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Differing limnological responses to late Holocene climate variability in the Cordillera Vilcanota, Peruvian Andes

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Abstract In recent decades, climate change in Peru's Cordillera Vilcanota has resulted in massive reductions to its cryosphere and the upslope migration of species and agriculture. Little, however, is known about the response of the region's many lakes that support local biodiversity and supply water to downstream populations. We analyzed fossil diatom assemblages in dated sediment cores from three lakes with differing morphometry and catchment characteristics to document the limnological response to climate variability over the late Holocene. The study lakes contained similar dominant diatom taxa but recorded markedly different assemblage shifts over time. The two deeper lakes, Laguna Sibinacocha ($z_{max} = 92 \text{ m}$) and Chaca Cocha ($z_{max} = 18$ m), contained diatom assemblages that oscillated in dominance between benthic fragilarioids (Staurosirella pinnata.

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INAIGEM – Dirección de Investigación en Ecosistemas de Montañas, Huaraz, Peru e-mail: ptapia@inaigem.gob.pe Pseudostaurosira brevistriata) and the planktonic Discostella stelligera. The Chaca Cocha diatom record closely matched the mean state changes in climate inferred from independent proxy records, whereas the record from the glacially influenced Laguna Sibinacocha did not match independent records. In contrast, the shallow study site, Lado del Quelccaya ($z_{max} = 5 \text{ m}$), recorded a complacent diatom profile dominated by benthic fragilarioids with negligible planktonic taxa. The disparate diatom trajectories among the study lakes reflect variations in morphometry and glacial influence and the assemblage shifts appear best explained by climate-driven alterations to thermal stratification. These data offer insight into the primary mechanisms driving limnological change in this region and how different lake types throughout the Andes may respond to future warming.

Keywords Diatoms · High-altitude · Climate change · Tropical Andes · Glacial lakes

Introduction

Mountain ecosystems show some of the clearest indications of twentieth century warming (Moser et al. 2019). This is perhaps best exemplified in the Cordillera Vilcanota in the Peruvian tropical Andes, where numerous studies have revealed the type of climate-driven changes relevant to mountain regions worldwide. For example, rising temperatures in recent decades (Michelutti et al. 2019a) have led to massive reductions in this mountain range's cryosphere (approximately 30% of area and 45% of volume since 1985; Salzmann et al. 2013), including the world's largest tropical glacier (Quelccaya Ice Cap), which has rapidly retreated (~ 300 m in 25 years) to limits unprecedented within the past six millennia (Thompson et al. 2013). Freshly deglaciated terrain has allowed anurans to set new altitude records for amphibians globally (5244-5400 m asl) and led to upward range extensions for soil microbes and pathogens (Schmidt et al. 2008; Seimon et al. 2007; Nemergut et al. 2006). Cultivation practices have also shifted several hundred meters upslope to elevations where agriculture was previously non-viable (Halloy et al. 2005). Considered together, these studies offer little doubt that ecosystem-scale effects of recent warming are well underway in the Cordillera Vilcanota. However, limnological research and, in particular, the response of lakes to climate change has been largely neglected in this region.

Glacier shrinkage in the Cordillera Vilcanota (Drenkhan et al. 2018) threatens the water supply for thousands of downstream users. A large-scale hydrological project has already occurred in response to concerns over reductions in the dry season flow from glacier-fed rivers. In 1996, the region's largest lake, Laguna Sibinacocha, was dammed to ensure adequate flow for agricultural, hydropower and household needs for hundreds of thousands of people downstream. The Cordillera Vilcanota's many lakes also support local populations and their livestock and help maintain the region's high biodiversity (Raven 2011).

Although the future of aquatic ecosystems in the Cordillera Vilcanota is closely connected to changing climate conditions, data on how the lakes have responded to climate over recent or long-term time-scales are lacking. A limnological survey of lakes and ponds in this region (Michelutti et al. 2019a) provided baseline data to assess future change, but offers no long-term perspective. Lake sediments, however, provide a means to reconstruct limnological histories and, indeed, are amongst the most widely distributed archives of past change throughout the Andes (Stansell et al. 2013; Bird et al. 2011; Bush et al. 2005).

Here we present paleolimnological records, spanning the late Holocene, from three lakes in the Cordillera Vilcanota (Fig. 1). Although there have been a few paleolimnological studies in this region, they concern clastic sediment delivery as a means to infer regional ice cover (Stroup et al. 2015; Rodbell et al. 2008) and atmospheric Hg deposition (Beal et al. 2014). Our focus was to assess long-term limnological change in response to climate variability, specifically by examining subfossil diatom (algal) bioindicators preserved in sediment cores. The Cordillera Vilcanota contains a diverse waterscape and much of the presentday limnological variability is driven by waterbody size and whether or not lakes receive glacial meltwater (Michelutti et al. 2019a). With this in mind, we selected three study lakes of different size and glacial influence. These include: (1) Laguna Sibinacocha, a large and deep lake that receives glacier meltwater inputs; (2) Chaca Cocha, a medium sized lake located in a glacier-free catchment; and (3) Lado del Quelccaya, a small, shallow lake that receives no direct glacial inputs, but is located near the Quelccaya Ice Cap (Fig. 1).

