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Sherilyn C. Fritz
University of Nebraska-Lincoln, sfritz2@unl.edu

P. A. Baker
Duke University, pbaker@duke.edu

Pedro M. Tapia
University of Nebraska-Lincoln

Trisha L. Spanbauer
University of Nebraska-Lincoln, tspanbauer@austin.utexas.edu

Karlyn S. Westover
University of Nebraska–Lincoln

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S. C. Fritz,[1,2] P. A. Baker,[3] P. Tapia,[1] T. Spanbauer,[1] and K. Westover [1]

1. Department of Earth and Atmospheric Sciences, University of Nebraska–Lincoln, Lincoln, NE 68588-0340 USA
2. School of Biological Sciences, University of Nebraska–Lincoln, Lincoln, NE 68588-0340 USA
3. Division of Earth and Ocean Sciences and Nicholas School of the Environment, Duke University, Durham, NC 27708 USA

Corresponding author — S. C. Fritz, Department of Earth and Atmospheric Sciences, University of Nebraska–Lincoln, Lincoln, NE 68588-0340, USA; sfritz2@unl.edu

Abstract

In recent years, deep drilling undertaken as part of the International Continental Drilling Program has generated multiple long lacustrine sedimentary records to reconstruct continental paleoclimate. In many cases, the tectonic and geomorphic history of these basins is under-constrained and poorly known, which affects the interpretation of climate history from geophysical, geochemical, and paleobiotic proxies in the sedimentary record. In addition, non-analog biotic assemblages that reflect evolutionary processes may constrain the reconstruction of past environments. In the drill-core record of Lake Titicaca, spanning the last ~ 370 ka, the diatom stratigraphy reflects both the influence of climate and the long-term evolution of the lake basin and its biota. In the upper part of the drill-core sequence, glacial intervals were deep and dominated by freshwater planktic taxa, and peak interglacial intervals were shallow and dominated by benthic species, some with saline affinities. In the basal sections of the drill-core record, benthic diatoms are dominant in both glacial and interglacial units, with freshwater taxa dominating the glacial strata. This suggests that the ancient lake basin was shallower during intervals of both wet and dry climate, and that the modern deep lake may result from a progressive subsidence and deepening of the basin over time. In addition, morphological evolution in one of the major lineages of planktic diatoms, *Cyclostephanos*, indicates substantial change in the limnological environment that affected species morphology and may have driven speciation.

Keywords: South America, Andes, Paleoclimate, Lake-level, Quaternary, Speciation

1. Introduction

Large long-lived lakes have the potential to produce archives of environmental dynamics spanning hundreds of thousands to millions of years. As a result, many of these systems have been the targets of recent lake drilling projects, because they can elucidate climatic processes operating at these long temporal scales (Williams et al., 2001; Fritz et al., 2007; Scholz et al., 2007). Long-lived lakes also have the potential to reveal evolutionary processes, including diversification, speciation, and extinction of aquatic biota (Khursevich et al., 2001; Williams et al., 2001), as well as the long-term ontogeny of the lake basin itself.

A number of the large lakes that have been targeted for drilling are located in tectonically active settings (e.g. Lake Titicaca, Bear Lake, Lake Qinghai, Lake Van, and the Dead Sea), and it is likely, especially on longer timescales, that some of these lacustrine sedimentary sequences were impacted by structural and geomorphic processes that affected the watershed and the lake basin itself, including its hydrologic thresholds (both inlets and outlets). These factors can affect the physical, chemical, and biological dynamics of the lake and in turn the lake's water balance and rate and style of sedimentation. In cases where the tectonic or hydrogeomorphic setting has been altered, the response of the ancient lake and landscape to climate may be different from the system of recent times (Bradbury, 1997; Colman, 1998; Kowalewska and Cohen, 1998). As

a result, "correct" interpretation of climate history from long sedimentary sequences can be challenging without *a priori* knowledge of geomorphic and tectonic history.

Many large long-lived lakes are known for their high degree of endemism, and the sedimentary record can reveal the conditions associated with the diversification of aquatic biota and hence the potential drivers of evolutionary change (Brooks, 1950; Johnson et al., 1996; Theriot et al., 2006). At the same time, ancient organisms may have gone extinct (Khursevich et al., 2001; Williams et al., 2001), and hence their ecology cannot be determined from modern analogs. In such cases, ecological tolerances can only be inferred from generic analogs, morphological characteristics, or the co-occurrence of extinct taxa with assemblages of other organisms with known ecological affinities or with distinctive geochemical or sedimentary features.

Lake Titicaca (14°09′ – 17°08′ S, 68°03′ – 71°04′W) is a large high-elevation (3,812 m) lake in the tropical Andes (Figure 1). The lake has been the focus of several decades of paleoclimatic study (Servant and Fontes, 1978; Wirrmann and Mourguiar, 1995; Abbott et al., 1997; Baker et al., 2001a), because of its potential for reconstructing the long-term history of precipitation variation in tropical South America, for understanding the factors that force tropical climate variability on paleoclimatic time scales, and for evaluating the impact of climate on the evolution of high tropical biodiversity. In 2001 we drilled

Figure 1. Map of Lake Titicaca showing the LT01-2B drill core site (marked by a filled circle). Inset map shows the location of the outlet, the Rio Desaguadero, and other large lake basins in the Bolivian Altiplano that have been hydrologically connected to Lake Titicaca at times in the past.
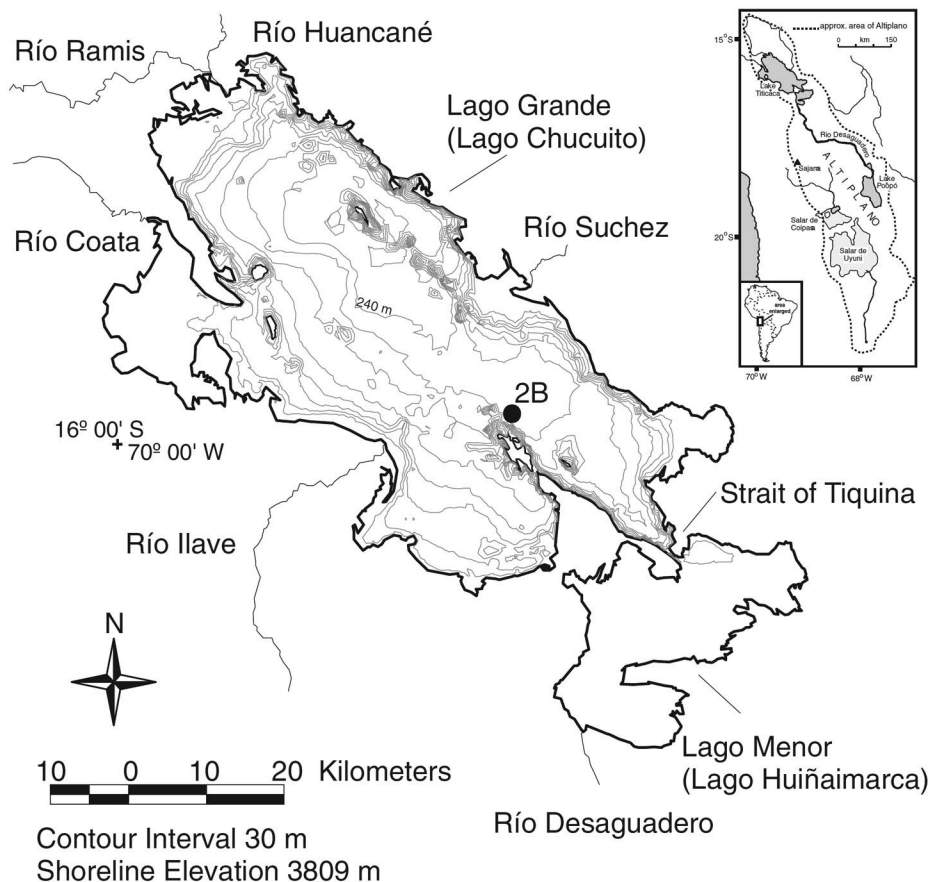
the sediments of Lake Titicaca to obtain a paleoclimatic record that extended to periods prior to the Last Glacial Maximum (LGM). Here, we use the detailed diatom stratigraphy of one of those cores to interpret the lake-level history of Lake Titicaca, to evaluate the role of climate relative to basin alteration in affecting lake-level change, and to document morphological change in a major lineage of planktic diatoms. A synthesis of the biotic and geochemical data and a detailed discussion of the climatic context for our studies are contained in prior papers (Fritz et al., 2007, 2010).

