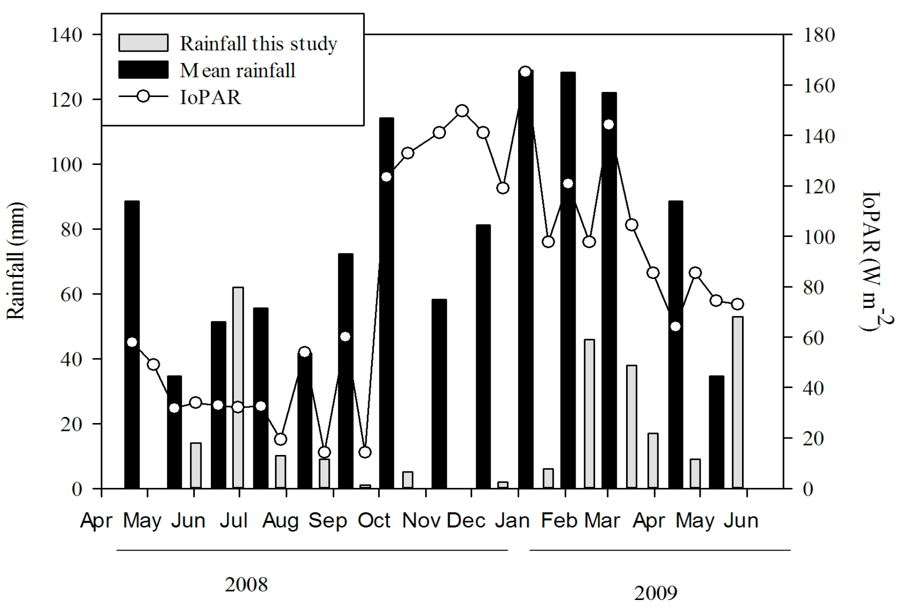

Figure 3. **Mean monthly rainfall (mm) accumulated between 2005 to 2007 and temporal rainfall together to incident photosynthetic active irradiance (I_0PAR: W m^{-2}) measured during sampling period.**

= 0.19). The analysis of similarities (ANOSIM) in the structure of microbial communities over time revealed significant temporal changes for PP, HF and ciliates in the clear lake; whereas in the turbid one, only the picoplankton structure varied among seasons, with very high initial Pcy abundances decreasing significantly over the period Autumn 08 - Summer 09 (Table IV, Fig. 6), thus showing asynchronous behaviors among both lakes.

The Figs. 7a, b displays the results of the variation partitioning performed to evaluate the segregation of intrinsic and extrinsic factors that explain the structure of each community in each lake. As many abiotic factors were excluded from the analysis due to high correlations or inflation factor > 20, only a small set significantly explained variation. In all cases, the extrinsic factors selected by the model were I_0PAR and rainfall; while different sets of intrinsic factors were selected for each microbial community.

In general, all communities of turbid lake were mostly regulated by intrinsic factors. On the other hand, in the clear lake, pure extrinsic factors mostly explained the picoplanktonic distribution; whereas a combination of both factors account for HF and ciliates abundances. The RDAs plots for each lake showing that both the first axis and the sum of all canonical axes were significant ($p < 0.05$) for all microbial communities. For El Triunfo, 35.4 %, 28.3 % and 30.7 % (for PP, HF and ciliates; respectively) of the total adjusted variation was explained by the model (Fig. 7a). Picoplanktonic communities were mostly related to extrinsic I_0PAR and rainfall (15.7 %). The RDA shows that the first axis was negatively correlated mainly with I_0PAR (r = -0.64), Temp (r = -0.52) and Chl-*a* (r = -0.49); while the second axis was positively associated to Alk (r = 0.42). Thereby, samples of PP distributed on the left side of the diagram indicate abundant HB during warm seasons. Abundances of heterotrophic flagellates in El Triunfo were strongly explained strongly by intrinsic factors (25.5 %), with the first axis in the RDA positively associated to Alk (r = 0.57), therefore concentrating samples from last autumn, characterized by a high proportion of the 5-10 μm fraction on the lower right quadrant. Second axis, in turn, was negatively correlated with SRP (r = -0.37). Ciliates of this clear lake also showed a community mostly regulated by

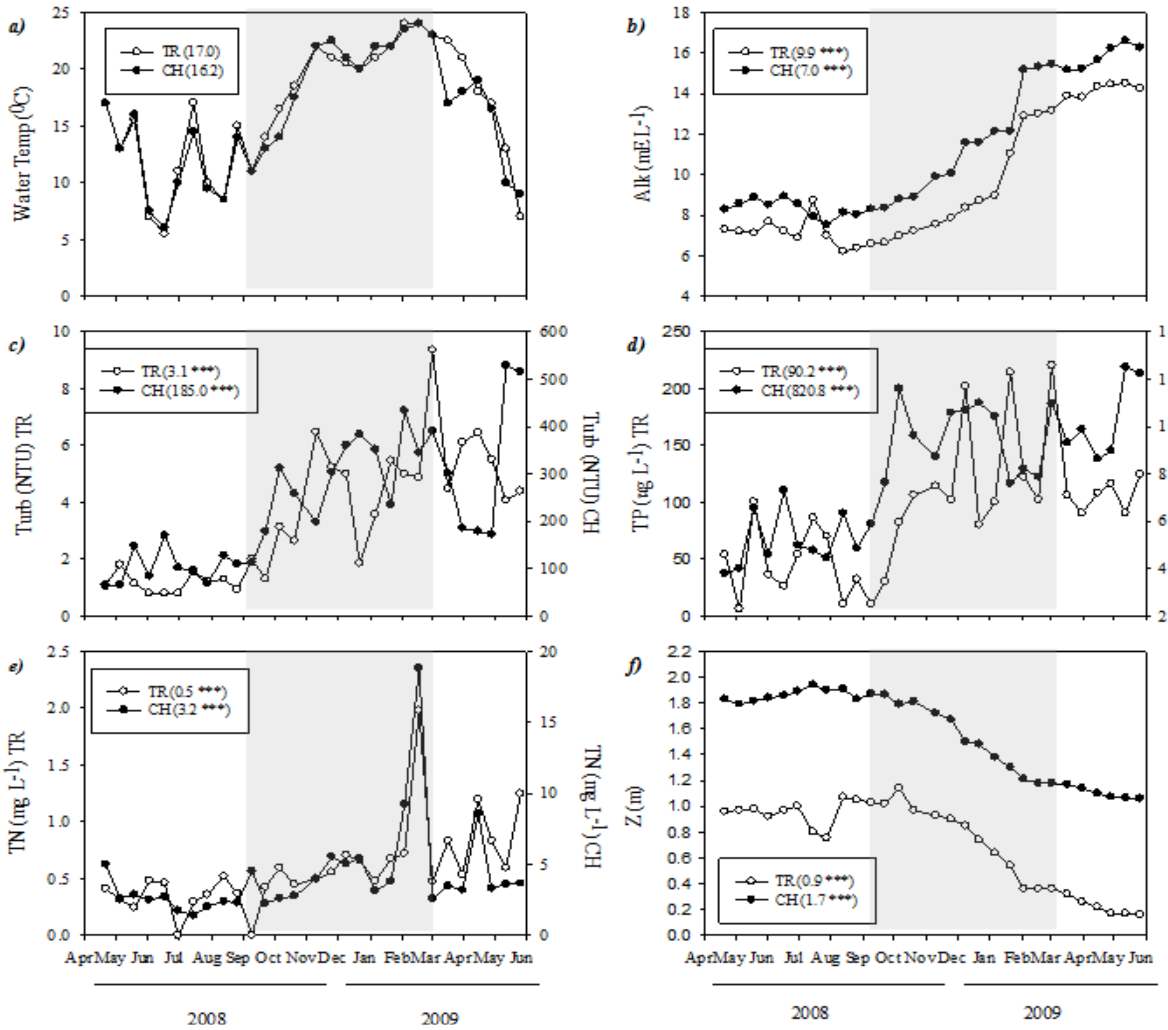

Figure 4. Temporal variation in chemical and physical parameters measured in the two lakes during sampling period: (a) Water Temperature (Temp: °C), (b) Alkalinity (Alk: mEq L^{-1}), (c) Turbidity (NTU), *(d)* Total Phosphorous (TP: µg L^{-1}), (e) Total Nitrogen (TN: mg L^{-1}), (f) Water depth (Z: m). TR: El Triunfo. CH: Chascomús. Numbers in parentheses after variable and site name in legends indicate the median value for each site and * indicate significantly different median after Mann Whitney test (*p* < 0.001). Grey areas correspond to warm (Spring and Summer) seasons.**

intrinsic factors (16.3 %), as the first axis of the RDA was correlated positively with TP (*r* = 0.65), TSS (*r* = 0.42) and Alk (*r* = 0.38), and the second axis was mainly associated with I_0PAR (*r* = 0.40). As a consequence, the abundance of small and mid-sized ciliates was mostly associated with warmer conditions, as shown in Fig. 6. As a result of the three RDA plots, we observed that as the warm season proceeded, I_0PAR increased and both HB and Peuk were associated with this parameter. TP and TSS showed higher values in Summer and Pcy, smaller ciliates and to a lesser extent large HF were associated to these conditions. Notably, abiotic conditions in Autumn 09 were very different from those of the previous year, and this fact was clearly reflected by the different communities.

