



Structure of plankton and waterbird communities under water level fluctuations: two case studies in shallow lakes of the Patagonian steppe

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Received: 21 June 2023 / Accepted: 26 April 2024
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Abstract

The Buenos Aires Lake Plateau, a unique semi-arid environment and priority area for waterbird conservation in Argentina, has recently shown reductions in lake sizes due to scarce rainfall. This study assessed the impact of contrasting hydrological conditions on the abiotic variables of lakes Chapu and Cervecero, as well as on the structure of plankton and how this affected the use of the lakes by waterbirds. We show that hydrological conditions shape the abiotic and biological features of these lakes. In 2015, both lakes were vegetated, but by 2016, their water level had dropped, causing decreased macrophyte coverage. In 2017, the lakes dried up completely, but were refilled the following year. The partial drought of 2015-2016 led to reduced concentrations of nutrients and food that support a high density and richness of birds, which are mostly aquatic and terrestrial feeders. After the extreme drought in 2017 and refilling phase in 2018, there was an improvement in the water quality of lake Chapu, as indicated by its increased clarity compared to that in 2015, while Cervecero remained turbid. Increased homogenization in plankton and waterbird species composition became evident in both lakes. There was a cyanobacteria bloom in Cervecero, while in Chapu Gammaproteobacteria were dominant. Both lakes supported few waterbirds, of which aquatic-terrestrial feeders and terrestrial herbivores were dominant. The abundance of the endemic and endangered hooded grebe (*Podiceps gallardoi* Rumboll 1974) declined with the cover of macrophytes, which these birds use when establishing their colonies. In sum, this study revealed changes in the conditions of lakes Chapu and Cervecero and their plankton communities in response to hydrological shifts, with implications for waterbird assemblages and, thus, biodiversity conservation.

Keywords Bacterioplankton · Phytoplankton · Zooplankton · Waterbirds · Drought · Cyanobacterial bloom

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Introduction

In aquatic ecosystems, the effects of climate change include alterations in water levels as a consequence of changes in precipitation patterns, an increase in the mean temperature, and changes in the carbon, nutrient, and hydrological cycles (Bates et al. 2008; Jeppesen et al. 2011, 2014, 2021). These impacts on water bodies have recently become more evident, with lakes increasingly considered sentinels and integrators of climate change (Williamson et al. 2008; Adrian et al. 2009; Schindler 2009). Shallow lakes are the most common type of aquatic system among the earth's landscapes, and may be of global significance as a result of their high rates of material processing (e.g., carbon, nitrogen, water, sediment, and nutrients) (Downing et al. 2006). Shallow lakes are particularly affected by decreasing rainfall, which typically leads to an increase in conductivity, turbidity, concentrations of ions, nutrients, and dissolved organic carbon, and variability in pH (Lake 2011). Furthermore, reduced runoff due to drought may increase internal loading and, consequently, total nutrient concentrations (Schindler and Vallentyne 2008; Jeppesen et al. 2009). Climate change also exacerbates the effects of eutrophication in shallow aquatic systems (Jeppesen et al. 2010).

These processes can influence the aquatic communities that inhabit shallow lakes by favoring species that are resistant to severe environmental disturbances (Bouvy et al. 2001; Costa et al. 2019; Cardoso et al. 2022). Drought intensification often affects lake biodiversity (Thomaz et al. 2007; Cardoso et al. 2022), causing, for example, the homogenization of communities due to increasing environmental filtering (Klamt et al. 2020). Indeed, it is considered that, over the next decades, climate change will be the primary cause of biodiversity loss on a global scale (Urban 2015; Reid et al. 2019).

The impact of extreme weather on freshwater planktonic communities can vary depending on the environmental context. During severe drought, water can undergo physicochemical deterioration, with cases of cyanobacteria and Actinobacteria being dominant in water bodies used to supply drinking water (Figueiredo et al. 2012). Patterns of reduced precipitation and increased global temperatures can stimulate cyanobacteria blooms, as these organisms are adapted to warm conditions and have high growth rates at high temperatures, with cyanobacteria outcompeting eukaryotic algae as a consequence [Paerl and Otten (2013) and references therein]. Thus, climate change can promote and stabilize the dominance of cyanobacteria in phytoplankton communities, and lead to the expansion of cyanobacterial blooms to higher latitudes (Wiedner et al. 2007; Paerl and Otten 2013). Zooplankton species

composition is also known to vary in response to major changes in environmental conditions (Starks et al. 2014). Zooplankton diversity among lakes was found to decrease in drought years in fishless ephemeral ponds (Chase 2007), while other work has shown that zooplankton assemblages differ more widely across lakes in drought years than in pluvial periods, as indicated by greater taxonomic diversity. Panarelli et al. (2008) observed that the zooplankton richness of lake Cavalos, southeastern Brazil, was lowest during an intense drought. However, zooplankton richness increased as the lake entered the recovery phase, and peaked when the lake exhibited more stable hydrologic conditions.

The consequences of climate change may be more severe in arid ecosystems where freshwater is already a scarce and limited resource. As global temperatures rise and precipitation patterns shift, the availability of freshwater in these regions is likely to become even more constrained, with potential ripple effects on the ecological dynamics of these fragile ecosystems (Döll and Siebert 2002). The availability of water is a key factor in avian diversity, and in arid regions in particular, aquatic ecosystems represent a vital habitat for waterbirds (Mendelsohn et al. 2007). For example, González-Gajardo et al. (2009) identified wetland area and water level fluctuations as the most important variables determining bird abundance in wetlands of central southern Chile. However, bird species abundance may change in response to changes in water depth, vegetation cover, and other habitat features over time (Riffel et al. 2001). Furthermore, eutrophication is often closely linked to changes in lake use by waterbirds (McKinnon and Mitchell 1994; Boldreghini and Santolini 1997; Mitchell and Wass 1997). In a study of equilibrium states of lakes, Moreno-Ostos et al. (2008) found that more waterbirds were attracted to them during the clear-water phase, with increased water transparency and macrophyte growth, which led to greater abundance and brood recruitment of dabbling and diving waterbirds as compared to turbid water phases. In fact, water clarity is crucial for restoring breeding waterbird communities, and can serve as an indicator of lake restoration success (Fox et al. 2019). For example, Fox et al. (2020) showed that by improving water quality, lake restoration can enhance conditions for locally breeding duck species, as long as these conditions support submerged macrophyte communities that are suitable for waterbird nesting.

The Patagonian steppe is characterized by low precipitation (Jobbágy et al. 1995; Paruelo et al. 1998) and includes unique semi-arid environments (Olson et al. 2001). Recognized as one of the most endemic-species rich regions of the world, its conservation is considered of vital importance (Dinerstein et al. 1995; Olson and Dinerstein 2002; Epele et al. 2021). Nevertheless, global conservation targets are far from being met for Patagonian aquatic systems, which may

disappear due to climate change (Barros et al. 2014; Epele et al. 2021). Fishless aquatic systems located on the basaltic plateaus of the steppe (47°S–51°S) are crucial for various species, and notably a diverse waterbird community that includes the endangered hooded grebe (*Podiceps gallardoi* Rumboll 1974), an endemic and critically endangered diver (Roesler et al. 2012; BirdLife International 2022). Most of the plateaus of the Patagonian steppe are considered of high importance for bird conservation in Argentina (Scott and Carbonell 1986; Di Giacomo 2005).

The inclusion of the central southern area of the Buenos Aires Plateau in the Patagonia National Park has proven a positive conservation step, as it provides crucial habitats for aquatic species such as the hooded grebe (Roesler 2016). However, the hydrology of these water bodies is dynamic due to significant variations in rainfall that can lead to a reduction in water level and even the existence of a lake, and has even resulted in the evaporation of water in lakes critical for the hooded grebe (Roesler et al. 2012; Lancelotti et al. 2020). These changes underscore the vulnerability of Patagonian aquatic ecosystems to climate change and the need for efforts to conserve them.

Patagonia's arid climate is characterized by extremely strong winds (Cabrera 1976; Paruelo et al. 1998) which, combined with reduced water levels, can increase sediment resuspension and turbidity (Hamilton and Mitchell 1996) and thus impact phytoplankton biomass and community structure (Allende et al. 2009; Jeppesen et al. 2015). Many lakes on the Patagonian plateau are shallow and exhibit a clear water state, with submerged vegetation (Izaguirre et al. 2018; Saad et al. 2018; Porcel et al. 2019). Field studies carried out from 2006 to 2017 showed a significant decrease in the water level of most arctic basins of a high number of lakes of the Patagonian plateau, which was further confirmed through a time series analysis of climate data and satellite images (Lancelotti et al. 2020). A decreased water level may trigger a regime shift in shallow lakes, as observed in some water bodies on the Patagonian plateau, which changed from a clear vegetated to a phytoplanktonic turbid regime, with the loss of submerged macrophytes (Izaguirre et al. 2018; Lancelotti et al. 2020). Droughts have been recently proposed as the potential cause of macrophyte degradation, with a consequent impact on the breeding cycle of the hooded grebe (Roesler et al. 2021).

