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ORIGINAL PAPER

Climate-driven changes in lakes from the Peruvian Andes

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Abstract The consequences of recent warming in the Andes have been dramatic, most iconically visualized by the rapid retreat of tropical mountain glaciers. Of all the ecosystems in the tropical Andes, lakes have received amongst the least research attention. We examined subfossil diatom and chrysophyte assemblages to chronicle recent (past ~150 years) ecological change in lakes from the Peruvian Andes. We recorded abrupt increases in planktonic diatoms and scaled chrysophytes beginning in the early 1900s. These changes are consistent with enhanced periods of thermal stratification, brought on by rising temperatures that have been documented throughout the Andes. These data indicate that ecological and likely physical limnological changes associated with Anthropocene warming are already under way in tropical high mountain lakes.

Keywords Peruvian Andes · Paleolimnology · Diatoms · Chrysophyte scales · Climate change

Introduction

Equatorial mountain lakes have been a scientific curiosity for decades (Hutchinson and Löffler 1956), mainly because of their unique limnological characteristics, imparted by their tropical, high-altitude location (Aguilera et al. 2013; Gunkel and Casallas 2002). More recently, these lakes are being recognized for their sensitivity to climate change, and in particular for their sediment records that allow for long-term reconstructions of environmental changes (Michelutti et al. 2015; Stansell et al. 2013; Bird et al. 2011; Cooke et al. 2009). The highest abundance of tropical mountain lakes occurs in the South American Andes, a region where recent climate change has outpaced most other parts of the planet (Vuille et al. 2003). Air temperatures in the Andes are exceeding the upper limits of variability documented by historical meteorological data, and climate models forecast a "no analog" scenario by the end of the century (Urrutia and Vuille 2009). Climate-related changes are already impacting Andean water resources via alterations to the amount and patterns of regional precipitation (Thibeault et al. 2010; Haylock

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et al. 2006; Vuille et al. 2003), and reduced runoff from rapidly melting glaciers (Rabatel et al. 2013; Vuille et al. 2008). The consequences of these changes are given immediacy by the tens of millions of people who depend on Andean freshwater resources for their livelihoods (Herzog et al. 2011). As a result, there is high conservation value attached to Andean lakes, yet they remain amongst the least studied of all ecosystems in the tropical Andes (Maldonado et al. 2011).

We investigated the effects of recent climate change on lakes in the Andes of Peru. Modern environmental change in the Peruvian Andes is probably best embodied by the rapid melting of tropical glaciers over the past few decades, which has been directly linked to rising temperatures (Thompson et al. 2013). However, lakes are also important sentinels of climate change (Williamson et al. 2009; Smol and Douglas 2007a, b) and their abundance throughout the tropical Andes allows for a dense network of monitoring sites.

In this study, we analyzed fossil diatom and chrysophyte assemblages from dated sediment cores recovered from two lakes in the Peruvian Andes located between Huancavelica and Cusco (Fig. 1). The two study sites, Laguna Yanacocha and Laguna Yauricocha, are located ∼250 km apart within the Cordillera Central of Peru, southeast of Lima (Fig. 1). Both study lakes are situated in remote, undeveloped catchments with little activity other than llama herders occasionally grazing their animals on the ichu grass (*Jarava ichu*) that dominates the surrounding vegetation.

Fig. 1 Location of study lakes Laguna Yanaoc属cha and Laguna Yauricocha in the Peruvian Andes

We selected these lakes for detailed biological analyses because they are located at similar altitudes and have comparable limnological characteristics with respect to water chemistry and morphology. In a general sense, this study revealed how tropical mountain lakes from this region of Peru are responding to modern climate change. More specifically, this study complemented previous research in the southern Sierra of Ecuador where an identical paleolimnological approach was used to show that the ecological and physical states of lakes have changed in response to recent warming (Michelutti et al. 2015). Taken together, these study sites span a north–south gradient of over 1000 km, which allowed us to assess the impacts of warming along a latitudinal gradient in the tropical Andes.

