




Recent cyanobacteria abundance in a large sub-tropical reservoir inferred from analysis of sediment cores

Daniela Gangi · María Sofía Plastani · Cecilia Laprida · Andrea Lami ·
Nathalie Dubois · Facundo Bordet · Claudia Gogorza · Diego Frau ·
Paula de Tezanos Pinto 

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Abstract Salto Grande is a large South American reservoir on the border between Uruguay and Argentina that was impounded in 1979 and experiences recurrent, massive cyanobacteria blooms. A water-monitoring program was initiated 20 years after the dam was built, hence the causes and onset of cyanobacteria blooms remain poorly known. We collected two sediment cores from the old river channel in the reservoir ($z = 17$ m) and used physical, chemical and biological variables in the sediments,

along with existing limnological data, to explore the history of cyanobacteria in the sub-tropical water body. Cyanobacteria fossil pigments were present at low concentrations during the first 24 years after impoundment, but more than doubled thereafter. Phytoplankton abundance tracked shifts in cyanobacteria pigment concentration, indicating an overall increase in all primary producers. Several sediment variables indicate a decline in water quality after 2003, such as increases in the number of photosynthetic sulfur bacteria and a reduction in sediment magnetic susceptibility. Akinetes (dormant cyanobacteria cells,

Daniela Gangi and María Sofía Plastani share first authorship.

D. Gangi
Laboratorio de Limnología. Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

M. S. Plastani · C. Laprida
Laboratorio de Sondeos de Ambientes Continentales y Marinos (SACMa) IDEAN (UBA-CONICET), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina

A. Lami
CNR-Water Research Institute, Verbania, Italy

N. Dubois
Department of Earth Sciences, ETH Zürich, Zurich, Switzerland

N. Dubois
Surface Waters – Research and Management, Eawag, Swiss Federal Institute of Aquatic Science and Technology, Dübendorf, Switzerland

F. Bordet
Área de Gestión Ambiental, Gerencia de Ingeniería y Planeamiento, Comisión Técnica Mixta de Salto Grande (CTM), Concordia, Argentina

C. Gogorza
Centro de Investigaciones en Física e Ingeniería del Centro de la Provincia de Buenos Aires (CIFICEN-CONICET - UNCPBA - CICPBA), Tandil, Argentina

D. Frau
Instituto Nacional de Limnología (CONICET-UNL), Ciudad Universitaria Paraje El Pozo, 3000 Santa Fe, Argentina

P. de Tezanos Pinto (✉)
Instituto de Botánica Darwinion. Buenos Aires, Argentina. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina
e-mail: ptezanos@darwin.edu.ar

Order Nostocales) in recent reservoir deposits were abundant and five species germinated under laboratory conditions, underscoring the ability of akinetes to initiate cyanobacteria blooms. The germinated assemblage reflected closely the composition of cyanobacteria blooms in the reservoir. Recorded increases in air temperature and decreases in wind speed, together with other variables (e.g. nutrients), can promote the large, recurrent cyanobacteria blooms. Invasion of the bivalve *Limnoperna fortunei* apparently promoted cyanobacteria blooms by preferential feeding on other phytoplankton taxa, and perhaps by altering nutrient concentrations and ratios. This work highlights the potential for using multiple variables in sediment cores from large reservoirs to better understand the responses of biota to multiple environmental stressors.

Keywords Akinetes · Cyanobacteria · Pigments · Paleolimnology · Reservoir

Introduction

Cyanobacteria blooms occur in many water bodies around the world and can have negative ecological (Huisman et al. 2005; Ibelings and Havens 2008) and economic impacts (Merel et al. 2013), as some blooms are toxic to wildlife and humans. Many studies indicate that recent increased intensities and frequencies of cyanobacteria blooms are responses to eutrophication (O’Neil et al. 2012; Taranu et al. 2015), but climate change (Paerl and Paul 2012), hydrologic changes (IPCC 2014) and biological invasions (Carpenter et al. 1995; Boltovskoy et al. 2013) can also increase risks of cyanobacteria blooms.

Regular monitoring is crucial for assessing changes in the magnitude, frequency and duration of cyanobacteria blooms in inland waters. Direct observations and monitoring programs, however, have usually been initiated only recently and often lack data of high temporal resolution, precluding an understanding of longer-term environmental changes in aquatic ecosystems (Dearing 2013). Paleolimnology, the stratigraphic study of variables in sediment cores from inland water bodies, can provide long-term perspectives on past ecological conditions, even prior to the initiation of monitoring programs (Williamson et al. 2009; Kowalewski et al. 2016).

Among paleolimnological variables, pigments in sediments can be used as indicators of past relative algae and cyanobacteria abundances (Riedinger-Whitmore et al. 2005; Kowalewski et al. 2016). Riedinger-Whitmore et al. (2005) used sedimentary pigments, in combination with other sediment variables, to assess the timing and possible causes behind cyanobacteria proliferation in several sub-tropical water bodies in Florida, USA. In some of their lakes, abrupt pigment increases in sediments were linked to cultural eutrophication, whereas in other cases, long histories of high pigment concentrations reflected local edaphic (natural) conditions (Riedinger-Whitmore et al. 2005). Pigments in lake and reservoir sediments can also be used to infer past redox conditions (Guilizzoni 2012; McGowan 2013) and grazing pressure (Leavitt et al. 1993).

Among cyanobacteria, one group, the Order Nostocales, is capable of developing dormant cells called akinetes under unfavorable growth conditions. These specialized cells represent an important intermediate phase between past and future blooms, as akinetes form during blooms, can remain dormant, and then germinate to initiate new blooms (Legrand et al. 2017). Water bodies with large populations of planktonic cyanobacteria in the Order Nostocales usually possess large numbers of akinetes in their sediments (Hellweger et al. 2008). Akinetes in surface sediments can be used to assess the potential for development of new planktonic populations (Hellweger et al. 2008; Cirés et al. 2013), through quantification of akinetes in uppermost sediments and germination experiments.

During the twentieth century, extensive damming of rivers worldwide transformed many water bodies, formerly unsuitable for cyanobacteria growth, into artificial ecosystems where cyanobacteria proliferate (Znachor et al. 2006); mainly because of increased water retention times (Kalff 2002) and reduced turbulence. Today, many reservoirs around the world experience cyanobacteria blooms (Amé et al. 2003; Rahman et al. 2005; Znachor et al. 2006; Li et al. 2010; Joung et al. 2011; Te and Gin 2011).