Diatoms (Bacillariophyceae) respond sensitively to the types of climate-driven changes expected to impact lakes in the tropical Andes. For example, meltwater from retreating glaciers may alter limnological properties by disrupting thermal stratification and mixing regimes (Sienkiewicz et al. 2017), affecting light penetration (Sommaruga 2015), enhancing nutrient inputs (Saros et al. 2010) and releasing metals



Fig. 1 Map showing the location of the study lakes (appearing as dark objects) and the Quelccaya Ice Cap (QIC; appearing as white) in the Cordillera Vilcanota region of Peru

and contaminants previously deposited on and contained within the ice sheet (Fortner et al. 2011; Blais et al. 2001). As a result, diatom assemblages from lakes within and outside glacial catchments often track different aspects of limnological change through time. In a similar vein, shallow waterbodies (Giles et al. 2018) respond differently to climate change compared to deep lakes (Michelutti et al. 2015). Although often overlooked, shallow lakes are prominent features of the tropical Andes and typically outnumber their deeper counterparts (Mosquera et al. 2017). They are usually adjacent to wetlands, locally referred to as *bofedales*, and are important to regional biodiversity, water regulating capacity and carbon sequestration (Cooper et al. 2010).

Lake histories often show individual characteristics because of differences in basin morphometry and catchment characteristics (Bräuning 2009). With this understanding, we selected study sites that spanned a range of size and glacial influence to assess limnological variability through time and to determine how prominent features of past climate change are expressed in lakes from this region. We chose the Cordillera Vilcanota as a study region, in part, because annually resolved ice-core records extending back to \sim 1800 years BP are available from the nearby Quelccaya Ice Cap (Fig. 1), and provide high-resolution paleoclimate data over the late Holocene with which to compare our paleolimnological records (Thompson et al. 2013). In particular, we were interested in the response of diatom assemblages to local expressions of distinct climate intervals identified by the Quelccaya ice core records, including the Medieval Climate Anomaly, Little Ice Age, and Current Warm Period.

Site description

The Cordillera Vilcanota is located in southeastern Peru ($\sim 14^{\circ}$ S, 71° W) at the eastern margin of the Andes (Fig. 1). It is amongst the most glacierized mountain ranges in the country, second only to the Cordillera Blanca to the north, and contains the Quelccaya Ice Cap, which is the world's largest tropical glacier. Seasonality is defined by a rainy period during the austral summer from October to March and a dry period during winter from April to September (Rabatel et al. 2013). Temperature differences between the summer and winter seasons are small, typically 1–2 °C; however, diurnal temperatures can vary by as much as \sim 18 °C.

Long-term meteorological records are rare within the Cordillera Vilcanota; however, there are two stations near the study lakes, run by the Peruvian National Weather Service (Servicio Nacional de Meteorología y Hidrología (SENAMHI)), which have data who extend back to the mid-1960s. The Ccatcca station (3729 m asl), \sim 60 km WNW of the study lakes, recorded mean minimum and maximum daily temperatures of 1.3 and 15.3 °C, respectively, and mean annual precipitation of 608 mm over the periods 1965-2014. The Pomacanchi station (3200 m asl), \sim 60 km WSW of the study lakes, recorded mean minimum and maximum daily temperatures of 2.8 and 17.2 °C, respectively, and mean annual precipitation of 851 mm over the periods 1985-2014 (Michelutti et al. 2019a).

The Ccatcca and Pomacanchi climate stations have recorded significant trends in temperature and precipitation since records first began in 1965 to 1985, respectively. The Ccatcca station shows increases of $0.23 \text{ °C} (r^2 = 0.001, P < 0.001)$ in maximum daily temperatures and 1.08 °C ($r^2 = 0.01$, P < 0.001) in minimum daily temperatures over its 49-year history (1965–2014). Precipitation at Ccatcca shows a significant increase of 139 mm from 1965 to 2014 (tau = 0.218, P = 0.029). The Pomacanchi station shows increases of 0.37 °C ($r^2 = 0.004$, P < 0.001) in maximum daily temperatures and 0.80 °C ($r^2 = 0.014$, P < 0.01) in minimum daily temperatures over its 29-year history (1985-2014). Precipitation at Ccatcca shows a significant increase of 457 mm from 1965 to 2014 (tau = 0.355, P = 0.007). Mean monthly wind velocity, obtained from the NOAA NCEP/NCAR reanalysis dataset (Kalnay et al. 1996), using data from the 600 hPa pressure level, recorded a minor and nonsignificant decreasing trend over the 38-year record (i.e. 1979–2017; tau = -0.001, P = 0.965; Michelutti et al. 2019a).