Although data on the physical limnology of tropical mountain lakes are scant, in general they are considered cold polymictic, exhibiting frequent circulation and brief periods of thermal stratification, if any (Steinitz-Kannan 1997; Löffler 1964). Gunkel (2000) suggested that, in the equatorial Andes, lakes less than ∼20 m deep should be polymictic. However, many variables factor into thermal stability. For example, Laguna Pumacocha in the Peruvian Andes is permanently stratified because of its steep-sided morphometry and sheltering by local topography (Bird et al. 2011). Lake Titicaca, a large and deep lake on the border of Peru and Bolivia, is warm monomictic (Kittel and Richerson 1978), however it is located at 15° south latitude where seasonal variations are greater relative to the equator. Our data suggest that the strength and duration of thermal stratification events have likely increased in the study lakes over the past several decades. This has implications for ecological restructuring over this time period in these remote alpine lakes.

Materials and methods

Core recovery and processing

Sediment cores were recovered from the deepest part of each lake (Yanacocha in June 2007; Yauricocha in June

2008) using a percussion corer fitted with a 6.5-cm-diameter polycarbonate tube. Cores were extruded on-site and sampled at 0.5-cm intervals. Excess ^{210}Pb activities with a constant-rate-of-supply model were used to calculate chronology over the past ~100 years. The dating model for Yanacocha is reported in Cooke et al. (2009) and relevant data for Yauricocha are provided in Electronic Supplementary Material (ESM) Table 1. Preparation of slides for siliceous microfossil analysis followed standard protocols (Battarbee et al. 2001). Diatom assemblages are presented in stratigraphies as percent relative abundance. Certain diatom taxa, although identified individually, were grouped together when presented in the stratigraphy mainly because they have similar ecological characteristics. These included *Fragilaria tenera* and *Fragilaria nanana*, as well as small benthic fragilarioids (*Staurosirella pinnata*, *Staurosira venter*, *Staurosira construens*, *Pseudostaurosira pseudoconstruens*, *Staurosira brevistriata*). A minimum of 300 diatom valves was enumerated for each sediment interval in both cores. Because the scales of only one species of chrysophyte (*Mallomanas lychenensis*) were recorded in Yauricocha sediments, these data were reported as the ratio of *M. lychenensis* scales to total diatom valves enumerated. No chrysophyte scales were recorded in Yanacocha.

Results

Meteorological data from the study region are sparse and generally of short duration. The stations nearest the study lakes with the longest, continuous records span from 1996 to present. Abancay station (elevation = 2750 m asl) is ~12 km from Yauricocha and reports a mean annual temperature (MAT) of 15.4 °C during the period of record, with a seasonal temperature range of ~13–18 °C. Acobomba station (elevation = 3236 m asl) is ~40 km from Yanacocha and reports a MAT of 12.2 °C during the period of record, with a seasonal temperature range of ~9–14.5 °C. Key features of the study lakes are summarized in Table 1. In brief, both lakes occupy a similar elevation (~4300 m asl), but Yauricocha is slightly larger and considerably deeper than Yanacocha. Water chemistry measurements recorded on-site indicate the lakes are circum-neutral and dilute (Table 1).

In Yanacocha, diatom assemblages in sediment below 10-cm depth (i.e. older than ~1966) are dominated by benthic taxa, primarily small fragilarioids (*S. pinnata*, *S. venter*, *S. construens*, *P. pseudoconstruens*, *S. brevistriata*) and *Achnanthidium minutissimum* (Fig. 2). Planktonic or tychoplanktonic taxa are also present, but in small percentages, including *F. tenera* and *F. nanana*, *Aulacoseira alpigena*, and trace amounts of *Tabellaria flocculosa*. Above 10-cm core depth (post AD ~1966), there is a marked increase in the planktonic *F. tenera* and *F. nanana*, up to >70 % relative abundance, and subsequent declines in benthic fragilarioids and *A. minutissimum*. Above 6-cm depth (post AD ~1990), *F. tenera* and *F. nanana* begin to decrease to <40 % relative abundance, and *T. flocculosa* increases from near zero values to consistently averaging ~10 % relative abundance. The small benthic fragilarioids increase after AD 1990, especially in the topmost sediment interval; however, planktonic taxa (*F. tenera*, *F. nanana*, *T. flocculosa*) also remain in high abundances.