1.1. Site description

Lake Titicaca (Figure 1) consists of a large (7,131 km^2) deep (max depth 284 m, mean depth 125 m) main basin (Lago Grande) and a smaller (1,428 km^2) shallower (max depth 42 m, mean depth 9 m) basin (Lago Huiñaimarca), which are connected at the Straits of Tiquina by a sill at 25 m depth. In the contemporary lake, inter-annual variation in lake level is most strongly influenced by precipitation (Baker et al., 2001a), which enters the lake in both direct rainfall (~ 47%) and inflow (~ 53%) from six major rivers. In the 20th century, water loss via evaporation (~ 91% of total losses) is less variable from year to year than precipitation over the lake. Less than 9% of water is lost via the sole surface outlet, the Rio Desaguadero (3,804 m elevation) (Roche et al., 1992). Thus, the lake is effectively a closed basin and has moderately elevated salinity (~ 1 g L^{-1}). Waters are of the NaCl(SO$_4$) type.

Lake Titicaca is a warm monomictic lake, and the water column is commonly stratified between October and June. Stratification is usually relatively weak, with a temperature difference between the epilimnion and hypolimnion of < 5 °C (Kittel and Richerson, 1978). In many years, winter mixing is incomplete, particularly in years of high winter temperatures (Richerson et al., 1992). The lake is nitrogen-limited (Wurtsbaugh et al., 1985, 1992), with a dissolved inorganic nitrogen to soluble reactive phosphorus ratio of < 3:1. The major source of nitrogen is nitrogen fixation; most external nitrogen and phosphorus loading occurs in stream flow during summer months. Silica concentrations in the epilimnion (0.5-1.8 mg L^{-1}) (Iltis et al., 1992) are frequently below concentrations limiting for diatom growth (Wurtsbaugh et al., 1985). The contemporary algal flora is composed primarily of chlorophytes (43–57%), cyanophytes (10–12%), and diatoms (27–39%) (Iltis, 1992). Diatoms bloom primarily during isothermal mixing; during years when mixing is not as deep, diatom biomass is greatly reduced (Richerson et al., 1992).

2. Methods

Overlapping drill cores were obtained in 2001 from three locations in Lake Titicaca, using the GLAD 800 drilling platform and coring system. The analyses reported here are from site LT01-2B (Figure 1) to the east of Isla del Sol in 235 m water depth. The site was drilled to a total depth of 136 meters below the sediment floor of the lake (mblf). The cores were shipped back to the U.S. and are stored at the University of Minnesota Lacustrine Core Repository (LacCore).

Photographs and detailed sedimentological descriptions were made of the core, which was sub-sampled at a resolution of 10 cm in units of apparently uniform lithology and at 2-cm intervals in units of more variable lithology. Diatom species composition was determined at 20-cm intervals (~ 700 samples) throughout the drill-core sequence. Samples for diatom analysis were treated with 10% hydrochloric acid to remove carbonates and cold hydrogen peroxide to oxidize

organic matter and then were rinsed to remove oxidation by-products. Prepared samples were dried onto coverslips, and the coverslips were mounted onto slides with Naphrax. Species were identified on a Zeiss Axioskop 2 microscope with a 100× (N.A. = 1.40) oil immersion objective. At least 300 diatom valves were counted on each slide. Diatom abundance in each sample is expressed as a percent of the total diatom valve count. Ecological affinities of diatom taxa are based on prior regional studies (Servant-Vildary and Roux, 1990; Servant-Vildary, 1992; Sylvestre et al., 2001; Tapia et al., 2003).

In initial counts (Fritz et al., 2007), planktic diatom taxa were identified to the highest possible taxonomic level (usually species or subspecies), but benthic taxa were lumped together into a single category (Figure 2). Subsequently, samples from core units with high (> 20%) benthic diatom abundance were re-counted to enumerate benthic taxa to the highest possible taxonomic level (Figure 3). Diatom assemblage zones were established based on stratigraphically constrained cluster analysis (CONISS) of square-root transformed diatom abundance data using the program psimpoll 4.27 (Bennett, 2007). Statistical significance of zones was tested using the broken-stick model (Bennett, 1996). Two separate cluster analyses were carried out: (1) on the differentiated planktic taxa plus the combined benthic group considered as a "taxon" (Figure 2), and (2) a second data matrix that included only the differentiated benthic taxa for those levels where the benthic percent abundance is > 20% (Figure 3). Zones created with the benthic-only data matrix are labeled with a "B". If the two data sets show similar clustering of stratigraphic sequences, this indicates that the diatom assemblage zones represent consistent paleoenvironmental patterns.

Samples for geochemical analysis were dried, powdered, weighed, and leached in buffered (pH = 5.5) ammonium acetate-acetic acid. Weight percent calcium carbonate was calculated from dissolved calcium concentration as measured by atomic absorption spectrophotometry (Perkin Elmer 5000), assuming that all the calcium was originally present as calcium carbonate. The acid-insoluble residue was rinsed in reagent-grade water, and portions of this residue were dried and weighed prior to determination of TOC and its stable isotopic composition. $\delta^{13}C_{org}$ was measured on a Finnegan MAT Delta Plus XL mass spectrometer in the Duke University Environmental Stable Isotope Laboratory, and carbon isotopic ratios are reported relative to the PDB standard. The precision for measurements was ± 0.2‰.