Salto Grande reservoir, the focus of this study, is a large (750 km²), sub-tropical South American reservoir that experiences massive, recurrent blooms of cyanobacteria that belong to the Orders Chroococcales and Nostocales. Sporadic cyanobacteria blooms were observed in the reservoir after the dam was constructed in 1979 (Berón 1990), and by 2000–2002,

cyanobacteria relative abundance was high (Chalar 2009). Massive, recurrent blooms have been documented since 2007 (O'Farrell et al. 2012; Bordet et al. 2017). The reservoir was also invaded by the filter-feeding bivalve *Limnoperna fortunei* (Boltovskoy et al. 2006) and the watershed has undergone major land use changes (Drozd and Arturi 2017).

The Salto Grande hydroelectric dam (31.26° S latitude, 57.93° W longitude) was built on the Uruguay River in 1979, forming a large (783 m²), shallow ($z_{\text{mean}} = 6.4$ m) reservoir between Argentina and Uruguay. Regular monitoring of reservoir water quality started only after year 2000, leaving an information gap about limnological conditions during the first 21 years of dam operation. The almost 2 decades of monitoring data from Salto Grande reservoir provide information about physical, chemical and biological water column variables (Table 1), yet prior to this study, sediments in the reservoir had

never been investigated. Data collected since 2000 yielded important information about water quality in the reservoir, but it remains unclear whether cyanobacteria were abundant since the time of dam construction, or if they increased only later in the reservoir's history. Paleolimnological variables were studied to infer environmental conditions in the reservoir since the year of dam construction (1979), up to the year when regular monitoring was initiated (2000).

We analyzed two sediment cores from Salto Grande reservoir to explore the history of cyanobacteria populations in the water body. We used physical, chemical, and biological measures in the sediment, along with available historical environmental data, to address the following questions: (1) Have cyanobacteria in the reservoir increased since the dam was constructed, and if so, when did that occur? (2) What are the potential environmental drivers that trigger

Table 1 Physical and chemical characteristics of the Salto Grande reservoir. For chemical variables, only the values of the river-like area of the reservoir, where the cores were obtained,

are presented. Nutrient concentrations are expressed as mean and standard deviation

Salto Grande reservoir	Lat. S 29°43' to 31°12', Long. W 57°06' to 57°55'	
Reservoir area	750 km ²	Bordet et al. (2017)
Reservoir basin area	224,000 km ²	Chalar (2009)
Reservoir length	144 km (with its major axis running in a NS direction)	Bordet et al. (2017)
Reservoir physiognomy	Dendritic; one main channel and 5 lateral arms	O'Farrell and Izaguirre (2014)
Reservoir mean volume	5000 hm ³	Bordet et al. (2017)
Depth	Maximum: 35 m; average: 6.4 m	O'Farrell et al. (2012)
Mean water retention time	2 weeks (during low-water periods this can increase to 9 weeks or more)	Chalar (2006); O'Farrell et al. (2012)
Average yearly water discharge	4640 m ³ s ⁻¹ (although with pronounced seasonal variations)	Bordet et al. (2017)
pH	Slightly alkaline	O'Farrell et al. (2012); Bordet et al. (2017)
Trophic level	Eutrophic	O'Farrell et al. (2012); Bordet et al. (2017)
Mixing regime	Polymictic (with short thermal stratification during low discharge periods)	Bordet et al. (2017)
Nitrogen	Total: 850 ± 490 µg L ⁻¹ ; dissolved inorganic: 570 ± 260 µg L ⁻¹	Bordet et al. (2017)
Phosphorus	Total: 30 ± 20 µg L ⁻¹ ; reactive soluble: 20 ± 10 µg L ⁻¹	Bordet et al. (2017)
Mean air temperature	Annual: 19 °C winter: 7 °C; summer: 30 °C	Bordet et al. (2017)
Mean annual rainfall	1260 mm	O'Farrell et al. (2012)
Local winds	NE direction; mean monthly velocities between 10 and 12 m s ⁻¹	Bordet et al. (2017)

cyanobacteria blooms? We quantified akinete concentrations in recent deposits and in conjunction with laboratory germination experiments addressed the following questions: (3) How dense is the “akinete bank” in recent sediments? (4) Do relative abundances of germlings (filaments arising from germinated akinetes) reflect the cyanobacteria populations in the water column?

Materials and methods

Field sampling

Field sampling was carried out in Austral summer 2015, in the river-like area of the Salto Grande reservoir (Fig. 1). This area was selected because it has the greatest water depths (average: 10–20 m). Sediment cores were collected from a Regnicoli 630 boat, anchored at a water depth of 17 m. We obtained two cores: Core 1 (C1, at 31.20761° S, 57.91955° W), and Core 2 (C2 at 31.20806° S, 57.91857° W). Cores were taken with a hammer corer that had a ~ 1-m-long, 7.5-cm-ID core barrel. When the cores were brought to the reservoir surface, the sediment–water interface in both was intact, and no degassing

occurred. Cores were immediately covered with dark plastic to prevent exposure to light and were transported from the study site to the laboratory in a vertical position to prevent sediment mixing. In the laboratory, the cores were stored in a dark room at 4 °C to prevent pigment degradation.

Physical, geochemical and biological variables

Before the cores were opened, they were X-rayed to identify internal sediment structures. Afterwards, cores were split lengthwise, photographed, and their stratigraphy was described. Colors were defined according to the Munsell Soil Color Chart. Volume magnetic susceptibility was measured at 0.5-cm intervals using a Bartington MS3 and results were used to establish stratigraphic correlation between cores, and as a first-order indicator of the concentration of magnetic (*sensu lato*) minerals in the sediment (Thompson and Oldfield 1986). Next, each core was subsampled at 1-cm resolution using a small lab spatula. Core chronology was determined by ^{210}Pb dating. Ten subsamples from each core, of 4–5 g dry weight, were measured on a high-purity germanium (HPGe), well-type gamma spectrometer (Canberra Industries Inc.) at EAWAG, Switzerland.