In 2015, most lakes on the Buenos Aires Plateau were in a clear, vegetated state, ideal for waterbird nesting. The period of drought that began in 2016 led to a significant drop in water levels. As a result of extreme drought in 2017, some lakes dried up completely, but were refilled the following year as a consequence of melting snow that fell in the winter. These events allowed a comparison to be made of changes in the freshwater community structure of two shallow lakes in Patagonia National Park in response

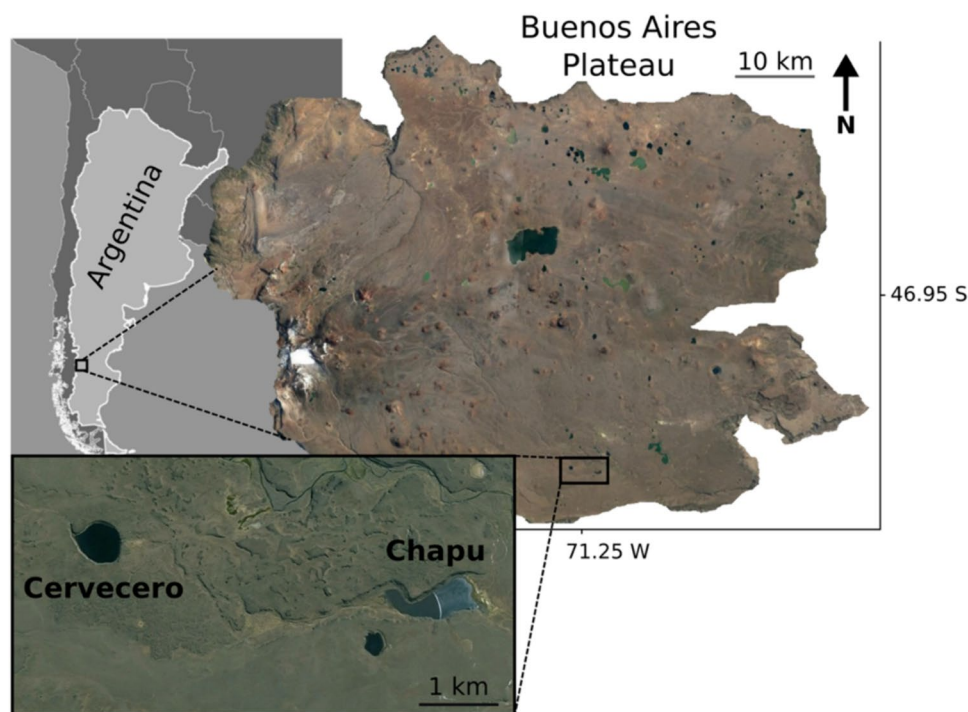
to changing biological and abiotic conditions. Lake regime shifts were assessed in 3 years of showing a high variation in water levels to determine changes that arose following drought and their effects on limnological factors, planktonic community diversity (bacteria, phytoplankton, and zooplankton), and lake use by waterbirds. We hypothesize that drought-induced shifts from vegetated to turbid non-vegetated regimes negatively impact water quality for planktonic and aquatic bird biodiversity in shallow lakes of the basaltic plateaus.

Materials and methods

Site description

We studied two shallow lakes, Chapu and Cervecero, located in northwest Santa Cruz province, Argentina, in the Buenos Aires Lake Plateau, which comprises part of the Patagonian steppe (Fig. 1). Rainfall in this region ranges from 16.8 to 290.8 mm year⁻¹, and temperature from 9.1 to 20.7 °C (Lancelotti et al. 2020). Snow covers the area from early autumn to late spring. The plateau, which has a surface area of 3650 km², is relatively flat; the highest altitude is ~1800 m a.s.l., in the west, and it decreases in an easterly direction, to just under 700 m a.s.l. (Roesler 2016). This plateau holds more than 150 endorheic basins, most of which are shallow (<5 m maximum depth) and naturally fishless, and range from temporary ponds to lakes larger than 17 km² (Porcel et al. 2020) that are fed by snow in autumn and winter (Pereyra et al. 2002). These water bodies are exposed to high irradiance and are usually fully mixed by strong winds from the west (Lancelotti 2009). They are thus dynamic systems with significant interannual hydrological fluctuations (Lancelotti et al. 2010, 2020) and vary widely in trophic status, from oligotrophic to eutrophic, including turbidity caused by suspended inorganic matter, where the conductivity is high; turbidity due to the presence of phytoplankton; and various vegetated states (Izaguirre et al. 2018; Porcel et al. 2019). Water milfoil (*Myriophyllum quitense* Kunth) (Lancelotti 2009), commonly known in the region as *vinagrilla*, is dominant in some of the lakes, which provide a crucial habitat for numerous endemic and threatened species, e.g., the hooded grebe (Menu-Marque et al. 2000; Perotti et al. 2005; Ortubay et al. 2006; Roesler et al. 2012; Fjeldså 1986). Chapu and Cervecero lakes comprise part of the Patagonia National Park, which was created with the primary goal of protecting the hooded grebe (under law no. 27081/2014, enacted in December 2015). Lake Cervecero (47°09'S, 71°16'W; Fig. 1) in particular has successfully hosted hooded grebe colonies in recent years (Roesler et al. 2012; Adami 2016).

Fig. 1 Geographic location of the shallow lakes surveyed



Sampling, limnological analyses, and climate data

Samples were collected during the summer in three successive field campaigns, which were carried out in March 2015, January 2016, and February 2018. Both lakes showed high interannual fluctuations in water level, as follows: highest water level in 2015; lower water level/partial drought in 2016; extreme drought in 2017 (when sampling was not possible); and higher water level during refilling in 2018. These categories were determined by depth, lake surface area, mean annual precipitation, and observations of the watermark on lake shores.

Sampling and measurements of abiotic parameters were carried out for the subsurface layer (~30-cm depth). Conductivity and pH were measured using a Horiba D-54 portable sensor and dissolved oxygen with a HachTM HQ30 dm meter. Unfiltered water samples were collected and preserved frozen ($-20\text{ }^{\circ}\text{C}$) for measurement of total phosphorus (TP) and total nitrogen (TN), which was conducted after sample digestion (Valderrama 1981), and determined using a HachTM DR/2800 spectrophotometer and the corresponding reagent kits. Samples for the measurement of dissolved organic carbon (DOC), chlorophyll *a* (Chl *a*), and organic suspended solids (OSS) were immediately filtered through Whatman GF/F filters (Whatman, UK). Samples for DOC determinations were acidified (to a pH of 2) and analyzed using a Shimadzu analyzer TOC-5000A with a high-temperature platinum catalyst oxidation method, following the recommendations of Sharp et al. (1993). Concentrations of Chl *a* (corrected for phaeopigments) were determined by

spectrophotometry using acetone as the solvent. The equations published by Marker et al. (1980) were used for the calculations. The samples for the measurement of OSS were filtered using filters that had been previously heated in a muffle furnace at $500\text{ }^{\circ}\text{C}$ and then weighed. The filters with the OSS were dried in an oven at $103\text{ }^{\circ}\text{C}$, weighed, and heated once again in a muffle furnace at $500\text{ }^{\circ}\text{C}$. OSS values were then estimated by difference by using the values of the inorganic suspended solids fraction. A LI-COR radiometer equipped with a Spherical Underwater Quantum Sensor (Li-193 SA; LI-COR, USA) was used to measure photosynthetically active radiation (PAR) at different depths in the water column. The vertical attenuation coefficient of PAR ($K_{d\text{PAR}}$) was calculated for the two lakes in accordance with Kirk (1994). Water transparency was estimated with a Secchi disc. Depth was measured with a portable sounder (Speedtech). The cover of submerged macrophytes was estimated semi-quantitatively for both of the lakes, according to two categories: without vegetation ($<25\%$ cover), with vegetation ($\geq 25\%$ cover).

To quantify the lake area, i.e., the area covered by water, throughout the study years, we analyzed Landsat-8 Level 1 images corresponding to the Buenos Aires Plateau. We selected images that showed low cloud cover or were cloud-free and had been acquired on dates close to the sampling events (24 February 2015, 10 January 2016, 15 January 2018). We downloaded, pre-processed, and clipped the images and conducted raster calculations to obtain the modified normalized difference water index (Xu 2006) to identify wet pixels in the images. The resultant raster was

polygonized to each lake, and the lake surface area was calculated. The fetch of each lake was calculated from Landsat-8 images for each year (24 February 2015, 10 January 2016, 15 January 2018) for the south-west quadrant as the predominant wind direction in the area is south-west. The analyses were conducted with QGIS 3.24.3-Tisler.

Precipitation data from 2015 to 2018 were provided by the Argentine National Meteorological Service (Servicio Meteorológico Nacional) from Perito Moreno, a town located 25 km from the Buenos Aires Plateau.

Plankton community analyses

Picoplankton

The abundance of photosynthetic picoplankton (PPP) and heterotrophic bacteria (HB) was analyzed using flow cytometry. Samples (4 mL) were fixed with a solution of 10% cold glutaraldehyde plus paraformaldehyde to a final concentration of 1%. Cryovials were transported in liquid nitrogen to the laboratory and then stored at -80°C until analysis. Two subsamples were taken for separate counts of HB and PPP. Fluorescent beads were added at a known concentration as the internal standard to the thawed fixed samples, which were then analyzed with a FACSAria II flow cytometer at the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. A fluorochrome (SyBGreen) was added to 400 μL of sample for HB determination; the sample was kept in the dark for about 10 min to complete nucleic acid staining. This technique allowed the separation and quantification of at least two HB populations: high nucleic acid content (HNA) and low nucleic acid content (LNA) bacterioplankton, which can be detected by their signature in plots of side scatter light versus green fluorescence of nucleic acid-bound stains [FL1; fluorescein isothiocyanate, 488-nm excitation, 530/30-nm band pass (BP) emission] (Gasol et al. 1999; Bouvier et al. 2007). For PPP quantification, the cytometric populations were identified in plots of side scatter light versus blue laser-dependent red fluorescence [FL3; peridinin-chlorophyll-protein, 488-nm excitation, 670-nm longpass emission], orange fluorescence (FL2; phycoerythrin, 488-nm excitation, 585/42-nm BP emission) versus FL3, and red laser-dependent far-red fluorescence (FL4; allophycocyanin 635-nm excitation, 661/61 nm BP emission) versus FL3 (Olson et al. 1993). Cytograms were analyzed using FlowJo 7.6.