In Yauricocha, the planktonic diatom *Discostella stelligera* (basionym: *Cyclotella stelligera*) is the dominant taxon throughout the sediment sequence (Fig. 3). Above 5-cm depth (post ~1998), *T. flocculosa* increases from near-zero values to consistently being present above 5 % relative abundance. A dramatic rise in the scaled chrysophyte *Mallomonas lychenensis* occurs at the 21-cm depth (AD ~1911) and continues in high abundance to present-day. Prior to the rise in *M. lychenensis*, the mean percent abundance of *D. stelligera* at all intervals (n = 11) was 43 %; following the *M. lychenensis* rise, the mean percent abundance of *D. stelligera* at all intervals (n = 21) increased to 55 %.

Discussion

Major species shifts were recorded in the fossil assemblages of both study lakes over the past ~150 years, consistent with warming-induced changes to lakewater properties (Figs. 2, 3). The impacts of warming reflected by abrupt shifts in diatom assemblages have been documented in hundreds of lakes globally, but primarily in the more-intensively studied lakes of the northern hemisphere (Hobbs et al. 2010; Rühland et al. 2008, 2015).

Table 1 Summary of key descriptor variables for the two study sites

	Elevation (m asl)	Area (km^2)	Zmax (m)	pH	COND (μS cm^{-1})	Latitude, Longitude
Yanacocha	4323	0.03	15	6.6	25	12°49′53.88″S, 74°55′26.76″W
Yauricocha	4305	0.04	37	6.2	10	13°42′1.24″S, 72°47′54.01″W