In the upper 48 m of the core, the chronology was established based on radiocarbon measurements in the uppermost 25 m and uranium-series ages on discrete aragonite laminae that were relatively free of detrital sediments. ^{14}C dates were calibrated using CALIB 4.4.2 for ages less than 20,000 ^{14}C years before present (BP) (Stuiver et al., 1998) and the calibration curve of Hughen and coworkers (Hughen et al., 2004) for older sediments. Below 48 m (~ 122.8 ka), an age model was derived by tuning peaks in calcium carbonate concentration to peak (enriched) values in the Vostok CO_2 record (Petit et al., 1999). The rationale for this approach is the coincidence in the upper 48 m of high calcium carbonate concentrations, which represent times of lowered lake level, with the global warm intervals of the mid-Holocene and MIS5e. The rationale for the age model construction is discussed in detail in Fritz et al. (2007). Application of this age model to the drill core sequence indicates that the 136-m core sequence spans approximately the last 370,000 years.

3. Results

3.1. Lithology

Sediments at site LT01-2B primarily consist of two alternating lithologic units: (1) gray mud that has high magnetic sus-ceptibility values, no carbonate, and low organic carbon concentrations; and (2) tan to green-gray mud that is laminated or thinly bedded and contains carbonate, high organic carbon concentrations, and has low magnetic susceptibility values. We interpret the sediments of the first unit to be of glacial–fluvial origin, derived primarily from glacial erosion in the surrounding cordillera (Fritz et al., 2007). In contrast, the second unit is composed primarily of autochthonous lacustrine material that was deposited during times when glacial extent was reduced in the watershed and when lake level fell below the outlet threshold, leading to calcium carbonate supersaturation and precipitation (Baker et al., 2001a; Seltzer et al., 2002). Thus, the second lithologic unit represents times of reduced precipitation that affected both glacial extent and lake level. The drill core sequence at LT01-2B consists of four major cycles of these two lithologic units, which suggests that the core spans four major cycles of regional glacial expansion and retreat.

3.2. Diatom stratigraphy

The diatom flora (Figures 2 & Figure 3) of the Lake Titicaca sediments includes planktic and benthic species that are characteristic of freshwater to saline environments. Above 95 m (~ 250 ka BP) the massive non-laminated units are dominated by freshwater planktic species, including *Cyclostephanos andinus*, *Cyclotella stelligera*, *Aulacoseira granulata*, and a group of undescribed morphotypes in the genus *Cyclostephanos*. Thus, the massive units are inferred to represent times when Lake Titicaca was deep and fresh, with lake level at or above the outlet. In these units, benthic diatom abundance is commonly < 25%, except in a small number of samples (Figure 2). In contrast, benthic diatoms dominate most of the non-laminated glacial unit from ~ 95 to 114 mblf, except the basal part (111–114 mblf), which contains a high proportion of the planktic genus *Cyclostephanos*. The high abundance of benthic diatoms suggests that lake level in much of this glacial unit was lower than in the non-laminated glacial units above. The benthic species composition (Figure 3) of this lower glacial unit in the core is more diverse than in benthic-dominated units higher up in the sequence; abundant taxa include *Cocconeis placentula*, *Gomphonema minutum*, *Hippodonta capitata*, *Navicula veneta*, *Navicula lauca*, *Navicula incarum*, *Navicula chungara*, *Navicula circumtexta*, *Planothidium lanceolatum*, and *Staurosirella pinnata*. These species can span a salinity gradient from fresh to sub-saline (0–5 g L^{-1}); the representation of obligate saline taxa is low. Together the data suggest that Lake Titicaca in this interval was shallow but a relatively fresh lake. In the lowest unit of massive sediments (>~123 mblf) diatom abundance is very low.