Samples for bacterial DNA analyses were also collected within the euphotic zone. Water samples were prefiltered with a 51- μm mesh and transported in the cold to the field laboratory using plastic bottles previously rinsed with 2% HCl and MilliQ water. Samples were sequentially filtered through an 18- μm mesh and then a 0.2- μm pore-size polycarbonate filter (Millipore, US). The filters were maintained

in liquid nitrogen throughout the sampling campaigns and conserved at -80°C in the laboratory. DNA was extracted using CTAB lysis buffer and chloroform/isoamyl alcohol, following the protocol described in Fernández Zenoff et al. (2006). The environmental DNA thus obtained was processed using paired-end sequencing, using an Illumina Miseq 2×300 (Macrogen, Korea), with previous amplification of the V3-V5 variable region of the 16S subunit of ribosomal RNA with the 341F-805R primer set (Herlemann et al. 2011). Raw paired-end sequencing reads from the Illumina MiSeq were analyzed using the DADA2 package (Callahan et al. 2016) in R. Taxonomic classification was achieved by using the SILVA database as a reference. The analyses involved quality filtering and trimming of forward and reverse sequences using the parameter $\text{truncLen } c = (260, 190)$ and $\text{maxEE} = c(2, 5)$, merging of sequences, removal of chimera, and taxonomic assignment of the amplicon sequence variants (ASVs). The data in the ASV table thus obtained were further filtered as follows: ASVs with less than 50 reads and those that were taxonomically affiliated to chloroplasts, mitochondria, and Archaea were eliminated. Samples were then normalized to the number of reads of the sample with the fewest reads (C_{\min}) using the SRS pipeline, which preserves the relative abundance of ASVs after normalization to as close as possible as that of the original datasets (Beule and Karlovsky 2020). Abundant ASVs were defined as those with a frequency $> 1\%$. A table with all ASVs for each lake is available in Supplementary material 1a. The raw sequence data are available from the European Nucleotide Archive, and have the following access numbers (where sampling year is given in parentheses): ERS5215491 (2015), ERS5215496 (2016), and ERS5215541 (2018) for lake Cervezero; and ERS5215495 (2015), ERS5215501 (2016), and ERS5215540 (2018) for lake Chapu. The taxonomic affiliations of ASVs identified as dominant across samples were revised through a BLAST search using the NCBI 16S ribosomal RNA project database (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) to assign these ASVs at the species level.

Phytoplankton

In both lakes, phytoplankton samples for qualitative analyses were taken with a 15- μm -mesh net and immediately fixed with 2–3% formaldehyde. Observations were made under a binocular optical microscope (Olympus CX31) at 1000 \times magnification. Algae were identified according to the specialized literature. Unfiltered samples for quantitative phytoplankton analyses were obtained from the upper layer of the lakes, which integrate water from the surface to 50-cm depth. Samples (250 mL) were fixed with 1% Lugol's iodine solution. Phytoplankton counts [individuals (ind.) per milliliter] were performed using an inverted Olympus CKX41

microscope, following Utermöhl (1958), and the count error was estimated according to Venrick (1978). Biovolumes were calculated by using appropriate geometric formulae (Hillebrand et al. 1999; Sun and Liu 2003). Algal biomass was estimated from biovolume, by assuming unit-specific density.

Zooplankton

Samples for the determination of zooplankton were taken from each lake with two 20-cm-diameter opening plankton nets of different mesh sizes (55 and 115 μm for rotifers and microcrustaceans, respectively), which were towed horizontally for 10 m. The sampling volume was estimated geometrically as a 10-m high cylinder with a base equivalent to the surface area of the net mouth. Samples were immediately preserved in 4% formaldehyde. Rotifers, adult copepods, and cladocerans were identified to the lowest possible taxonomic level (mostly species, and genus in a few cases). Zooplankton abundance was calculated as number of individuals per liter. Rotifers were counted under a binocular microscope by using a 1-mL Sedgwick–Rafter cell, and microcrustaceans in a 5-mL Bogorov counting chamber under a stereoscopic microscope. The mean biomass of each species was estimated by applying biovolumetric formulae for rotifers (Ruttner-Kolisko 1977) and then transforming the data to dry weight (Dumont et al. 1975) or from body length-dry weight relationships (Bottrell et al. 1976; Pilati and Martínez 2003). The total biomass of each water body was calculated by multiplying the abundance of each species by its biomass and then adding up all the values.

Waterbird census

Aquatic bird censuses were carried out for both lakes by two experienced observers in the summers of 2015–2018, between 15 December and 15 January; 10 \times 42 binoculars and a 20–60 \times 60 spotting scope were used for this purpose. Both observers counted every species present, and the total number of birds was the maximum number recorded. In the case of diving species (associated with a higher chance of underestimation), each observer counted the birds twice. In the case of the critically endangered hooded grebe, each observer counted the birds three times using a species-specific technique (see Roesler 2016).

Data analyses

Principal component analysis (PCA) of the limnological variables, with standardization in RStudio environment (version 1.2.5042; RStudio Team 2020) with the vegan package (Oksanen et al. 2019) was used to evaluate relationships between them.

Lake regimes were defined for both lakes according to the dominant producer community, using the models of Scheffer et al. (1993) and Liboriussen and Jeppesen (2003) as reference models.

Species richness (S), Shannon's diversity index [$H' = -\sum p_i \ln(p_i)$], Simpson's diversity index ($D = 1/\sum p_i^2$), and evenness ($E_H' = H'/\ln S$) were calculated for bacteria, phytoplankton, zooplankton, and waterbird assemblages with Past 4.04 software (Hammer et al. 2001).

Results

Climate and limnological analyses

Temporal variation in the area covered by water was evident in both lakes during the study (Table 1). The average rainfall recorded in the region ranged from 2 to 49 mm year^{-1} ; the lowest average rainfall was recorded in 2015 and 2016, while the highest, which led to the lakes refilling in 2018, was recorded in 2017. In 2016, the area of Chapu and Cervecero reduced by 1.3 and 1.6 ha relative to that in 2015, respectively, as a consequence of the drop in water level. In 2018, refilling of lake Chapu increased the water level relative to that of 2015, and the area of the lake was 1.82 km^2 ; in Cervecero, the water level was close to that of 2015, and the area of the lake was 1.14 km^2 (Table 1). There was also temporal variation in depth in both lakes, with the lowest depths recorded during 2016 (0.90 m in Chapu and 1.30 m in Cervecero). The fetch was almost twice as long in Chapu as in Cervecero in the three periods analyzed. Between 2015 and 2016, there was a 28-m reduction in fetch in Cervecero, whereas there was a slight increase, of 2 m, in Cervecero. In 2018, due to lake refilling, the fetch was 59 m greater than that in 2015 in Chapu and 34 m less than that in 2015 in Cervecero.

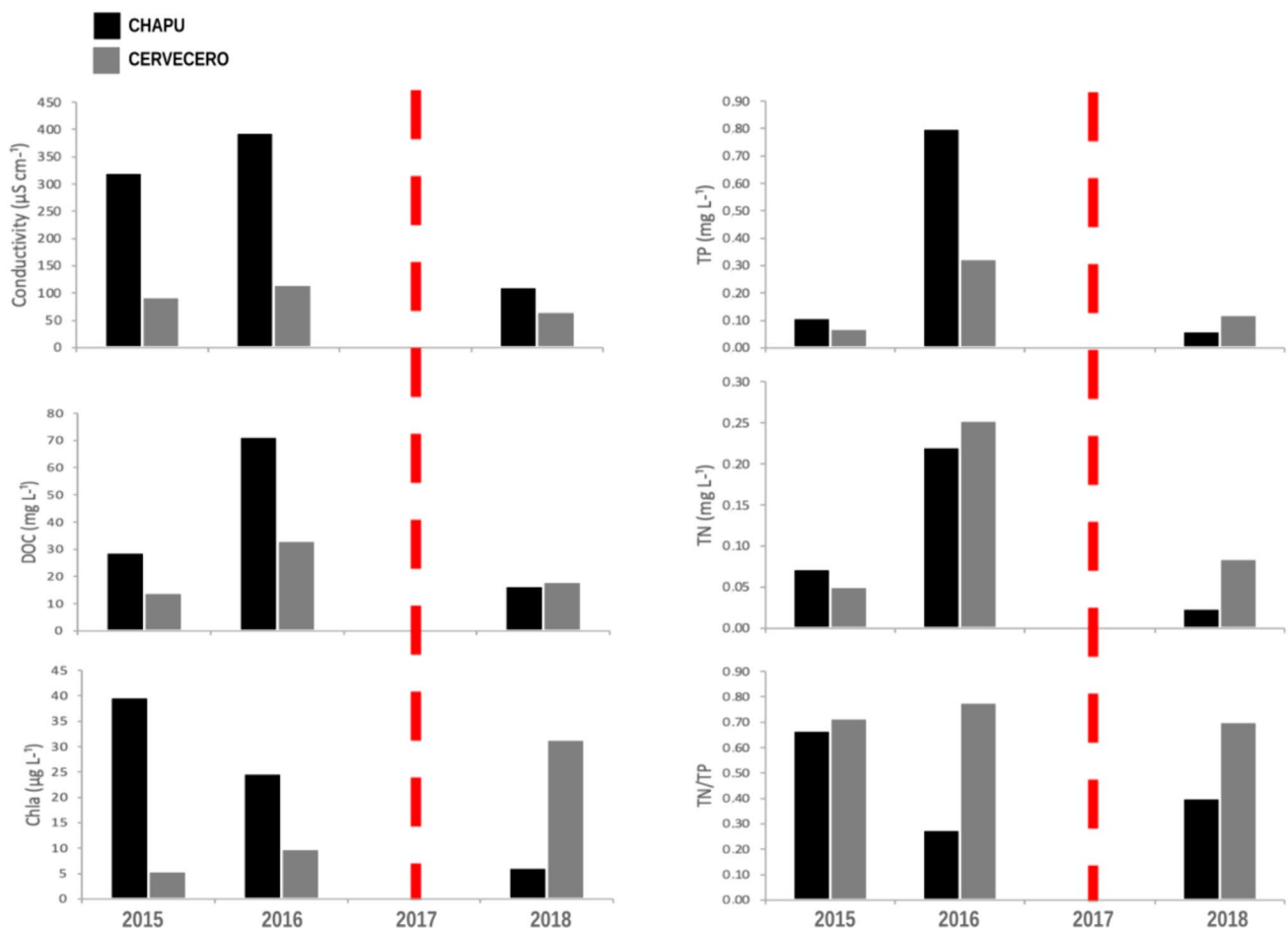
In both lakes, conductivity, DOC, TP, and TN values tended to be higher in 2016, when water levels were lowest, compared to 2015 (Fig. 2); this difference was particularly notable for conductivity, which was 74 $\mu\text{S cm}^{-1}$ higher in Chapu and 23 $\mu\text{S cm}^{-1}$ higher in Cervecero in 2016 compared to 2015. When comparing the data for 2016 and 2018, Chapu showed the greatest differences in these parameters, while Cervecero showed a large difference in the TN concentration (Fig. 2). The TN:TP ratio varied greatly between these years in Chapu—ranging from 0.28 to 0.67—but was relatively stable in Cervecero, with values between 0.70 and 0.78. The lakes showed differences in the Chl *a* concentration in the period 2015–2018, with Chapu showing a decreasing trend (39.7, 24.7, and 6.11 μL^{-1}), and Cervecero an increasing trend, that ranged from 5.4 to 31.3 μL^{-1} (Fig. 2). Cervecero also showed a trend of increasing $K_{d\text{PAR}}$ (2.7–24.9 m^{-1}) and OSS (7–44 mg L^{-1} ; Table 1). Chapu