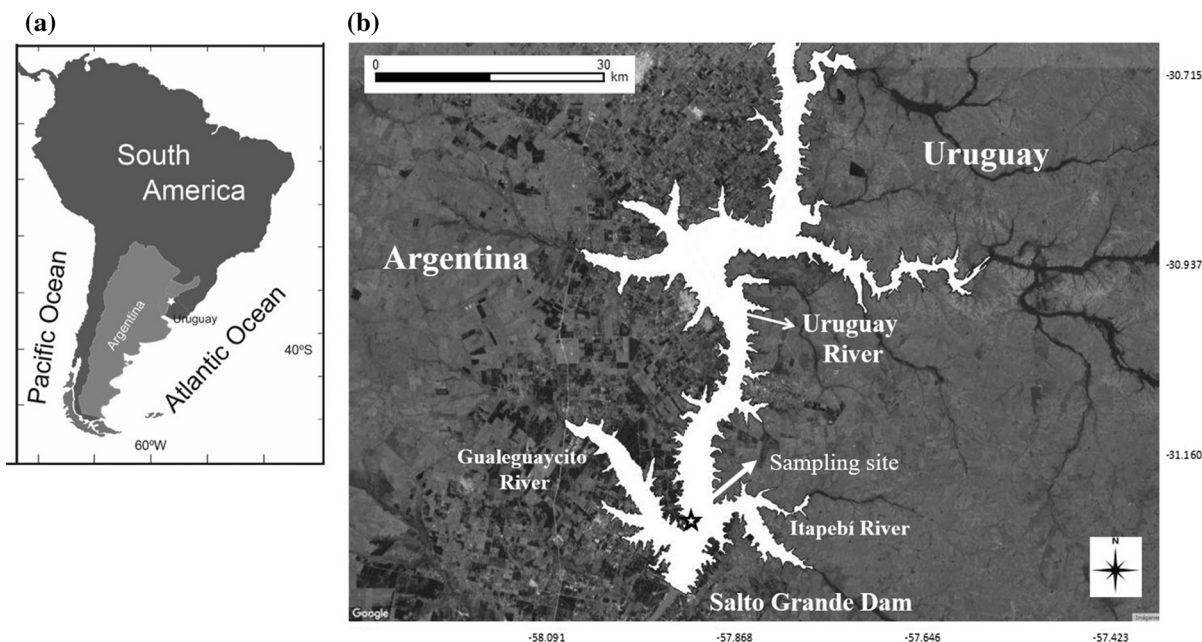


Fig. 1 Map of the Salto Grande reservoir showing the location (a) and morphology (b) of the reservoir. The star depicts the sampling site

Water content was measured on each 1-cm-resolution sample in both cores, by drying sediments at 60 °C for at least 24 h. Next, organic matter content was estimated by loss-on-ignition (Heiri et al. 2001). Sedimentary pigments were measured in each 1-cm-resolution sample from C1. Pigments were extracted from ~ 1 g of wet sediment with 5 mL of 90% acetone solution overnight in the dark at one atmosphere of nitrogen. Then, sediments were centrifuged at 3000 rpm for 10 min. The extract was used to quantify pigments using High Pressure Liquid Chromatography, with an Ultimate 3000 system (ThermoFisher) that consisted of a quaternary pump, an autosampler and a DAD detector. The elution program and the method for pigment identification, taxonomic specificity and quantification followed the procedures of Lami et al. (2009). The herbivory index, i.e. a proxy for grazing pressure, was calculated as the pigment ratio (chl a + pheophytin a)/pheophorbide (Leavitt et al. 1993). Finally, the wavelength absorption ratio 430 nm:410 nm was used as an index of pigment preservation, which can be used in cases where lakes are not acidified (Lami et al. 2000), as is the case for the Salto Grande reservoir (Table 1). Stratigraphic zones for each variable were determined using Optimal Partition (Birks and Gordon 1985). Statistical significance was determined by comparison against null models estimated by the Broken-stick model SSQ with the program BSTICK version 1.0 (Bennett 1996).

Sediment age–depth relationships and sedimentation rate calculations

To establish sediment age–depth relationships and calculate sedimentation rates, the constant flux constant sedimentation rate (CF-CSR), constant initial concentration (CIC) and constant rate of supply (CRS) models were utilized. The CRS model assumes a constant flux of excess ^{210}Pb to the sediment, but can accommodate variable sedimentation rate. In this model, the sediment age at depth is given by the ratio of excess ^{210}Pb activity below that point to the total excess ^{210}Pb activity in the sediment column (Appleby and Oldfield 1983). Thus, the CRS model is applicable to longer-term sedimentation, i.e. when at least ~ 100 years of sediment has accumulated. Because the dam was built in 1979, the reservoir sediment column is shorter than the equilibrium depth (age), i.e. the depth at which total ^{210}Pb would be in equilibrium

with the supported ^{210}Pb (^{226}Ra), which would require an age of about five ^{210}Pb half-lives, or ~ 110 years. Thus we could not measure the “complete” unsupported core inventory. Because the total unsupported inventory ^{210}Pb is important for application of the CRS model (Appleby 2001; MacKenzie et al. 2011), we opted instead to apply the constant initial concentration (CIC) model (Pennington et al. 1976). The CIC model assumes that the initial concentration of excess ^{210}Pb remained constant throughout the history of sediment accumulation, regardless of changes in the rate of sediment deposition (Pennington et al. 1976). The CIC model assumes that the sedimentation rate has remained constant through time, or that the flux of excess ^{210}Pb changed proportionally with changes in sediment accumulation. The CIC model has been applied successfully in aquatic environments where excess ^{210}Pb inputs are dominated by fluxes of sediment, and associated ^{210}Pb , mobilized from the surrounding catchment, as can be the case with urban reservoirs (McCall et al. 1984). When excess ^{210}Pb fluxes and sediment accumulation rates are both constant, the CRS and CIC models converge to the CF-CSR model and the excess ^{210}Pb activity declines exponentially with mass depth (Appleby 2001). Since ^{210}Pb decays logarithmically with time from its initial activity, with a decay constant of 0.03114 a^{-1} , the sediment age at any depth is given by: $t_z = (l/k) \text{Ln}(A_0/A_1)$ where t_z = age at depth z , k = ^{210}Pb decay constant, A_0 = initial unsupported ^{210}Pb activity per unit mass, and A_1 = unsupported ^{210}Pb activity per unit mass at depth z .