Seasonality in the tropical Andes is driven by precipitation variability, which is governed by the strength of the South American Summer Monsoon (SASM). Although only first described in the late-1990s (Zhou and Lau 1998), SASM variability in Peru has been the focus of numerous paleoclimate studies (Reuter et al. 2009; Bird et al. 2011; Stansell et al. 2013; Kanner et al. 2013; Bustamante et al. 2016). The SASM displays distinct seasonality, beginning in

October, with a mature phase between December and February, before declining in April. The demise phase begins between March and May when the monsoon loses strength, eventually leading to a dry winter season (Vuille et al. 2012). The SASM is influenced over inter-annual timescales by variability in mean-state conditions of the El Niño Southern Oscillation (ENSO), the Pacific Decadal Oscillation (PDO), and the Atlantic Decadal Oscillation (ADO), among others (Vuille et al. 2012). Also of importance is the position of the Intertropical Convergence Zone (ITCZ) during the austral summer (December–March), which influences SASM intensity (Bird et al. 2011).

Paleoclimate studies from tropical South America often focus on reconstructing SASM variability and/or temperature and include diverse climate proxies in archives such as lake sediments (Bird et al. 2011), ice cores (Thompson et al. 2013), cave speleothems (Reuter et al. 2009), tree rings (Morales et al. 2012), and marine sediment cores (Haug et al. 2001). Although we consider all relevant paleoclimate reconstructions when interpreting our lake sediment records, we focus primarily on ice core data from the Quelccaya Ice Cap because of its proximity to the study lakes and the fact that it offers annually resolved δ^{18} O and net accumulation histories, reflecting temperature and precipitation, respectively, for the past \sim 1800 years (Thompson et al. 2013). The ice core data reveal several distinct climate intervals, including the: (1) Medieval Climate Anomaly (MCA) from \sim 1100 to 1300 CE, characterized by warm and dry conditions; (2) Little Ice Age (LIA) from \sim 1520 to 1880 CE, characterized by cool temperatures and alternating between wet conditions in the early portion (1520–1680) and dry conditions in the latter portion (1681-1880 CE); and (3) Current Warm Period (CWP) from 1880 CE to present, characterized by a return to warmer and wetter conditions relative to the late LIA (Thompson et al. 2013).

The study sites are located within 20 km of one another on a plateau (\sim 4800 m asl) in the region near Laguna Sibinacocha (Fig. 1). Limnological details for the study sites, and from other waterbodies from this region, are given in Michelutti et al. (2019a), and are summarized briefly below and in Table 1.

Laguna Sibinacocha (13° 54.072 S; 71° 00.741 W) is the largest of the three study lakes (Fig. 1; Electronic Supplementary Figure [ESM] Fig. 1). Situated at an altitude of 4870 m asl, with an area of

 \sim 3000 ha and a maximum depth of 92 m, it is a dominant landscape feature of the region and one of the largest, high-elevation lakes on the planet. The lake is a primary source of the Vilcanota-Urubamba River, a major tributary to the Amazon River. Laguna Sibinacocha has been stocked with rainbow trout (Oncorhynchus mykiss) and serves as an important fishery for a small number of local people who live in and around its catchment. In response to climaterelated concerns over decreases in dry season flow from glacially fed rivers, a dam (~ 357 m long by 12 m high) was constructed in 1996 at the lake's outflow to ensure adequate flow for downstream needs. Water supplied from Laguna Sibinacocha is used primarily for agriculture (50%), followed by energy (36.5%) and households (11.6%; MINAM 2018). Since 2013, water levels have dropped below the maximum capacity of the dam, which did not happen in previous years (MINAM 2018). This suggests either an increase in water consumption and/or enhanced drought periods in recent years. Despite being a critical water resource for hundreds of thousands of people, only recently have basic limnological data been gathered (Michelutti et al. 2019a). Briefly, the lake is circum-neutral (pH 7.9), ultraoligotrophic (total phosphorus = $3.3 \mu g/L$) and relatively dilute (conductivity = 380μ S/cm; Table 1). It is a cold-water lake (temperatures < 12 °C) that experiences only short periods of weak thermal stratification (Michelutti et al. 2019a). An actively melting glacier (Seimon et al. 2017) drains into the northern basin of the lake, but this does not result in any temperature gradient along its \sim 15-km length (Michelutti et al. 2019a).

Chaca Cocha (13° 57.758 S; 71° 04.672 W) is the second largest of the study lakes (Fig. 1; ESM Fig. 1). Situated at an altitude of 4860 m asl, it has an area of 167 ha and a maximum depth of ~ 18 m. The lake is circum-neutral (pH 7.29), oligotrophic (total phosphorus = 9.7 μ g/L) and dilute (conductivity = 19 μ S/ cm; Table 1). There are no data on annual circulation or thermal stratification, but an adjacent lake of similar size and depth, Uma Cocha (Fig. 1), recorded a relatively well-mixed water column with only brief periods of weak thermal stratification over a 1-year period from 2016 to 2017 (ESM Fig. 2). The lake is not located within a glacial watershed and the nearest glaciers are ~ 20 km away, including the glaciers to the north of Laguna Sibinacocha and the Quelccaya

	рН	COND (µS/cm)	DOC (mg/L)	TN (mg/L)	TP (µg/L)	Area (ha)	Zmax (m)	Elev (m asl)	Coring location
Sibinacocha	7.84	380	2.5	0.220	3.3	3000	92	4870	13° 54.072 S; 71° 00.741 W
Chaca Cocha	7.29	19	3.7	0.283	9.7	166.57	18	4860	13° 57.758 S; 71° 04.672 W
Lado del Quelccaya	7.04	7	7.3	0.565	13.1	2.21	5	4825	13° 56.876 S; 70° 54.055 W

Table 1 Select limnological variables and data for the study lakes

Ice Cap to the east (Fig. 1). The lake is fed primarily by precipitation. During high-water periods, the lake drains from an outlet along its southern shore into nearby Uma Cocha (Fig. 1). There is no development within the catchment and the only human impacts are from herders who periodically graze their animals near the lake.