Table 1 Morphometric and environmental measurements for lakes Chapu and Cervecero in 2015, 2016, and 2018, indicating lake state [vegetated (V); clear vegetated (CV); clear not vegetated (CNV); organic turbid (OT)]

	Shallow lakes		Chapu			Cervecero	
	2015	2016	2015	2016	2018	2015	2016
Altitude (m a.s.l.)		1193				1037	
Year	2015	2016	2015	2016	2018	2015	2016
State	V	OT	CNV	CV	CV	CV	OT
Depth (m)	2.00	0.90	2.00	2.00	1.30	2.20	
Lake area (km ²)	1.46	1.33	1.82	1.29	1.13	1.14	
Water level	High	Low	High	High	Low	High	
Macrophyte cover (%)	50	No	No	50	25	No	
Fetch (m)	650	652	709	379	351	345	
pH	8.40	8.71	8.90	7.96	7.88	9.40	
DO (mg L ⁻¹)	11.11	8.99	9.14	8.15	9.28	8.31	
K _d _{PAR} (m ⁻¹)	–	4.04	4.35	2.72	9.52	24.90	
Secchi (m)	0.24	0.42 ^a	0.39 ^a	1.25	0.18 ^a	0.24	
OSS (mg L ⁻¹)	3.00	37.00	16.00	7.00	18.00	44.00	

DO Dissolved oxygen, K_d_{PAR} vertical attenuation coefficient of photosynthetically active radiation (PAR), OSS organic suspended solids

^aValues estimated from K_d_{PAR}

**Fig. 2** Conductivity (Conduct), dissolved organic carbon (DOC), total phosphorus (TP), total nitrogen (TN), TN:TP ratios, and chlorophyll *a* (Chl *a*) concentrations in lakes Chapu and Cervecero in 2015, 2016,

and 2018. Red dashed lines indicate the absence of data for 2017, when the lakes dried up due to the extreme drought

had a mean Kd_{PAR} of 4.2 m^{-1} and the highest OSS value (37 mg L^{-1}) during the partial drought of 2016. Both lakes had approximately 50% macrophyte cover in 2015. In 2016, the vinagrilla cover in Cervecero was still good (25%), while Chapu exhibited a drastic decline in the cover of submerged vegetation. In 2018, neither lake had submerged macrophytes.

The PCA analysis (Fig. 3) revealed difference in water chemistry characteristics of the two lakes, with Cervecero being associated with higher DOC, TP, and TN values and Chapu with higher conductivity and Chl *a*. Moreover, samples/dates showed clear ordination for the two principal components. PC1 explained 59.68% of the variance and was associated with DOC (correlation=0.92), TP (correlation=0.90), TN (correlation=0.84) and Chl *a* (correlation=0.51). PC2 explained 23.43% of the variance and was more closely related to conductivity (correlation=-0.62) and lake area (correlation=-0.81).

Plankton community analyses

Picoplankton

A total of 1145 ASVs were obtained from 279,414 reads after all filtering steps and sample normalization to 46,569 reads (Supplementary material 1a). As the rarefaction curve of each sample before normalization reached a plateau, sampling depth and sequencing coverage were considered adequate (Supplementary Figure 1). ASVs were taxonomically affiliated to 29 phyla, where the highest relative abundances were for Proteobacteria (37.9%), Bacteroidota (23.4%), Verrucomicrobiota (19.2%), and Actinobacteria (9.6%) in that order (Fig. 4a). The most abundant classes were Gammaproteobacteria (30.9%), Bacteroidia (23.3%), Verrucomicrobiae (19.0%), Actinobacteria (8.5%), and Alphaproteobacteria (7.0%) (Fig. 4b).

In 2015 and 2016, Chapu and Cervecero showed similar diversity and relative bacterial abundance. The most abundant phyla were Proteobacteria, Bacteroidota, Verrucomicrobiota, Actinobacteria, and Firmicutes, in that order (Fig. 4a). In 2018, however, the lakes showed differences in bacterial composition and relative abundance (Fig. 4). In

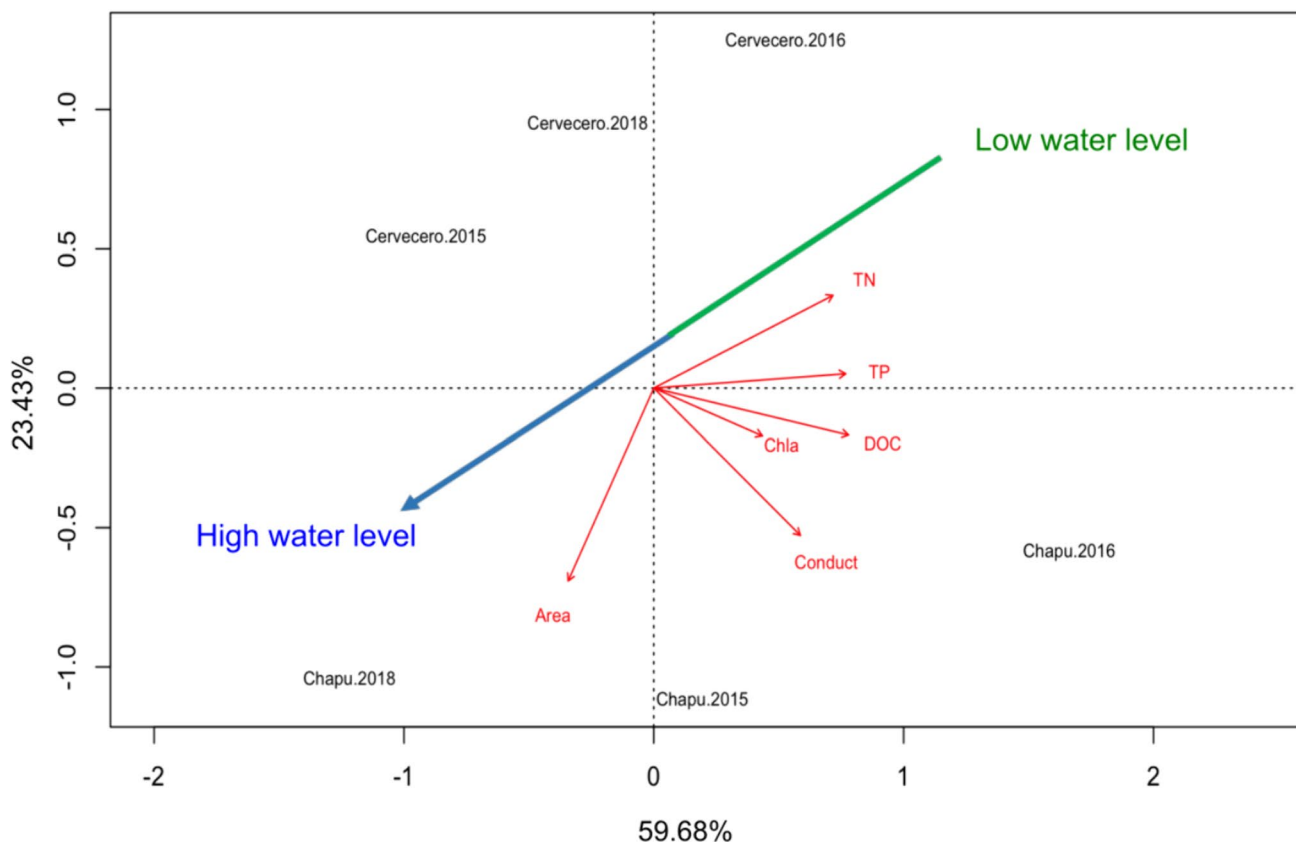
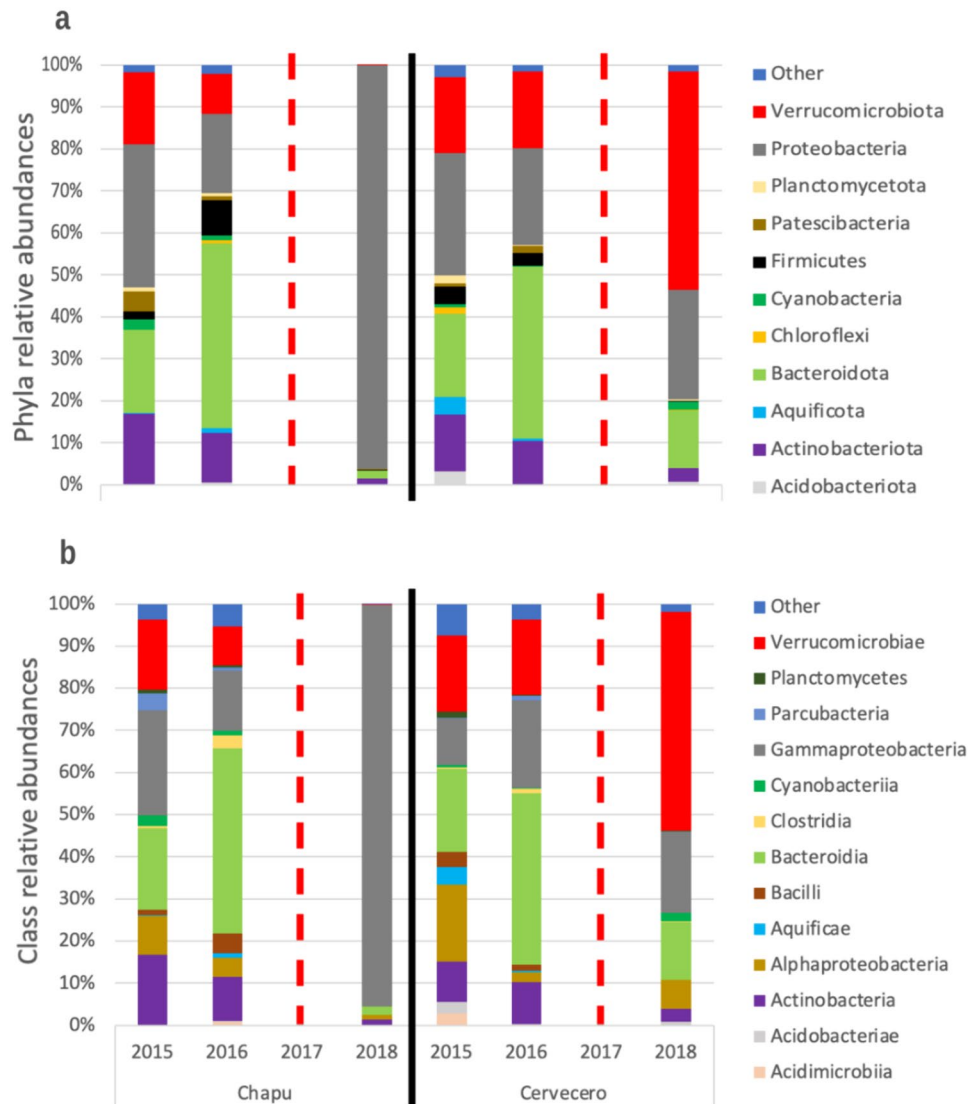