Historical environmental data

Historical data on air temperature, wind speed, and precipitation were provided by the weather station EEA, INTA (Estación Experimental Agropecuaria, 31.22531° S, 58.06551° W), located about 20 km southwest of the Salto Grande reservoir, and were available from 1967, prior to dam construction, to 2017. Water level and water flow data were provided by the Comisión Técnica Mixta and measured at the Salto Grande reservoir, and were available from 1994, 15 years after the dam was constructed, to 2017. We calculated annual mean values for air temperature, wind speed, water flow, and water level, and determined cumulative annual precipitation values. Temporal trends in these variables were analyzed

statistically using the non-parametric Mann–Kendall test (Gilbert 1987).

Cyanobacteria abundance

The three uppermost samples (3–2, 2–1, 1–0 cm) in cores C1 and C2 were used to assess recent cyanobacteria abundance. To characterize akinete density in each of the samples, about 0.5 g of wet sediment was diluted in 50 mL distilled water, and fixed with Lugol's solution. Akinete quantification was performed using a Palmer Cell with a Zeiss Standard 18 light microscope, at a magnification of 400 \times . At least three chambers were counted for each sample. Akinete density was first calculated as akinetes mL⁻¹, applying the formula: Akinetes mL⁻¹ = (C * a) F⁻¹, where C = total number of akinetes counted (unit = akinetes), a = the area of view, derived from the magnification and microscope used, and the depth of the counting chamber (mL⁻¹), and F = number of fields counted. Next, akinete density was converted into akinetes g⁻¹ dry weight, which accounts for the dilution applied (50 mL water) and the water content of sediments.

The akinete germination experiment was run under controlled laboratory conditions. Each treatment was run with three pseudo-replicates (2 cores * 3 layers [3–2, 2–1, 1–0 cm] * 3 pseudo-replicates = 18 experimental units). Each experimental unit contained 1 g of wet sediment in 150 mL of sterile WC culture medium (Guillard 1975). Total nitrogen and total phosphorus concentrations in the standard WC culture medium were modified to mimic historical nutrient levels in the reservoir; all other nutrient concentrations were those of WC medium. The experimental units were exposed to: light (100 μ mol photon m⁻² s⁻¹), temperature (25 °C) and photoperiod of 14 h light:10 h dark. These variables are similar to the ones used in our previous laboratory studies run with cyanobacteria at the population and community level (de Tezanos Pinto and Litchman 2010a, b). The experiment was run in batch regime (without replenishment of the culture medium) and lasted 2 weeks. This time frame is recognized as sufficient for observing filaments in germination experiments (Cirés et al. 2013). At the onset and end of the experiment, 15 mL samples were taken and fixed with Lugol's solution. Sampling at the beginning of the experiment was done to test for the absence of filaments in the

culture medium. If filaments are absent at the outset, then those observed at 15 days should have arisen from akinete germination, as well as from asexual reproduction of filaments from akinete germination. Filament density [filaments mL⁻¹ = (C * a) F⁻¹] was estimated using a Palmer cell with a Zeiss Standard 18 light microscope at a magnification of 160 \times , and at least five counting chambers were counted for each sample. Results are expressed as relative filament density because filament density in the culture media may result from either the germination of one akinete or from the asexual division of previously germinated filaments.

Results

Sediment description

Combined analysis of the X-ray radiographs and sedimentology of C1 (Fig. 2a) showed cm-scale laminations (very thin to thin-bed) throughout the core. Some discrete, isolated burrows disrupted the primary fabric in the middle and base of core C1, but did not disrupt the laminations (Fig. 2a). Analysis of sediment color showed layers of light (red and dark reddish brown) and dark (dark brown to very dark grey) sediments, reflecting siliciclastic sediments. The X-radiographs in C2 also showed cm-scale laminations, but without burrows (Fig. 2b). In C2, the upper 35 cm were composed of intercalated light and dark, silty siliciclastic sediments, similar to those in C1. Sediments below 35 cm, however, were composed of very dark (blue-black and dark gray) clayey silts with roots and terrestrial plant debris, which displayed the features of a mature soil (Fig. 2b). Organic matter and water content were in the range of 9–16% and 50–60%, respectively, in both cores (Fig. 2a, b). In C2, in particular, organic matter was low below 35 cm, i.e. in the underlying soils (Fig. 2b).

Core chronologies and correlation

In C1, excess ²¹⁰Pb activity did not decrease with depth (Fig. 2a). In C2, the excess ²¹⁰Pb activity profile displayed an overall exponential decrease with depth and was used to date the core. After removing an outlier at 20.5 cm depth, the CF-CSR model suggested a linear sedimentation rate of 0.67 cm a⁻¹ between 4.5

