CLIMATIC AND LACUSTRINE MORPHOMETRIC CONTROLS ON DIATOM PALEOPRODUCTIVITY IN A TROPICAL ANDEAN LAKE

Bao, R.[1*]; Hernández, A.[2]; Sáez, A.[3]; Giralt, S.[4]; Prego, R.[5]; Pueyo, J.J.[3]; Moreno, A.[6] and Valero-Garcés, B. L.[6]

[1]Centro de Investigacións Científicas Avanzadas (CICA), Facultade de Ciencias, Universidade da Coruña, 15701 A Coruña, Spain

[2]Instituto Dom Luiz (IDL), Faculdade de Ciências, Universidade de Lisboa, Lisbon 1749-016, Portugal

[3]Faculty of Geology, Universitat de Barcelona, C/ Martí Franquès s/n, 08028 Barcelona, Spain

[4]Institute of Earth Sciences Jaume Almera - CSIC, C/Lluís Solé i Sabarís s/n, 08028 Barcelona, Spain

[5]Instituto de Investigaciones Marinas – CSIC, Eduardo Cabello 6, 36208 Vigo, Spain

[6]Pyrenean Institute of Ecology - CSIC, Av. Montañana 1005, 50059 Zaragoza, Spain

***Correspondence to:**

Roberto Bao

Centro de Investigacións Científicas Avanzadas (CICA), Facultade de Ciencias, Universidade da Coruña, 15701 A Coruña, Spain

Phone: +34 881 012 101

Fax: +34 981 16 70 65

E-mail: roberto.bao@udc.es

ABSTRACT

The coupling of lake dynamics with the catchment biogeochemistry has been considered the key element controlling primary production in mountain lakes at time scales of a few decades to millennia. Yet, little is known on the effects produced by changes in the morphometry of lakes throughout their ontogeny. Lake Chungará (Central Andean Altiplano, northern Chile) experienced long-term lake-level fluctuations that strongly modified its area:volume ratios, making it an ideal system to explore the relative role that long-term climatic shifts and changes in morphometry play on biosiliceous lacustrine productivity. In this paper we review previous data on percent content of total organic carbon, total inorganic carbon, total nitrogen, total biogenic silica, isotopic composition of organic matter, carbonates, and diatom frustules, as well as on the abundances of the chlorophycean *Botryococcus braunii* in this lake for the period 12,400-1,300 cal yr BP. We also include new data on organic carbon and biogenic silica mass accumulation rates and diatom assemblages composition of an offshore core dated with ^{14}C and U/Th.

Biosiliceous productivity was primarily influenced by shifts in allochthonous nutrient inputs related to precipitation variability. Humid phases dated at c. 12,400 to 10,000, 9,600 to 7,400 and 3,550 to 1,300 cal yr BP, coincide with periods of elevated productivity. Conversely, falls in productivity were recorded during arid phases dated at c. 10,000 to 9,600 and 7,400 to 3,550 cal yr BP (Andean mid-Holocene Aridity Period). Yet, morphometry-related in-lake controls provoked that there was not a linear response of productivity to precipitation variability. During the late Glacial to early Holocene, lowstands facilitated complete water column mixing, prompting the episodic massive blooms of a large centric diatom, *Cyclostephanos* cf. *andinus*. Irrespective of aridity, moderate productivity could therefore be maintained by this phenomenon of morphometric eutrophy during the early history of the lake. The subsequent net increase in lake-level introduced modifications in the area of the epilimnion sediments versus the total volume of the epilimnion that prevented complete overturn. Surpassing a certain depth threshold at c. 8,300 cal yr BP caused the cessation of morphometric eutrophy conditions associated with the *Cyclostephanos* cf. *andinus* superblooms. After 7,300 cal yr BP, the lake experienced a decrease in biosiliceous productivity and a change of state that involved a stronger

dependence on precipitation variability, a shift to a bicarbonate-dominated system, and a lesser contribution of diatoms to total primary productivity. Our results show that interpretation of lacustrine paleoproductivity records as paleoclimatic archives need to take into account the effects of changes in morphometry associated with the ontogeny of lakes.

Keywords: lake paleoproductivity, lake ontogeny, laminated sediments, diatoms, Andean Altiplano, Holocene

1. INTRODUCTION

Photosynthetic activity in periodically stratified lakes is generally restricted by phosphorous and nitrogen concentrations in the epilimnion, because the waters underneath, although richer in these limiting nutrients, do not receive sufficient light to sustain significant primary productivity (Sterner, 2008). This vertical segregation is usually eliminated when deep mixing of the water column brings the bottom nutrient-rich waters to the euphotic zone. Nutrient and mixing gradients are therefore primary drivers of phytoplankton dynamics and productivity in aquatic ecosystems (Winder & Hunter, 2008). Morphometric characteristics of the lake basin influence the total epilimnion volume and the degree of water column mixing and, therefore, can be an important influence on lake productivity (Imboden & Wüest, 1995; Wetzel, 2001).

The relative role that lake morphology plays in affecting productivity likely varies geographically and through time. In a classical paper, Rawson (1955) reviewed data from a series of large lakes and concluded that lake morphometry was a determinant factor in lacustrine productivity, a result that could not be reproduced by Brylinsky & Mann (1973), who considered morphometry as relatively unimportant in affecting phytoplankton production. These ecological studies relied on space-for-time substitution approaches (Smol, 2008) and did not take into account changes in productivity that could be associated with modifications in the morphology of an individual lake over long periods of time. Moreover, in spite of evidence generated by Quaternary paleoecologists (Engstrom et al., 2000), many limnologists still assume a traditional model of progressive eutrophication of lakes over time (Deevey, 1955). Temporal change in phytoplankton communities and their function is a time-scale dependent process whose study has largely ignored the long-term variability resulting from lake ontogeny (Anderson, 1995). Data analyses on broad time scales provide new insights on the role that both climate and local physiographic factors can have in affecting the productivity of lake systems. Disentangling the relative importance of these two factors is required in Quaternary paleoclimatic reconstructions that rely in part on the study on changes in paleoproductivity inferred from biosiliceous proxy data (e. g., Johnson et al., 2004; Mackay, 2007; Castañeda et al., 2009).

Lakes in the Central Andean Altiplano experienced strong lake-level fluctuations during the Late Quaternary that altered their surface area:volume ratios (Placzek et al., 2009). This variation makes them ideal systems to explore the relative role that long-term climatic shifts and changes in morphometry play in affecting lacustrine productivity. The millennial scale moisture balance of the Atlantic-Amazon-hydrologic system is strongly influenced by precessional changes in solar insolation (e. g. Rowe et al., 2002), although changes in Equatorial Pacific sea-surface temperature (SST) and El Niño-Southern oscillation (ENSO) variability also may have played a role (Polissar et al., 2013). All of these factors contributed to changes in lake-levels that, in turn, affected the composition of planktonic communities (e. g. Tapia et al., 2003). In spite of this, very little is known regarding the effects of long-term lake-level variability on functional properties, such as lacustrine productivity, of regional limnological systems.

Lake Chungará (Central Andean Altiplano, northern Chile) is a surficially closed lake that has undergone significant changes in water level in the last 12,400 years (Sáez et al., 2007). Due to its complex bottom topography, these changes produced important modifications in the surface:volume ratio during its ontogeny, making it a good system to test the relative importance that climate and morphometric characteristics of the lake have on primary productivity variation. There is a former appreciable knowledge of the main changes that occurred in the lake since the Late Glacial based on multiproxy evidence. These included sedimentary facies characterization (Sáez et al., 2007), isotopic composition of bulk organic matter ($\delta^{13}C_{org}$, $\delta^{15}N_{org}$; Pueyo et al., 2011), carbonates ($\delta^{18}O_{carbonate}$, $\delta^{13}C_{carbonate}$; Pueyo et al., 2011), and diatom frustules ($\delta^{18}O_{diat}$, $\delta^{13}C_{diat}$; Hernández et al., 2008, 2010, 2011, 2013), as well as a moisture balance reconstruction based on magnetic susceptibility, X-ray Fluorescence (XRF), X-ray Diffraction (XRD), Total Carbon and Total Organic Carbon (TC and TOC), Biogenic Silica (BSi) and grey-colour curve of the sediment data (Giralt et al., 2008). But, in spite of the large number of proxies analyzed, an overall picture on the causes behind changes in paleoproductivity in the lake is still lacking.

In this paper we integrate these previous and new (diatom assemblages composition, organic carbon and biogenic silica mass accumulation rates) multiproxy data on the paleoenvironmental evolution of Lake Chungará, to develop an evolutionary model of long-term productivity trajectories in

a high altitude tropical lake. We also study the relationship between changes in productivity and the main climatic events recorded in the Central Andean Altiplano, as well as the potential role that changes in lake morphometry could have also played. We show how the imprinting of primary climatic forcing signals in the sedimentary record is decisively modulated by the effects of changes in the morphometry of the basin throughout the ontogeny of the lake.