On the other hand, in Chascomús lake, between 67.4 %, 23.2 % and 14.4 % (for PP, HF and ciliates; respectively) of the total adjusted

Table III. Summary of Spearman rank correlation analysis to examine coherence between different parameters between lakes.

Parameters	*r*	*p*
Temp	0.98	< 0.0001
Alk	0.92	< 0.0001
Cond	0.79	< 0.0001
Z	0.78	< 0.0001
Turb	0.64	< 0.0001
TSS	0.62	< 0.0001
TN	0.68	< 0.001
K_dPAR	0.62	< 0.05

We show only significant correlations ($p < 0.05$) with $r > 0.60$ (Temp: water temperature; Alk: alkalinity; Cond: conductivity; Z: water depth; Turb: turbidity; TSS: total suspended solid; K_d PAR: attenuation coefficient of photosynthetic active radiation).

variation was explained by the model (Fig. 7b). All communities respond mainly to intrinsic factors. The RDA for PP shows that axis 1 was negatively correlated with Chl-*a* (r = -0.67), SRP (r = -0.65), I_0PAR (r = -0.61) and Temp (r = -0.60), while axis 2 was positively correlated mainly with rainfall (r = 0.54). The strong response of HB and Peuk to the high nutrient and light availability during the warmer season accounts for the highest explanatory power of the model. In the RDA plot for HF shows axis 1 correlated positively with SRP (r = 0.57) and Chl-*a* (r = 0.41), and the second one was mainly associated with rainfall (r = 0.41). Finally, axis 1 in the RDA plot for ciliates was positively correlated with Alk (r = 0.30) and the second axis with I_0PAR (r = 0.37). Yet, the abundances of the different size fractions of both HF and ciliates do not follow a clear pattern in relation with these variables, as shown by the low explanatory power of the model for these communities.

DISCUSSION

Factors affecting organisms abundances are diverse and their dynamics are influenced by different drivers that operate from outside and within a system (Cohen et al. 2003, Kent et al. 2007). A high degree of temporal coherence evidences some external control operating similarly across lakes; thereby, it is suited for prediction of ecosystems evolution and regionally applied management schemes in the context of global changes and intensive land uses (Adrian et al. 2009, Roland et al. 2012). Inversely, lack of synchrony suggests internal controls that are lake-specific and less docile to prediction and management (Knowlton & Jones 2007, Kent et al. 2007, Caliman et al. 2010). This study evidenced that physical and chemical variables were more coherent between both shallow lakes than biological ones, and hence do not suffice to explain the abundances and distribution of microorganisms. Instead, microbial communities seem to be mainly affected by local effects, with the steady state playing a major role in structuring their composition and dynamics.

Temporal coherence in the dynamics of physical-chemical parameters of the lakes

In general, nutrients and Chl-*a* concentrations were within the characteristic values for eutrophic (El Triunfo: TP mean = 230 μgL^{-1}, Chl-*a* mean = 2.7 μgL^{-1}) and hypertrophic (Chascomús: TP mean = 630 μgL^{-1}, Chl-*a* mean = 130 μgL^{-1}) systems of Pampa Plain (Allende et al 2009, Silvoso et al. 2011). The contrasting steady states of these lakes are clearly reflected in their physical and chemical features (Allende et al. 2009, Pérez et al. 2010). While high Alk and pH

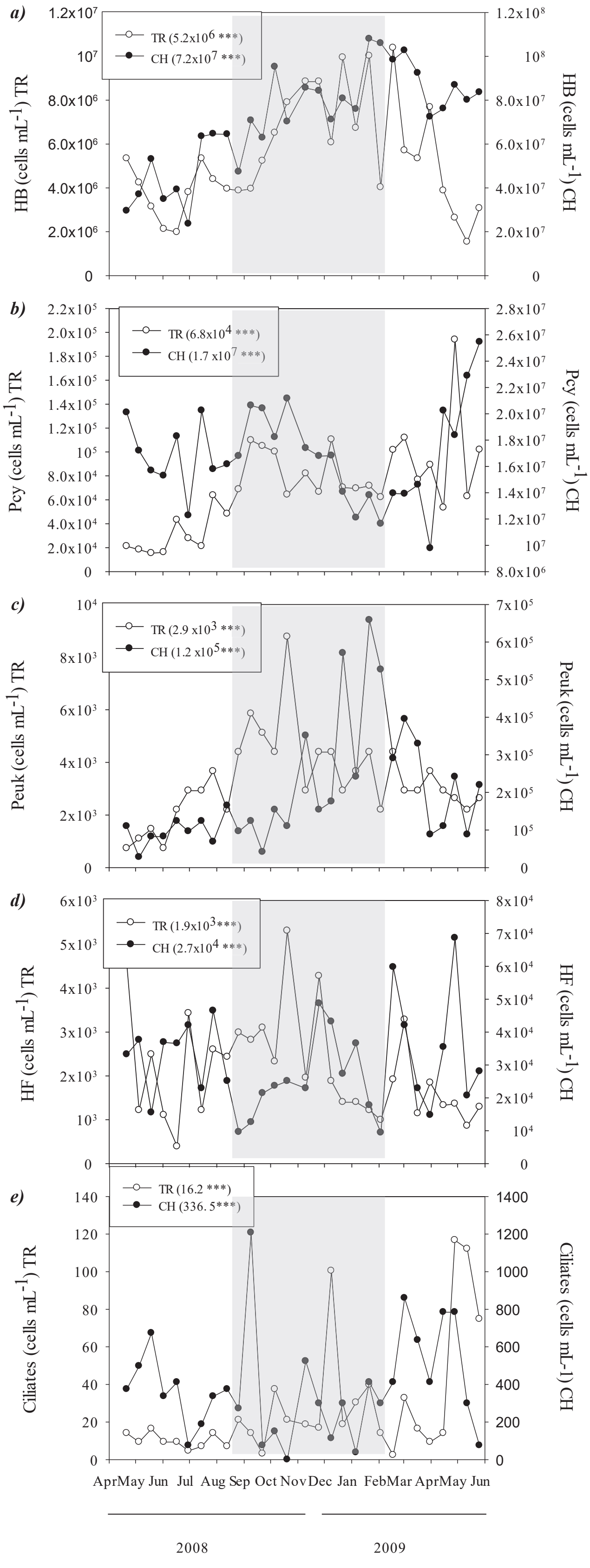

Figure 5. Temporal variation of microbial communities measured in the two lakes during sampling period: (a) Heterotrophic bacteria (HB: cells mL^{-1}), (b) Picocyanobacteria (Pcy: cells mL^{-1}), (c) Picoeukaryote (Peuk: cells mL^{-1}), *(d)* Heterotrophic flagellates (HF: cells mL^{-1}), (e) Ciliates (cells mL^{-1}). TR: El Triunfo. CH: Chascomús. Numbers in parentheses after variable and site name in legends indicate the median value for each site and *** indicate significantly different median after Mann Whitney test (*p* < 0.001). Grey areas correspond to warm (Spring and Summer) seasons.

values in both lakes can be explained by the high concentrations of sodium and calcium in the catchment (Fernández-Cirelli & Miretzky 2004), the dissimilar nutrient concentrations and conductivity were due not only to direct precipitations and groundwaters but also to the land use in the surrounding area (Quirós et al. 2006, Castro-Berman et al. 2019). Also, even though the wind regime is the same for both lakes, the surface of El Triunfo is one order of magnitude smaller than that of Chascomús, thus having a reduced fetch and allowing the profuse growth of aquatic vegetation. Notably, the water column of El Triunfo was colonized by submerged and emergent macrophytes (Allende et al. 2009), which could cause a negative effect on the turbulence, avoiding resuspension of sediment particles (Scheffer et al. 1993). As a consequence, a lower inorganic matter in the seston was found in the clear lake. This feature is also reflected in the different light attenuation coefficient (K_dPAR) since El Triunfo presented significant lower K_dPAR values as compared to Chascomús lake. Also, the nature of particulate matter contributes to underwater light transmission (Pérez et al. 2013). Lakes with high color indicate a larger input of allochthonous DOC and should be more heterotrophic than productive high-TP lakes (Webster et al. 2008, Torremorell et al. 2015). This was true for our study, since El Triunfo showed significantly higher aCDOM$_{440}$ ($p = 0.004$) and aCDOM$_{440}$/Chl-a ratio ($p < 0.001$) than Chascomús.