Nearly all of the laminated sediments in the LT01-2B drill core sequence have a high abundance of benthic taxa (Figure 2). In the uppermost ~ 2 m of the core, which dates from the mid-Holocene, dominant benthic species (Figure 3) include *Cocconeis placentula*, which grows on macrophytes, and the hardwater taxon *Epithemia argus*, mixed with the planktic taxon *Cyclotella meneghiniana* and the tychoplanktic *Chaetoceros muelleri*. Both of the latter are characteristic of sub-saline to saline waters (≥ 3 g L^{-1}). The penultimate laminated unit, which is correlated with Marine Isotope Stage (MIS) 5e, has very high proportions of sub-saline to saline diatoms, and the species composition suggests that this was the most saline interval represented in the drill-core sediments. The tychoplanktic *Chaetoceros muelleri*, which is restricted to waters with salinity greater than 2 g L^{-1}, is abundant in the upper part of this laminated unit, and the saline *Paralia sulcata* is abundant at the base. Common benthic taxa (Figure 3) include *Tabularia tabulata*, *Tryblionella compressa*, *Tryblionella constricta*, *Achnanthes brevipes*, *Cocconeis titicaensis*, *Cocconeis placentula*, and *Achnanthes amoena*, and this assemblage of benthic species is distinctive relative to all other benthic-dominated samples. Two very
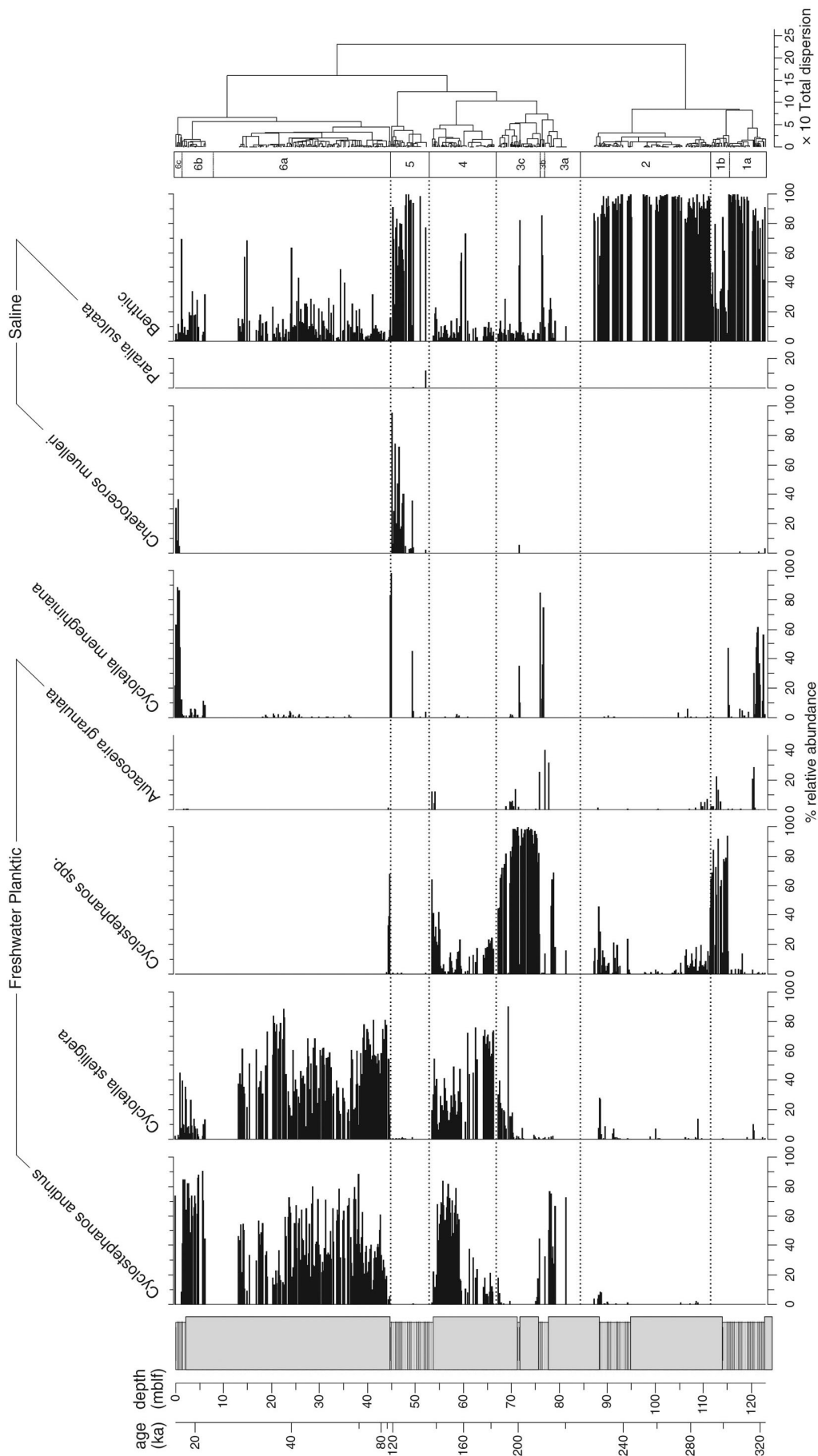
Figure 2. Diatom stratigraphy of Lake Titicaca showing percent relative abundance of common pelagic species relative to the abundance of benthic taxa. The primary axis is sediment depth (meters below lake floor, mblf); associated ages (ka) are show in the left-hand column. The gray units are gray mud, and the striped units are laminated carbonate-rich mud (see text for additional information). Diatom zones were determined by stratigraphically constrained cluster analysis.
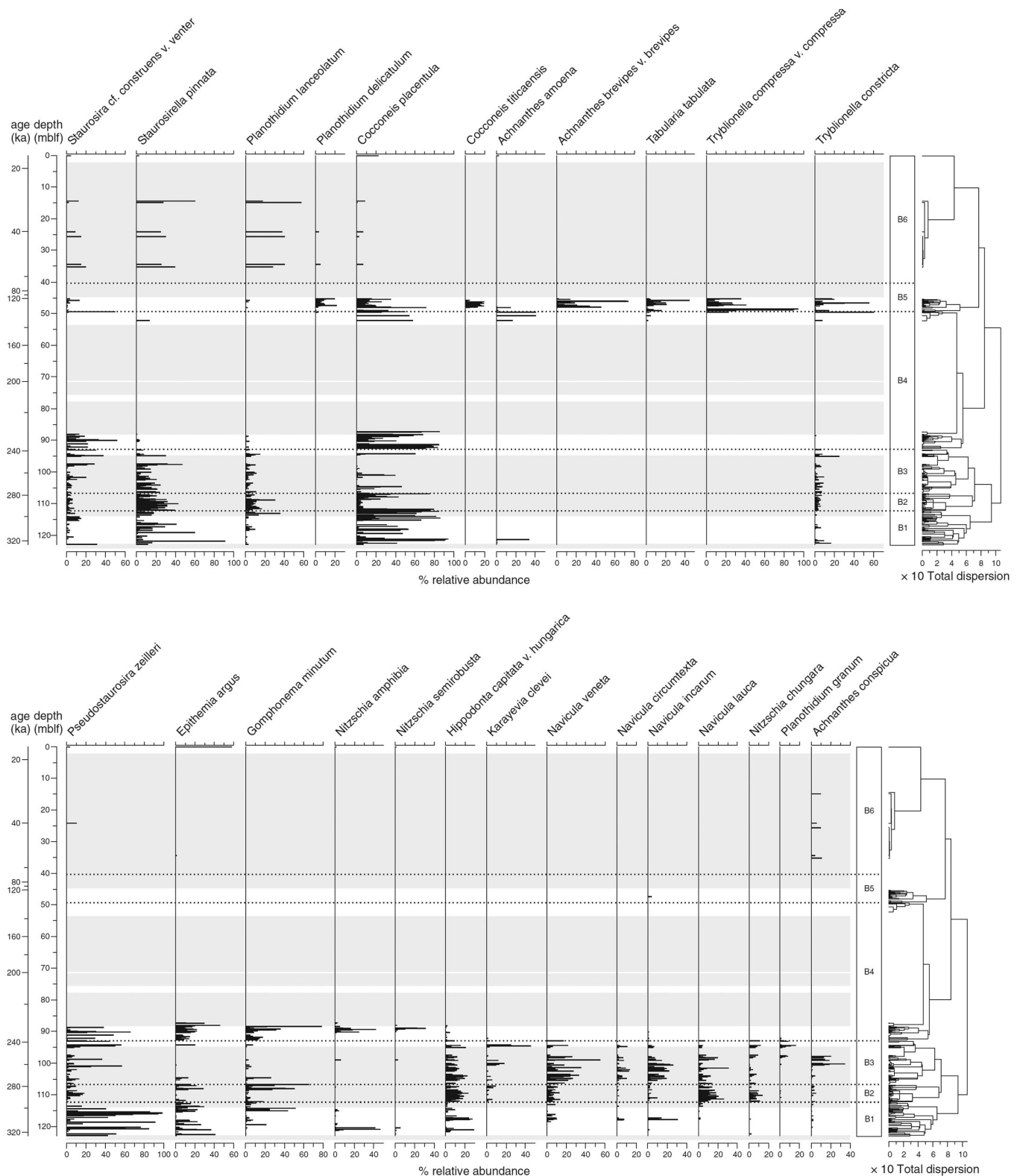
Figure 3. Common benthic taxa (%) in the benthic-dominated zones of the Lake Titicaca drill core. Note that detailed assessment of the species composition of the benthic flora was only carried out in samples with benthic relative abundance > 20%. The primary axis is sediment depth (meters below lake floor, mblf); associated ages (ka) are shown in the left-hand column. Shaded areas are the units of gray mud, whereas the non-shaded areas are laminated units. Benthic diatom zones were determined by stratigraphically constrained cluster analysis.

thin laminated lenses occur within the massive sediment unit that spans from ~ 54 to 88 mblf. These sediments differ from the other laminated units in that they have high proportions of the tychoplanktic *Aulacoseira granulata* and *Cyclotella meneghiniana* (Figure 2) and relatively low proportions (< 20%) of ben-

thic diatoms. The two laminated units at the base of the core (~ 88–95 and 114–123 mblf) contain a diverse array of benthic species (Fig, 3), including the epiphytic *C. placentula*, which can tolerate a range of salinities, *Pseudostaurosira zelleri*, which is characteristic of sub-saline to saline conditions, and other

taxa that are typical of fresh to sub-saline waters (*E. argus, G. minutum, Nitzschia amphibia, Staurosira construens* var. *venter*).