Lado del Quelccaya (13° 56.876 S; 70° 54.055 W; unofficial name) is the smallest of the study lakes (Fig. 1; ESM Fig. 1). Situated at an altitude of 4825 m asl, it has an area of 2.2 ha and a maximum depth of ~ 5 m. This shallow lake is located in close proximity $(\sim 5 \text{ km})$ to the Quelccaya Ice Cap, but does not receive any glacial hydrologic input. The lake is fed mainly by precipitation. The lake is circum-neutral (pH 7.04), slightly mesotrophic (total phosphorus = 13.1 μ g/L) and extremely dilute (conductivity = 7 μ S/cm; Table 1). Temperature loggers placed at 1-m depth intervals over a period of 1 year (2016-2017) recorded isothermal conditions, with only short-lived periods of weak thermal stratification, similar to the larger and deeper lakes of the region (Michelutti et al. 2019a). The catchment is free from human disturbances other than the occasional presence of grazing animals. A small rock dam (of unknown origin) was constructed at the lake's outlet along the northwest shore, perhaps to maintain high water levels for livestock during the dry season.

Materials and methods

Sediment cores were recovered in 2015 (Laguna Sibinacocha) and 2016 (Chaca Cocha, Lado del Quelccaya) using a 7.6-cm (internal diameter) gravity corer (Glew et al. 2001). All cores were sectioned onsite into 0.5-cm intervals using a Glew et al. (2001) extruder. The core from Laguna Sibinacocha was taken in the southern basin at ~ 28 m water depth (Table 1). Chaca Cocha and Lado del Quelccaya were

cored in their deepest basins at depths of 28 m and 5 m, respectively.

Geochronology on the uppermost sediments from all cores was established by applying the constantrate-of-supply (CRS) model to excess ²¹⁰Pb activities. Sediment samples were counted at Queen's University on a digital high-purity germanium spectrometer (DSPEC, Ortec[®]) with a well-type gamma detector consisting of a germanium crystal with lithiumdiffused electrodes. The CRS dates were developed using ScienTissiME dating software (ScheerSoftware Solutions, Barry's Bay, ON, Canada; ESM Fig. 3). Sediments beyond the range of ²¹⁰Pb dating were dated using Accelerator Mass Spectrometry (AMS) radiocarbon (¹⁴C) on available macrofossil remains, including fragments of plant material, chitinous cocoons, and charcoal. Terrestrial macrofossils were isolated, identified, and prepared by A. Telka of Paleotec Services. The isolated macrofossils were analyzed at the Keck Carbon Cycle Accelerator Mass Spectrometry Laboratory at the University of California, Irvine Earth System Science Department (Keck Carbon Cycle AMS Laboratory, 2011). The radiocarbon age was calibrated to years before present (cal yr BP, where BP = 1950) using the program Calib Rev 7.0.4. An age-depth model was established for Chaca Cocha using Bacon version 2.2 (Blaauw and Christen, 2011; ESM Fig. 4).

Preparation of sediment for siliceous microfossil analysis followed standard techniques (Battarbee et al. 2001). Diatoms were examined using a $100 \times$ oil immersion objective (numerical aperture = 1.3) and a $10 \times$ ocular, with condenser lens, on a Leica DMRB microscope equipped with differential interference contrast optics. A minimum of 300 diatom valves was identified and enumerated for each sediment interval. Diatoms were identified to the lowest taxonomic level possible (species and variety), following the taxonomy of Antoniades et al. (2008), and Krammer and Lange-Bertalot (1986, 1988, 1991a, b). Diatom data were converted into relative abundances and plotted using the program C2 version 1.5.1 (Juggins 2007). Because of difficulties identifying the large number of fragilarioid-type diatoms found in girdle view, *Staurosirella pinnata, Pseudostaurosira construens*, and *Staurosira construens* var. *venter* were grouped together as *Fragilaria* sensu lato complex. Principal component analysis (PCA), an unconstrained ordination technique that models species responses along synthetic variables (axes), was used to reveal the main direction of variation in fossil assemblages in Chaca Cocha, to make comparisons with other climate proxy records.

Results

Laguna Sibinacocha

Excess ²¹⁰Pb activity showed a slight down-core increase in the uppermost sediments before declining steadily to background values near 10-cm depth (ESM Fig. 3). The ¹⁴C age at 22-cm depth gave a calibrated age range of 5042–4900 BCE (Table 2), which is approximately 3000–4000 years older than what is typical for other lake sediment cores in this region of the Andes (Stroup et al. 2015; Rodbell et al. 2008). The basal ¹⁴C age at 36-cm depth gave a calibrated age range of 2724–2699 BCE, which is over 2000 years younger than the age at 22-cm depth (Table 2).