Pampas wetlands are also influenced by hydrometeorological conditions (Sosnovsky & Quirós 2006). At a regional, long-term scale, Elisio et al. (2015) observed that average air temperature in Chascomús City increased significantly 1.4° C over 47 years. This variable showed a good fit with water surface temperature, which in our study showed a high degree of coherence between lakes. Furthermore, during the analyzed hydrological cycle, the region experienced a drought period with half of the annual rainfall for the region (Pérez et al. 2015, Elisio et al. 2015); resulting in a pronounced general decline of the hydrometric level in all lakes of the area. This was reflected in an enhancement of turbidity toward the end of the period, and was also reflected in conductivity and alkalinity, which presented a high synchronism between lakes. These results agree with those of Quirós et al. (2002) who noted that saline concentration of

Table IV. **Analysis of similarities (ANOSIM) among fractions of different microbial groups over time.**

Lakes **Microbial community**	**El Triunfo**		**Chascomús**	
	Overall (R)	**Significant season**	**Overall (R)**	**Significant season**
PP	0.32***	Win 08 - Spr 08*	0.49***	Aut 08 - Spr 08* Aut 08 - Sum 09* Win 08 - Sum 09**
HF	0.28***	Win 08 - Aut 09*	-0.65 ($p = 0.87$)	NS
Ciliates	0.21**	Aut 08 - Sum 09*	-0.02 ($p = 0.63$)	NS

(Aut: Autumn, Win: Winter, Spr: Spring, Sum: Summer)(* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Pampean lakes follows both the annual and interannual variation of rainfall.

Regardless of the absolute values of abiotics variables, both systems showed a high degree of temporal coherence which highlight the influence exerted by extrinsic factors on these lakes (Elisio et al. 2015, Torremorell et al. 2015). Moreover, within the descriptors of climatic change proposed by Adrian et al. (2009), we observed that water temperature, water level and alkalinity were the most appropriate indicators of environmental change because of their rapid response and extremely high synchronicity between lakes.

Microbial communities from the two lakes did not evidence temporal coherence in their dynamics

Even though abiotic parameters were highly coherent among lakes, this synchronicity was not reflected in temporal patterns of most microorganisms. Only HB abundances correlated positively ($r = 0.5$, $p < 0.01$), despite an unusual draught causing very disparate values during the last autumn. While, Chascomús depth diminished from about 1.9 to 1.2 m, El Triunfo almost dried out, thus undergoing much more extreme changes. In all, extrinsic factors accounted for most of the explained variation only for the picoplankton of El Triunfo clear lake.

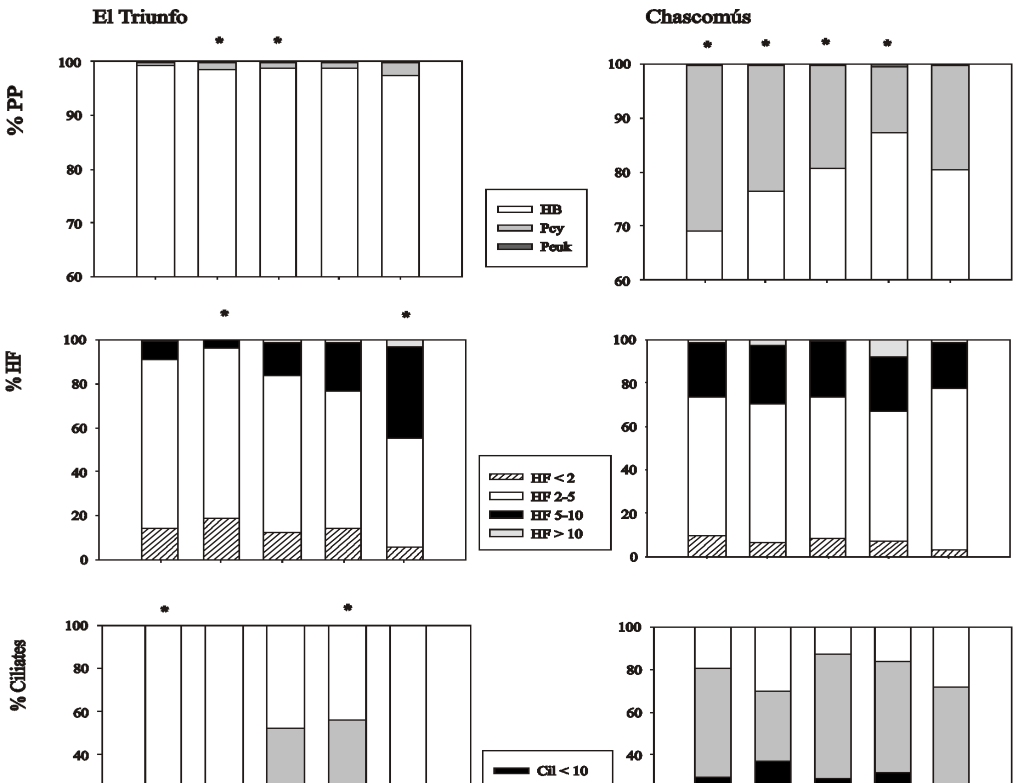

Figure 6. Relative seasonal importance of microbial abundances in the two studied lakes. Picoplankton -PP-: Heterotrophic Bacteria -HB-, Picocyanobacteria -Pcy- and Picoeukaryote -Peuk-; Heterotrophic Flagellates -HF-: HF < 2 µm, HF 2-5 µm, HF 5-10 µm and HF > 10 µm and ciliates -Cil- : Ciliates < 10 µm, Ciliates 10-20 µm; Ciliates > 20 µm. (Aut: Autumn, Win: Winter, Spr: Spring, Sum: Summer). TR: El Triunfo. CH: Chascomús. * indicate significant differences after ANOSIM (Table IV).

In clear lakes, vegetation plays an important role in the stabilization of the clear water phase, as macrophytes have a negative effect on phytoplankton (Scheffer et al. 1993) by diminishing underwater light (Izaguirre et al. 2010) as well as nutrient availability. Unlike in previous studies (Allende et al. 2009, Silvoso et al. 2011), we registered high HB abundances relative to total PPP in El Triunfo (annual mean 98.5 % in TR, 78.8 % in CH) (Fig. 6). The significant correlations of HB abundances with abiotic factors and Chl-*a* concentrations (Figs. 2a and 7a) and the lack of correlation with the abundances of predators, suggest that HB were more regulated by resource availability than predation and highlights the importance of phytoplankton-supplied labile DOC (Torremorell et al. 2015). In the turbid lake, Chl-*a* together with nutrients and I_0PAR made up an even larger percentage of the variation in the abundance of bacterial components than in the clear one (Fig. 7b), thus indicating that total phytoplankton biomass and HB abundances were tightly coupled (Fig. 2b). In previous studies of Pampean lakes, the bacterial community was related to phytoplankton biomass in the high-nutrient lakes, while this relationship was weaker in clear ones, where HB could depend of other organic matter sources (*i.e* macrophytes) (Muylaert et al. 2002, Torremorell et al. 2015). In a field molecular research in Pampa lakes, Llames et al. (2017) demonstrated that bacterial communities showed physiological adaptations to persist when these systems undergo a regime shift, and convergent taxonomic and phylogenetic indices showed that environmental abiotic control was maximized under turbid conditions. Previous surveys demonstrated that in Chascomús lake, phytoplankton primary production is directly related to incident solar radiation and light limitation drives the seasonal patterns of seston and water transparency (Torremorell et al. 2009, Llames et al. 2009). Therefore, the high turbidity would be explained by the large phytoplankton enabled by the hypertrophic turbid state of this water body. Overall, bacterial communities in both lakes varied seasonally with maximum values during summertime, suggesting the importance of extrinsic factors for this community and indicating a bottom-up control (Van der Gucht et al. 2001, Yanarell et al. 2003).