Fig. 3 Principal component analysis (PCA) for Chl *a*, DOC, Conduct, TN, TP, and lake area for Chapu and Cervecero in 2015, 2016, and 2018. For abbreviations, see Fig. 2

Fig. 4 Relative abundance of the dominant bacteria at phylum level (a) and class level (b) in Chapu and Cervecero in 2015, 2016, and 2018, based on 16S rRNA gene sequencing. Red dashed lines indicate the absence of data for 2017, when the lakes dried up due to the extreme drought



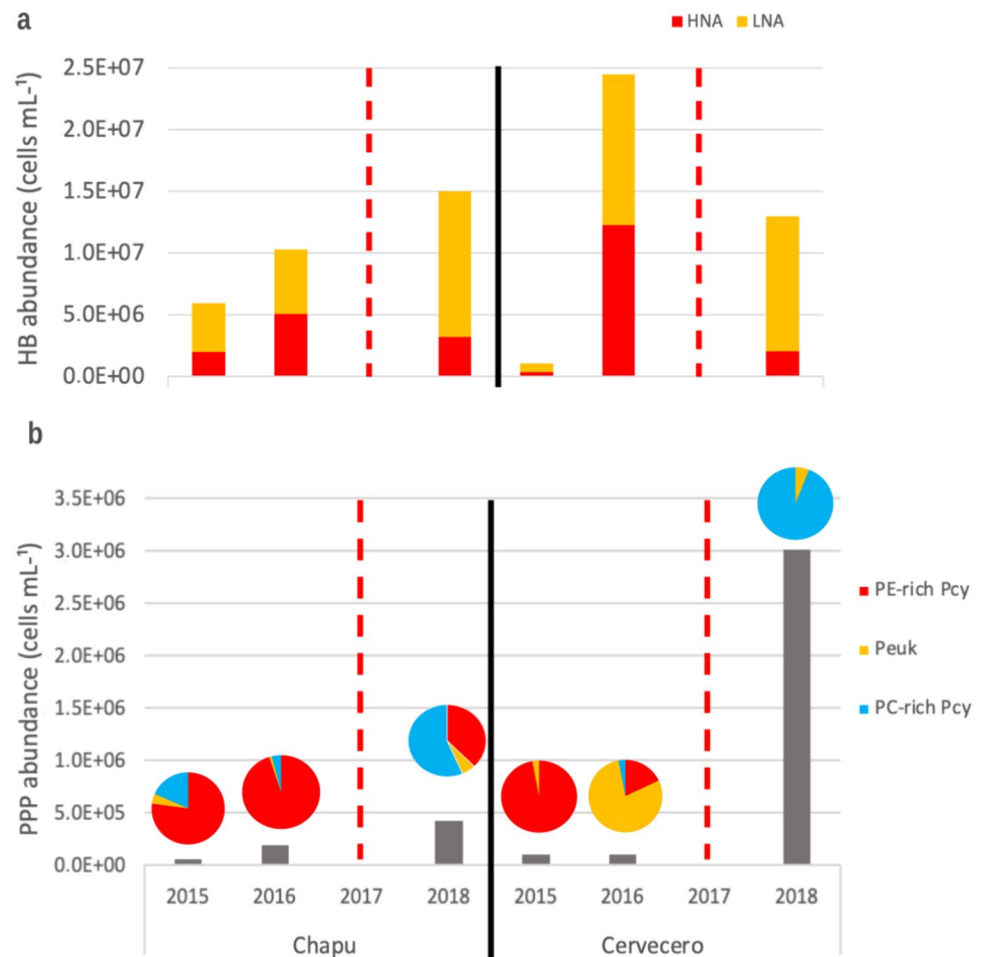
that year, Proteobacteria were clearly dominant in, 95.2% of which were Gammaproteobacteria (Fig. 4b), mainly in the genus *Pseudomonas*. Blasting of the corresponding ASV against the NCBI database identified *Limnohabitans parvus* (98.36%) (Supplementary material 2). Meanwhile, Cervecero showed a more diverse bacterial community, which was dominated by Verrucomicrobiota, with class Verrucomicrobiae accounting for 51.9% of the phylum, and mainly comprising the FukuN18-freshwater-group genus. Blasting against the NCBI database identified *Silvanigrella aquatica* (95.12%) (Supplementary material 2), followed by Proteobacteria (classes Gammaproteobacteria and Alphaproteobacteria, with 19.3% and 6.9%, respectively), Bacteroidota (13.8% of the class Bacteroidia), and Actinobacteriota (3.1%; class Actinobacteria, mostly corresponding to the family Microbacteriaceae) and phylum Cyanobacteria (2%; Aphanizomenon_NIES81 and Leptolyngbya_ANT.L52.2 genera; Fig. 4; Supplementary material 1a).

Bacterial abundance in both lakes tended to be higher in 2016 and 2018 as compared to 2015, with a larger difference in Cervecero (Fig. 5a). The HNA and LNA bacterioplankton fractions were proportionally the same in the two lakes in 2016, while LNA bacterioplankton were dominant in 2015 and 2018. In both lakes, PPP concentration was highest in 2018, with evident dominance of phycocyanin-rich picocyanobacteria (Pcy). In addition, a large increase in picoeukaryotes was observed in Cervecero during the partial drought of 2016 (Fig. 5b).

Phytoplankton

The phytoplankton community (> 2 µm) in the period under study comprised a total of 127 species in Chapu and Cervecero lakes, with Chlorophyceae, Cyanobacteria, Bacillariophyceae, Euglenophyceae, Chrysophyceae, and Cryptophyceae as the most representative

Fig. 5 Abundance of heterotrophic bacteria (a) and photosynthetic picoplankton (b) in Chapu and Cervecero in 2015, 2016, and 2018 determined by flow cytometry. Red dashed lines indicate the absence of data for 2017, when the lakes dried up due to the extreme drought