2. STUDY SITE

2.1 *Physiographic and limnological features*

Lake Chungará (18º15' S, 69º09' W, 4,520 m a.s.l., Fig. 1) was formed between 15,000 and 17,000 yr BP after the partial collapse of the Parinacota volcano (Hora et al. 2007; Sáez et al., 2007). The lake has a maximum length of 8.75 km, a maximum water depth of 40 m, a surface area of 21.5 km^2, and a volume of 400 x 10^6 m^3 (Mühlhauser et al., 1995; Herrera et al., 2006). The western and northern lake margins are steep, whereas the eastern and southern margins are gentle, forming extensive shallow (less than 7 m deep) platforms (Fig. 1B). The main inlet to the lake is the Chungará small stream (300-460 l s^{-1}), while the main water loss is by evaporation (3.10^7 m^3 yr^{-1}). The groundwater outflow to the near Cotacotani lakes has been estimated as about 6-7 10^6 m^3 yr^{-1} (Risacher et al., 1999; Dorador et al., 2003).

Lake Chungará is a cold-polymictic and moderately saline lake, which thermally stratifies from January to April (Mühlhauser et al., 1995). It contains 1.2 g l^{-1} of Total Dissolved Salts, with a conductivity ranging between 1,500 and 3,000 μS cm^{-1}, and a water chemistry of Na-Mg-HCO_3-SO_4 type (Mühlhauser et al., 1995; Dorador et al. 2003). The lake has been classified as oligo-mesotrophic or meso-eutrophic according to chlorophyll-a concentration and photosynthetic activity, respectively (Mühlhauser et al., 1995). Most of the primary productivity is by diatoms, but cyanobacteria and chlorophyceans contribute more during spring and summer (Dorador et al., 2003; Márquez-García et al., 2009). Large concentrations of phosphorous were measured at present (Mühlhauser et al., 1995), but the lake is limited by nitrogen (Dorador et al., 2003; Márquez-García et al., 2009).

The lake receives precipitation from the Atlantic Ocean. Annual rainfall in the Chungará region is about 350 mm yr^{-1}, but the range is variable (100-750 mm yr^{-1}). Mean temperature is 4.2ºC. Humidity in the region is advected from the Amazon Basin by the South American Summer Moonson (SASM), which is linked to the Intertropical Convergence Zone (ITCZ) (Zhou & Lau, 1998). The wet season occurs during the austral summer months, when a weak easterly flow prevails over the Altiplano as a consequence of the southward migration of the subtropical jet stream and the establishment of the Bolivian High Pressure system (Baker et al. 2005; Garreaud et al. 2009; Polissar et al., 2013). In addition, a significant fraction of the inter-annual changes in summer precipitation is currently also related to ENSO (Garreaud et al., 2003).

2.2 *The lake sedimentary inflill*

A 3D depositional model based on seismic imagery and sedimentary facies analyses of 15 sediment cores identified a total of 6 sedimentary units composed of 7 offshore, 3 littoral-nearshore, and 2 volcaniclastic facies (Sáez et al., 2007) (Fig. 1C). Sediments in the offshore-deepest central plain are made up of laminated (Unit 1) and non-laminated diatomaceous oozes with interbedded tephra layers (Unit 2). The diatomaceous laminated sediments of Unit 1 show rhythmites made up of triplets (4 to 24 yr) of white, light- and dark-green laminae (Hernández et al., 2008, 2011) (Fig. 2). Green laminae are composed of a mixture of the euplanktonic diatom *Cyclostephanos andinus* (always smaller than 50 µm), diatoms of the *Discostella stelligera* complex, and a diverse mixture of tychoplanktonic and benthic diatoms. White laminae show an almost monospecific composition of very large valves of *Cyclostephanos andinus* (>50 µm), which resulted from the deposition of massive short-term blooms of this taxon. These superblooms have been interpreted as triggered by strong influx of nutrient-rich waters from the lake bottom to the photic zone or, less frequently, by nutrient inputs associated with increased runoff (Hernández et al., 2011). The dark laminae are considered to represent the background limnological conditions. The diatomaceous oozes of Unit 2 show no lamination or indication of massive short-term blooms of large *Cyclostephanos andinus*.

3. MATERIALS AND METHODS

In November 2002, 15 sediment cores up to 8 m long were retrieved from the lake with a Kullenberg corer. From the core lithostratigraphic correlation, a composite core spanning the whole sedimentary infill of the offshore zone (minimum thickness of 10 m) was constructed. The chronological framework of the sedimentary sequence of Lake Chungará was generated from 17 AMS ^{14}C dates of bulk organic matter and aquatic plant macrofossils, and by one $^{238}U/^{230}Th$ date from carbonates (see further details of age model in Giralt et al., 2008).

Samples for analyses were taken every 5-10 cm from core CHUN11A (Fig. 1). TC and total inorganic carbon (TIC) content were measured using a UIC model 5011 CO2 Coulometer, with TOC determined by subtraction of TIC from TC. Total nitrogen (TN) was determined in a Variomax C/N following the Dumas' method (Ma & Gutterson, 1970). BSi was extracted following the alkaline leaching technique (Mortlock & Froelich, 1989), measuring the resulting extract by the molybdate blue colorimetric method (Hansen & Grashoff, 1983) using an AutoAnalyser Technicon II. TOC, TIC and TBSi results are expressed in the form of percent values of the sediment dry weight. For the calculation of dry bulk densities the samples were dried to remove free water. Fluxes of TOC and BSi to the sediments were estimated calculating mass accumulation rates (MARs, mg cm^{-2} yr^{-1}) by multiplying their concentrations by the sediment dry densities and sedimentation rates at each depth. By calculating the fluxes, the input of each component is independent of the effects of sediment dilution (Boyle, 2001). Although neither percent values nor MARs can provide on their own precise paleoproductivity reconstructions, their use in combination can help in the identification of the main trends in productivity (Engstrom & Wright, 1984; Boyle, 2001).

Samples for diatom analysis were processed using standard techniques (Renberg, 1990). At least 400 valves were counted per sampled interval. All counts were made at X1000 with Nomarski differential interference contrast optics. Diatom preservation was estimated using the *F* index (Flower & Likhoshway, 1993). Identifications of diatom taxa were based upon the available diatom floras from the region (Rumrich et al., 2000) and elsewhere (e. g., Krammer & Lange-Bertalot, 1986-1991; Lange-Bertalot, 2000-2005). Raw valve counts were converted to percentage abundance data. All statistical

analyses were carried out on a diatom relative abundance matrix of those taxa attaining a frequency of more than 2% in at least one sample. Data were transformed by square-root transformation. Definition of the main Diatom Assemblage Zones (DAZs) was performed using stratigraphically constrained cluster analysis based on squared Euclidean dissimilarity (CONISS, Grimm, 1987), as implemented in Psimpoll 4.10 (Bennett, 2002). Zonations with variances that exceeded values generated by a broken-stick model of the distribution of variance were deemed statistically significant (Bennett, 1996).

Ordination analyses (Detrended Correspondence Analysis-DCA, and Principal Component Analysis-PCA) were conducted with the CANOCO 4.5 computer program (ter Braak & Smilauer, 1998) to identify the main underlying environmental gradients explaining the variability of the diatom abundance data (Jongman et al., 1987). Although a transfer function for ionic concentration and salinity was developed in the near Bolivian Altiplano (Sylvestre et al., 2001), most of the taxa present in Lake Chungará do not occur in that dataset, and it was not useful for quantitative paleoenvironmental studies. Therefore, only qualitative diatom-based paleoenvironmental reconstructions were performed, carefully informed by contemporary data on diatom ecology (following Sayer et al., 2010). In this case, the qualitative approach was made on the basis of the study of modern analogues in Lake Chungará (Dorador et al., 2003) and the nearby Lake Titicaca (Theriot et al., 1985; Iltis, 1992; Servant-Vildary, 1992; Tapia et al., 2003, 2004). Diatom autoecologies derived from a survey on the literature (e. g. Servant-Vildary & Roux, 1990; Gasse et al., 1995; Sylvestre et al., 2001) have also been used.