Constrained cluster analysis of the entire diatom flora divides the stratigraphic sequence into 6 major zones (Figure 2). Overall, the diatom zones are correlated with the alternation between massive and laminated units, and the majority of the even numbered zones are correlated with glacial intervals, and the odd numbered zones are correlated with inter-glacial times (Fritz et al., 2007). Subzone 6c is correlated with the upper mid-Holocene laminated unit, subzones 6a and 6b are correlated with the massive sediments from the last Glacial period, zone 5 is correlated with the laminated sediments of MIS5e, and zone 4 is correlated with the penultimate glacial interval (MIS6). Zone 3 is the interval of massive sediments with the thin inter-bedded laminated sequences, and this lithologic unit has been correlated with the upper part of MIS7. The upper part of zone 2 (88–94 mblf) is correlated with the laminated sediments that have been dated to MIS7e, whereas the lower portions of zone 2 (94–110 mblf) form the massive unit that represents MIS8. Zone 1 is split into two subzones that are related to different lithologies: subzone 1b (110–114 mblf) is the massive sediment unit dominated by *Cyclostephanos* sp., whereas subzone 1a (114–123 mblf) is the basal laminated unit. Constrained stratigraphic cluster analysis of the detailed benthic diatom counts (Figure 3) suggests zones and subzones (labeled with B) that match the zonation of the complete flora (Figure 4).

4. Discussion

4.1. The last glacial cycle (marine isotope stages 1–5)

The age of the uppermost 46 m of the drill core sequence is constrained by radiocarbon and U-series dates, which indicate that this section of core spans the last glacial cycle (MIS 1–5). The uppermost 26 m of sediment fall within the range of radiocarbon (< 42 ka), whereas a series of U-series dates on aragonite layers place the uppermost part of the penultimate laminated section (45.842 mblf) in MIS5e (122.8 ka) (Fritz et al., 2007). Most of the sediment between the basal radiocarbon date and the U-series ages is massive carbonate-poor sediment with high magnetic susceptibility values, thus a lithology that suggests that the sediments originate from glacial erosion in the surrounding cordillera. Extrapolation of the radiocarbon chronology to the base of this glacial unit (42 mblf) yields an age of 60 ka. A comparison of this extrapolated age with the U-series age of ~ 122 ka at 45 mblf suggests either a hiatus or very slow sediment accumulation in the intervening interval (most of MIS5a-5d) (Fritz et al., 2007). In this interval, the diatom flora shows an abrupt sequence of change from the obligate saline taxon *Chaetoceros muelleri* to the salinity tolerant *Cyclotella meneghiniana* to an unknown morphotype of *Cyclostephanos* sp. to the freshwater *Cyclostephanos andinus* within 0.7 m of core (Figure 2).

The dominance of freshwater planktic diatoms in the glacial age sediments (1–42 mblf; ~ 10–60 ka) indicates that Lake Titicaca was a deep freshwater lake as a result of high precipitation associated with the South American summer monsoon (Baker et al., 2001a). Within the glacial period, an alternation between *Cyclostephanos andinus* and *Cyclotella stelligera* (Figure 2) suggests a fluctuating limnological environment, although it is unclear whether the two are responding to changing nutrient concentrations or modest changes in lake depth or both. Both of these taxa co-occur in the modern Lake Titicaca (Tapia et al., 2003): *C. andinus* grows in the pelagic regions of the lake, whereas *C. stelligera* is more common in nearshore regions (< 25 m), as well as in shallower glacial lakes in the surrounding cordillera.

The penultimate laminated unit (~ 52–44.8 mblf) dates from MIS5e. The carbonate laminations, enriched $\delta^{13}C_{org}$, and diatom composition (Figure 5) are indicative of an arid period
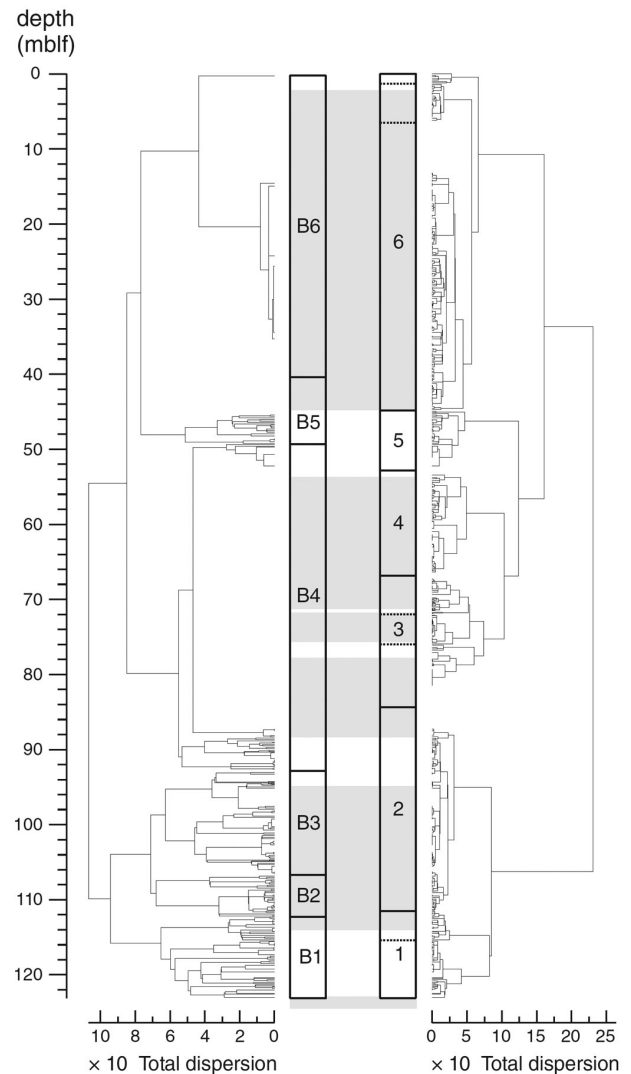
Figure 4. The diatom zones determined from the benthic species compositional data (left-hand column, zones labeled with a B) compared with the zones determined from the differentiated planktic species plus the sum of all benthic taxa treated as a single taxon (right hand column). See text for further details.

when lake level was lowered below the outlet threshold. As a result calcite supersaturation and salinity increased, as did the input of organic carbon from littoral macrophytes, which are heavier in isotopic composition than carbon from pelagic algae (Cross et al., 2000). In the lower portion of the unit (52.2–49.6 mblf, zone B-4b), the diatom assemblage (Figure 3) is dominated by the epiphytic *Cocconeis placentula*, which suggests macrophyte expansion, and by the benthic taxa *Achnanthes amoena* and *Staurosirella pinnata*. Above this (zone B-5) is an increase in saline taxa, including the tychoplanktic *Chaetoceros muelleri* (Figure 2) and the benthic species, *Tabularia tabulata, Tryblionella compressa*, and *Tryblionella constricta* (Figure 3). Together, this assemblage indicates that salinity during this stage was the highest of the entire LT01-2B drill core sequence. Pollen data from this interval also suggest extreme aridity and warmth (Hanselman et al., 2005)