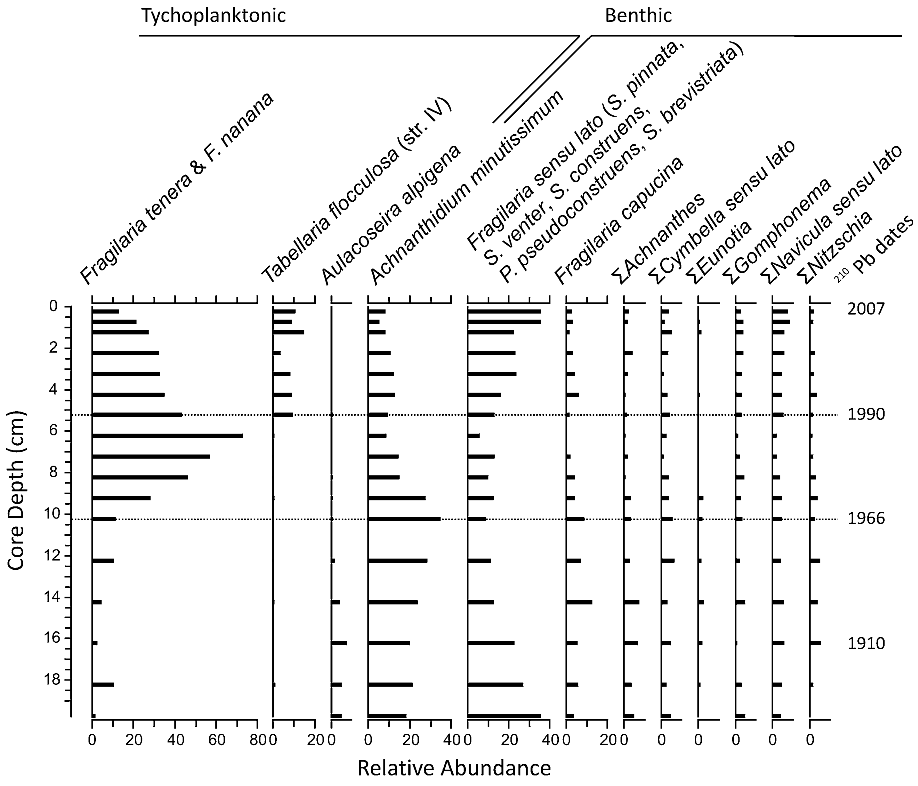

Fig. 2 Diatom profile from Laguna Yanacocha showing fossil diatom assemblages expressed as percent abundances. ^{210}Pb dates are presented on the right-most side of the profile

Although diatoms have been directly linked to changes in water temperature (Weckström et al. 1997; Pienitz et al. 1995), their response to warming is believed to be primarily indirect and regulated through: (1) reductions in the extent and duration of ice cover, which increase habitat availability and length of growing season; and/or (2) increased duration and strength of thermal stratification (Rühland et al. 2008, 2015). In Yanacocha and Yauricocha, which lack seasonal ice cover, the diatom response appears consistent with enhanced periods of thermal stratification caused by warming.

In Yanacocha, following AD ~1966, there is a clear assemblage shift from predominantly benthic to planktonic diatoms (Fig. 2). Both *F. tenera* and *F. nanana* are believed to be primarily planktonic and indeed are commonly recorded in the plankton of oligotrophic lakes (Kelly et al. 2005; Cremer and Wagner 2004; Cremer et al. 2001). The cells of these diatoms can link via spines to form ribbon-like colonies, which is a clear adaptation to remaining suspended in the water column. Likewise *T. flocculosa* (str. IV), although capable of attaching to hard substrates, is often recorded in the plankton, where it

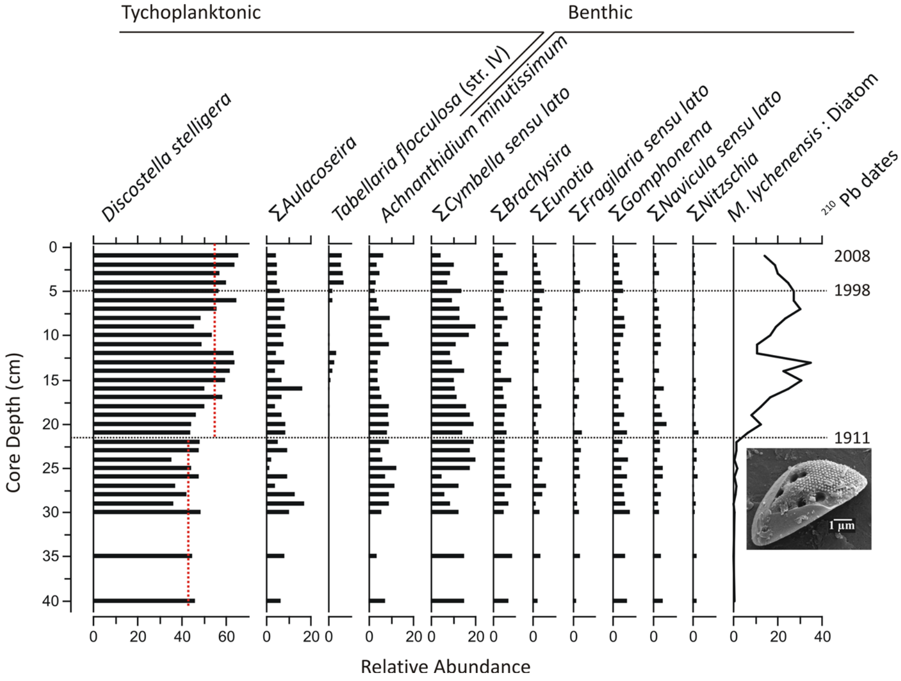

Fig. 3 Diatom and chrysophyte scale profile from Laguna Yauricocha expressed as percent abundances. ^{210}Pb dates are presented on the right-most side of the profile. The vertical red line denotes the mean *D. stelligera* percent abundances prior to (43 %) and following (55 %) the onset of the rise of *M. lychenensis* (pictured *inset*)