The fossil diatom record is characterized by a gradual switch in dominance between the planktonic *Discostella stelligera* (Cleve & Grunow) Houk & Klee and benthic fragilarioids, namely *Staurosirella pinnata* Ehrenberg and *Pseudostaurosira brevistriata* Grunow. Beginning at ~ 22-cm depth, *D. stelligera* begins to decline from > 80% relative abundance to near-negligible values above ~ 8-cm depth, whereas

S. pinnata and P. brevistriata increase from < 5% relative abundance below ~ 24 -cm depth to > 80% relative abundance above ~ 10 -cm depth. Taxa belonging to the genera Achnanthes sensu lato, Amphora, Nitzschia, as well as Tabularia fasciculata (C. Agardh) D.M. Williams and Round 1986, show minor (< 10%) increases in relative abundance beginning at ~ 20 -cm depth towards the surface (Fig. 2).

Chaca Cocha

Excess ²¹⁰Pb activity showed a monotonic down-core decline from the surface, until reaching supported levels at \sim 4-cm depth (ESM Fig. 3), representing the slowest near-surface sedimentation rate among the study sites. The ¹⁴C ages gave calibrated age ranges of 1311-1359 CE at 11.25-cm depth and 553-642 CE at 28.25-cm depth (Table 2). The 32-cm record encompasses approximately 1600 years of sediment accumulation (ESM Fig. 4). The fossil diatom record is characterized by alternating dominance between the planktonic Discostella stelligera (Cleve & Grunow) Houk & Klee and benthic fragilarioids, namely Staurosirella pinnata Ehrenberg and Pseudostaurosira brevistriata Grunow, with lesser representation from the genera Navicula sensu lato, Pseudostaurosira, Achnanthes, and Nitzschia (Fig. 3). Specifically, fragilarioids (S. pinnata and P. brevistriata) dominate near the bottom (\sim 450–600 CE) and top (~ 1700–2016 CE) sections of the core, whilst D. stelligera dominates the middle portion of the record (~ 750–1600 CE).

Lado del Quelccaya

Excess ²¹⁰Pb activity showed a slight down-core increase in the uppermost sediments, but subsequently

Sample name	Core depth midpoint (cm)	UCIAMS #	¹⁴ C age (BP)	Calibrated age ranges (2σ) cal yr CE/BCE	Rel. area under prob. distr.
Chaca Cocha	11.25	200793	575 ± 20	1311–1359 CE	0.64
Chaca Cocha	28.25	200794	1470 ± 25	553–642 CE	1
Sibinacocha	22.25	200795	6060 ± 25	5042-4900 BCE	0.98
Sibinacocha	35.75	170773	4200 ± 20	2724-2699 BCE	0.58

Table 2 Radiocarbon ages from Chaca Cocha and Laguna Sibinacocha

Fig. 2 Fossil diatom assemblage profile for Laguna Sibinacocha. Radiocarbon ages are reported on the left side below the ²¹⁰Pb dates. "Tab." is an abbreviation for the genus *Tabularia*



declined steadily to background values near 20-cm depth (ESM Fig. 3). The bottom portion of this core was not ¹⁴C-dated. The diatom assemblages were dominated throughout the entire record by benthic fragilarioids, including *S. pinnata*, *P. brevistriata*, and *Staurosira construens* var. *venter* (Ehrenberg) P.B. Hamilton. There was a slight, but notable, decrease in the relative abundances of these fragilarioids, from \sim 70 to 60% at 20-cm depth, largely caused by small increases in *Achnanthidium minutissimum* (Kützing) Czarnecki and *Encyonopsis krammeri* E. Reichardt. There was a further slight decline in the fragilarioid relative abundances at \sim 8-cm depth, largely caused by increases in *Brachysira vitrea* (Grunow) R. Ross (Fig. 4).

Discussion

The study lakes show strikingly different diatom trajectories over time, despite recording similar dominant taxa in their fossil assemblages (Figs. 2, 3, 4). The two deep lakes, Laguna Sibinacocha and Chaca Cocha, record shifts in dominance between benthic fragilarioids and the planktonic *Discostella stelligera*, whereas the shallow Lado del Quelccaya records no planktonic taxa and a comparatively complacent profile dominated by benthic taxa, mainly *Fragilaria* sensu lato species. The disparate fossil diatom profiles reflect variations in lake morphometry and catchment characteristics among the study sites, and offer insights into how different lake types in this region could respond to future warming.