A tentative qualitative lake-level curve was constructed combining the previous and new multiproxy data. These included i) the abundances of euplanktonic vs. periphytic diatoms, ii) changes in the lithofacies, particularly the presence of carbonates (Sáez et al., 2007), iii) oxygen isotopic data on diatom frustules ($\delta^{18}O_{diat}$) for the late Glacial and early Holocene, with $\delta^{18}O_{diat}$ enrichments and depletions mostly indicating low and high lake-levels, respectively (Hernández et al., 2013), iv) the oxygen isotopic characterization of carbonates ($\delta^{18}O_{carbonate}$), starting to precipitate at 10,200 cal yr BP, with $\delta^{18}O_{carbonate}$ depletions and enrichments indicating water volume increases, and more evaporated waters, respectively (Pueyo et al., 2011), v) the abundances of *Myriophyllum* sp. and *Botryococcus braunii* (Sáez et al., 2007), and vi) the moisture balance reconstruction of Giralt et al. (2008).

4. RESULTS

4.1 Diatom Assemblages

A total of 109 taxa have been identified. Percent abundance data of 21 common diatoms were plotted stratigraphically (Fig. 3). The diatom record is dominated by euplanktonic diatoms (mainly *Cyclostephanos andinus* and diatoms of the *Discostella stelligera* complex), with subdominant freshwater tychoplanktonic and benthic taxa (mainly *Staurosira construens* aff. *venter*, *Cocconeis placentula* and *Nitzschia tropica*). The diatom dissolution index *F* shows moderately well preserved valves in Unit 1, whereas diatom dissolution effects were more prominent in Unit 2 (Fig. 3). The broken-stick model of the distribution of variance allowed the definition of eight DAZs (Table 1 and Fig. 3).

Previous preliminary examination of smear slides (Hernández et al., 2008, 2011) did not allow precise determinations at the species level. In this study, routine counts allowed taxonomic differences to be identified in specimens of *Cyclostephanos andinus* in the laminated sediments. Whereas the valves found in the green laminae could be ascribed to the published description of *Cyclostephanos andinus* (Tapia et al., 2004), the larger specimens preserved in the white laminae showed striking differences under the microscope. Later SEM ultraestructural examination of the valves confirmed the uncertain taxonomic identity of the larger *Cyclostephanos andinus*, which in the future may be assigned to a new closely related species (cf. Fritz et al., 2012) or, alternatively, may be considered *Cyclostephanos andinus* of extreme morphology (Edward Theriot, pers. comm.). Until its taxonomic affinity is affirmed, it will be referred to as *Cyclostephanos* cf. *andinus* in this publication.

A DCA was performed to estimate the length of the dominant gradient in the diatom assemblages and to evaluate whether the taxa in the core samples followed a unimodal or linear distribution (Jongman et al., 1987). Results indicated that the longest gradient was 2.08 SD units, suggesting a linear response (Leps & Smilauer, 2003). For this reason a PCA was subsequently performed. During the implementation of the PCA we wanted to restrict our analyses to the identification of the main long-

term environmental forcings on the composition of the diatom assemblages. However, the white and light green laminae of Unit 1 (Facies A and B), made up of a quasi-monospecific assemblage of *Cyclostephanos* cf. *andinus*, represented very short-term conditions (extraordinary diatom blooms) interrupting any long term trend (Hernández et al., 2008, 2011). This taxon was not present in the banded and massive Unit 2 (Facies D, E and F). To partial out the effects of both sources of variation, we performed a Partial PCA using the lithological units (laminated, i. e., Unit 1, vs. non-laminated, i. e, Unit 2) as covariables (ter Braak & Smilauer, 1998; Leps & Smilauer, 2003). This procedure allows us to ascertain whether there is still any environmental explanation of the long-term changes in the diatom record once the effects of the short-term variability imposed by the white laminae are removed.

The first two principal components of the partial PCA (PC1 and PC2) explained 83.6% of the total variance (λ_1 = 0.625; 69.4%, and λ_2 = 0.128; 14.2%). *Cyclostephanos andinus* shows the highest score for the first main direction of variation (PC1), and the diatoms of the *Discostella stelligera* complex acquiring the most negative score (Fig. 4). The second ordination axis (PC2) shows highest scoring for *Cyclostephanos* cf. *andinus*, with most of the periphytic taxa (e. g. *Nitzschia tropica*, *Staurosira construens* aff. *venter*, *Fragilaria capucina*) also showing positive scores. At the opposite side of the gradient, *Cyclostephanos andinus* shows the most negative score. Variations of the first two principal components throughout the core are plotted in the diatom abundance diagram (Fig. 3).

4.2 Geochemical proxy data

Depositional evolution of Lake Chungará has been reconstructed based on sedimentary facies analyses and a number of geochemical proxies. The percent values and MARs of TOC and TBSi, percent content of TIC, and the TOC/TN atomic ratio are plotted along with the percent abundance of benthic diatoms, used here as a rough indicator of changes in water depth, and the scores of the first two axis derived from the PCA conducted on the diatom abundance data (Fig. 5). Additionally, previous isotopic data on organic matter, carbonates, and diatom frustules, and the percent abundance of *Botryococcus braunii* observed in palynological slides (Sáez et al., 2007) are also included.

4.2.1 *Unit 1*

TBSi content in Unit 1 is high, ranging from 41 to 54%. Fairly stable values in TBSi occur from the bottom to 531 cm (c. 9,350 cal yr BP), comprising Subunit 1a and the lower part of Subunit 1b. The fairly constant percent content of Subunit 1a and the lower part of Subunit 1b is, however, not mirrored by TBSi MARs data, which show a rising trend from 6.6 mg TBSi cm^2 yr^{-1} to a maximum flux for the whole sedimentary record of 29.2 mg TBSi cm^2 yr^{-1} recorded in Subunit 1a at 652 cm (c. 10,600 cal yr BP). This trend is followed by a decline to a mimimum value of 5.4 mg TBSi cm^2 yr^{-1}, which is again not accompanied by significant variations in the percentage of TBSi. Maximum values for percent content of TBSi are recorded in the top half Subunit 1b, with a maximum of 75% at 474 cm (c. 8,600 cal yr BP), declining afterwards. This rise is paralleled by an increase in the TBSi flux to the sediments, which reached values as high as 19.2 mg TBSi cm^2 yr^{-1}.

Whereas TOC and TBSi MARs follow a similar pattern, other differences stand out, especially when %TOC is considered. The bottom of Subunit 1a shows a declining trend in %TOC, followed by an overall persistent rising trend throughout subunits 1a and 1b. This trend starts at 787 cm (c. 11,600 cal yr BP), when a minimum of 2.5% TOC is recorded, coinciding with the onset of the Holocene. The highest values in the whole unit for TOC (8.3%) and its accumulation rate (4.0 mg TOC cm^2 yr^{-1}) correspond to the 682 cm level (c. 10,950 cal yr BP), when a small decrease in both the content of TBSi and its MAR is recorded. The TOC flux to the sediments declines after this peak, until a minimum of 0.9 mg TOC cm^2 yr^{-1} at 550 cm (c. 9,600 cal yr BP). %TOC shows, however, a general rising trend, which fluctuates between 4.7 to 8.6%.

This unit ends at 450 cm (c. 8,300 cal yr BP) with a strong reduction in the flux of TBSi and TOC to the sediments, as well as with the diminution of their percent content, which is concomitant with the first occurrence of carbonate-rich layers and a sharp increase in %TIC (3.8%). Although a previous TIC peak occurred at 550 cm (c. 9,500 cal yr BP) it was not associated to discrete carbonate laminae.

The atomic TOC/TN ratio shifts between 6.9 and 12.6 throughout this unit (a large fall at 712 cm, c. 11,000 cal yr BP, can certainly be attributed to an analytical error), and although a rising trend is visible throughout subunits 1a to 1b, most of the values fall in the <10 range.

4.2.2 *Unit 2*

Unit 2 starts yielding flux values of 24.4 mg TBSi cm^2 yr^{-1} and 3.6 mg TOC cm^2 yr^{-1}. After the %TIC peak that separates Unit 1 and Unit 2, %TBSi rises to a maximum of 62.8 for the whole unit at 422 cm (c. 8,000 cal yr BP), whereas %TOC also increases to 9.2 at the same level. Immediately after, there is a declining trend from this level onwards, involving a sharp fall in the case of TBSi after 337 cm (c. 7,200 cal yr BP). TBSi MARs and %TBSi reach the lowest values for the whole record from this time to present, with values that range between 1.8 to 8.8 mg TBSi cm^2 yr^{-1} and 6.3 to 34.8%, respectively. TOC fluxes are also strongly reduced, ranging from 0.4 to 2.5 mg TOC cm^2 yr^{-1}, but maintaining values above those of the Late Glacial. In contrast, %TOC shows substantial fluctuations, with a peak at 22 cm (c. 1,500 cal yr BP) of 9.7%. Reductions of TOC and TBSi content are, however, magnified by the presence of tephra layers at 224, 56 and 39 cm. In spite of the general decrease in the geochemical paleoproductivity proxies, a consistent rising trend is recorded between 308-255 cm (c. 6,900-6,400 cal yr BP), when %TBSi and %TOC show a parallel increase coincident with a maximum value of 4.4 for TIC.