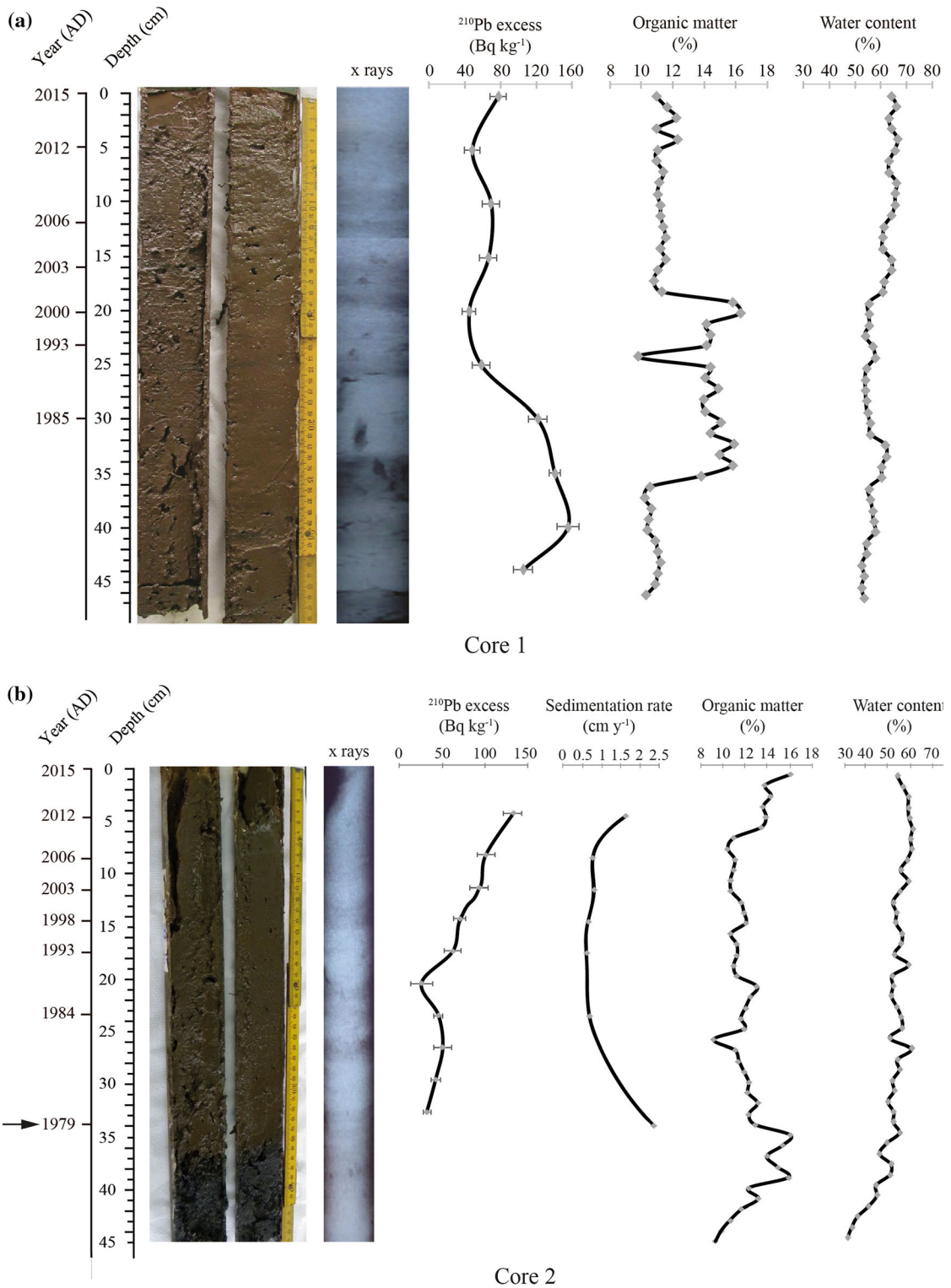


Fig. 2 Photograph of X-ray view, ^{210}Pb activity curve (with the error bars), organic matter (LOI) and water content for cores C1 (a) and C2 (b). Linear sedimentation rate is included for C2. The

black arrow in C2 (b) depicts the onset reservoir sedimentation above underlying soil (blue-black color in the photograph). (Color figure online)

and 32.5 cm ($R^2 = 0.96$). The final age model was established using two anchor points, in conjunction with the CIC model (Fig. 2b): (1) surface sediment (0 cm) was assigned a date of 2015, i.e. the coring year, and (2) the transition between soil and lacustrine sediments (35 cm) was assigned a date of 1979, the year the dam was constructed. Using only these two anchor points yields a mean linear sedimentation rate of 0.94 cm a^{-1} , somewhat higher than the value from the CF-CSR model (0.67 cm a^{-1}). According to the CF-CSR model, linear sedimentation rate was high when the dam was constructed (1979) and then declined until 1984. Thereafter it was stable until 2006, but increased afterwards (Fig. 2b). The ^{137}Cs activities were below detection limit in both cores, which is not surprising for sediments from the Southern Hemisphere deposited > 15 years after the peak year of atmospheric bomb testing, 1963.

Core correlation using magnetic susceptibility was based on five tie points above 27 cm in C2 and 32 cm

in C1 (Fig. 3). Correlation enabled establishment of an age model for C1, using the chronology of C2 (Fig. 3). In both cores, magnetic susceptibility declined by half after 2003 (Fig. 3). In C2, magnetic susceptibility was very low in sediments below 35 cm (1979), i.e. in the underlying soils (Fig. 3).

Fossil pigments

Pigments in sediments showed two significant zones, one from 1979 to 2003 and another from 2003 to 2015 (Fig. 4). Specific pigments for cyanobacteria, i.e. echinenone, zeaxanthin and myxoxanthophyll, were present throughout the core. Concentrations were low from 1979 to 2003, but increased after 2003 by 2.5- to 3-fold (Fig. 4). Likewise, pigments linked to phytoplankton (beta carotene), eukaryotic algae (diatoms, cryptophytes and chlorophytes) and photosynthetic sulfur bacteria were present at low concentrations from 1979 to 2003, but increased > 2.5 -fold after 2003

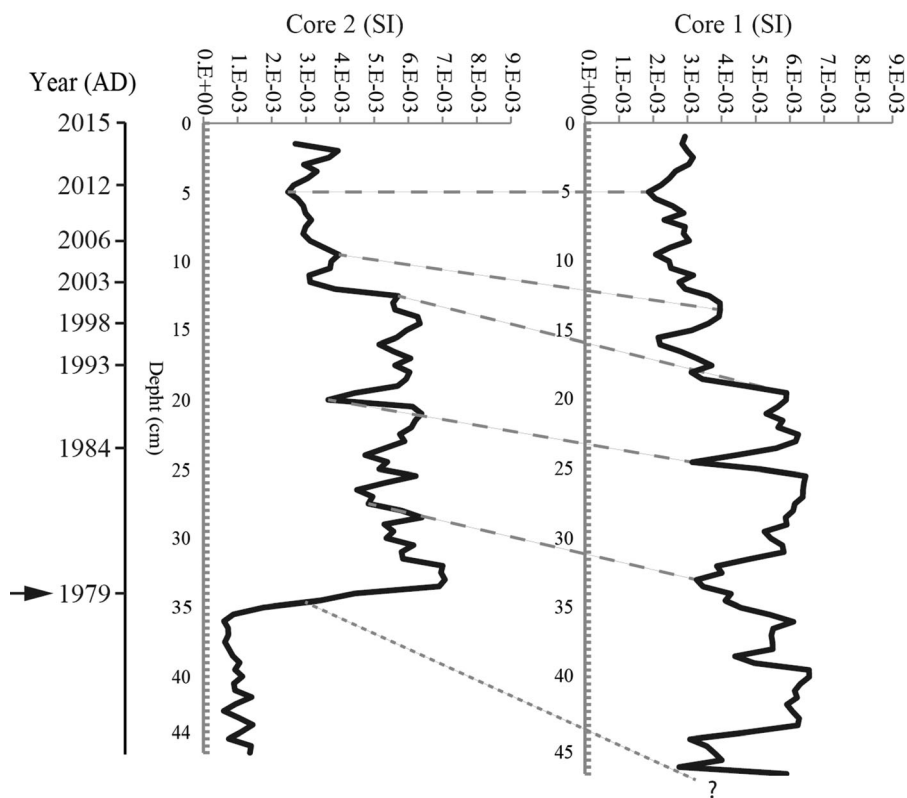


Fig. 3 Magnetic susceptibility and cross correlation of cores C1 and C2. Five tie points (dashed lines) enabled dating of C1 using the ^{210}Pb chronology of C2. The black arrow in C2 depicts

the shift between soil and lacustrine sediments, below which the magnetic susceptibility is very low