4.2. Long-term evolution of the lake basin and its biota

4.2.1. Diatom evolution and extinction

The Lake Titicaca drill core sequence documents morphological evolution in a major lineage of planktic diatoms, the genus

Figure 5. Summary diagram that shows the relative abundance of benthic and saline diatoms during the last 370 ka in comparison with major lithologic units and selected geochemical data from the drill core. Shaded areas are the units of gray mud, whereas the non-shaded areas are laminated units. On the diatom panel, the solid black line indicates benthic diatoms, and the dashed line indicates the relative abundance of saline taxa. Diatom zones are indicated to the right of the diatom curves and are based on the composite planktic and benthic flora (see Figure 2). Marine Isotope Stages (MIS) of the global interstadial periods are labeled in the far right-hand column (CO_2 data are from Petit et al., 1999).
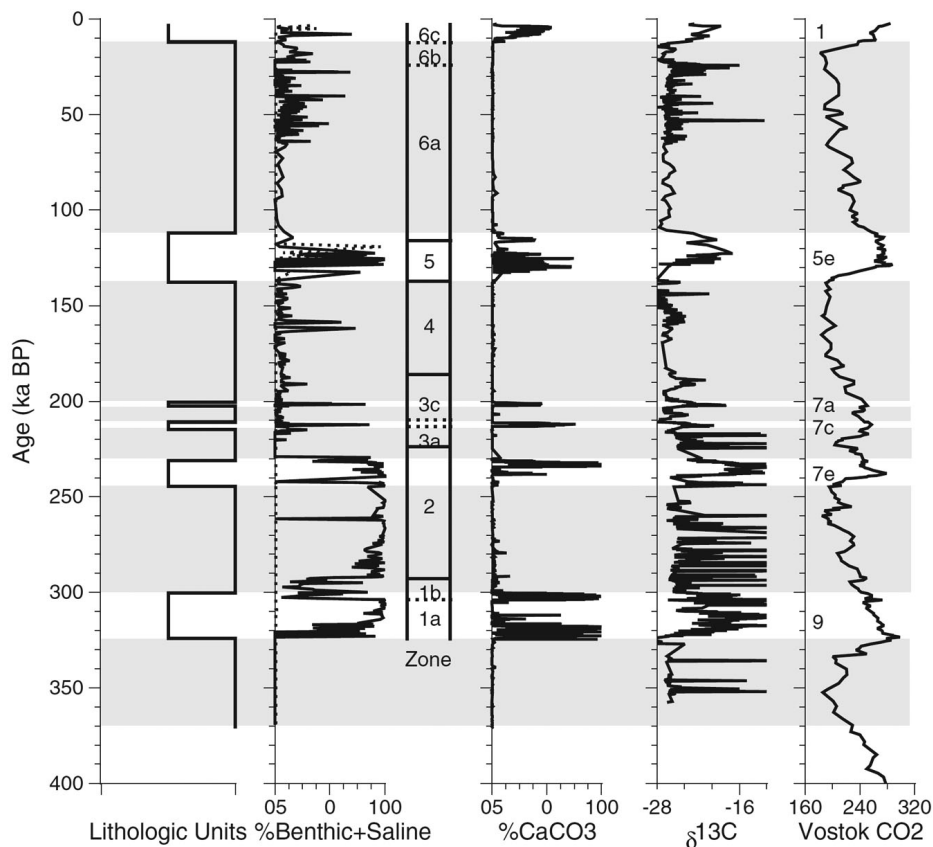
Cyclostephanos. In the modern lake, *Cyclostephanos andinus* is the dominant planktic diatom, and it blooms during times of deepened water-column mixing (Theriot et al., 1985). *C. andinus* was first described from Lake Titicaca and was originally thought to be endemic to the basin. Subsequently, it has been reported from other Andean fossil locations and in one contemporary site (Tapia et al., 2004; Ekdahl et al., 2008; Hernandez et al., 2011). These data suggest that the taxon occurs outside the Lake Titicaca basin, although its distribution appears to be restricted to the tropical Andes. *C. andinus* is dominant in the drill core sequence throughout the most recent interval of late-Pleistocene glaciation (depths < 44.3 mblf, MIS2-4). In earlier planktic dominated phases of the lake, the morphology of the *Cyclostephanos* species is more diverse and includes at least two additional morphotypes that may be different species (Figure 6). These differ from the modern *Cyclostephanos andinus* in size, valve curvature, and density of the pores. The valve face of *C. andinus* has subtle undulation and a large range in valve diameter, between 13.2 and 72.4 µm (Tapia et al., 2004). The prevalent morphotype in samples between 44.5 and 81 mblf (~ 105–220 ka) is characterized by extreme undulation of the valve face, and the valve diameter reaches sizes larger than the *C. andinus* range. *Cyclostephanos* morphotypes occurring in samples below 81.5 mblf (> 220 ka) generally have undulate valve faces, and valve diameters are often smaller than the *C. andinus* size range.

In some samples between 44.3 and 81 mblf (~ 105–220 ka), *C. andinus* and the other morphotypes co-occur, whereas in other samples in this interval, they do not co-occur. In the lower portion of the drill core (> 89 mblf, > 232 ka), *C. andinus* is rare, and it is absent in the basal sediments (> 109 mblf, > 285 ka), where other *Cyclostephanos* morphotypes are common. It is unclear whether or not the different morphotypes represent different species, although the presence of three

planktic morphotypes apparently living in sympatry suggests that they are indeed biological species. In any case, the morphological changes through time suggest significant variation in the limnological environment.

Evolution in major planktic lacustrine diatom lineages during the Pleistocene has been documented in Lake Baikal (Edlund and Stoermer, 2000; Khursevich et al., 2001), as well as in Yellowstone Lake during the warming just prior to the onset of the Holocene (Theriot et al., 2006). In Lake Baikal evolution and subsequent extinction among pelagic taxa is recurrent – each of the precessionally paced interglacials of the last 800,000 years has a distinctive paleo-assemblage (Khursevich et al., 2001). In comparison, the diatom flora of Lake Titicaca is relatively stable. The stratigraphic data in Lake Titicaca do not provide unequivocal evidence of an environmental trigger for the emergence of the modern *C. andinus* morphotype, although the earliest occurrence in the drill core sequence (109 mblf, 285 ka) is associated with the onset of glacial sedimentation. The last occurrence of the other *Cyclostephanos* spp. morphotypes occurs at the transition out of the penultimate interglacial (MIS5e), following an interval of very slow sediment accumulation that may be a hiatus. The other *Cyclostephanos* morphotypes are absent in the most recent interval of extensive regional glaciation (2–44 mblf, MIS 2–4), as well as in the modern flora, where *C. andinus* is the dominant planktic diatom.