The TOC/TN curve shows oscillations throughout the record, although maintaining a general increasing trend towards the present. This is most evident when the flux of TBSi is strongly reduced after 337 cm (c. 7,200 cal yr BP). As is the case for %TBSi, %TOC and %TIC, there is also a consistent increase in the TOC/TN ratio between 308-255 cm (c. 6,900-6,400 cal yr BP) when the highest values for the whole record (14.0 and 14.5) are reached.

5. DISCUSSION

5.1 Meaning of the diatom assemblages

Lake Chungará has a diatom record characterized by shifting dominance of large vs. small taxa, typified by *Cyclostephanos andinus* and *Discostella stelligera*, respectively. These are interrupted by episodes of exclusive dominance of a very large diatom, *Cyclostephanos* cf. *andinus*, manifested in the deposition of the white, beige, and very light green laminae. Both *Cyclostephanos andinus* and the

diatoms of the *Discostella stelligera* complex represent high lake-level conditions without elevated concentration of salts (Tapia et al., 2003).

Cyclostephanos is a genus of euplanktonic diatoms characteristic of well-mixed waters under isothermal conditions (Håkansson, 2002), whereas the diatoms of the *Discostella stelligera* complex thrive well in stratified low energy environments (e. g. Rühland et al., 2008). Large cells, such as those of *Cyclostephanos andinus* and *Cyclostephanos* cf. *andinus*, require well-mixed conditions to avoid sinking in the water column (Margalef, 1978). On the other hand, their larger size increases their nutrient requirements, and their low surface to volume area (S/V) reduces nutrient uptake. For these reasons they only thrive well under high nutrient concentrations (Finkel et al., 2005; Litchman et al., 2009). Conversely, enhanced buoyancy of small-sized phytoplankton, such as the components of the *Discostella stelligera* complex, gives an advantage under thermal stratification, and their high S/V ratio facilitates nutrient uptake under lower nutrient situations. Although other factors besides water column mixing regime can simultaneously act to explain the abundances of centric diatoms in sedimentary records (Saros & Anderson, 2014), comparison with modern analogues shows that ecophysiological adaptations to avoid sinking are the most likely main driver of *Cyclostephanos* and *Discostella* abundances in Lake Chungará. Diatoms of the *Discostella stelligera* group are currently more abundant during the austral summer, when stratification is favored (Dorador et al., 2003). This taxon is also most abundant in the nearshore regions of Lake Titicaca, where waters are warmer (Tapia et al. 2003). By contrast, *Stephanodiscus astraea*, the former name for *Cyclostephanos andinus* (Theriot et al., 1985; Tapia et al., 2004), was found as the main component of the phytoplankton assemblages in the cold season, when mixing by isothermal conditions can be prompted (Dorador et al., 2003). This result also fits with the known ecology of the species in Lake Titicaca, where it is associated with the breakdown of thermal stratification and very high levels of nutrients (Theriot et al., 1985). Iltis (1992) also reported blooms, when 100% of the diatom assemblage can be made up by *Cyclostephanos andinus* (Servant-Vildary, 1992).

Results of the PCA indicate that changes in the water column mixing regime and depth are the primary controllers of the composition of the diatom assemblages. PC1 mainly reflects variations in the large centric diatom *Cyclostephanos andinus* relative to small diatoms of the *Discostella stelligera*

complex. Thus it measures the euplanktonic diatom size distribution, which is related to water turbulence (Fig. 5). The high abundance of *Cyclostephanos andinus* throughout the history of the lake suggests that intervals of isothermal mixing were persistent. Nevertheless, their duration varied in comparison with the stratification periods, as indicated by fluctuations in the relative abundance of the *Discostella stelligera* group.

Changes in water depth are suggested by PC2, since it reflects variation in a set of periphytic diatoms (e. g. *Nitzschia tropica*, *Staurosira construens* aff. *venter*, *Fragilaria capucina*.), vs. the euplanktonic *Cyclostephanos andinus* (Fig. 4). On the other hand, *Cyclostephanos* cf. *andinus* shows a close relationship with periphytic taxa, which suggests that, although euplanktonic, it needs moderately shallow waters to develop blooms. An association with shallow waters has also been found for other large species of the *Cyclostephanos andinus* complex, which became extinct during the Quaternary (Fritz et al., 2012) and by large sized cells of the nominate *Cyclostephanos andinus* in Lake Titicaca (Servant-Vildary, 1992). Also, its very large size indicates not only a well-mixed water column, but an enhanced nutrient storage capacity (Litchman et al., 2009). Thus, *Cyclostephanos* cf. *andinus* superblooms, and therefore the deposition of the white laminae, would be triggered by increased nutrient input during shallow water periods. A lamina by lamina isotopic diatom characterization showed that deposition of the white laminae occurs mainly at times of increase in $\delta^{18}O_{diat}$ values, indicating reduced external hydrologic inputs to the lake, and depletions in the $\delta^{13}C_{diat}$, an indicator at this sampling scale of light carbon upwelled from the hypo- to the epilimnion (Hernández et al., 2011). All these data support the interpretation of *Cyclostephanos* cf. *andinus* as a suitable indicator of conditions when nutrients stored in the hypolimnion are released to the epilimnion during relative lowstands that favor entrainment of hypolimnetic waters into surface waters.

5.2 Paleoecological evolution of Lake Chungará and relationship with major climatic events

Sedimentological, micropaleontological, and geochemical indicators were used to define the depositional evolution of Lake Chungará and a qualitative paleohydrological history characterized by several low and highstand phases during the period 12,400-1,300 cal yr BP (Figs. 5 and 6). The

multiproxy approach followed in this review also allowed us to identify up to seven distinct productivity-related stages in the paleoenvironmental evolution of the lake.

5.2.1 *Stage 1 (c. 12,400–12,100 cal yr BP)*

Reduced productivity conditions are recorded at this initial stage, as indicated by the relatively low fluxes of TOC and TBSi to the sediments (Fig. 5). Minimum depth conditions for the whole record were reached (Fig. 6), as suggested by the highest percent abundance of benthic diatoms. Low lake-level is supported by the presence of pollen belonging to the aquatic macrophyte *Myriophyllum* sp. and a very low concentration of the chlorophycean *Botryococcus braunii* (Sáez et al., 2007). Although values of PC1 suggest complete water column mixing to the bottom and nutrient release coherent with low lake-level, cold conditions associated with the Late Glacial prevented high productivity, as the TOC and TBSi MARs indicate.

5.2.2 *Stage 2 (c. 12,100–10,800 cal yr BP)*

This stage shows a significant reduction in benthic diatoms which, however, still maintain high values, indicating that shallow waters persisted. A progressive increase in %TOC, starting at c. 11,400 cal yr BP, as well as the highest MARs values for TBSi and TOC, indicate a period of enhanced productivity (Fig. 5), an interpretation also supported by the $\delta^{13}C_{diat}$ and $\delta^{15}N_{org}$ enrichments (Pueyo et al., 2011; Hernández et al., 2013) (Fig. 5). This rise is concomitant with a sudden warming at the onset of the Holocene (Thompson et al., 1998) and with increased nutrient inputs by runoff (highstand P1).

The *Discostella stelligera* complex dominated the first part of this stage (DAZ CHUN11A-02, Fig. 3), which suggests a stratified water column (Fig. 6). Relatively shallow waters during this first part of this interval were, however, also favorable for the development of *Cyclostephanos* cf. *andinus* superblooms, leading to the intermittent formation of white laminae (Facies A). The dominant stratified conditions were therefore disturbed by sporadic and short-term episodes of strong turbulence. As the change in the PC1 shows, the second part of this stage (most of DAZ CHUN11A-03) was characterized by long periods of a well-mixed water column and high nutrients in surface waters,

concomitant with a peak in productivity conditions indicated by TOC and TBSi MARs (Fig. 5). The change in the mixing regime is also reflected in the $\delta^{13}C_{org}$ depletion, which occurred between the two parts of this period (Pueyo et al., 2011) and is likely related to the enrichment of the epilimnion with light carbon under periods of enhanced mixing (Meyers, 1997; Cohen, 2003). The fact that the magnitude of the $\delta^{13}C_{diat}$ enrichment does not keep pace with the increase in TOC and TBSi MARs was also interpreted as an evidence of the intensificaction of mixing, since this would have released isotopically depleted CO_2 from the hypolimnion, buffering the $\delta^{13}C_{diat}$ increase due to enhanced productivity. Intermittent peaks in *Botryococcus braunii*, an indicator of increased water column-stability (Margalef, 1983), suggest however a marked seasonality in the mixing regime.