forms predominantly zig–zag filaments (Hallstan et al. 2013; Spaulding et al. 2010). We interpret the recent rise of *F. tenera*, *F. nanana*, and *T. flocculosa* as an increase in planktonic diatoms that are now able to flourish as warming lengthens the duration and extent of thermal stratification. This interpretation is further strengthened by the disappearance of the heavily silicified *A. alpigena*, which requires a more turbulent water column to remain in the photic zone (Rühland et al. 2008, 2015).

Numerous studies report the rise of pennate planktonic diatoms such as *Fragilaria* and *Tabellaria* taxa in response to modern warming. For example, Rühland et al. (2013) documented an increase in *F. tenera* (concurrent with the planktonic *D. stelligera*) in four lakes from the Canadian subarctic that occurred with a regional shift to substantially warmer temperatures. *Fragilaria nanana* was found to increase following warming in the Pyrenees (Catalan et al. 2002), and was also identified as a taxon indicative of warmer conditions in European alpine lakes in general (Catalan et al. 2009). In a survey of Swedish boreal lakes, Hallstan et al. (2013) identified *T. flocculosa* as a species for which the length of growing season or extreme warm temperatures are important. Likewise, Hobaek et al. (2012) linked recent increases in *T. flocculosa* in Lake Mjøsa, a large and deep lake in southeastern Norway, to increased temperature. The diatom assemblage shift recorded in Yanacocha provides an example of the rise of pennate planktonics in response to recent warming in the southern hemisphere.

In Yauricocha, the planktonic *D. stelligera* dominates the assemblage throughout the full history of the sediment core (Fig. 3). Yauricocha ($z_{max} = 37$ m) is over twice as deep as Yanacocha ($z_{max} = 15$ m) and the presence of *D. stelligera* throughout the sediment core indicates that the lake is stratified or at least stratifies long enough for this planktonic taxon to dominate the assemblage. In the tropical Andes, it is typically the shallow lakes ($z_{max} < 20$ m) that tend to be polymictic (Gunkel 2000), and the depth of Yauricocha may account for its apparent thermal stratification, although many factors, e.g. wind, air temperature, topography, can influence physical lake properties. The fossil diatom assemblages in Yauricocha do not show marked changes denoting enhanced stratification as in Yanacocha; however, there is a dramatic rise in the scaled chrysophyte *M. lychenensis* beginning in the early 1900s (Fig. 3).

Similar to diatoms, scaled chrysophytes have been shown to respond sensitively to limnological change including pH (Smol 1995) and other water quality variables (Paterson et al. 2001). Importantly, they are euplanktonic, and are therefore favoured during thermal stratification (Paterson et al. 2004). Under conditions of a stable epilimnion, the flagellated chrysophytes are at an advantage compared to more turbulent conditions during which their flagellar motility is far more hampered. Several studies have associated increases in scaled chrysophytes in recent decades to greater strength and duration of thermal stratification driven by warming (Haig et al. 2013; Ginn et al. 2010; Paterson et al. 2004).

In Yauricocha, we interpret the post ~1900 rise of *M. lychenensis* as a response most likely driven by a more stable water column brought on by rising temperatures (Vuille et al. 2003; Michelutti et al. 2015). This is supported by greater relative abundances of the planktonic *D. stelligera*, which increases, on average, by 12 % following the sharp rise in *M. lychenensis* (Fig. 3). *Cyclotella* taxa, such as *D. stelligera*, are known to become more competitive as the water column stratifies with warming (Rühland et al. 2008, 2013, 2015; Hadley et al. 2013; Hobbs et al. 2010). In their meta-analysis of over 200 northern hemisphere lakes, Rühland et al. (2008) defined a *Cyclotella* species rise as an increase >5 % above background relative abundance. In Yauricocha, the mean percentage increase following the *M. lychenensis* rise is over twice that value. Further support for enhanced thermal stratification in Yauricocha is the small rise in *T. flocculosa* after AD ~1998, which also increased around the same time in Yanacocha (Fig. 2).