By contrast, PPP abundances showed dissimilar temporal patterns in both lakes. Previous studies found that at extremely high Chl-*a* concentrations, Pcy densities cannot be predicted and the relative importance of each phytoplankton size fraction remains unclear (Vörös et al. 1998, Fermani et al. 2015). Pampas lakes strongly differ from Northern Hemisphere counterparts, as nutrients concentrations stand as extremes of the trophic-state continuum (Quirós et al. 2002, Diovisalvi et al. 2015) promoting differences in the distribution and abundances of the communities (Izaguirre et al. 2012, Fermani et al. 2015). In most temperate lakes of the Northern Hemisphere, Pcy numbers remain low for most of the year ($1x10^3$ cells mL^{-1}) with a Spring or early Summer peak and second peak during Summer-Autumn (Callieri 2010 and references therein). On the other hand, tropical lakes show high Pcy abundances ($1x10^5$-$1x10^6$ cells mL^{-1}) (Sarmento et al. 2008), but depending upon the interactions with other phytoplankton groups, could develop an early Spring-Summer peak or stable abundances throughout the year (Sarmento et al. 2006, Callieri 2010). Our results showed not only abundances in the same order of magnitude than HB but also a distinct temporal pattern with high Pcy abundances throughout the winter, as already reported by Huber et al. (2017). These findings are different from those expected for temperate eutrophic water bodies (Callieri 2007 and references therein), but in

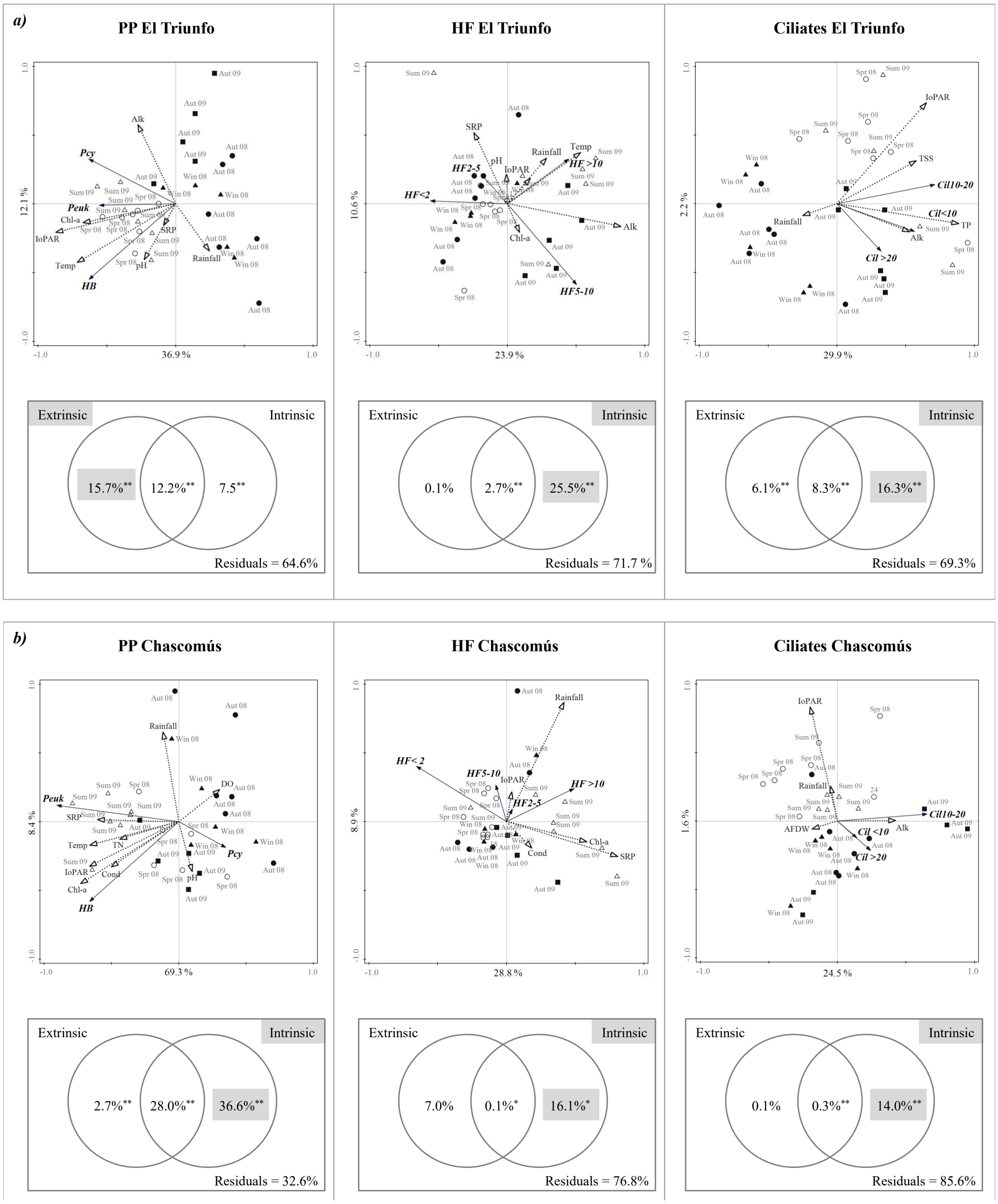

Figure 7. Biplot of RDA method and venn diagrams showing the variation partitioning performed with the microbial abundance explained by unique and joint effects of extrinsic and intrinsic factors: (a) El Triunfo: extrinsic: I_0PAR and rainfall. Intrinsic PP: Temp., Chl-*a*, Alk; HF: pH, Temp., Chl-*a,* SRP; Ciliates: Alk, TSS and TP. (b) Chascomús: extrinsic: I_0PAR and rainfall. Intrinsic PP: pH, Temp, DO, Cond, Chl-*a*, TN, SRP; HF: Chl-*a*, Cond, SRP; Ciliates: AFDW, Alk. Solid black, dashed black arrows and points represents microbial community, environmental factors and sites, respectively; and each arrow points in the direction of the steepest increase of the corresponding values. I_0PAR: photosynthetic light intensity, Chl-*a*: chlorophyll *a*, Temp: water temperature, TN: total nitrogen, SRP: soluble reactive phosphorous, DO: dissolved oxygen, TP: total phosphorous, Alk: alkalinity, TSS: total solid suspended, AFDW: ash free dry weigh. PP: Picoplankton. HB: Heterotrophic Bacteria, Pcy: Picocyanobacteria, Peuk: Picoeukaryote, HF: Heterotrophic Flagellates, Cil: ciliates (Autumn 08 -Aut 08-, Winter 08 -Win 08-, Spring 08 -Spr 08- , Summer 09 -Sum 09-, Autumn 09 -Aut 09-).