Lake-level remained relatively shallow during this period, although a progressive rise is suggested by the relative decrease in benthic diatoms. However, the paleohydrological change seems smaller than further north, where wet conditions occurred in Lake Titicaca between c. 13,000 to 11,000 cal yr BP (Baker et al., 2001; Tapia et al., 2003), correlating with the wet Coipasa lake cycle in most of the Bolivian Alitplano (Servant et al., 1995).

5.2.3 *Stage 3 (c. 10,800–10,000 cal yr BP)*

This stage is characterized by a decrease in benthic diatoms after a significant peak at the onset of this phase. Interestingly, the $\delta^{18}O_{diat}$ record during this interval shows an enrichment which is contradictory with a highstand situation (Hernández et al., 2008) (Fig. 5). It was suggested that flooding of the shallow east and south platforms (Fig. 1B) at this time increased the whole S/V ratio of the lake, and therefore evaporation, explaining the $\delta^{18}O_{diat}$ enrichment. In this scenario, the peak in benthic diatoms at the start of this stage could therefore be a product of not a lake-level drop, but a consequence of the topographic effect of increased availability of shallow littoral habitats when the flooding took place (Stone & Fritz, 2004; Wigdhal et al., 2014).

Flooding of the shallow platform is paralleled by two significant changes. On one hand, the apparent decrease in productivity, as shown by the reduction in the TOC and TBSi MARs (Fig. 5). On the other, the mixing status changes from well mixed, represented by the dominance of *Cyclostephanos andinus*, to stratified conditions, represented by the dominance of the *Discostella*

stelligera group later on. In between this change, *Cyclostephanos* cf. *andinus* superblooms develop and trigger white laminae deposition, as a consequence of easier nutrient recycling in now extensive shallow areas of the lake.

Whereas the TOC flux declines, %TOC shows an increase during this stage (Fig. 5). The postulated reduced mixing of the water column could have maintained low or anoxic conditions at the lake bottom, as the values of $\delta^{13}C_{carbonate}$ around 7‰ also suggest (Pueyo et al., 2011) (Fig. 5). This would increase organic matter preservation and therefore %TOC values. This organic matter is predominantly of phytoplanktonic origin, as indicated by TOC/TN values around 10 (Meyers, 1997, 2003). The increase in %TOC, while %TBSi maintains similar levels, indicates a greater contribution of the non-diatom component of the original phytoplanktonic community. This replacement of diatoms, probably by motile phytoplankton, is what is expected with decaying turbulence (Margalef, 1978).

This stage coincides with declining summer insolation (Berger & Loutre, 1991) and a weakened SASM concomitant with the northward ITCZ displacement (Haug et al., 2001; Cruz et al., 2005). Under this scenario, a period of reduced moisture, and not a humid phase, would be expected in the Andean Altiplano. ENSO variability has, however, been invoked to explain changes in moisture in the tropical area during this period, so the recorded late Glacial to early Holocene humid conditions could be triggered by the dominance of La Niña-like conditions at this time (Betancourt et al., 2000; Koutavas et al., 2002; Hernández et al., 2010; Zech et al., 2010).

5.2.4 *Stage 4 (c. 10,000–9,600 cal yr BP)*

Benthic diatoms record their highest relative abundances in Holocene times during this stage, suggesting a short-lived lowstand situation (Fig. 6). Lake-levels would be again similar to those of the first part of stage 3 that maximized the extension of shallow habitats. The rise in the TOC/TN ratio suggests increased contribution of the non-algal component, likely littoral macrophytes, to the organic matter flux to the sediments. The peak in the abundance of the mesosaline *Nitzschia tropica* might indicate a saline concentration associated with a decline in lake-level (e. g. Bao et al., 1999), a common feature at present, when precipitation is reduced (Dorador et al., 2003). A carbonate peak also occurs at this time. Intense photosynthetic activity during the superblooms of *Cyclostephanos* cf.

andinus is the most probable driver of carbonate precipitation by removal of CO_2 (Pueyo et al., 2011). However, the decline in TOC and TBSi MARs suggests that although primary productivity was extraordinarily high during the short-lived superblooms of *Cyclostephanos* cf. *andinus*, these had no major effect in the total biomass production over the long term, which decreased during this stage.

During this event a significant change towards a more turbulent regime took place (Fig. 6). This part of the sedimentary record exhibits the highest values of Mn, as recorded by XRF analyses (Moreno et al., 2007). Mn precipitation usually indicates the oxygenation of a previously anoxic hypolimnion (Cohen, 2003), suggesting that the well-stratified conditions during the previous Stage 3 would have produced seasonal or persistent anoxia, which is favorable for increased Mn concentration in the water column.

The short-lived lowstand that characterizes this stage points to a dry event in the region. Additional data on $\delta^{18}O_{diat}$ (Hernández et al., 2013), the development of brown-white interbedding and carbonate-bearing laminated diatomite facies (Sáez et al., 2007), and high-resolution multiproxy geochemical and mineralogical data (Giralt et al., 2008) supports this interpretation. The recorded fall in water level matches with the summer insolation minimum at 10,000 yr (Berger & Loutre, 1991), which would favor a northward shift of the ITCZ, a reduction in the strength of the SASM, and therefore a period of reduced moisture (Garreaud et al., 2009). This short-lived dry period might be related to a similar event detected in Lake Titicaca at approximately 11,000 to 10,000 cal yr BP (Baker et al., 2001; Tapia et al., 2003). Uncertainties associated with age models constructed for lacustrine sequences in the central Andean Altiplano (Quade et al., 2008), and different climatic responses due to latitudinal effects (Abbott et al., 2003) might account for the observed differences in timing between the two records. The Lake Pacucha sedimentary record from the Peruvian Andes (Hillyer et al., 2009) shows a lowstand that peaked at c. 10,000 cal yr BP, closely fitting the shallow water conditions in Lake Chungará.

5.2.5 *Stage 5 (c. 9,600–7,400 cal yr BP)*

This stage shows a significant lake-level rise (highstand P2) manifested by the very low percent values of benthic diatoms and a $\delta^{18}O_{diat}$ depletion (Fig. 5). The record shows however a carbonate

precipitation peak at 8,300 cal yr BP, which is more probably related to Ca availabilty once prolonged leaching of volcanic rocks in the catchment increased the concentration of Ca in lake waters (Pueyo et al., 2011). Productivity is high, with a peak in %TBSi and increases in %TOC, as well as in TBSi and TOC MARs. These conditions are also associated with $\delta^{13}C_{org}$ and $\delta^{15}N_{org}$ record peaks (Pueyo et al., 2011) and a net increase in $\delta^{13}C_{diat}$, another indicator of elevated productivity at this time (Hernández et al., 2013) (Fig. 5). The main factor responsible for high productivity may be enhanced nutrient inputs from the catchment associated with increased water availability (Giralt et al., 2008). Lake water rise, however, would have a counteractive effect, which is a restriction in the vertical mixing down to the hypolimnion (Fig. 6). Weakly mixed waters prevailed during this stage, as indicated by a decrease in the PC1 and the start of the steady increase of *Botryoccocus braunii* (Fig. 5). This chlorophycean is currently the main component of the phytoplankton in Lake Chungará during the warmest summers when intense stratification develops (Dorador et al., 2003). The high values of $\delta^{13}C_{org}$ also recorded at this time (Fig. 5) may not only be related to increased productivity, but also to enhanced stratification that enriches DIC in ^{13}C (Meyers, 1997; Cohen, 2003). Because of reduced mixing and a deeper water column, complete water column overturn would be hindered, preventing the necessary nutrient release from the lake bottom that allows the maintenance of large centric diatoms. As a consequence of the restriction in the lake's internal nutrient cycling, the *Cyclostephanos* cf. *andinus* superblooms cease, and a transition from laminated (facies B) to massive (facies C) sediments occurs.

This humid phase can be adscribed to a wet period spanning 10,000 to 8,000 cal yr BP, when Lake Titicaca showed overflowing lake-level conditions (Baker et al., 2001; Tapia et al., 2003). Both the similar duration of this period in Chungará and Titicaca, and a similar time lag experienced by the previous dry event, suggest that corresponds to the same phenomenon. Wetter conditions between 8,400-7,200 cal yr BP were also recorded in Lake Paco Cocha (Abbott et al., 2003). Shorter wet episodes that also match in age with this Lake Chungará stage are known for Lake Pacucha (Hillyer et al., 2009) at c. 8,730 and 8,300 cal yr BP, and Lake Potosí (Bolivia) at about 8,000 cal yr BP (Wolfe et al., 2001).