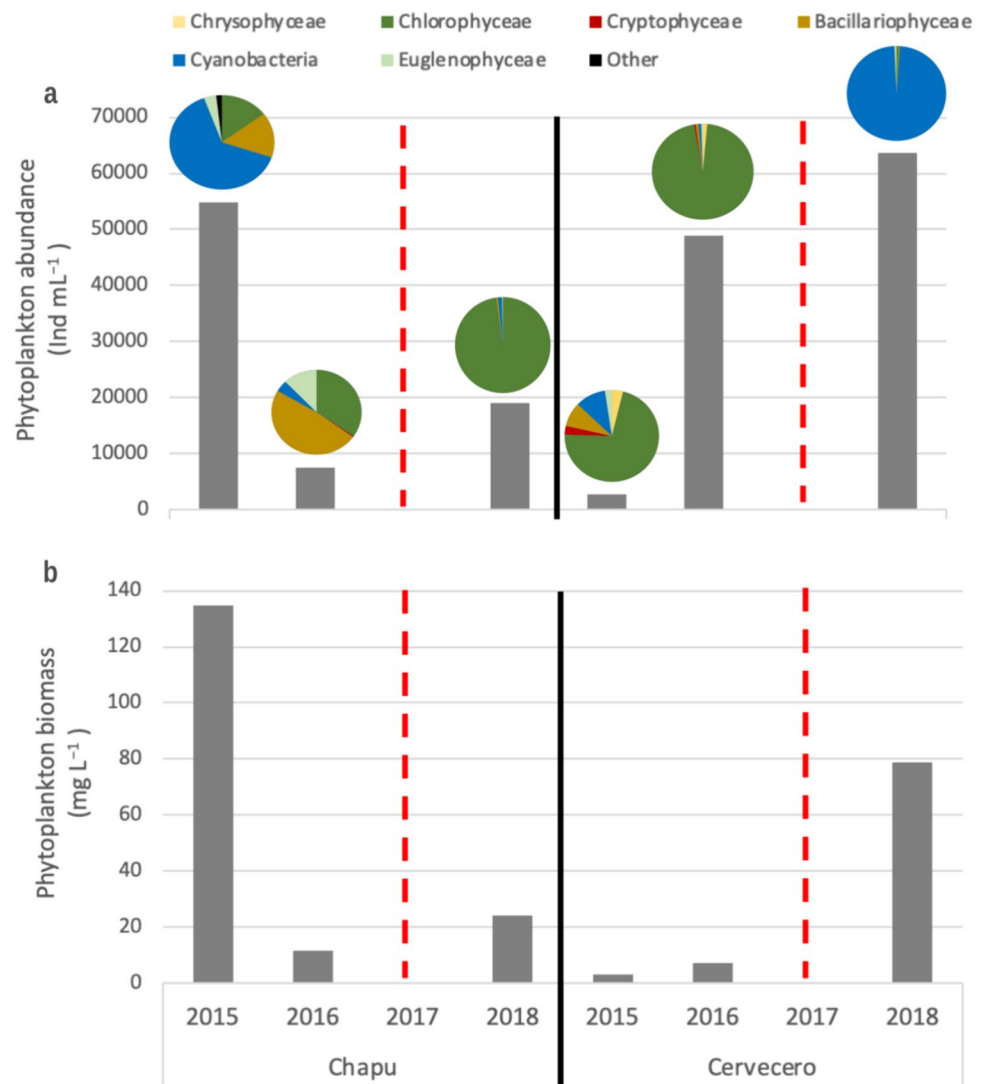


groups (Supplementary material 1b). This community showed different compositions in each lake during the studied years (Fig. 6). Phytoplankton abundance and biomass tended to be higher in Chapu in 2015 than in 2016 and 2018 [54,789 individuals (ind.) mL⁻¹, 135 mg L⁻¹, respectively], while Cervecero had greater abundance and biomass in 2018 (63,622 ind. mL⁻¹, 79 mg L⁻¹, respectively). In both lakes, taxonomic groups were more diverse in 2015, cyanobacteria were dominant (*Planktothrix*, *Dolichospermum*, and *Pseudanabaena catenata*) in Chapu and chlorophytes (*Monoraphidium subclavatum*) in Cervecero. In the partial drought of 2016, diatoms and chlorophytes were dominant in Chapu but only chlorophytes were dominant in Cervecero (*Chlorolobion braunii*, 43,425 ind. mL⁻¹). In 2018, when the water bodies had refilled with water, chlorophytes (*Oocystis* spp., 16,640 ind. mL⁻¹) were dominant in Chapu, while in Cervecero there was a cyanobacteria bloom of *Dolichospermum flos-aquae* (61,312 ind. mL⁻¹) (Fig. 6a).

Zooplankton

Zooplankton assemblages comprised 14 species of rotifers, seven of cladocerans, and five of copepods (Supplementary material 1c). Over the years studied, zooplankton abundance and biomass generally increased in both lakes (Fig. 7). The taxonomic composition remained stable in Chapu but was more variable in Cervecero over the years (Fig. 7a). In 2015, both water bodies showed lower zooplankton abundance and biomass than in 2016 and 2018 (respectively, 98 ind. L⁻¹ and 620 µg L⁻¹ in Chapu, 39 ind. L⁻¹ and 827 µg L⁻¹ in Cervecero), with rotifers and copepods prevailing in Chapu and copepods in Cervecero. In the partial drought of 2016, zooplankton abundance and biomass increased in both water bodies as compared to 2015 (respectively, 169 ind. L⁻¹ and 1599 µg L⁻¹ in Chapu, 151 ind. L⁻¹ and 1847 µg L⁻¹ in Cervecero). Also, in 2016, copepods were dominant (69%) in Chapu, while in Cervecero mostly cladocerans (64%) and rotifers (27%) were dominant. The highest proportion

Fig. 6 Abundance and taxonomic composition (a) and biomass (b) of phytoplankton in Chapu and Cervecero in 2015, 2016, and 2018. Red dashed lines indicate the absence of data for 2017, when the lakes dried up due to the extreme drought



of the study years nauplii larvae was recorded in 2016. Upon lake refilling in 2018, zooplankton abundance increased in both Chapu and Cervecero (302 ind. L⁻¹ and 1617 ind. L⁻¹, respectively; Fig. 7a), while zooplankton biomass increased in Chapu (3742 µg L⁻¹) but decreased in Cervecero (1456 µg L⁻¹; Fig. 7b). In 2018, rotifers (*Keratella kostei*) were highly dominant in Cervecero, and in Chapu, copepods (*Boeckella michaelsoni*), cladocerans (*Daphnia commutata*), and rotifers (*K. kostei*) were dominant.

Plankton diversity indexes

Between 2015 and 2016, phytoplankton richness decreased in both of the lakes. The richness of bacterial ASVs decreased in Cervecero in both years, whereas in Chapu it tended to be higher in 2015 than in 2016. Zooplankton richness followed the opposite trend, as it increased in Cervecero and decreased in Chapu (Table 2). After

lake refilling in 2018, both water bodies showed a drastic decrease in phytoplankton and bacterioplankton richness as compared to 2015–2016, while zooplankton richness recovered in Chapu and further increased in Cervecero. Phytoplankton, zooplankton, and bacterial ASV evenness values tended to be lower in 2018 than in 2015–2016.

Overall, the diversity indexes (Simpson's *D* and Shannon's *H'*) were highest for the plankton communities in 2015 and 2016 and lowest in 2018 in both lakes. More specifically, bacterial diversity was highest in 2015 in both lakes and decreased over the remainder of the study period. Phytoplankton diversity followed the same pattern in Cervecero, but in Chapu it peaked in 2016 and decreased in 2018. In Chapu, zooplankton diversity was highest in 2015, followed by 2016 and 2018, while in Cervecero it was higher in 2016 than in 2015, and lowest in 2018 (Table 2).

Fig. 7 Abundance and taxonomic composition (a) and biomass (b) of zooplankton in Chapu and Cervecero in 2015, 2016, and 2018. *Red dashed lines* indicate the absence of data for 2017, when the lakes dried up due to the extreme drought

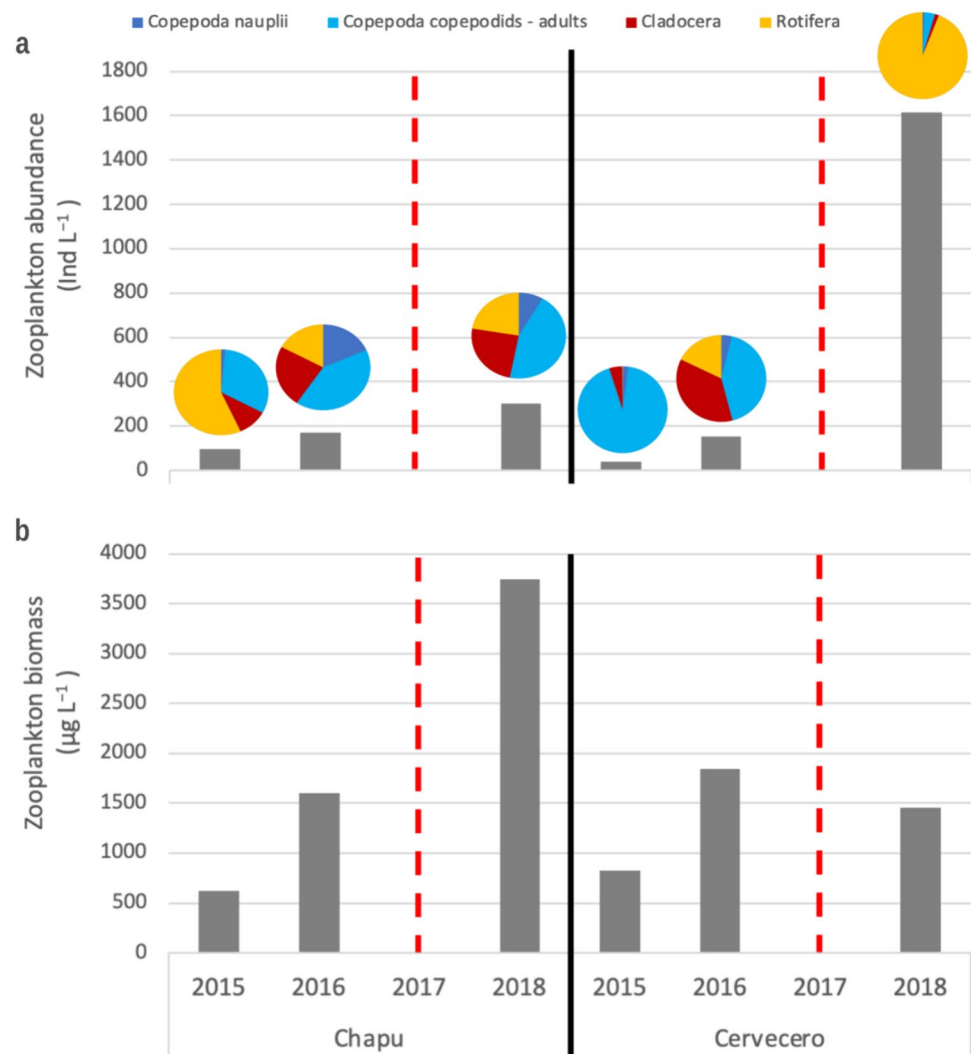


Table 2 Richness, Simpson's diversity index ($D=1/\sum p_i^2$), Shannon's diversity index [$H' = -\sum p_i \ln(p_i)$], and evenness calculated for Chapu and Cervecero in 2015, 2016, and 2018 based on bacterial amplicon sequence variants (ASVs), and phytoplankton and zooplankton compositions

Community	Index	Chapu			Cervecero		
		2015	2016	2018	2015	2016	2018
Bacterioplankton	Richness	386	465	71	489	405	162
	Simpson's	0.9634	0.9353	0.2314	0.984	0.9498	0.7338
	Shannon's	4.335	4.421	0.724	5.109	4.106	2.375
	Evenness	0.1978	0.1789	0.02905	0.3385	0.1499	0.06635
Phytoplankton	Richness	50	45	23	43	35	15
	Simpson's	0.8831	0.9315	0.5557	0.6243	0.2093	0.07111
	Shannon's	2.698	3.093	1.255	1.943	0.6074	0.2403
	Evenness	0.297	0.4898	0.1525	0.1623	0.05245	0.08478
Zooplankton	Richness	15	11	13	8	10	20
	Simpson	0.8836	0.8148	0.6787	0.4835	0.7659	0.3394
	Shannon's	2.346	1.889	1.424	1.071	1.728	0.8434
	Evenness	0.6965	0.6012	0.3197	0.365	0.5631	0.1162