line with others surveys in the region (Silvoso et al. 2011, Fermani et al. 2015). In addition, the area surrounding Chascomús lake comprises extensive farmlands wherein agricultural practices involve the use of glyphosate (Castro-Berman et al. 2019). As demonstrated by many authors (Pérez et al. 2007, Pizarro et al. 2016, Śliwińnska-Wilczewska et al. 2018), glyphosate could promote the growth of Pcy, enhancing the effect of hypertrophic nutrient concentrations. Additionally, light quality could be a key factor determining Pcy distribution (Vöros et al. 1998, liwińnska-Wilczewska et al. 2018). In turbid environments, highly efficient in light harvesting phycocyanin-rich Pcy predominate (Allende et al. 2009, Felföldi et al. 2009) contributing with higher biomass during periods of shorter days (Iachetti & Llames 2015, Huber et al. 2017), though it is also possible that Pcy development in Chascomús was favoured by a more stable water column and a high retention time (Camacho et al. 2003). Our study also detected an unusual progressive replacement of Pcy by Peuk during the warmer season which could be explained by the grazing by small cladocerans (Callieri & Stockner 2002). Generally, in oligotrophic systems, large filter-feeder cladocerans, like *Daphnia* sp., can feed over a wide range of particle size (Sommer & Sommer 2006, Lepère et al. 2006). However, in highly eutrophic environments (*i.e* Chascomús), the zooplankton composition is dominated by small cladocerans (*i.e Bosmina* sp. and *Moina* sp.) (Work & Havens 2003, Diovisalvi et al. 2010). Huber et al. (2017) demonstrated in the field that Pcy abundance was negatively correlated with the density of small cladocerans in Chascomús lake (r = 0.51, p < 0.05); and experimentally, when these species dominated, the proportion of grazing resistant morphologies (*i.e.* Pcy-ag) is higher, as found in this study (Table II). On the other hand, in the clear El Triunfo lake, Pcy abundances were positively related to Turb and TSS (Fig. 2a) and followed the radiation pattern in the RDA (Fig. 7a). Also, the average Pcy:Peuk ratio was much lower (21.4 and 83.9, respectively), in accordance with previous findings in similar water bodies (Silvoso et al. 2011, Fermani et al. 2015). It has been shown that light quality and quantity constitute a key driver of PPP structure, and the proportion of Pcy/Peuk is affected by the turbidity (Callieri 2007). Our observations agree with some studies found that under clear-vegetated conditions, Pcy reached intermediate values, whereas in the turbid lakes they were either too high or too low (Vörös et al. 1998, Fermani et al. 2015). While temperature and nutrients accounted for Peuk growth in temperate water bodies (Callieri 2007), in our study both lakes these small algae were coupled with HB in both lakes. In fact, HB, Peuk abundances and Chl-*a* concentrations were more tightly coupled in the turbid lake than in the clear one, suggesting a stronger influence of biological processes on community structure (Callieri & Stockner 2002).

Seasonal dynamics of HF and ciliates can be regulated by factors relating to trophic state, season, food availability and predation pressure, as widely reported by e.g. Auer & Arndt (2001), Burns & Galbraith (2007) and Chróst et al. (2009). Studies focusing on their dynamics and temporal coherences, are scarce (Mieczan et al. 2015, Simon et al. 2015, Weisse et al. 2016). While Lansac-Tôha et al. (2008) observed a moderate synchronicity in microzooplankton abundances in a Brazilian tropical reservoir, our study did not reveal any significant coherence between lakes. According to different authors (Auer & Arndt 2001, Burns & Galbraith 2007, Chróst et al. 2009), HF abundances are positively related to trophic state. In line with those authors, almost all size fractions as well as total were one order of magnitude higher in Chascomús than in El Triunfo. In both lakes the HF community was largely composed of small bacterivorous flagellates (HF 2-5 µm); however, seasonal differences were found amongst them. In the clear lake, total HF reached their maximum abundance in Spring, following the trend of small autotrophs, as found in temperate lakes of the Northern Hemisphere (Auer & Arndt 2001, Wieltschnig et al. 2001, Kalinowska 2004). Notably, the high correlation between both HF 5-10 µm and Cil 10-20 with Pcy ($r = 0.64$ and 0.68; respectively, $p < 0.001$) suggests that these organisms are mainly herbivorous (Arndt & Mathes 1991, Meira et al. 2018). On the contrary, fluctuations in total HF abundance did not follow a seasonal pattern in Chascomús lake, as found in Huber et al. (2017), and size structure remained stable throughout the study period (Fig. 6, Table IV). In addition, no significant correlations between total HF and HB abundances were found and the average HB:HF ratio was greater ($3x10^3$) than expected ($1x10^3$) if HF exerted a strong predation pressure on bacteria (Sanders et al. 1992). It is known that when trophic status increases, zooplankton can exert a strong control over HF abundances, resulting in a higher decoupling between HF and their preys (Gasol 1994, Pernthaler 2005). Our results suggest that such biotic interactions not studied here could regulate HF abundances in the turbid lake (Sommer & Sommer 2006, Burian et al. 2013).

Total abundances of ciliates in both lakes were among the values reported for other eutrophic lakes (Kalinowska 2004, Burns et al. 2007, Chróst et al. 2009) and numbers were significantly lower in the clear than in the turbid one, as reported by Wichelen et al. (2013). Most of them were small (<30 µm) and mainly bacterivorous (Beaver & Crisman 1989, Nakano et al. 1998); however, no clear relationship between ciliates and HB abundances was found in either lake, probably due to indirect effects. In the clear lake, abundances were high during the warmer period (Fig. 5e) in line with the results of Boenigk & Novarino (2004) and Kammerlander et al. (2016), who largely ascribed the temporal distribution of the community to the relative solar irradiance. At that time, Pcy also were abundant and medium sizes ciliates dominated. The highly significant correlation between them (Fig. 2a) suggests that the ciliates could be mainly controlled by the resource availability (Calleri et al. 2002). Also, the sheltering effect of plants from larger predators could partially explain the predominance of large protists in vegetated environments (Scheffer et al. 1993, Mieczan 2010), by reducing zooplankton grazing (Özen et al. 2018). Ciliates dynamics in turbid Chascomús lake was markedly different. Neither abundances of total ciliates nor those of the different size fractions correlated to any abiotic variable selected by the RDA and results of the ANOSIM showed no significant seasonal differences throughout the study (Table IV, Fig. 6). However, the RDA shows that ciliates may be at least indirectly affected by the amount of incident light and AFDW (Fig. 7b). Boenigk & Novarino (2004) observed that in turbid, turbulent environments, suspended sediment is directly linked to light penetration, and some ciliates were affected due to interference in the uptake of particles. Moreover, this inverse relationship could be explained by the stochiometric imbalances induced by increasing light supply (Urabe & Sterner 1996); since some studies found that food quality is lower when the incident light increases (Diehl 2007, Bramm et al. 2009). In Chascomús, the phosphorous content of seston decreases with increasing incident solar radiation (Lagomarsino et al. 2011), and thus grazers could be more affected by the quality than quantity of available food (Llames et al. 2009). Therefore, the differences found in both water bodies seem to be attributed to the alternative stable state and related variables, as found by Wichelen et al. (2013), in 66 shallow lakes of Europe.

Overall, the divergent dynamics of microbial components indicates the dominance of site-specific controls wherein alternative state overrides extrinsic factors in determining the structure and dynamics of microbial heterotrophic communities.

Implications of the findings

Several studies describe shallow lakes as valuable sentinels of global climate change, though effects of the latter depend on geographic location, morphometry, climate, vegetation and other natural and anthropic drivers (Adrian et al. 2009, Beklioğlu et al. 2016), and shallow lakes with alternative states complicate theoretical predictions of warming effects. Meehorf et al. (2012) summarized the effects of climate change on a number of freshwater communities (fishes, zooplankton, macroinvertebrates, periphyton, phytoplankton) from different regions, but microbial heterotrophic communities have been less investigated. In order to fill in this knowledge gap, this work analyzed the coherence of the yearly dynamics of abiotic and biotic factors in two temperate shallow lakes with contrasting alternative states. Our results evidenced that, in addition to pronounced differences in microbial abundances, divergent dynamics of microbial components was found despite the strong temporal coherence in abiotic features imposed by extrinsic factors. Furthermore, biotic and abiotic drivers were different in each lake. Communities from the turbid, hypertrophic Chascomús lake responded mostly to intrinsic factors expressed by turbidity-related features; and the decoupling among extremely abundant Pcy and their microbial predators suggests a strongly steady state less prone to be affected by climatic effects. On the other hand, microbial components of El Triunfo responded to a combination of extrinsic and intrinsic factors, and bottom-up regulation of the trophic web was more evident through correlations among potential predators and preys. Such biotic relationships, in turn, can be sensitive to draught-driven changes in the vegetated clear state of the lake. Therefore, in addition to the findings of Sosnovsky & Quirós (2006), who found that smaller Pampean lakes are more susceptible to changes in rainfall –and hence to changes in climate- we hypothesize that clear lakes would perform better as sentinels of climate change in the Pampa wetland. As regards microbial communities, only HB showed some degree of coherence among lakes, though this trend was not observed in higher trophic levels, rendering them of little use as indicators of climate change (Adrian et al. 2009) and highlighting the importance of the alternative state to govern them. By contrast, in this work, water temperature, water level and alkalinity would be suitable indicators in these Pampas lakes, as Adrian et al. (2009) proposed. Additionally, we recommend further exploring sinchronicity among microbial communities of clear Pampean lakes to evaluate their potential as climate change sentinels.