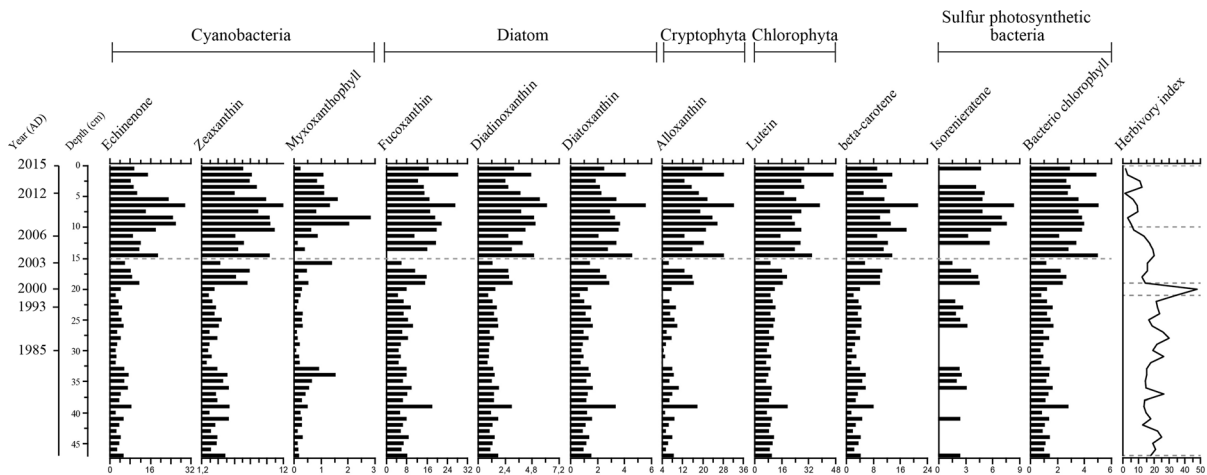


Fig. 4 Pigments denoting carotenoids specific for cyanobacteria, bacteria and phytoplankton (nMoles g^{-1} LOI) sorted by taxonomic affinity, and the herbivory index, (chl

(Fig. 4). The contribution of photosynthetic sulfur bacteria pigments was always low (mean isorenieratene concentration before and after 2003 = 2.4 and 5.5 nMoles g LOI $^{-1}$, respectively, and mean bacterio-chlorophyll before and after 2003 = 1.3 and 3.5 nMoles g LOI $^{-1}$, respectively) (Fig. 4).

The radiation absorption ratio 430 nm:410 nm in the sediment profile displayed values just below 1.0 (mean = 0.84, range = 0.75–0.89), without major changes before and after 2003 (Fig. 5). Values of the radiation absorption ratio 430 nm:410 nm near 1.0 indicate generally good preservation (Lami et al. 2000). The herbivory index (HI), for which lowest values indicate higher grazing (Leavitt et al. 1993), showed four significant zones, with an overall trend of increased grazing through time (Fig. 4). The four significant zones were: 1979–1997 (high and constant HI, low grazing), 1997–2001 (highest HI values, low grazing), 2001–2009 (decreased HI values, high grazing) and 2009–2015 (lowest HI values, highest grazing) (Fig. 4).

Historical environmental data

Mean annual air temperature increased significantly throughout the period analyzed (tau: 0.321, $p = 0.002$) by about 0.5–1 °C (Fig. 6), with a period of lower annual mean temperatures from 1968 to 1992 (< 19 °C) and an increasing trend from 1993 to 2009 (> 19 °C) (Fig. 6). Mean annual wind speed,

a + pheophythin a)/pheophorbide, for which lower values denote higher grazing on phytoplankton. Dashed lines separate significantly different zones for the variables analyzed

decreased significantly (tau: 6.04, $p < 0.0001$) by about 44% from 1967 to 2017: values were highest in 1967 (8.5 km h^{-1}), intermediate up to 1985 (< 8.5–> 6.05 km h^{-1}), and lowest (< 5.5 km h^{-1}) after 1985 (Fig. 6). There was no significant trend in annual precipitation (tau: 0.14, $p = 0.130$), with values ranging between 786 and 2193 mm (Fig. 6). Mean annual values of water discharge and water level also yielded non-significant trends (tau: 0.254, $p = 0.088$, tau: – 0.210, $p = 0.160$, respectively) with higher values in the intervals 1994–2005 and 2012–2017, and lower values from 2004 to 2012 (Fig. 6).

Current cyanobacteria abundance

Akinete abundance in the six sediment samples analyzed ranged from 3.5×10^4 to 1.8×10^5 akinetes g^{-1} dry, with a mean and standard deviation of $9.2 \times 10^4 \pm 5.7 \times 10^4$ akinetes g^{-1} dry. We did not observe colonies of *Microcystis* spp. (Order Chroococcales) in the six sediment samples.