Laguna Sibinacocha

Interpretation of the Laguna Sibinacocha diatom profile is hampered by the ¹⁴C-dating uncertainties of the sediment record. The ¹⁴C age range of the basal sediment (2724–2699 BCE), although not implausible, seems anomalously old based on the ²¹⁰Pb age-depth profile, as well as ¹⁴C ages recorded in other sediment cores from this region (Stroup et al. 2015; Rodbell et al. 2008). The ¹⁴C age reversal at \sim 22-cm

Fig. 3 Fossil diatom assemblage profile for Chaca Cocha. The age model developed in Bacon version 2.2 (Blaauw and Christen, 2011) using ²¹⁰Pb dates and two ¹⁴C ages is shown on the left side of the figure, beside core depth. "Dip." and "G." are abbreviations for the genera *Diploneis* and *Gomphonema*, respectively



depth (an age range of 5042–4900 BCE) confirms the presence of an old carbon source. Similar ¹⁴C dating reversals also occurred in sediment cores taken from the middle and northern basins of the lake, indicating this is a lake-wide phenomenon and not an anomaly within a single core (B. Konecky unpublished). The source of the old carbon is unknown, but could be related to carbon introduced from glacial inputs. Interestingly, ¹⁴C age reversals were also found in a nearby (~ 15 km away) pro-glacial lake, Challpacocha, which drains the Quelccaya Ice Cap (Stroup et al. 2015). Not all glacial-fed lakes in this region, however, record ¹⁴C age reversals (Rodbell et al. 2008).

Despite ¹⁴C dating challenges, the Laguna Sibinacocha sediment record reveals important information about past limnological change. ²¹⁰Pb dating of the uppermost sediments produced a reliable chronology for the past ~ 130 years (0–9-cm depth; ESM Fig. 3). During that period, the fossil assemblages (dominated by benthic fragilarioids; Fig. 2) were relatively stable and showed no clear response to either the rising temperatures of recent decades or the construction of the dam in 1996 that raised water levels by ~ 2 m.

The complacency of the diatom profile since \sim 1880 CE belies the striking assemblage shift that occurred earlier in the record (beginning at \sim 22-cm depth) when the planktonic *D. stelligera* steadily declined from near dominance (> 90% relative abundance) to negligible abundances, as benthic *Fragilaria* sensu lato species rose in abundance to dominate the fossil record. This assemblage shift represents a major ecological change because the switch from planktonic to benthic diatoms often implies a change in the physical structure of the water column (Michelutti et al. 2015; Rühland et al. 2008, 2015).

Populations of small-celled and fast-growing cyclotelloid taxa such as *D. stelligera* are often favoured under conditions of strengthened thermal stratification (Rühland et al. 2008, 2015; Winder et al. 2009; Winder and Hunter 2008). In Laguna Sibina-cocha, the gradual shift from *D. stelligera* to benthic fragilarioids beginning at 22-cm depth suggests a breakdown of thermally stratified conditions, towards a water column that is continually mixing. This inference is supported, in part, by depth-time contour

Fig. 4 Fossil diatom assemblage profile for Lado del Quelccaya. "Enc." and "Brach." are abbreviations for the genera *Encyonema* and *Brachysira*, respectively



plots of temperature that show Laguna Sibinacocha is presently isothermal, with only brief periods of weak thermal stratification throughout the year (Michelutti et al. 2019a).

The diatom profile in Laguna Sibinacocha (which is not currently thermally stratified) is opposite to hundreds of paleolimnological records from across the Northern Hemisphere (Rühland et al. 2008; Smol et al. 2005), as well as in the tropical Andes (Michelutti et al. 2015), which show distinct shifts from benthic fragilarioid taxa to small planktonic cyclotelloid species, linked to greater periods of thermal stratification resulting from twentieth century warming (Rühland et al. 2015). The current nearisothermal state of Laguna Sibinacocha may be a consequence of the disruption of thermal stratification from increased inputs of cool glacial meltwater. Glaciers draining into the north end of the lake have been in decline since 1931 CE, with ice margins currently retreating by as much as 13 m/year over the past decade (Seimon et al. 2017). Similarly, Sienkiewicz et al. (2017) concluded that a disruption of thermal stratification in a Spitsbergen lake, caused by an intensification of catchment erosion processes with twentieth century warming, resulted in a shift in dominance of diatom assemblages from *Cyclotella* sensu lato taxa to benthic species. In Laguna Sibinacocha, enhanced glacial inputs from retreating glaciers may explain the present-day absence of small cyclotelloid taxa that thrive in thermally stratified waters. However, the decline of *D. stelligera* began much

earlier than the modern glacier retreat, indicating an earlier trigger for the diatom assemblage shift.

The ¹⁴C-dating problem in Laguna Sibinacocha makes it impossible to pinpoint the onset of the major assemblage shift and to identify possible triggers for changes to the physical structure of the water column. Net annual accumulation histories from Quelccaya ice core records, however, document an unprecedented wet period from ~ 1520 to 1680 CE (Thompson et al. 2013). This wet period had a major influence on water levels in Laguna Sibinacocha. For example, a recently discovered archaeological site, containing pre-Hispanic artifacts and architecture, sits ~ 4 m under water in the nearshore environment of the lake, indicating a rise in lake level since the initial occupation of the site. Analysis of a sediment sequence preserved within an Inca pot recovered from this site indicates that lake level rose during the late-1600s CE, following an extended period of aboveaverage precipitation that began \sim 1520 CE, and water levels have remained high until present (Michelutti et al. 2019b).