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REFERENCES

ADRIAN R ET AL. 2009. Lakes as sentinels as climate change. Limnol Oceanogr 54(6, part 2): 2283-2297.

ALLENDE L, TELL G, ZAGARESE H, TORREMORELL A, PÉREZ G, BUSTINGORRY J, ESCARAY R & IZAGUIRRE I. 2009. Phytoplankton and primary production in clear and turbid shallow lakes from the pampa plain (Argentina). Hydrobiologia 624: 45-60.

ANDERSEN T, CARSTENSEN J, HERNÁNDEZ-GARCÍA E & DUARTE CM. 2009. Ecological thresholds and regime shifts: approaches to identification. Trends Ecol Evol 24: 49-57.

ANDRUS MJ, WINTER D, SCANLAN M, SULLIVAN S, BOLLMAN W, WAGGONER JB, HOSMER AJ & BRAIN RA. 2013. Seasonal synchronicity of algal assemblages in three Midwestern agricultural streams having varying concentrations of atrazine, nutrients, and sediment. Sci Total Environ 458-460: 125-139.

APHA. 1998. Standard Methods for the Examination of Water and Wastewater, 20th ed. American Public Health Association, Washington, DC, USA.

ARNDT H & MATHES J. 1991. Large heterotrophic flagellates form a significant part of protozooplankton biomass in lakes and rivers. Ophelia 33: 225-234.

AUER B & ARNDT H. 2001. Taxonomic composition and biomass of heterotrophic flagellates in relation to lake trophy and season. Freshw Biol 46(7): 959-972.

BEAVER JR & CRISMAN TL. 1989. The role of ciliated protozoa in pelagic freshwater ecosytems. Microb Ecol 17: 111-136.

BEKLIOĞLU M, MEERHOFF M, DAVIDSON TA, ALI GER K, HAVENS KE & MOSS B. 2016. Preface: Shallow lakes in a fast changing world. Hydrobiologia 778: 9-11.

BRAMM ME, KJELDAHL LASSEN M, LIBORIUSSEN L, RICHARDSON K, VENTURA M & JEPPESEN E. 2009. The role of light for fish–zooplankton–phytoplankton interactions during winter in shallow lakes—a climate change perspective. Freshw Biol 54: 1093-1109.

BOENIGK J & NOVARINO G. 2004. Effect of suspended clay on the feeding and growth of bacterivorous flagellates and ciliates. Aquat Microb Ecol 34: 181-192.

BURIAN A, SCHAGERL M & YASINDI A. 2013. Microzooplankton feeding behaviour: grazing on the microbial and the classical food web of African soda lakes. Hydrobiologia 710: 61-72.

BURNS C & GALBRAITH LM. 2007. Relating planktonic microbial food web structure in lentic freshwater ecosystems to water quality and land use. J Plankton Res 29: 127-139.

CALIMAN A ET AL. 2010. Temporal coherence among tropical coastal lagoons: a search for patterns and mechanisms. Braz J Biol 70: 803-814.

CALLIERI C. 2007. Picophytoplankton in Freshwater Ecosystems: The Importance of Small-Sized Phototrophs. Freshw Rev 1(1): 1-28.

CALLIERI C. 2010. Single cells and microcolonies of freshwater picocyanobacteria: a common ecology. J Limnol 69(2): 257-277.

CALLIERI C & PINOLINI ML. 1995. Picoplankton in Lake Maggiore, Italy. Int Rev gesamten Hydrobiol 80: 491-501.

CALLIERI C & STOCKNER JG. 2002. Freshwater autotrophic picoplankton: a review. J Limnol 61: 1-14.

CAMACHO A, MIRACLE MR & VICENTE E. 2003. Which factors determine the abundance and distribution of picocyanobacteria in inland waters? A comparison among different types of lakes and ponds. Arch Hydrobiol 157: 321-338.

CANO MG, CASCO MA, SOLARI LC, MAC DONAGH ME, GABELLONE NA & CLAPS MC 2008. Implications of rapid changes in chlorophyll-a of plankton, epipelon and epiphyton in a Pampean shallow lake: an interpretation in terms of a conceptual model. Hydrobiologia 614: 33-45.

CARON DA, WORDEN AZ, COUNTWAY PD, DEMIR E & HEIDELBERG KB. 2009. Protists are microbes too: a perspective. ISME J 3: 4-12.

CARPENTER S ET AL. 1987. Regulation of lake primary productivity by food web structure. Ecology 68: 1863-1876.

CASTRO-BERMAN M, LLAMES ME, MINOTTI P, FERMANI P, QUIROGA MV, FERRARO M, METZ S & ZAGARESE HE. 2019. Field evidence supports former experimental claims on the stimulatory effect of glyphosate on picocyanobacteria communities. doi.org/10.1016/j.scitotenv.2019.134601 0048-9697/.

CASTRO-BERMAN M, MARINO DJG, QUIROGA MV & ZAGARESE H. 2018. Occurrence and levels of glyphosate and AMPA in shallow lakes from the Pampean and Patagonian regions of Argentina. Chemosphere 200: 513-522.

CHRÓST RA, TOMASZ A, KALINOWSKA K & SKOWRONSKA A. 2009. Abundance and structure of microbial loop components (Bacteria and Protists) in lakes of different trophic status. J Microbiol Biotechn 9: 858-868.

CRUMP BC & HOBBIE JE. 2005. Synchrony and seasonality in bacterioplankton communities of two temperate rivers. Limnol Oceanogr 50: 1718-1729.

COHEN JE, JONSSON T & CARPENTER SR. 2003. Ecological community description using the food web, species abundance, and body size. Most 100(4): 1781-1786.

DIEHL S. 2007. Paradoxes of enrichment: effects of increased light versus nutrient supply on pelagic producer-grazer systems. Amer Naturalist 169: 173-191.

DIOVISALVI N, BOHN VY, PICCOLO MC, PERILLO GME, BAIGÚN C & ZAGARESE HE. 2015. Shallow lakes from the Central Plains of Argentina: an overview and worldwide comparative analysis of their basic limnological features. Hydrobiologia 752: 5-20.

DIOVISALVI N ET AL. 2010. Chascomús: estructura y funcionamiento de una laguna pampeana turbia. Ecol Austral 20: 115-127.

ELISIO M, VITALE A & MIRANDA L. 2015. Influence of climate variations on Chascomús shallow lake thermal conditions and its consequences on the reproductive ecology of the Argentinian Silverside (Odontesthes bonariensis—Actinopterygii, Atherinopsidae). Argentine Pampean Shallow lake. Hydrobiologia 752: 155-166.

FELFÖLDI B, SOMOGYI B, MÁRIALIGETI K & VÖROS L. 2009. Characterization of photoautotrophic picoplankton assemblages in turbid, alkaline lakes of the Carpathian Basin (Central Europe). J Limnol 68(2): 385-395.

FERMANI P, TORREMORELL A, LAGOMARSINO L, ESCARAY R, UNREIN F & PÉREZ G. 2015. Microbial abundance patterns along a transparency gradient suggest a weak coupling between heterotrophic bacteria and flagellates in eutrophic shallow Pampean lakes. Argentine Pampean Shallow lake. Hydrobiologia 752: 103-123.

FERNÁNDEZ-CIRELLI A & MIRETZKY P 2004. Ionic relations: a toll for studying hydrogeochemical processes in Pampean shallow lakes (Buenos Aires, Argentina). Quat Int 114(1): 113-121.

GASOL JM. 1994. A framework for the assessment of top-down vs bottom-up control of heterotrophic nanoflagellate abundance. Mar Ecol Progr Ser 113: 291-300.

HAMMER Ø, HARPER DAT & RYAN PD. 2001. PAST: Paleontological Statistics software for education and data analysis. Palaeontol Electron 4(1): 1-9.