Although undoubtedly the *Cyclostephanos* are planktic, other ecological characteristics of the taxonomically undescribed morphospecies in the drill core can only be inferred from their association with diatom species of known ecological affinities. In some levels, the unknown *Cyclostephanos* spp. co-occur with *Aulacoseira granulata*, a tychoplanktic taxon that is characteristic of high nutrients and low light and is common in a variety of shallow and well-mixed systems (Kilham and Kilham, 1975; Anderson, 2000). In other samples, moderate percentages (< 25%) of
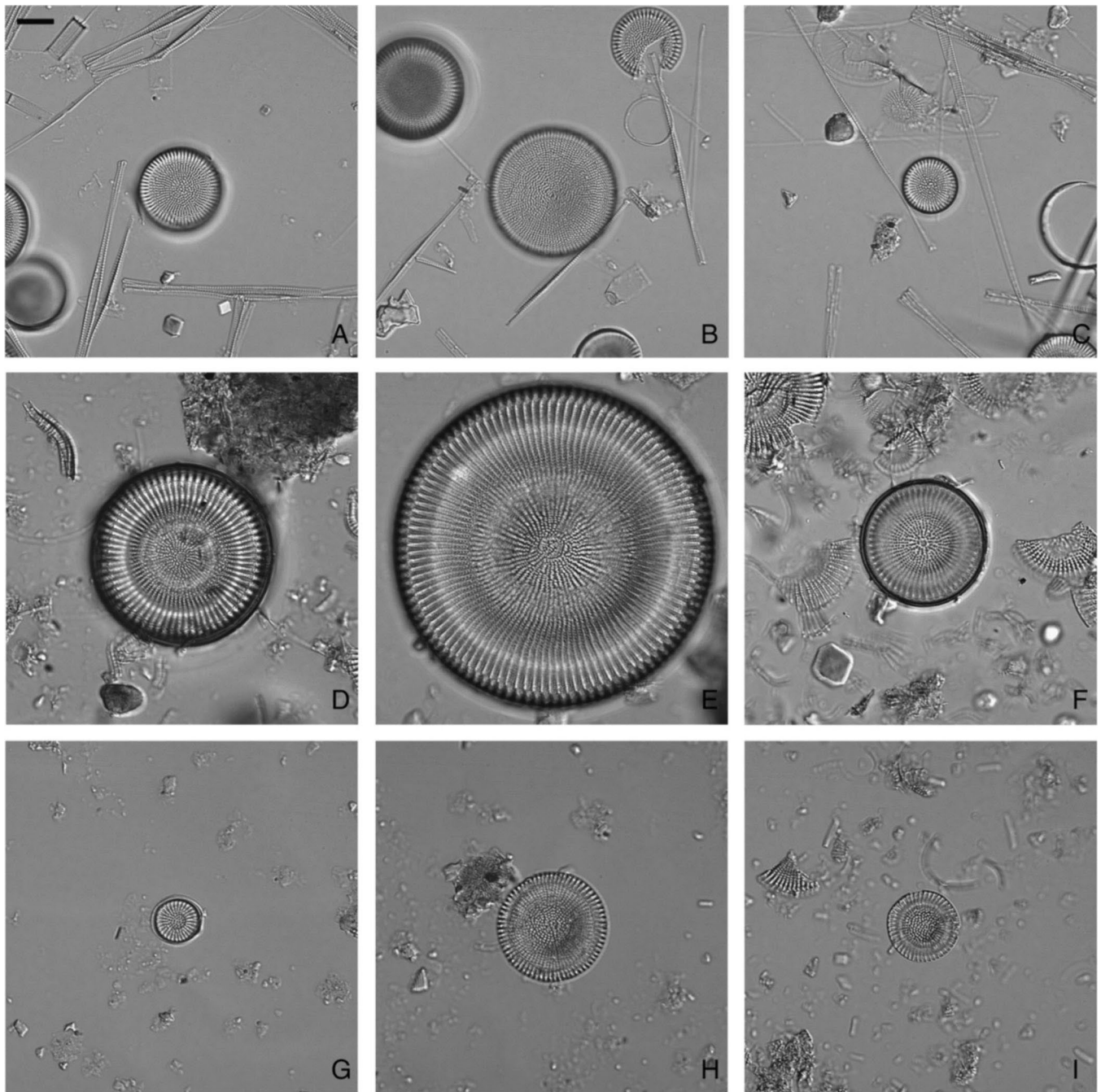
Figure 6. Light micrographs of *Cyclostephanos* morphotypes from Lake Titicaca (Bolivia, Peru). Scale bar = 10 μm. A–C: *Cyclostephanos andinus* holotype from modern plankton samples; D–F: *Cyclostephanos* spp. from core samples located ~ 70–75 mblf; G-I: *Cyclostephanos* spp. from core samples located ~ 100–115 mblf. See text for additional description of the morphotypes.

*Cyclostephano*s spp. occur in benthic-dominated intervals. These associations suggest that the unknown *Cyclostephanos* morphotypes may be favored in conditions associated with shallower water than *C. andinus* and that the planktic-dominated intervals in the basal part of the core may be shallower than those of the last glacial cycle. In any case, the diatom stratigraphy suggests that the contemporary planktic diatom assemblage of Lake Titicaca has existed only for the last ~ 80 ka.

4.2.2. Limnological evolution of the Lake Titicaca basin
Several characteristics of the diatom flora in the sediments that pre-date MIS5e (> 53.7 mblf) suggest that the earlier limnological environment of Lake Titicaca differed from that of the last glacial cycle. Foremost is the occurrence and frequent

dominance of several undescribed morphotypes in the planktic genus *Cyclostephanos*, as described above. Another distinctive characteristic of the basal part of the drill core is the long intervals of dominance by benthic diatom species, which suggest that Lake Titicaca was shallow for much of the period between ~ 230 and 323 ka (87–123 mblf). Although benthic diatom dominance is expected in the shallow lake intervals inferred for the laminated units, the long interval (95–111.5 mblf, ~ 244–292 ka) of massive high-susceptibility sediment – indicative of extensive glacial erosion in the catchment – also is dominated by benthic species. The glacial interval from 111.5 to 115.4 mblf (~ 292 to 303 ka) is the only section in the lower part of the drill core record (diatoms are absent below 123 mblf, ~ 323 ka) where *Cyclostephanos* morphotypes are abundant. In

the basal glacial unit (zones B2, B3), the benthic diatom species composition is distinctive and different from that of laminated units, as indicated in the constrained cluster analysis (Figure 3). Benthic diatom diversity is high, and many of the taxa, such as those in the Naviculaceae and several of the *Nitzschia* spp. (Figure 3), do not occur in the sediments of the last glacial cycle. Overall, the species composition suggests that Lake Titicaca during this lower glacial interval (correlative with MIS8) was relatively fresh, and this conclusion is corroborated by the absence of carbonate in the gray silty clay that dominates this unit (Figure 5) (Fritz et al., 2007).