One possibility to explain the shift from D. stelligera to benthic fragilarioids in Laguna Sibinacocha is that higher-than-normal precipitation raised water levels and disrupted thermal stratification. Enhanced glacial melt in the twentieth century would continue to keep the lake in a near-isothermal state, despite recent warming. Changes in lake surface area and effective fetch that occur with water level fluctuations may also have affected mixing regimes. With a rise in lake level of ~ 4 m since the late 1600s CE, Laguna Sibinacocha would have a larger surface area and longer effective fetch that could result in increased water column mixing (Stone et al. 2019). The rise in water level during the cool LIA may have also introduced old carbon from the sides of the basin into the lake, accounting for the ¹⁴C dating anomalies. This interpretation remains speculative until an accurate agedepth profile can be established for this lake.

Chaca Cocha

In the Chaca Cocha diatom profile (Fig. 3), the oscillating dominance between *D. stelligera* and *Fragilaria* sensu lato taxa (and other benthic species) suggests changes in the mixing regime, which alternately favoured planktonic and benthic diatom assemblages. The lake is not located within a glacial

watershed and is far from human activities, other than some livestock grazing, and thus any changes should be solely climate-driven. The PCA axis 1 scores of diatom relative abundances, which largely reflect the shifts in abundance between *D. stelligera* and the *Fragilaria* sensu lato complex, broadly match mean state changes in climate inferred from the Quelccaya ice core records, as well as a Southern Hemisphere temperature reconstruction ensemble (Fig. 5; Neukom et al. 2011).

During the MCA ($\sim 1100-1300$ CE), *D. stelligera* dominated the fossil assemblage (Figs. 3, 5). The warm and dry conditions that characterized this period would have promoted enhanced periods of thermal stratification and favoured the establishment of small planktonic cyclotelloids (Rühland et al. 2015). With the onset of the LIA ($\sim 1520-1880$ CE), *D. stelligera* declined in abundance as benthic taxa increased, consistent with the breakdown of thermal stratification during cooler conditions. The CWP (~ 1880 CE-present) is characterized by increasing abundances of *D. stelligera*, suggesting a return to greater periods of thermal stratification with rising temperatures.

Southern Hemisphere climate proxy records indicate that recent decades have been the warmest of the past 1000 years (Neukom et al. 2011), and rising temperatures have been implicated in the current retreat of the Quelccaya Ice Cap margin to limits unprecedented within the past 6000 years (Thompson et al. 2013). In Chaca Cocha, the D. stelligera increase is unprecedented within the context of the past ~ 200 years; however, this planktonic taxon reached much higher abundances during the MCA (Figs. 3, 5). This apparent "muted" response to recent warming may be attributed to slow sedimentation rates (~ 28 yr/cm since 1900 CE) and climate variables other than temperature, such as precipitation and windiness, which can affect thermal stratification. Nonetheless, the Chaca Cocha diatom record does seem to track mean state change in climate over the late Holocene as inferred from independent paleoenvironmental archives (Fig. 5).

Lado del Quelccaya

The dominant diatoms in Lado del Quelccaya (e.g. *S. pinnata, S. construens var venter, P. brevistriata, A. minutissimum, B. vitrea, E. neogracile*) are commonly recorded in shallow, oligotrophic, and circum-neutral



Fig. 5 The PCA axis 1 diatom species scores for Chaca Cocha (far right) shown in comparison with (from left) decadal averages of δ^{18} O and net accumulation in the Quelccaya Summit Dome (QSD) ice core (Thompson et al. 2013), as well as the 30-year loess filtered ensemble mean temperature

lakes (Giles et al. 2018) and accurately reflect its water chemistry and morphometry (Table 1). These taxa, however, are ubiquitous and found in a wide range of environments (Tapia 2008), making them relatively poor indicator species. Explanations for the slight increases in *B. vitrea* and *E. neogracile* at ~ 1900 CE, from near negligible values, remain speculative. One explanation is changes to habitat availability such as increased macrophyte biomass. Of potential importance is a small rock dam of unknown origin, constructed at the lake's outlet, which my have affected habitat availability as well as water chemistry. In a survey of 77 subarctic Canadian lakes, Rühland et al. (2003) found the highest abundance of B. vitrea in lakes with the highest concentrations of TN and DOC, both of which would be expected to increase with longer water residence time, associated with damming. In fact, Lado del Quelccaya recorded the highest concentrations of TN and DOC among all lakes (n = 12) in a prior limnological survey (Michelutti et al. 2019a). Alternatively, warming-induced changes in catchment vegetation may also have caused elevated TN and DOC concentrations.