At the onset of the germination experiment, we found no filaments in the culture medium of any of the 18 experimental units (2 cores * 3 depths * 3 pseudo-replicates). After 2 weeks, at the end of the experiment, we found filaments of five species: *Dolichospermum planctonicum* (Brunnthal) Wacklin, L. Hoffmann & Komárek, *D. circinalis* Rabenhorst ex Bornet et Flahault and *D. cf. pseudocompactum* (M. Watanabe), *Cuspidothrix issatschenkoi* (Usacev

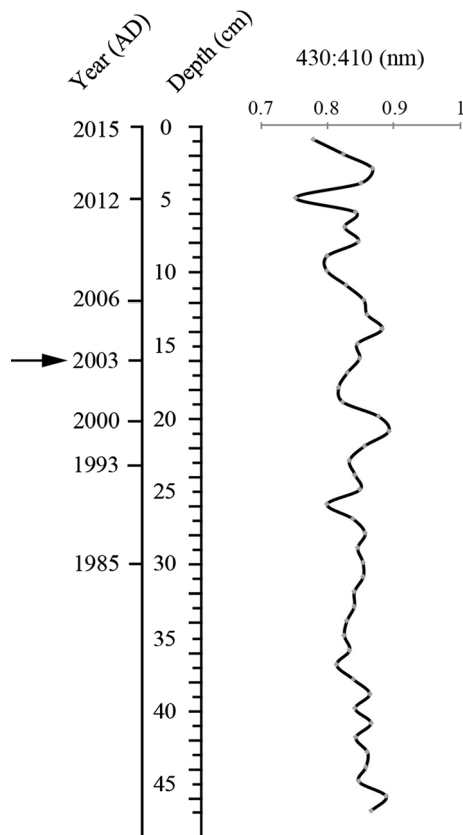


Fig. 5 Depth versus the radiation absorption ratio 430 nm:410 nm, an index of pigment preservation, for which values close to 1.0 indicate high pigment preservation. The arrow depicts the year 2003, when the shift towards increased productivity occurred. Note that the pigment preservation remains relatively constant before and after 2003

Rajaniemi, Komárek, Willame, Hrouzek, Kastovská, Hoffmann & Sivonen and *Aphanizomenon* sp. All 18 samples still lacked colonies of *Microcystis* spp. Filament relative abundances at day 15 were rather similar across samples (Fig. 7). The species with the highest relative contribution was *D. planctonicum* (mean 58%), followed by *Cuspidothrix* and *D. circinalis* (means of 20% and 17%, respectively), and smaller contributions of *Aphanizomenon* and *D. cf. pseudocompactum* (means of 3.5% and 1.6%, respectively) (Fig. 7). The three *Dolichospermum* species together represented about 76% of Nostocales abundance (Fig. 7).

Discussion

Core 2 (C2) was composed of a pre-inundation soil that was overlain by lacustrine sediments. The former was characterized by dark color, presence of roots, low values of magnetic susceptibility, and low organic matter content. Core 1 (C1), however, was composed exclusively of lacustrine sediments. X-ray analysis revealed laminae in both cores, which was confirmed by visual inspection of the sediments. The few burrows observed in C1 did not cause substantial bioturbation, as shown by the persistence of laminations, the ability to match the magnetic susceptibility records between cores, and the clear structure of the pigment profile. Although ^{210}Pb activity was measured in both cores, a reliable ^{210}Pb chronology could not be established for C1 because excess ^{210}Pb activity did not decrease with depth in the core. In C2, however, excess ^{210}Pb activity displayed a generally exponential decrease with depth and was used to date the sediments and calculate sedimentation rate. Linear sedimentation rate was high right after dam construction, stabilized thereafter, and showed a marked increase again in recent years.

We dated C1, based on the chronology of C2, by correlating the magnetic susceptibility profiles between cores, using five tie points. Magnetic susceptibility, used as a first-order indicator of the concentration of magnetic (sensu lato) minerals (Thompson and Oldfield 1986), dropped by half after 2003 in both cores. This decline in magnetic minerals (Thompson and Oldfield 1986) was probably related to reducing conditions and concomitant destruction of ferrimagnetic grains by diagenesis, associated with sulfate reduction (Kawamura et al. 2007). More studies, however, are needed to confirm this interpretation.

Fossil pigments in the cores enabled us to infer what happened between dam construction in 1979, and the onset of the limnological monitoring program in 2000, thereby filling in the 21-year information gap. Cyanobacteria fossil pigments echinenone, zeaxanthin and myxoxanthophyll were present in low abundances during the first 24 years after dam construction. The data confirm that blooms occurred in the reservoir immediately after the dam was constructed, but blooms at that time were evidently sporadic (Berón 1990). By 2000–2002, however, cyanobacteria dominated the phytoplankton assemblage (Chalar 2009). A large change occurred in 2003, and is documented by a



Fig. 6 Temporal trends through time for annual mean air temperature (significant increase, $p < 0.05$), annual mean wind speed (significant decrease, $p < 0.05$), annual precipitation, annual mean water flow and annual mean water level. The dark

arrow denotes the year when the dam was built (1979) and the gray arrow denotes the year when the shift towards increased cyanobacteria occurred (2003)

2.5- to 3-fold increase in cyanobacteria pigment concentrations. This paleolimnological result is consistent with what was observed in the water monitoring program, which shows that blooms have been massive and recurrent since at least 2007 (O’Farrell

et al. 2012; Bordet et al. 2017). As observed for pigments of cyanobacteria, pigments of eukaryotic phytoplankton (diatoms, chlorophytes, cryptophytes) and photosynthetic sulfur bacteria were present at low

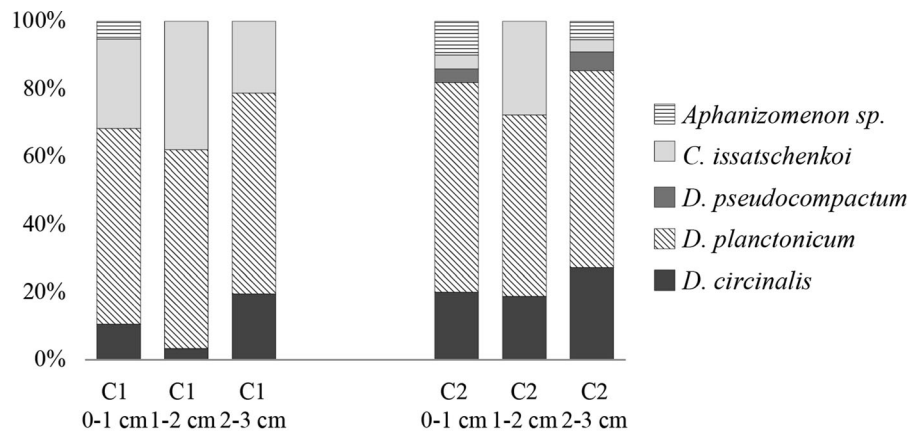


Fig. 7 Relative filament abundance for the cyanobacteria species of the Order Nostocales at the end of the germination experiment (day 15), in both cores (C1 and C2), and the three analyzed depths in near-surface sediments (3–2, 2–1, 1–0 cm)

concentrations during the first 24 years after impoundment, but increased substantially, $> 2.5\times$ after 2003.