Two alternative scenarios could account for the dominance of benthic diatoms during an interval of expanded glaciation in the surrounding cordillera. One is that the lake was stratified for extended periods, potentially meromictic, such that pelagic diatom production was low, because of reduced nutrient recycling into surface waters. Limnological surveys of the lake have shown that hypolimnetic entrainment is reduced in some years, although observed impacts on total primary production were limited (Richerson et al., 1986). Alternatively the lake may have been shallow, and several characteristics of the sedimentary sequence suggest that lake level was relatively low at this time. Although carbonate is absent in the silty clay that comprises most of the unit, there are occasional thin lenses of carbonate. In addition, several layers of peaty sediment are interspersed throughout the unit, and the heavy $\delta^{13}C_{org}$ (Figure 5) (Fritz et al., 2007) suggests high inputs of macrophyte-derived organic matter (Cross et al., 2000). Modeling studies of glacial mass balance in the central Andes suggest that Pleistocene glacial advance required precipitation amounts at least as high as today (Kull et al., 2008); thus a primary climatic control on reduced lake level at this time seems unlikely. A more probable explanation is that the lake basin itself was shallower, because of geomorphic or tectonic influence on basin morphometry. Based on very limited available geological and geophysical observations, we surmise that three main tectonic/geomorphic processes have been significant in the Lake Titicaca basin during the ~ 400 ka span of the drill core record and have affected lake-level trends: (1) changing basin morphology, (2) regional tilting, and (3) changing geometry (elevation) of the outlet of the lake.

A progressive subsidence and deepening of the basin floor explain the main observations of this paper, and several lines of evidence are consistent with the hypothesis that the basic morphology of the lake has changed from an aerially large and shallower basin in earlier times to the present, relatively small, but deep basin. Abundant geologic evidence exists for the prior existence of much larger lakes (higher lake stands) in the Lake Titicaca basin. Newell (1949) mapped the nearly flat-lying lacustrine sediments of the Rio Azangaro Formation (RAF), extending more than 60 km north of the present-day shoreline: he believed that these sediments were deposited in a paleolake "Ballivian" that was antecedent to Lake Titicaca. Outcrops of these sediments occur at elevations up to about 3920 meters above sea level (masl), approximately 110 meters above the present (variable) level of Lake Titicaca, and the RAF was said by Newell to reach a maximum thickness of 100 m. Newell believed that the RAF was "pre-glacial", but he had no radiometric or fossil data supporting this conclusion. In the nearby Rio Ramis valley to the north of Lake Titicaca, Farabaugh and Rigsby (2005) measured a stratigraphic section along the Rio Iquilo that is comprised of several meters of fine-grained, laminated, organic-rich blue-gray clay, containing abundant gastropods and ostracodes. These sediments were very likely deposited in a pelagic lacustrine environment. The top of this section lies at about 3880 meters above sea level, approximately 70 meters above the modern level of Lake Titicaca. The sole radiocarbon date on fossil shells from this unit

yielded an apparently finite uncalibrated radiocarbon age of 39,500 ± 610 ^{14}C years BP. While it is possible that these sediments are inset into Newell's RAF, there are as yet no studies of the stratigraphic relations of the units. Stable oxygen isotopic data (Baker, unpublished results) from several shell samples within the Rio Iquilo section strongly support the conclusion that these sediments were deposited in a through-flow lake that was much fresher than modern Lake Titicaca. Thus, these data suggest that as recently as MIS3, Lake Titicaca was far larger than today.

To the south of Lake Titicaca, nearly flat-lying lacustrine sediments outcrop along the northern Rio Desaguadero valley at elevations of 3865 masl, approximately 55 meters above the modern level of Lake Titicaca (Servant and Fontes, 1978). These sediments have been radiocarbon dated at ca. 30,000 cal yr BP (Rigsby and Baucom, 1998) and are likely correlated with the Rio Iquilo section north of Lake Titicaca. This conclusion suggests that there may have been a basin-wide southeastward tilting of ~ 15 m in the past 30 to 40 ka.

Changes in the outlet threshold of Lake Titicaca over time are suggested by two observations. The lacustrine sediments along the Rio Desaguadero described above outcrop only to the north (upstream) of a 40-meter deep canyon on the Rio Desaguadero that separates Ulloma from Callapa (~ 100 km south of the Lake Titicaca outlet). Thus, most of the downcutting of this Ulloma-Callapa sill likely took place since their deposition. In addition, stratigraphic evidence from the Salar de Uyuni to the south suggests that Salar de Uyuni may not have been hydrologically connected to Lake Titicaca and the northern Altiplano via the Rio Desaguadero prior to ~ 60 ka (Fritz et al., 2004). After that time, outflow from Lake Titicaca, through the Rio Desaguadero, contributed to the formation of the large paleolakes "Minchin" and "Tauca" on the southern Altiplano (e.g. Baker et al., 2001b; Nunnery et al., 2010).

These observations spanning the last 30–60 ka of changing basin morphology, tilting, and downcutting document tectonic and geomorphic processes that are likely to have been active over much of the longer drill core record. Clapperton (1993) assembled a marvelous review of the history of the studies of the past lake levels on the Altiplano. One of his main conclusions still stands: that the many different strandlines identified in the northern Altiplano "have not yet been clearly distinguished on a stratigraphical and chronological basis." Our continued lack of knowledge of the tectonic and geomorphic history of this basin continues to limit our ability to decipher its paleoclimatic record.

5. Conclusions

The diatom species composition of Lake Titicaca spanning the last 370 ka shows changes that reflect lake-level variation, likely driven by both climate and non-climatic processes. During the last glacial cycle, planktic diatoms dominate during glacial states (MIS2-4), whereas benthic diatoms are most common during the mid-Holocene and penultimate global interglacial (MIS5e). The species assemblage of MIS5e suggests that this interval had the highest salinity and lowest lake level of the past 400 ka, and multiple lines of evidence suggest that this was the driest period in the drill-core record.

Several aspects of the diatom record suggest the influence of tectonic and geomorphic processes in affecting lake-level trends, particularly in the older strata. During the last glacial cycle, multiple lines of evidence show that the lake was fresh and overflowing during glacial intervals and much shallower and saltier during the peak of the interglacials (Fritz et al., 2007). The planktic-dominated glacial intervals in the upper part of the core are dominated by *Cyclostephanos andinus,* a diatom that is abundant in the contemporary lake. But prior

to MIS4, the diatom record contains several distinct morphotypes in the genus *Cyclostephanos* that are now extinct and are possibly undescribed species. In addition, benthic diatoms dominate the assemblage for most of the period prior to MIS6, including both glacial and interglacial intervals. Although relevant geophysical and geological data are scant, it is likely that progressive subsidence and deepening of the basin floor and associated changes in the geometry of the outlet have affected lake-level trends in Lake Titicaca and thus the composition and evolution of its diatom flora.

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