HUBER P ET AL. 2017. Phenotypic plasticity in freshwater picocyanobacteria. Environm Microbiol 19: 1120-1133.

IACHETTI CM & LLAMES ME. 2015. Light limitation helps stabilize the phytoplankton assemblage steady-state in a temperate and highly turbid, hypertrophic shallow lake (Laguna Chascomús, Argentina). Hydrobiologia 752: 33-46.

IZAGUIRRE I, ALLENDE L, ESCARAY R, BUSTINGORRY J, PÉREZ G & TELL G. 2012. Comparison of morpho-functional phytoplankton classifications in human-impacted shallow lakes with different stable states. Hydrobiologia 698: 203-216.

JÜRGENS K & JEPPESSEN E. 2000. The impact of metazooplankton on the structure of the microbial food web in a shallow, hypertrophic lake. J Plankton Res 22: 1047-1070.

KALINOWSKA K. 2004. Bacteria, nanoflagellates and ciliates as components of the microbial loop in three lakes of different trophic status. Pol J Ecol 52(1): 19-34.

KAMMERLANDER B, KOINIG KA, ROTT E, SOMMARUGA R, TARTAROTTI B, TRATTNER F & SONNTAG B. 2016. Ciliate community structure and interactions within the planktonic food web in two alpine lakes of contrasting transparency. Freshw Biol 61: 1950-1965.

KENT AD, YANNARELL AC, RUSAK JA, TRIPLETT EW & MCMAHON KD. 2007. Synchrony in aquatic microbial community dynamics. ISME J 1: 38-47.

KÜPPERS MG & CLAPS MC. 2012. Spatiotemporal variations in abundance and biomass of planktonic ciliates related to environmental variables in a temporal pond. Argentina. Zool Stud 51(3): 298-313.

KNOWLTON MF & JONES JR. 2007. Temporal coherence of water quality variables in a suite of Missouri reservoirs. Lake Reservoir Manag 23: 49-58.

LAGOMARSINO L, PÉREZ G, ESCARAY R, BUSTINGORRY J & ZAGARESE HE. 2011. Weather variables as drivers of seasonal phosphorus dynamics in a shallow hypertrophic lake (Laguna Chascomús, Argentina). Fundam Appl Limnol 178(3): 191-201.

LANSAC-TÔHA FA, BINI LM, VELHO LFM, BONECKER CC, TAKAHASHI EM & VIEIRA LCG. 2008. Temporal coherence of zooplankton abundance in a tropical reservoir. Hydrobiologia 614(1): 387-399.

LEGENDRE P & BIRKS HJB. 2012. From classical to canonical ordination. In Birks HJB, Lotter AF, Juggins S & Smol JP (Eds), Tracking Environmental Change Using Lake Sediments, Data Handling and Numerical Techniques. Springer, Dordrecht: 201-248.

LEPÈRE C, BOUCHER D, JARDILLIER L, DOMAINZON I & DEBROAS D. 2006. Succession and regulation factors of small eukaryote community. Composition in a lacustrine ecosystem (Lake Pavin). Appl Environ Microbiol 72: 2971-2981.

LIEBHOLD A, KOENIG WD & BJØRNSTAD ON. 2004. Spatial synchrony in population dynamics. Annu Rev Ecol Evol S 35: 467-490.

LLAMES ME ET AL. 2009. The effects of different degrees of light availability in shallow, turbid waters: a mesocosm study. J Plankton Res 31(12): 1517-1529.

LLAMES ME, DEL GIORGIO PA, ZAGARESE H, FERRARO M & IZAGUIRRE I. 2013. Alternative states drive the patterns in the bacterioplankton composition in shallow Pampean lakes (Argentina). Environ Microbiol Rep 5: 310-321.

LLAMES ME, HUBER P, METZ S & UNREIN F. 2017. Interplay between stochastic and deterministic processes in the maintenance of alternative community states in Verrucomicrobia-dominated shallow lakes. FEMS Microbiol Ecol: 93: fix07.

LOPRETTO E & TELL G. 1995. Ecosistemas de aguas continentales. Metodologías para su uso. Tomo I. Ediciones Sur, La Plata.

MACEK M, PESTOVÁ D & MARTÍNEZ PÉREZ ME. 2008. Dinámica temporal y espacial de la comunidad de ciliados en un lago monomíctico-cálido Alchichica (Puebla, México). Hidrobiológica 18(1): 25-35.

MALVÁREZ AI & BÓ R. 2004. Bases ecológicas para un sistema nacional de clasificación e inventario de humedales (Eds), Buenos Aires, Argentina.

MANTEL N. 1967. The detection of disease clustering and a generalized regression approach. Cancer Res 27: 209-220.

MEERHOFF M ET AL. 2012. Environmental Warming in Shallow Lakes: A Review of Potential Changes in Community Structure as Evidenced from Space-for-Time Substitution Approaches. Adv Ecol Re 46: 259-349.

MEIRA B, LANSAC-TOHA FM, TREVIZAN SEGOVIA B, BRESSAN BUOSI PR, LANSAC-TÔHA FA & MACHADO VELHO LF. 2018. The importance of herbivory by protists in lakes of a tropical floodplain system. Aquat Ecol 52(2-3): 193-210.

MIECZAN T. 2010. Periphytic ciliates in three shallow lakes in Eastern Poland: a comparative study between a phytoplankton-dominated lake, a phytoplankton-macrophyte lake and a macrophyte-dominated lake. Zool Stud 49(5): 589-600.

MIECZAN T, TARKOWSKA-KUKURYK M, PECZULA W, PLASKA W & RECHLICZ J. 2015. Seasonal patterns of testate amoebae and ciliates in peatboags vs. bacteria and flagellates abundances. Teka Kom Ochr Kszt Środ Przyr – *OL PAN* 12: 46-53.

MUYLAERT K, GUCHT KVD, VLOEMANS N, MEESTER LD, GILLIS M & VYVERMAN W. 2002. Relationship between bacterial community composition and bottom-up versus top-down variables in four eutrophic shallow lakes. Society 68(10): 4740-4750.

NAKANO S, ISHII N, MANAGE PM & KAWABATA Z. 1998. Trophic roles of heterotrophic nanoflagellates and ciliates among planktonic organisms in a hypereutrophic pond. Aquat Microbial Ecol 16: 153-161.

ÖZEN A, TAVŞANOĞLU ÜN, ÇAKIROĞLU Aİ, LEVI EE, JEPPESEN E & BEKLIOĞLU M. 2018. Patterns of microbial food webs in Mediterranean shallow lakes with contrasting nutrient levels and predation pressures Hydrobiologia 806(1): 13-17.

PÉREZ GL ET AL. 2007. Effects of the herbicide ROUNDUP® on freshwater microbial communities: a mesocosm study. Ecol Appl 17(8): 2310-2322.

PÉREZ GL, LAGOMARSINO L & ZAGARESE HE. 2013. Optical properties of highly turbid shallow lakes with contrasting turbidity origins: the ecological and water management implications. J Environm Manage 130: 207-220.

PÉREZ GL, TORREMORELL A, BUSTINGORRY J, ESCARAY R, PÉREZ P, DIÉGUEZ M & ZAGARESE HE. 2010. Optical characteristics of shallow lakes from the Pampa and Patagonia regions of Argentina. Limnologica 40: 30-39.

PÉREZ S, SIERRA E, MOMO F & MASSOBRIO M. 2015. Changes in average annual precipitation in Argentina's Pampa Region and their possible causes. Climate 3: 150-167.

PERNTHALER J. 2005. Predation on prokaryotes in the water column and its ecological implications. Nat Rev Microbiol 3: 537-546.

PIZARRO H, VERA S, VINOCUR A, PÉREZ G, FERRARO M, MENÉNDEZ HELMAN, RJ & DOS SANTOS AFONSO M. 2016. Glyphosate input modifies microbial community structure in clear and turbid freshwater systems. Environ Sci Pollut R 23: 5143.

PORTER KG & FEIG YS. 1980. The use of DAPI for identifying and counting aquatic microflora. Limnol Oceanogr 25: 943-948.

QUIRÓS R, ROSSO JJ, RENNELLA AM, SOSNOVSKY A & BOVERI MB. 2002. Análisis del estado trófico de las lagunas pampeanas (Argentina). Interciencia 27(11): 584-591.