The shallow depth of Lado del Quelccaya was reflected by the dominance of benthic diatom taxa (Fig. 4). Although this lake contained taxa also found

reconstruction for the Southern Hemisphere (Neukom et al. 2011). Demarcations of the Current Warm Period (CWP), Little Ice Age (LIA), and Medieval Climate Anomaly (MCA) are based on climatological periods identified from the ice core records in Thompson et al. (2013)

in the deeper study sites, notably benthic fragilarioids and A. *minutissimum*, its diatom profile stands in stark contrast to its deeper counterparts in that it lacks planktonic taxa in appreciable numbers and shows no major species shifts throughout the record. The complacency of the diatom assemblages in the shallow site, relative to the deep study lakes, is consistent with research in the southern Ecuadorian Andes where deep lakes $(z_{max} > 10 \text{ m})$ recorded abrupt diatom shifts beginning in the mid-1900s, associated with rising air temperature and declining wind speed (Michelutti et al. 2015), and nearby shallow lakes $(z_{max} < 4 \text{ m})$ showed only modest diatom changes over the same time period (Giles et al. 2018). This stands in marked contrast to high-latitude regions, where diatom assemblages in shallow lakes respond sensitively, and record earlier shifts to warming temperatures, compared to deep lakes (Smol and Douglas 2007; Michelutti et al. 2003). In regions with winter ice cover, climate-driven changes to the length of the summer growing season are often the overriding factors driving limnological change (Smol 1988; Smol et al. 2005). This same mechanism does not apply to lakes in the tropical Andes that have year-round growing seasons with no winter ice cover. In remote lakes of the tropical Andes, an overriding factor driving limnological change is climate-induced changes to thermal stratification (Giles et al. 2018; Michelutti et al. 2016). In shallow lakes, wind can easily mix the entire water column. Thus, such water bodies do not experience limnological changes that are typically associated with enhanced thermal stratification.

Thermal stratification versus lake water-level change

We favor alterations in thermal stratification and mixing regimes as being the primary mechanism affecting diatom assemblages in our study lakes, particularly shifts between planktonic D. stelligera and benthic Fragilaria sensu lato species. Diatoms, however, are also known to respond to water-level changes in lakes (Wolin and Stone 2010), so the question arises as to whether lake-level fluctuations at our study sites caused the recorded shifts. Numerous paleolimnological studies from the Andes have used varying abundances of functional diatom groups to infer water-level fluctuations. Specifically, high abundances of planktonic taxa have been linked to high water levels and dominance by benthic taxa have been used to infer shallow water conditions (Baker et al. 2001; Fritz et al. 2004; Hillyer et al. 2009; Cardozo et al. 2014).

In Laguna Sibinacocha, benthic *Fragilaria* sensu lato taxa increased in recent sediments, while the planktonic *D. stelligera* declined to near negligible values (Fig. 6). Interpreting the rise in benthic taxa as a lake level reduction is not likely here, as Laguna Sibinacocha is deep ($z_{max} = 92$ m) and water levels have, in fact, risen by several meters during the last few centuries (Michelutti et al. 2019a, b). Similarly, in Chaca Cocha, the highest abundances of *D. stelligera* occur during the warm and dry MCA, when water levels would be expected to have been low. Also, *D. stelligera* declined markedly during the cool and wet period of the LIA (~ 1520–1680 CE), when water levels would have most likely risen (Figs. 5, 6).

Although changes in water level are apparent for lakes in the study region, and Laguna Sibinacocha in particular (Michelutti et al. 2019b), shifts in functional diatom groups appear unrelated to depth fluctuations. As discussed earlier with respect to Laguna Sibinacocha, however, changes in water depth alter the lake area and effective fetch, which could affect lake mixing regimes (Stone et al. 2019). Dramatic lake



Fig. 6 Summary of *Discostella stelligera*, the dominant planktonic taxon, relative to the *Fragilaria* sensu lato taxa (*Staurosirella pinnata, Pseudostaurosira brevistriata,* and *Staurosira construens* var. *venter*), the dominant benthic taxa, in the three study lakes

level fluctuations, by several tens of meters, such as those recorded at Lake Titicaca (Baker et al. 2001), are not likely to have occurred in our study lakes. This is because Lake Titicaca's enormous catchment area $(57,000 \text{ km}^2)$ integrates climate conditions over a large region (Abbott et al. 2003), whereas the lakes of the Cordillera Vilcanota have smaller catchments (Laguna Sibinacocha has a catchment area of 135 km²) and reflect local conditions. For these study lakes, and during the time period encompassed by the sediment cores, we favor alterations to thermal stratification regimes, or lack thereof, as the major factor driving diatom assemblage shifts. Similar conclusions have been reached in comparative studies of lakes in the Ecuadorian Andes, where accelerated warming over the past 30 years has led to protracted periods of thermal stratification (Labaj et al. 2018; Michelutti et al. 2016) and attendant shifts in phytoand zooplankton assemblages (Labaj et al. 2017; Michelutti et al. 2015).

Conclusions

Although the main mechanism driving limnological change in the Cordillera Vilcanota study lakes seems to be climate-induced alterations to thermal stratification, each site recorded markedly different diatom profiles over the late Holocene. The differing responses of the diatom communities are related to the morphometry and catchment characteristics of each site. For example, the shallowness of Lado del Quelccaya (< 5 m) ensures that wind can easily mix its entire water column and therefore it is not subject to limnological changes associated with thermal stratification. In contrast, differences in diatom profiles between the deeper study lakes, which are capable of thermally stratifying, seem to be driven by whether or not the lake receives direct glacial runoff. Chaca Cocha does not receive any glacial runoff and its diatom assemblage shifts match the mean state changes in regional climate recorded by independent climate proxy records. These data demonstrate that lakes in the tropical Andes could experience different limnological responses with future climate change.

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