5.2.6 *Stage 6 (c. 7,400–3,550 cal yr BP)*

This stage starts with a sharp increase in benthic diatoms and an enrichment in $\delta^{18}O_{carbonate}$, both indicating a reduction in water depth (lowstand P3). The flux of TOC and TBSi is strongly reduced, even to levels below those of the Late Glacial for TBSi. This is not accompanied by a decrease of the same magnitude in TOC (Fig. 5). The observation of a much greater reduction in TBSi than in TOC in both percent content and MARs suggests that other organisms are replacing in part the role of diatoms as primary producers. *Botryococcus braunii* increases its abundance during this phase (Sáez et al., 2007), and the TOC/TN ratio reaches the highest values for the whole record (Fig. 5). Both observations support the idea that at least chloropyceans and macrophytes increased their contribution to total primary productivity.

In spite of the strong reduction of the TBSi and TOC flux to the sediments, $\delta^{13}C_{org}$ maintained high values during this phase (Pueyo et al., 2011). The carbonate-bicarbonate system in Lake Chungará is currently dominated by HCO_3^-, with a molar distribution between free CO_2, bicarbonate and carbonate of 3:958:39 (Mülhauser et al., 1995). During long periods of stratification, rates of photosynthetic inorganic carbon uptake can exceed rates of resupply of CO_2, raising pH, but photosynthesis can continue making use of bicarbonate or via carbon concentration mechanisms (Hopkinson et al., 2011). Bicarbonate uptake by aquatic plants generally occurs when its concentration exceeds that of CO_2 by more than ten times (Wetzel, 2001), a figure currently largely surpassed in Lake Chungará. Under these circumstances, the carbon isotopic composition of algae becomes heavier (Meyers, 2003). This could explain why there is a net increase in $\delta^{13}C_{org}$ values during this stage in spite of the strong reduction in productivity. A rise in pH associated with alkalinizing base cations released by volcanoclastic inputs during this phase (Sáez et al., 2007) could also explain a change to a bicarbonate dominated system throughout this period. This hypothesis is also supported by the general trend towards higher $\delta^{13}C_{carbonate}$ (Pueyo et al., 2011).

The diatom record shows a reduction in the *Discostella stelligera* group and sharp increase in *Cyclostephanos andinus* during this phase, with both taxa codominating the assemblages (Fig. 3). A less stable water column, and lowstand conditions facilitating a more complete overturn, favored *Cyclostephanos andinus*. In spite of this, lowering of the lake water level never reached conditions that allowed superblooms of *Cyclostephanos* cf. *andinus*. The codominance between the *Discostella*

stelligera group and *Cyclostephanos andinus* suggests that although water column-stability decreased compared to the previous phase, thermal-stratification was very common. This is also supported by the high percentages of *Botryococcus braunii*.

This stage fits into the mid-Holocene aridity period in the Altiplano, roughly established between 9,000 to 4,000 cal yr BP, but whose intensity and exact timing is variable over the region (Abbott et al., 2003). Maximum aridity conditions are recorded in Lake Titicaca between c. 8,000 to 5,500 cal yr BP (Baker et al., 2001). This time range resembles the dry phase in Lake Chungará from c. 7,400 to 3,600 cal yr BP. Uncertainties in our age model are greatly reduced after 8,000 cal yr BP (Giralt et al., 2008), precluiding a clear correlation with the chronology of Lake Titicaca. Lake Chungará record also demonstrates that the mid Holocene period was not homogeneous, but fluctuating between dry and wet conditions. The driest conditions would have developed between 7,400 and 6,600 cal yr BP according to the diatom record, fitting with mineralogical and high-resolution XRF data (Giralt et al., 2008). In contrast, a wetter period took place between c. 6,600 to 6,000 cal yr BP. This correlates with a wet episode from 7,500 (7,000) to 6,500 (6,000) cal yr BP also recorded in Lake Titicaca (Baker et al., 2001; Rowe et al., 2002; Tapia et al., 2003).

5.2.7 *Stage 7 (c. 3,550–1,300 cal yr BP)*

This stage is represented by the record of Subunit 2b, where volcanoclastic materials constitute a great part of the sediments (Sáez et al., 2007). Marked fluctuations in %TOC and its MAR can partially be an artifact due to the presence of tephras. There is, however, a consistent trend in the first part of this stage to a general reduction in both TOC content and fluxes, as well as in the TOC/TN ratio. This is coincident with a depletion in the $\delta^{18}O_{carbonate}$, interpreted as the end of the previous arid phase (Pueyo et al., 2011). Because of this and the absence of any significant increase in the benthic diatom content, changes reflected in the organic matter reaching the lake bottom at this time are likely due to the increased contribution of allochthonous organic matter associated with enhanced runoff. The reduction of *Cyclostephanos andinus* and the increase of the *Discostella stelligera* group point to a strengthening water column stratification, likely associated to higher lake-levels (Fig. 6).

Sediment cores from lakes Titicaca, Lagunillas, and Umayo (Peru) show that this latest part of the Holocene corresponds to a highstand phase (Rowe et al., 2002; Ekdahl et al., 2008). Establishment of the over-flow conditions in lake Titicaca started after 4,000 to 3,100 cal yr BP (Baker et al., 2001; Tapia et al., 2003), which match with the onset of this paleoproductivity stage in Lake Chungará. Different lowstands have however been identified during this phase in Lake Titicaca, indicating that this period was far from stable (Abbott et al., 1997; Baker et al., 2005). Similar fluctuations correspond in Lake Chungará to small peaks in benthic diatoms at c. 2,800, 2,200 and 1,500 cal yr BP. Relatively deeper waters at the coring site might probably have downweighted the magnitude of change in benthic diatom abundance.

5.3 Main drivers of long-term changes in biosiliceous productivity

Paleoproductivity changes in Lake Chungará generally show a good agreement with the main paleoclimatic phases defined in the central Andean Altiplano from a set of of lacustrine records. Climate has exerted a fundamental influence on changes in productivity, modifying allochthonous nutrient inputs to the lake, as well as lake-levels and the water-column mixing regime. Changes in lake morphometry associated to those lake-level fluctuations however modulated the magnitude of the climate imprint in the sedimentary record.

5.3.1 *Nutrient availability associated with runoff*

Long-term variability in the external delivery of nutrients to the lake is the main responsible for paleoproductivity changes. Periods of enhanced productivity (Stages 2, 5 and 7, Fig. 6) are coincident with periods of increased runoff associated with elevated water availability in the Altiplano. Conversely, at times of aridity (Stages 4 and 6, Fig. 6) the lake experienced reduced biomass production. This is in agreeent with the present-day pattern of phytoplanktonic biomass reduction that accompanies water level falls in this lake (Dorador et al., 2003), and to the suggestion that the key

element controlling primary production in mountain lakes at time scales of a few decades to millennia is the coupling of lake dynamics with the catchment biogeochemistry (Catalan et al., 2006).

5.3.2 *Effects of lake morphometry on internal nutrient recycling*

Nutrient availability is dependent not only on external inputs, but on internal recycling due to the existing water column structure at a given time. Its change prompts shifts in phytoplankton communities, which, in turn, affect primary productivity and higher trophic production (e. g., Margalef, 1978; Winder & Hunter, 2008). Three stages of well-stratified waters dominated by small-sized diatoms of the *Discostella stelligera* group have been identified (Stages 3, 5 and 7, Fig. 6). Higher turbulence and mixing is associated with four periods in which the large *Cyclostephanos* species are more prominent (Stages 1, 2, 4 and 6, Fig. 6). The early phases in lake ontogeny (Stages 1 to 3, Fig. 6) show a clear correspondence between stronger mixing and elevated productivity, as shown by the correspondence between PC1 and TBSi and TOC MARs. An exception is the Late Glacial (Stage 1, Fig. 6) when, in spite of the dominance of isothermal conditions, productivity was low very likely due to cold temperatures. The highest productivity conditions in the whole lake history were recorded when increased turbulence is added to the effects of enhanced runoff (Stage 2, Fig. 6).