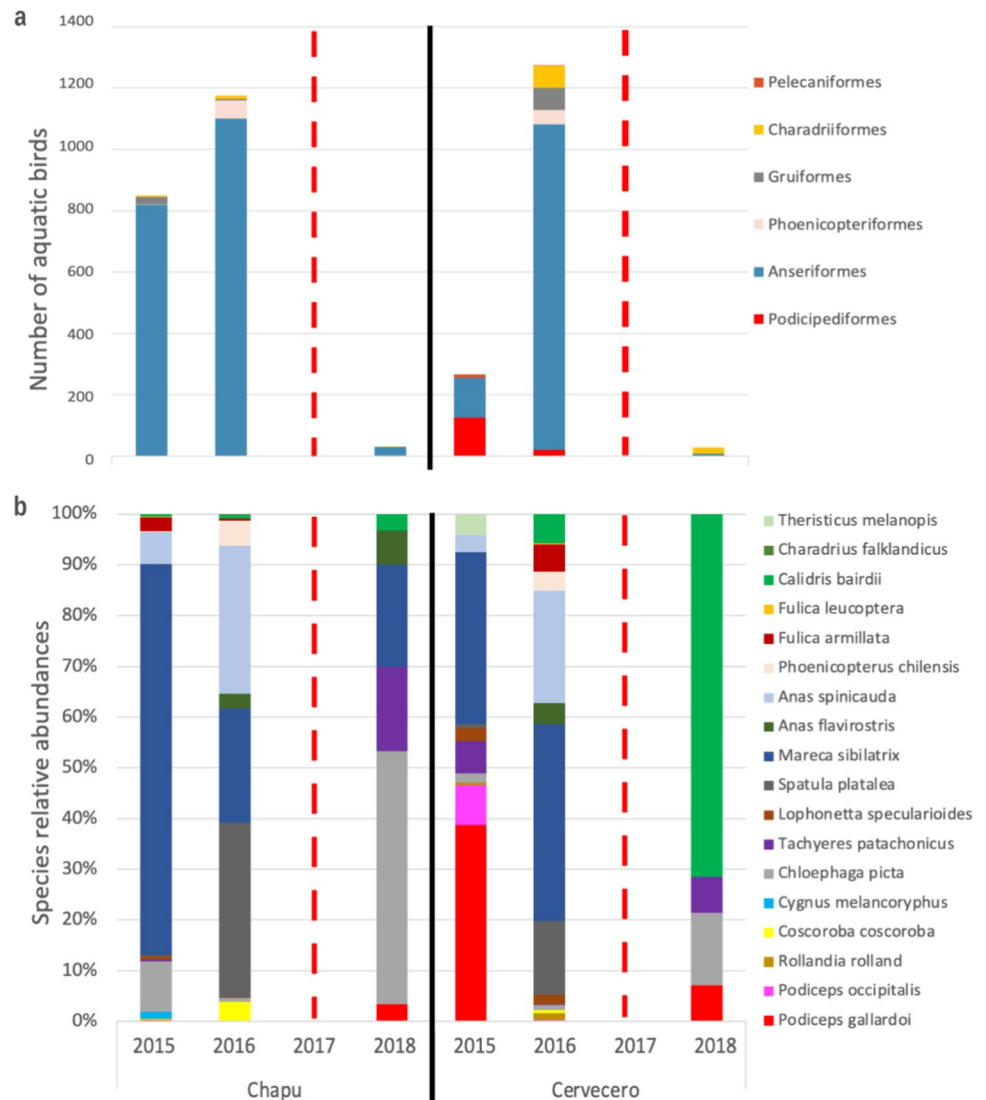
Lake use by waterbirds

The aquatic bird community was represented by 18 species in the 2015–2018 censuses in Chapu and Cervecero (Supplementary material 1d). These species belonged to the following avian orders: Anseriformes ($n=9$), Charadriiformes ($n=2$), Gruiformes ($n=2$), Pelecaniformes ($n=1$), Phoenicopteriformes ($n=1$), and Podicipediformes ($n=3$). Both lakes showed greater bird abundance in 2015 and 2016, when Anseriformes were dominant in both systems and Podicipediformes abundance was also high in Cervecero (Fig. 8a). In 2016, bird abundance in Cervecero had increased by 79% relative to 2015, with a total of 1274 birds, while in Chapu it had increased by 28%, with a total of 1175 birds. In 2018, bird abundance was lowest in both Chapu and Cervecero, with 30 and 28 individuals, respectively (Fig. 8a).

Mareca sibilatrix was one of the most abundant species in both lakes in 2015, with 657 individuals in Chapu and 90 in Cervecero (Fig. 8b). *Podiceps gallardoi* and *Podiceps occipitalis* were dominant in Cervecero in the high-water period of 2015, with 103 and 21 birds, respectively. However, in the partial drought of 2016 the dominant species in both lakes included *Mareca sibilatrix*, *Anas spinicauda*, *Spatula platalea*, *Anas flavirostris*, *Phoenicopus chilensis*, and *Coscoroba coscoroba*. In Cervecero, *Fulica armillata* (68 individuals) and *Calidris bairdii* (72 individuals) were also abundant in 2016. In 2018, *Chloephaga picta* (15 individuals) was dominant in Chapu and *Calidris bairdii* (20 individuals) in Cervecero (Fig. 8b). It is also worth highlighting that two hooded grebes were observed in these lakes in 2018 when the water level was high.

The highest waterbird richness was recorded for both lakes before the extreme drought of 2017 and the in 2018, after the lake refilling. Evenness for aquatic birds was closer

Fig. 8 Total number, relative abundance by order (a), and relative abundance of species of aquatic birds (b) in Chapu and Cervecero in 2015, 2016, and 2018. Red dashed lines indicate the absence of data for 2017, when the lakes dried up due to the extreme drought



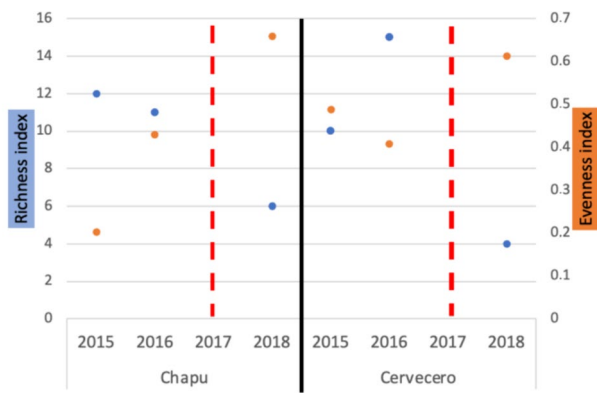


Fig. 9 Richness and evenness indexes for aquatic birds in Chapu and Cervecero for 2015, 2016, and 2018. Red dashed lines indicate the absence of data for 2017, when the lakes dried up due to the extreme drought

to 1 in 2018 in both lakes than in the other years of the study (Fig. 9).

Discussion

The results of this study indicate changes in the ecological regimes of two lakes resulting from marked interannual hydrological shifts, and the loss of aquatic vegetation during drought. These events led to a differential response of plankton communities and changes in waterbird assemblages, with implications for biodiversity conservation.

The lakes of the basaltic plateaus of arid Patagonia are dynamic systems that have shown increasing interannual variability over the last decades and a decreasing trend in surface area (Lancelotti et al. 2020) resulting from a reduction in local precipitation (Barros et al. 2014; Pessacq et al. 2020; Llanos et al. 2016; Scordo et al. 2018). Changes in the water levels of shallow lakes on these plateaus—triggered by prolonged drought or flash floods—have caused regime shifts from clear to turbid water, or vice versa. The evaporation of water during the partial drought in 2015–2016 resulted in a drastic increase in some of the main physical and chemical variables of lakes Cervecero and Chapu, such as total nutrient concentration, conductivity, DOC, and suspended solids. These effects led to a change in the regimes of both lakes; macrophyte cover was reduced and the structure of the plankton community changed, as reported for other lakes on the Patagonian plateau (Izaguirre et al. 2018) and other aquatic environments worldwide in response to drought (Chaparro et al. 2011; O’Farrell et al. 2011; Sánchez et al. 2015; Dembowska 2022). Although the lowest water levels were reached in both lakes during 2016, Chapu showed greater changes in abiotic variables than Cervecero,

including an increase in conductivity and the lowest depth and lake area recorded for the years of this study.

Between 2015 and 2016, when the partial drought occurred, there were different changes in the plankton communities. During 2015 and 2016, both lakes showed a similar diversity and relative abundance of bacteria. The most abundant phyla were Proteobacteria, Bacteroidota, Verrucomicrobiota, Actinobacteria, and Firmicutes; the first four have also been reported to be the most dominant phyla in other freshwater systems around the globe (Newton et al. 2011; Tessler et al. 2017). The members of these phyla have a global distribution (Tessler et al. 2017 and citations therein), apart from Firmicutes, which is considered a minor phylum of freshwater lakes. Members of the Firmicutes are commonly found in freshwater sediments (Newton et al. 2011), and the lowest water levels that were reported here, in 2016, might have favored wind-driven resuspension of bacteria from sediments. The highest HNA bacterial concentrations for both lakes were also measured in 2016, and are in agreement with the dominance of the HNA bacterial fraction reported in studies on aquatic environments with high nutrient loads (Harry et al. 2016; Pradeep Ram et al. 2016).

Regarding the PPP populations determined by flow cytometry, the highest density of picoeukaryotes in Cervecero, in 2016, is in agreement with other studies that reported dominance of picoeukaryotes over Pcy in less transparent and eutrophic lakes (Craig 1987; Vörös et al. 1998; Schiaffino et al. 2013; Izaguirre et al. 2014). This fraction, however, was not dominant in Chapu, and further research is needed where different strains are subjected to different light and nutrient conditions to characterize their adaptation to these. The greatest abundance of phycocyanin-rich Pcy, which was recorded in Cervecero in 2018, might have been related to the cyanobacteria bloom; indeed, Schallenberg et al. (2021) suggested that co-occurring cyanobacteria may cause strain-specific responses in Pcy. Certain Pcy have been shown to be associated with blooms of the larger filamentous cyanobacteria (Pick 2016), with both positive and negative relationships between them (Śliwińska-Wilczewska et al. 2018). Śliwińska-Wilczewska et al. (2017) showed that isolates of *Synechococcus* sp. had a positive effect on the growth of *Aphanizomenon flos-aquae* but a negative effect on other filamentous species. Various benthic and periphytic diatom taxa which are kept in suspension by wind-induced turbulence were dominant in Chapu in the low water period, and included *Achnanthes* sp., *Cocconeis* sp., *Cymbella* spp., and *Gomphonema* spp., which were also recorded under similar conditions in other environments (Allende et al. 2009; Padisák et al. 2009; Avigliano et al. 2014). In 2016, *C. braunii*, a species typically found in shallow eutrophic environments (Padisák et al. 2009), was dominant in Cervecero. These results are in line with those of other studies showing a drought-induced reduction in water level as a driving factor

of change in phytoplankton assemblages (Avigliano et al. 2014; da Costa et al. 2016).