Patterns of change in small *Cyclotella* taxa can be more complex than a direct response to changes in thermal stratification, as factors such as light and nutrients may also be important (Saros and Anderson 2015). Changes must be interpreted within the context of each lake (Rühland et al. 2015). In the Andes, warming temperatures have been an undeniable driver of ecosystem changes (Maldonado et al. 2011), and climate is inextricably linked to aquatic ecosystem processes that affect diatom resource requirements. Given that reduced mixing and enhanced periods of thermal stratification seem a likely scenario with increased warming, smaller-sized taxa, such as *D. stelligera*, with high surface area to volume ratios, will be more efficient at light harvesting and nutrient uptake (especially in oligotrophic systems) as they are better able to maintain a vertical position within the water column. In a recent review, Rühland et al. (2015) documented several examples of *D. stelligera* thriving in oligotrophic lakes, with many lakes recording an increase in this taxon with a reduction in nutrients and increased warming. Meanwhile, scaled chrysophytes such as *M. lychenensis* are well known to thrive when lakewater nutrients decrease, not increase (Smol 1985, 1995), and so nutrient enrichment is not a plausible alternate hypothesis for these changes.

Climate data from this region of Peru are sparse and of short duration. The two stations nearest the study lakes show trends of rising temperatures since the start of the records in the mid-1990s (Fig. 4). Although short in duration, these temperature records are consistent with warming trends, in general, throughout the Andes (Vuille et al. 2003), and support our interpretation that the changes we record in algal indicators are likely related to warming-induced

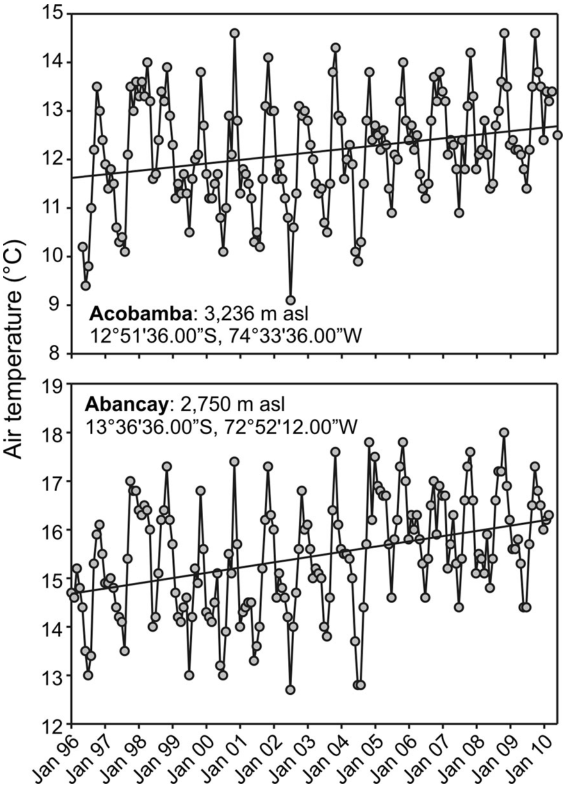

Fig. 4 Monthly mean air temperatures for the two meteorological stations closest to each study lake. Abancay station is ~12 km from Yauricocha and Acobomba station is ~40 km from Yanacocha

alterations to the stratification regime of the study lakes. Similar changes in timing and magnitude have been recorded in lakes from the southern Sierra of Ecuador, specifically abrupt increases in *Cyclotella* taxa (Michelutti et al. 2015). Although millennial-scale records are ultimately required to place the diatom changes recorded here in a truly long-term perspective (Hillyer et al. 2009; Ekdahl et al. 2008; Cross et al. 2000), these data show that the warming trend of recent decades is causing a restructuring of the ecological and physical states of the study lakes.

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