The rise in pigments of photosynthetic sulfur bacteria, which thrive under extreme environmental conditions, such as anoxia and darkness or low light, suggests an increase in bottom anoxia after 2003. Though such O_2 -free conditions could have enhanced pigment preservation, the radiation absorption ratio 430 nm:410 nm, a proxy for pigment preservation, yielded consistent, high values throughout the core, indicating there had been no change in pigment preservation. Thus, higher pigment abundances in the core after 2003 reflect a real shift in productivity and are not a simple artifact of pigment preservation.

Given the high magnitude and frequency of blooms in the reservoir observed during regular water monitoring (O'Farrell et al. 2012; Bordet et al. 2017), we expected to find a higher relative increase in cyanobacteria over eukaryotic phytoplankton. We found, however, that cyanobacteria trends tracked shifts in the phytoplankton community as a whole, without there having been major community reorganization. The latter can result from seasonal alternation of phytoplankton groups observed in the reservoir, with high relative cyanobacteria dominance during warm periods and high relative dominance of eukaryotic algae during winter (Bordet et al. 2017). It is possible that lack of sub-annual (seasonal) resolution in the sediment record from Salto Grande reservoir precludes identification of a seasonal signal. We note that bloom magnitude in this reservoir is highest in the dendritic, shallower areas of the water body, compared to

blooms in the river-like area, as the latter has higher flow and greater depth (O'Farrell et al. 2012; Bordet et al. 2017; Drozd et al. 2019).

Grazing pressure on phytoplankton was low from the year of dam construction (1979) until 2001, when it first significantly increased, then increased again after 2008. The onset of increased grazing (2001) coincided almost exactly with the expansion of the exotic bivalve *Limnoperna fortunei*, which was first detected in the reservoir in 2001, and by 2003 had reached densities up to 50,000 individuals m^{-2} (Boltovskoy et al. 2006). Cladoceran and copepod densities, however, were rather low, with annual records during 2004–2012 ranging from quasi-absent to 6 individuals L^{-1} (Boltovskoy et al. 2013). Hence, increased grazing seems to have been related more to bivalve expansion than to zooplankton grazing. Moreover, Cataldo et al. (2012) showed at the mesocosm scale, *L. fortunei* favors blooms of *Microcystis* by modifying nutrient concentrations and proportions, and by promoting the formation of larger cyanobacteria colonies. The bivalve is a filter feeder, capable of filtering 357 mL $ind^{-1} h^{-1}$ at 28 °C (Frau et al. 2013), and studies of its stomach contents found that its diet was mostly composed by euglenoids, diatoms and green algae (Rojas Molina et al. 2010). Such selective grazing could indirectly favor cyanobacteria over eukaryotic algae. Hence, grazing pressure exerted by the exotic bivalve *L. fortunei* seems to promote, rather than control cyanobacteria growth.

Several studies suggest that water quality in the Salto Grande reservoir declined in the 24 years after its construction, including a more than two-fold increase in cyanobacteria (and other phytoplankton) productivity, an increase in photosynthetic sulfur bacteria (though still low in concentration) and an increase in sedimentation rate. These results underscore that degradation of this sub-tropical reservoir occurred over the course of decades, as has been recorded in tropical reservoirs elsewhere (Wengrat et al. 2018).

Historical environmental data show that for the period 1967–2017, air temperature increased significantly and wind speed decreased significantly by 44%, whereas precipitation remained unchanged. The increase in air temperature was 0.5–1.0 °C and was higher after 1993. Higher temperatures may enhance cyanobacteria growth through direct effects on growth rate (Paerl 2017) and through interactive effects with nutrients (Wagner and Adrian 2009) and wind. Indeed, in the Salto Grande reservoir, Bordet et al. (2017) observed that cyanobacteria surface blooms developed whenever temperature was above 16.5 °C and wind speed was $\leq 3.5 \text{ km h}^{-1}$. Current mean annual wind speeds are $< 3.5 \text{ km h}^{-1}$, favoring the establishment of cyanobacteria that develop scum-type blooms that accumulate on the surface (*Microcystis* spp. and *Dolichospermum* spp. complex). Water discharge and water level showed similar trends during the period analyzed, the 23 years between 1994 and 2017, though this time frame may be too short to detect statistical changes. Cultural eutrophication was not assessed in this study, as the historical nutrient record is incomplete. Nevertheless, the water body is eutrophic (Table 1) and the area has experienced major changes in land use in the last 30 years (Drozd and Arturi 2017), and major increases in population, which probably affected nutrient concentrations in the reservoir.

The akinete (dormant cells) seed bank in the upmost sediments was large, and displayed concentrations similar to values in other reservoirs that experience cyanobacteria blooms (Cirés et al. 2013). Indeed, water bodies with large populations of planktonic cyanobacteria of the Order Nostocales usually contain large numbers of akinetes in their sediments (Hellweger et al. 2008). We found no *Microcystis* colonies in the sediments, even though sampled during a bloom, suggesting that this genus is unable to survive

in deep-water sediments (17 m) of the river-like area, even during the growing season. This finding is not surprising, as *Microcystis* is unable to produce dormant cells. In laboratory conditions we observed germination from near-surface sediments of five Nostocales species, underscoring the capacity of this group of cyanobacteria to recolonize the plankton from inocula in sediments, under favorable conditions. In situ germination in the river-like area, however, could be less successful because of less favorable environmental conditions, relative to those in the laboratory. Two of the *Dolichospermum* species found in the sediments were described as dominant in the water column of the reservoir by O'Farrell et al. 2012), where mostly scum-forming blooms develop (*Dolichospermum* and *Microcystis* complexes) (O'Farrell et al. 2012; Bordet et al. 2017). Moreover, the relative dominance of the germling community, 76% *Dolichospermum* spp., reflected closely the dominance patterns observed in the water column by O'Farrell et al. (2012) and Bordet et al. (2017).

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