Zooplankton biomass and abundance were greater in both lakes under low water level conditions. These findings are in line with those of Chaparro et al. (2011), who found greater mean abundances of rotifers, cladocerans, and copepods at low water levels. These results indicate that water level fluctuations are chiefly responsible for shaping zooplankton assemblages in fishless shallow lakes.

After the extreme drought in 2017 and the refilling phase in 2018, Chapu showed improved water quality as compared to 2015 and a clear state, while Cervecero showed the opposite pattern, with more turbid water and a deterioration in abiotic parameters as compared to 2015. A pattern of homogenization was evident in both lakes after the extreme drought in 2017, as indicated by lower diversity indexes for plankton and waterbirds than in 2015–2016, and was consistent with the results of other studies, including those on different taxonomic groups (Olden and Rooney 2006; Lougheed et al. 2008; Shaw et al. 2010; Chaparro et al. 2019; Zorzal-Almeida et al. 2021; Rusanov et al. 2022). Despite the proximity of these lakes (2.5 km apart) and common features, including basaltic origin, basins, and sediment type, their communities responded differently in the refilling phase. In Cervecero, a bloom of potentially toxic cyanobacteria (*D. flos aquae*) developed; to the best of our knowledge, this is the first report of this type of bloom occurring in a basaltic plateau lake. In Chapu, in contrast, the chlorophytes *Oocystis* spp., which are tolerant of high turbidity and low nutrient levels and inhabit clear, deeply mixed meso-eutrophic lakes (Reynolds et al. 2002; Padišák et al. 2009) were dominant. During the algal bloom in Cervecero there was a relative increase in phycocyanin-rich Pcy, which are more likely to occur in high-turbidity environments (Stomp et al. 2007; Schiaffino et al. 2013), and the rotifer *K. kostei*, a typical species of eutrophic systems (Marinone et al. 2006), was dominant.

The significant reduction seen in the biomass of zooplankton was consistent with the presence of filamentous cyanobacteria, which may be toxic to zooplankton, and are generally not consumed by them (Sivonen and Jones 1999; Havens 2008). However, rotifers, which are more selective feeders than filter feeders like *Daphnia*, thrive in the absence of cyanobacteria (Christoffersen et al. 1990; Frenken et al. 2018), and as members of the *Keratella* seem to prefer food particles with a diameter of $< 10 \mu\text{m}$ (Ronneberger 1998), *K. kostei* may have benefited from grazing on other sources of food (e.g., bacteria, zoospores) that were present during the cyanobacteria bloom (Christoffersen et al. 1990; Frenken et al. 2018).

Remarkable features of the bacterial homogenization in Chapu during the summer of 2018 were dominance of the genus *Pseudomonas* (Gammaproteobacteria) and, in

particular, affiliation of ASVs to *Limnohabitans parvus*. Although less evident than in Chapu, homogenization in Cervecero was also dominated by ASV14, which was affiliated to FukuN18_freshwater_group (Verrucumicrobiota) and *Silvanigrella aquatica* (with 95.1% identity). *Silvanigrella aquatica* is presently the only valid species within the family Silvanigrellaceae (phylum Proteobacteria), and was isolated from a small humic lake in the Black Forest mountain range in Germany (Hahn et al. 2017). Therefore, the extreme shift in the composition of the bacterioplankton community—particularly in Chapu with the extreme dominance of *Pseudomonas*—was an indicator of the sharp deterioration of bacterioplankton diversity that occurred after the drought in 2017.

Hydrological conditions influence the abiotic and biological characteristics of the lakes in arid Patagonia. Even though *M. quitense* can grow from seed (Orchard 1981), no macrophytes were detected in either lake after they had refilled in 2018. This indicates that the conditions were not optimal, or insufficient time had elapsed, for their germination and/or regrowth. An increase in phytoplankton biomass in turn increases turbidity, which has a negative effect on the development of macrophytes (Scheffer et al. 1993). In addition, some of the dominant cyanobacteria can produce cyanotoxins that have an allelopathic effect, which may have contributed to the macrophytes' decline (Mohamed 2017). Not only the reduction in water levels per se but also the absence of aquatic vegetation may have led to community homogenization, as macrophytes provide heterogeneous habitats in aquatic environments and distinct microhabitats for a variety of organisms (Lodge et al. 1988) such as rotifers (Duggan et al. 2001) and larger invertebrates, including zooplankton and macroinvertebrates (Cyr and Downing 1988).

As the data reported here cannot fully explain why these lakes, which are only 2.5 km apart, had such different abiotic and biotic conditions after drought and refilling, the effects of wind and lake morphometry should also be considered, since Cervecero has a typical pan-like shape, whereas Chapu is feather-shaped and has a longer fetch. As reported for lakes of the Pampean plain, the effects of drought vary with lake morphology (Seitz et al. 2020). Moreover, Chapu and Cervecero are isolated lakes that may be subjected to idiosyncratic forces or the effects of environmental variables that were not measured here.

Climate change has already led to a drastic reduction in the water levels of lakes of the Patagonian plateau, and has negatively impacted the availability of habitat for waterbirds of conservation importance in the region (Lancelotti et al. 2020). Variations in water levels in these lakes also have consequences for plankton communities, and the use of these aquatic systems by the hooded grebe. The use of lakes by birds also changes in response to habitat shifts, as seen in other aquatic systems (Riffel et al. 2001; González-Gajardo

et al. 2009). Although the partial drought altered the species composition and richness of waterbirds, their numbers remained high as compared to during the extreme drought and post-refilling phases, when bird density and richness were at their lowest. In 2015 and 2016 the conditions were much better for waterbirds than in 2018, and the greatest plankton community diversity was also seen in these earlier years. Despite the partial drought, waterbirds continued to use both lakes in 2016. The results indicate that the partial drought led to increased concentrations of nutrients and food, which supported a high density and richness of birds. Most of the dominant birds were species that feed in terrestrial aquatic zones, such as the Chiloé wigeon, yellow-billed pintail, yellow-billed teal, Chilean flamingo, red-gartered coot, and Baird's Sandpiper (Supplementary Table 1). However, when the water levels were high in 2018, both lakes only supported a few species, where Baird's Sandpiper—an aquatic-terrestrial feeder—was dominant in Cervecero and the upland goose—a herbivorous terrestrial feeder—in Chapu (Supplementary Table 1). These observations were made at the same time as the homogenization of plankton communities was observed as the lakes refilled. Although there were sources of food for most of the waterbird species during the partial drought of 2016, the decrease in the water level was disadvantageous for the hooded grebe, which was directly affected by the reduction in macrophytes. This endemic species avoids lakes with these types of conditions as they are not suitable for nesting and the establishment of colonies, which has implications for their reproduction (Roesler 2016). It also worth pointing out that Chapu, Cervecero, and other lakes on the plateau, recently dried up again, in 2022–2023 (SP, personal observations).

Conclusions

This study sheds light on the potential impact of drought on the aquatic ecosystems of the Patagonian steppe, including changes in abiotic factors such as water level, nutrient concentration, and water quality, as well as potential harm to the biotic community. Homogenization of communities was observed after the refilling phase of the lakes following the extreme drought, with the first record of a cyanobacteria bloom in Cervecero, which underlines the importance of conserving these ecosystems in a relatively pristine state. To the best of our knowledge, this is the first study to analyze changes in communities of three types of plankton—bacterioplankton, phytoplankton, and zooplankton—in lakes in a remote area of Patagonia. Patagonian lakes are crucial for the conservation of aquatic bird biodiversity in the region, and undergo drastic changes in water level as a result of climate change. Our results indicate that regular long-term

monitoring of these ecosystems is required to enable the preservation of their biodiversity and uniqueness.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00027-024-01083-w>.

Acknowledgements This work was supported by Fondo para la Investigación Científica y Tecnológica of Argentina (FONCYT PICT 2013-0794; PICT 2021-III-A-00090); Proyecto Macá Tobiano (Aves Argentinas/Ambiente Sur)—Programa Patagonia Aves Argentinas [Toyota Argentina, Nippon Car, Pan American Energy, CONTAIN/NERC-Latam, BirdLife International Preventing Extinction Programme (B. Olewine and S. and B. Thal), ICFC Canada, Toyota Environmental Activities Grant Programme, ZSL-EDGE, Secretaría de Ambiente de Santa Cruz, and the Whitley Fund For Nature]; Technical Advisory Agreement IEASA—CONICET—Macá Tobiano. We thank the staff and volunteers of Proyecto Macá Tobiano/Programa Patagonia (Aves Argentinas). We also thank the Dr. I. O'Farrell for their collaboration and V. Rago for field assistance, Dr. M.C. Diéguez for the DOC measurements, and D. Kachanovsky for assistance in processing the DNA data. We are grateful to the anonymous reviewers for their constructive comments, which greatly improved this article.

Author contributions SP performed the field work, was chiefly responsible for the microbial, phytoplankton and zooplankton analyses, performed data analyses, and wrote the manuscript. II and JL directed the project. MCM helped during the field campaigns and with zooplankton analyses. LF and IR were responsible for the aquatic bird censuses and gave valuable suggestions in this regard. MS carried out the BLAST analyses and helped with the bacterial DNA analyses. JL also participated in field trips and analyzed Landsat images with QGIS. CASG helped with bacterial DNA analyses and participated in two of the field campaigns. JS and II also helped with the field trips and with picoplankton and phytoplankton analyses. All authors were involved in the preparation and editing of this article.

Data availability Data are in supplementary information.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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