QUIRÓS R, BOVERI MB, PETRACCHI CA, RENNELLA AM, ROSSO JJ, SOSNOVSKY A & VON BERNARD HT. 2006. Los efectos de la agriculturación del humedal pampeano sobre la eutrofización de sus lagunas. Eutrofizaçaõ na América do Sul: Causas, conseqüências e tecnologias de gerenciamento e controle: 1–16. In: Tundisi JG, Matsmura-Tundisi T & Sidagis Galli C (Eds), Instituto Internacional de Ecologia, Instituto Internacional de Ecologia e

Gerenciamento Ambiental, Academia Brasileira de Ciências, Conselho Nacional de Desenvolvimento Científico e Tecnológico, InterAmerican Panel on Internacional Issues, InterAmerica Network of Academies of Sciences.

RASMUSSEN JB, GODBOUT L & SCHALLENBERG M. 1989. The humic content of lake water and watershed and lake morphometry. Limnol Oceanogr 34: 1336-1343.

ROLAND F, HUSZAR VLM, FARJALLA VF, ENRICH-PRAST A, AMADO AM & OMETTO JPHB. 2012. Climate change in Brazil: perspective on the biogeochemistry of inland waters. Braz J Biol Sci 72: 709-722.

SANDERS RW, CARON DA & BERNINGER UC. 1992. Relationship between bacteria and heterotrophic nanoplankton in marine and freshwaters: an interecosystem comparison. Mar Ecol Progr Ser 86: 1-14.

SARMENTO H, ISUMBISHO M & DESCY JP. 2006. Phytoplankton ecology of Lake Kivu (Eastern Africa). J Plankton Res 28: 815-829.

SARMENTO H, UNREIN F, ISUMBISHO M, STENUITE S, GASOL JM & DESCY JP. 2008. Abundance and distribution of picoplankton in tropical, oligotrophic Lake Kivu, eastern Africa. Freshw Biol 53: 756-771.

SEGOVIA BT, PEREIRA DG, BINI LM, MEIRA BR, NISHIDA VS, LANSAC-TÔHA FA & VELHO LFM. 2015. The role of microorganisms in a planktonic food web of a floodplain lake. Microb Ecol 69: 225-233.

SCHEFFER M, HOSPER SH, MEIJER ML, MOSS B & JEPPESEN E. 1993. Alternative equilibria in shallow lakes. Trends Ecol Evol 8: 275-279.

SCHEFFER M & JEPPESEN E. 2007. Regime shifts in shallow lakes. Ecosystems 10(1): 1-3.

SCHEFFER M & VAN NES EH. 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. Hydrobiologia 584(1): 455-466.

SCHIAFFINO MR, DIOVISALVI N, MARFETÁN MOLINA D, FERMANI P, LI PUMA C, LAGOMARSINO L, QUIROGA MV & PÉREZ GL. 2019. Microbial food-web components in two hypertrophic human-impacted Pampean shallow lakes: interactive effects of environmental, hydrological, and temporal drivers. Hydrobiologia 830(1): 255-276.

SHERR EB & SHERR BF. 1993. Protistan grazing rates via uptake of fluorescently labeled prey. In: Kemp P, Sherr B, Sherr E & Cole J (Eds), Handbook of methods in aquatic microbial ecology. Lewis Publ., Boca Raton, FL, 695-701.

SILVOSO J, IZAGUIRRE I & ALLENDE L. 2011. Picoplankton structure in clear and turbid eutrophic shallow lakes: A seasonal study. Limnologica 41: 181-190.

SIMON M, LÓPEZ-GARCÍA P, DESCHAMPS P, MOREIRA D, RESTOUX G, BERTOLINO P & JARDILLIER L. 2015. Marked seasonality and high spatial variability of protist communities in shallow freshwater systems. ISME J 1-13.

ŚLIWIŃNSKA-WILCZEWSKA S, MACULEWICZ J, BARREIRO FELPETO & LATAŁA A. 2018. Allelopathic and Bloom-Forming Picocyanobacteria in a Changing World. Toxins 10-48.

SOMMARUGA R. 1995. Microbial and classical food webs: A visit to a hypertrophic lake. Microb Ecol 17: 257-270.

SOMMER U & SOMMER F. 2006. Cladocerans versus copepods: the cause of contrasting top–down controls on freshwater and marine phytoplankton. Oecologia 147: 183-194.

SOSNOVSKY A & QUIRÓS R. 2006. Efectos de la intensidad de uso de la tierra en pequeñas lagunas pampeanas (Argentina). Ecol Austral 16: 115-124.

TER BRAAK CJF. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 6: 1167-1179.

TER BRAAK CJF. 1987. Ordination. In Jongman RHG, ter Braak CJF & van Tongeren OFR (Eds), Data analysis in community and landscape ecology. Cambridge University Press, Wageningen: 91-173.

TORREMORELL A, BUSTIGORRY J, ESCARAY E & ZAGARESE HE. 2007. Seasonal dynamics of a large, shallow lake, laguna Chascomú: the role of light limitation and other physical variables. Limnologica 37: 100-108.

TORREMORELL A, LLAMES ME, PÉREZ GL, ESCARAY R, BUSTINGORRY J & ZAGARESE HE. 2009. Annual patterns of phytoplankton density and primary production in a large, shallow lake: the central role of light. Freshw Biol 54: 437-449.

TORREMORELL A, PÉREZ G, LAGOMARSINO L, HUBER P, QUEIMALIÑOS C, BUSTINGORRY J, FERMANI P, LLAMES ME & UNREIN F. 2015. Microbial pelagic metabolism and cDOM characterization in a phytoplankton-dominated versus a macrophyte-dominated shallow lake. Hydrobiologia 752: 203-221.

URABE J & STERNER R. 1996. Regulation of herbivore growth by the balance of light and nutrients. Proc Natl Acad Sci 93: 8465-8469.

VAN DER GUCHT K, SABBE K, DE MEESTER L, VLOEMANS N, ZWART G, GILLIS M & VYVERMAN W. 2001. Contrasting bacterioplankton community composition and seasonal dynamics in two neighboring hypertrophic fresh-water lakes. Environm Microbiol 3: 680-690.

VÖRÖS L, CALLIERI C, BALOGH KV & BERTONI R. 1998. Freshwater picocyanobacteria along a trophic gradient and light quality range. Hydrobiologia 369-370: 117-125.

WEBSTER KE ET AL. 2008. An empirical evaluation of the nutrient-color paradigm for lakes. Limnol Oceanogr 53: 1137-1148.

WEISSE T, ANDERSON R, ARNDT H, CALBELT A, HANSEN PJ & MONTAGNES D. 2016. Functional ecology of aquatic phagotrophic protists – Concepts, limitations, and perspectives. Eur J Protistol 55: 50-74.

WETZEL RG & LIKENS GE. 2000. Limnological Analyses. Springer, New York.

WICHELEN V ET AL. 2013. Planktonic ciliate community structure in shallow lakes of lowland Western Europe. Eur J Protistol 49: 538-551.

WIELTSCHNIG C, KIRSCHNER A, STEITZ A & VELIMIROV B. 2001. Weak coupling between heterotrophic nanoflagellates and bacteria in a eutrophic freshwater environment. Microb Ecol 42: 159-167.

WORK KA & HAVENS KE. 2003. Zooplankton grazing on bacteria and cyanobacteria in a eutrophic lake. J Plankton Res 25: 1301-1306.

YANNARELL AC, KENT AD, LAUSTER GH, KRATZ TK & TRIPLETT EW. 2003 Temporal patterns in bacterial communities in three temperate lakes of different trophic status. Microb Ecol 46: 391-405.

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FERMANI PAULINA designed, planned, carried out the analyses, figures, the counting of flagellates and ciliates under microscope, and wrote the article.
LAGOMARSINO LEONARDO, ESCARAY ROBERTO and BUSTINGORRY JOSÉ carried out the sampling and the chemical analyses.
TORREMORRELL ANA performed picoplankton count under microscope.
LLAMES MARÍA collaborated with certain statistical analyses
PÉREZ GONZALO performed the optical properties and DOC measurements.
ZAGARESE HORACIO helped to prepare the draft manuscript
MATALONI GABRIELA helped to interpret the data and revised the manuscript for important intellectual content.
All the authors revised the manuscript and approved the final version.