A major paleoecological transition takes place after Stage 3, when phases with nutrient recycling by stronger turbulent conditions seem to be uncoupled from diatom productivity at the time scale of the sediment record. This is shown by the existence of periods characterized by well stratified waters with high productivity (Stage 5, Fig. 6) and others with less stratified conditions but reduced production (Stages 4 and 6, Fig. 6). In the absence of reliable paleoindicators of factors that affect water turbulence, such as wind stress, surface heat flux or turbidity currents, a very probable explanation for this decoupling is that changes in lake basin morphometry adjust the effects of mixing (Imboden & Wüest, 1995), causing a change in productivity levels. Lake Chungará shows a complex bottom topography, combining steep shorelines with extensive shallow platform areas (Fig. 1B). The water level fluctuations experienced during its history produced major changes in the relative extent of potential deep mixing areas in the lake. During lowstands, complete or almost complete mixing of the

water column to the lake bottom is facilitated. When the ratio of the area of the epilimnion sediments with respect to the total volume of the epilimnion is high, nutrient remineralization is rapid, enabling nutrients to be circulated back into the epilimnion (Fee, 1979). During the early stages (stages 1 to 3, Fig. 6) low water levels allow wind-driven turbulence to easily reach the nutrient-rich hypolimnion at times of enhanced vertical mixing. This prompts productivity, temperature permitting. As the lake-level rises during the early to the mid Holocene, complete vertical mixing becomes more restricted, and the effects of periods of strong turbulence on diatom productivity intensification are reduced.

The combined effect of water mixing and lake morphometry on internal nutrient supply is particularly well illustrated in the formation of the *Cyclostephanos* cf. *andinus* superblooms and, therefore, on the deposition of white laminae in lithological Unit 1. White laminae are predominantly formed during lowstand periods or when littoral platforms of the lake were flooded, forming extensive shallow areas (Hernández et al., 2011). Under these circumstances, nutrient release from the lake bottom is facilitated, triggering massive *Cyclostephanos* cf. *andinus* blooms. Maximum deposition of white laminae is recorded during a particularly pronounced lowstand in stage 4 after a long oligomictic to meromictic condition affected the lake (Fig. 6). The development of an oxygen-depleted hypolimnion (Stage 3, Fig. 6) would enrich the bottom waters with phosphorous (Cohen, 2003), which is ultimately released to the surface waters in the following stage, triggering the *Cyclostephanos* cf. *andinus* superblooms. This mechanism explains the deposition of almost pure diatom oozes at times of extended shallow conditions when, for this reason, the lake experiences a state of morphometric eutrophy *sensu* Rawson (1955). This ephemeral condition, which relies on nutrient recycling from the deep waters, has no great effect on the TBSi and TOC flux to the sediments in the long term (Fig. 5). Yet, the importance of morphometric eutrophy should not be neglected when compared to the recent parts of the record. Once a depth threshold is surpassed during the early to mid Holocene transition (corresponding to the change from the laminated deposits of Unit 1 to the massive Unit 2), mixing down to the bottom becomes more difficult, and the formation of the *Cyclostephanos* cf. *andinus* superblooms is hindered. Any ulterior lowstand, such as those recorded during the mid-Holocene aridity crisis, would have never put the lake-level below that depth threshold. Consequently, productivity can no longer solely rely on internal nutrient recycling, and biosiliceous productivity falls to

minimum levels. Compared to lowstands associated to more juvenile stages in lake ontogeny, when morphometric eutrophy was still possible, the TBSi flux is strongly reduced to levels below Late Glacial times.

Surpassing the depth threshold likely not only brought about termination of the *Cyclostephanos* cf. *andinus* superblooms, but also very probably produced the extinction of this taxon, which, so far, has not been found at present in other lake systems of the central Andean Altiplano. Undescribed new species of *Cyclostephanos* that went extinct have also been detected in Pleistocene sediments of Lake Titicaca (Fritz et al., 2012). In Lake Chungará, as is true of Lake Titicaca, some of the putative new morphospecies may be favored by conditions associated with shallower waters than the nominal *Cyclostephanos andinus*.

5.3.3 *Volcanism*

The Lake Chungará record shows that it became increasingly dependent on allogenic controls on its productivity during its evolution. Besides variations in runoff, another external forcing factor, volcanic ash deposition, could have affected biosiliceous productivity. Increased silica loads associated with ashfall during volcanic events have been reported as triggers of enhanced diatom productivity in some lake systems (e. g. Lotter et al., 1995; Cruces et al., 2006). The most significant change in Holocene volcanism in the area was the renewed activity of the Parinacota volcano after 7,500 cal yr BP (Giralt et al., 2008). However, in spite of increased silica availability by tephra deposition during the sedimentation of Unit 2, biosiliceous productivity was significantly lowered in Lake Chungará. Furthermore, no significant changes occurred in the diatom assemblages after the different periods of tephra deposition. Yet, the relationship between tephra deposition and diatom productivity is probably a time scale-dependent process. Some evidence points to short-term reorganization of the diatom assemblages, as well as changes in productivity, after volcanic disturbance, but these effects last for no more than 5 years (Cruces et al., 2006). Other observations indicate that volcanic silica loads do not provide the necessary sustained stimulus to enhance productivity, and that the long term trends in lake evolution are not fundamentally affected by tephra inputs (Telford et al., 2004). A more detailed sampling would therefore be necessary to definitely

confirm the short-term consequences of airborne tephras on the productivity conditions of Lake Chungará.

6. CONCLUSIONS

The sedimentary record of Lake Chungará reveals a complex interplay between climatic and lacustrine morphometric controls that influence paleoproductivity throughout its evolution. Precipitation variability over the Andean Altiplano has been the most important primary forcing factor for changes in allochthonous nutrient inputs and paleoproductivity during the studied period. The magnitude of changes in climate-driven impacts on the aquatic system are, however, modulated by morphometry-related in-lake controls that show that there is not a linear response of lacustrine productivity to changes in precipitation and, therefore, to climatic variability.

Variations in the water-column mixing regime acted as a key driver in long-term productivity conditions, compensating losses produced at times of decreased nutrient availability associated with runoff. This is particularly well exemplified during the early Holocene (10,800-9,600 cal yr BP), which includes two distinct paleoproductivity stages. During the first stage, the lake experienced dominant oligo to meromictic conditions that, irrespective of intervals of enhanced precipitation in the Andean Altiplano, lead to a significant decrease in productivity. During more arid phases in the early Holocene, the trend toward decreased productivity was mantained. However, complete overturn, facilitated by a lowstand situation, helped to sustain episodic moderate productivity conditions by nutrient recycling from the sediments. When this morphometric eutrophy occured, most of the biomass was produced by episodic superblooms of a very large diatom, *Cyclostephanos* cf. *andinus*, which is strictly dependent on the existence of deep water circulation and relatively shallow waters.

The effects of mixing of the water column therefore strongly depend on changes in the morphometry of the lake basin associated with its evolution. Lake Chungará experienced a net long-term lake-level increase since its origin up to c. 8,300 cal yr BP, when maximum depth conditions were reached. Because of the complex topography of the basin, this lake-level increase substantially

modified the area of the epilimnion sediments with respect to the total volume of the epilimnion. Once the depth threshold was surpassed, a deeper lake prevented complete mixing of the water column to the bottom, and the episodic superblooms of *Cyclostephanos* cf. *andinus* were no longer possible. This made the lake more dependent on allochthonous nutrient inputs and, therefore, on climate variability. As a result, the Andean mid-Holocene Aridity Period, lasting in Lake Chungará from c. 7,400 to 3,550 cal yr BP, brought a sharp decrease in productivity which, at least for diatoms, descended to levels below Late Glacial times. Crossing the depth threshold not only sharply decreased the lake productivity, but was also accompanied by a reduction in the relative role of diatoms as primary producers, and by a shift to a bicarbonate-dominated system. Subsequently, biosiliceous productivity never reached the levels of previous stages in the ontogeny of the lake.

Our results show that in this closed high mountain lake climatic changes constitute the primary driver in the long-term productivity conditions, but that the magnitude of change can be strongly amplified or reduced by factors intrinsic to the lake that vary during its ontogeny. This needs to be taken into account when interpreting lacustrine paleoproductivity records as evidences of late Quaternary climatic changes.

ACKNOWLEDGMENTS

The Spanish Ministry of Science and Innovation funded the research through the projects ANDESTER (BTE2001-3225), Complementary Action (BTE2001-5257-E), LAVOLTER (CGL2004-00683/BTE), GEOBILA (CGL2007-60932/BTE) and CONSOLIDER-Ingenio 2010 GRACCIE (CSD2007-00067). The Limnological Research Center (USA) provided the technology and expertise to retrieve the cores. We are grateful to CONAF (Chile) for the facilities provided in Parque Nacional Lauca. We are also indebt to Edward Theriot, who examined scanning electron microscope micrographs of the *Cyclostephanos* making up the laminated unit. Manel Leira is also thanked for his advice on statistical analyses.

REFERENCES

Abbott, M.B., Binford, M.W., Brenner, M., Kelts, K., 1997. A 3500 14C yr high-resolution record of water-level changes in Lake Titicaca, Bolivia/Peru. Quaternary Research 47, 169-180.

Abbott, M.B., Wolfe, B.B., Wolfe, A.P., Seltzer, G.O., Aravena, R., Mark, B.G., Polissar, P.J., Rodbell, D.T., Rowe, H.D., Vuille, M., 2003. Holocene paleohydrology and glacial history of the central Andes using multiproxy sediment studies. Palaeogeography, Palaeoclimatology and Palaeoecology 194, 123-138.

Anderson, N.J., 1995. Temporal scale, phytoplankton ecology and paleolimnology. Freshwater Biology 34, 367-378.

Baker, P.A., Fritz, S.C., Garland, J., Ekdahl, E., 2005. Holocene hydrologic variation at Lake Titicaca, Bolivia/Peru, and its relationship to North Atlantic climate variation. Journal of Quaternary Science 20, 655-662.

Baker, P.A., Seltzer, G.O., Fritz, S.C., Dunbar, R.B., Grove, M.J., Tapia, P.M., Cross, S.L., Rowe, H.D., Broda, J.P., 2001. The history of South American tropical precipitation for the past 25,000 years. Science 291, 640-643.

Bao, R., Sáez, A., Servant-Vildary, S., Cabrera, L., 1999. Lake-level and salinity reconstruction from diatom analyses in Quillagua formation (late Neogene, Central Andean Forearc, northern Chile). Palaeogeography, Palaeoclimatology, Palaeoecology 153, 309-335.

Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. New Phytol. 132, 155-170.

Bennett, K.D., 2002. Documentation for Psimpoll 4.10 and Pscomb 1.03, C Programs for Plotting Pollen Diagrams and Analising Pollen Data. Uppsala University.

Berger, A., Loutre, M.F., 1991. Insolation values for the climate of the last 10 million years. Quaternary Science Reviews 10, 297-317.

Betancourt, J.L., Latorre, C., Rech, J.A., Quade, J., Rylander, K.A., 2000. A 22,000-Year Record of Monsoonal Precipitation from Northern Chile's Atacama Desert. Science 289, 1542-1546.

Boyle, J.F., 2001. Inorganic geochemical methods in paleolimnology, In: Last, W.M., Smol, J.P. (Eds.), Tracking Environmental Change Using Lake Sediments. Volume 2: Physical and Geochemical Methods. Kluwer Academic Publishers, Dordrecht, pp. 83-141.

Brylinsky, M., Mann, K.H., 1973. An analysis of factors governing productivity in lakes and reservoirs. Limnology and Oceanography 18, 1-14.

Castañeda, I.S., Werne, J.P., Johnson, T.C., 2009. Influence of climate change on algal community structure and primary productivity of Lake Malawi (East Africa) from the Last Glacial Maximum to present. Limnology and Oceanography 54, 2431-2447.

Catalan, J., Camarero, L., Felip, M., Pla, S., Ventura, M., Buchaca, T., Bartomeus, F., De Mendoza, G., Miró, A., Casamayor, E.O., Medina-Sánchez, J.M., Bacardit, M., Altuna, M., Bartrons, M., Díaz de Quijano, D., 2006. High mountain lakes: extreme habitats and witnesses of environmental changes. Limnetica 25, 551-583.

Cohen, A.S., 2003. Paleolimnology. Oxford University Press, Oxford.

Cruces, F., Urrutia, R., Parra, O., Araneda, A., Treutler, H., Bertrand, S., Fagel, N., Torres, L., Barra, R., Chirinos, L., 2006. Changes in diatom assemblages in an Andean lake in response to a recent volcanic event. Archiv Fur Hydrobiologie 165, 23-35.

Cruz, F.W., Burns, S.J., Karmann, I., Sharp, W.D., Vuille, M., Cardoso, A.O., Ferrari, J.A., Silva Dias, P.L., Viana, O., 2005. Insolation-driven changes in atmospheric circulation over the past 116,000 years in subtropical Brazil. Nature 434, 63-66.

Deevey, E.S., 1955. The obliteration of the hypolimnion. Memorie dell'Istituto Italiano di Idrobiologia, Suppl 8, 9-38.

Dorador, C., Pardo, R., Vila, I., 2003. Variaciones temporales de parámetros físicos, químicos y biológicos de un lago de altura: el caso del lago Chungará. Revista Chilena de Historia Natural 76, 15-22.

Ekdahl, E.J., Fritz, S.C., Baker, P.A., Rigsby, C.A., Coley, K., 2008. Holocene multidecadal- to millennial-scale hydrologic variability on the South American Altiplano. The Holocene 18, 867-876.

Engstrom, D.R., Fritz, S.C., Almendinger, J.E., Juggins, S., 2000. Chemical and biological trends during lake evolution in recently deglaciated terrain. Nature 408, 161-166.

Engstrom, D.R., Wright Jr., H.E., 1984. Chemical stratigraphy of lake sediments as a record of

environmental change, In: Haworth, E.Y., Lund, J.W.G. (Eds.), Lake Sediments and Environmental History. Leicester University Press, Leicester, pp. 11-68.
Fee, E.J., 1979. A relation between lake morphometry and primary productivity and its use in interpreting whole-lake eutrophication experiments. Limnology and Oceanography 24, 401-416.
Finkel, Z.V., Katz, M.E., Wright, J.D., Schofield, O.M.E., Falkowski, P.G., 2005. Climatically driven macroevolutionary patterns in the size of marine diatoms over the Cenozoic. Proceedings of the National Academy of Sciences 102, 8927-8932.
Flower, R.J., Likoshway, Y., 1993. An investigation of diatom preservation in Lake Baikal, Fifth Workshop on Diatom Algae, March 16-20, Irkutsk, Russia, pp. 77-78.
Fritz, S.C., Baker, P.A., Tapia, P., Spanbauer, T., Westover, K., 2012. Evolution of the Lake Titicaca basin and its diatom flora over the last ~370,000 years. Palaeogeography, Palaeoclimatology, Palaeoecology 317, 93-103.
Garreaud, R., Vuille, M., Clement, A.C., 2003. The climate of the Altiplano: observed current conditions and mechanisms of past changes. Palaeogeography, Palaeoclimatology, Palaeoecology 194, 5-22.
Garreaud, R.D., Vuille, M., Compagnucci, R., Marengo, J., 2009. Present-day South American climate. Palaeogeography, Palaeoclimatology, Palaeoecology 281, 180-195.
Gasse, F., Juggins, S., Ben Khelifa, L., 1995. Diatom-based transfer functions for inferring past hydrochemical characteristics of African lakes. Palaeogeography, Palaeoclimatology, Palaeoecology 117, 31-54.
Giralt, S., Moreno, A., Bao, R., Sáez, A., Prego, R., Valero-Garcés, B., Pueyo, J., González-Sampériz, P., Taberner, C., 2008. A statistical approach to disentangle environmental forcings in a lacustrine record: the Lago Chungará case (Chilean Altiplano). Journal of Paleolimnology 40, 195-215.
Grimm, E.C., 1987. CONISS: a Fortran 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Computers and Geosciences 13, 13-35.
Håkansson, H., 2002. A compilation and evaluation of species in the general *Stephanodiscus*, *Cyclostephanos* and *Cyclotella* with a new genus in the family Stephanodiscaceae. Diatom Research 17, 1-139.
Hansen, H.P., Grashoff, K., 1983. Automated chemical analysis, In: Grashoff, M., Ehrhardt, M., Kremlin, K. (Eds.), Methods of Seawater Analysis. Verlag Chemie, Weinheim, pp. 368-376.
Haug, G.H., Hughen, K.A., Sigman, D.M., Peterson, L.C., Rohl, U., 2001. Southward Migration of the Intertropical Convergence Zone Through the Holocene. Science 293, 1304-1308.
Hernández, A., Bao, R., Giralt, S., Barker, P.A., Leng, M.J., Sloane, H.J., Sáez, A., 2011. Biogeochemical processes controlling oxygen and carbon isotopes of diatom silica in Late Glacial to Holocene lacustrine rhythmites. Palaeogeography, Palaeoclimatology, Palaeoecology 299, 413-425.
Hernández, A., Bao, R., Giralt, S., Leng, M.J., Barker, P.A., Pueyo, J.J., Sáez, A., Moreno, A., Valero-Garcés, B., Sloane, H.J., 2008. The palaeohydrological evolution of Lago Chungará (Andean Altiplano, northern Chile) during the Lateglacial and early Holocene using oxygen isotopes in diatom silica. Journal of Quaternary Science 23, 351-363.
Hernández, A., Bao, R., Giralt, S., Sáez, A., Leng, M.J., Barker, P.A., Kendrick, C.P., Sloane, H.J., 2013. Climate, catchment runoff and limnological drivers of carbon and oxygen isotope composition of diatom frustules from the central Andean Altiplano during the Lateglacial and Early Holocene. Quaternary Science Reviews 66, 64-73.
Hernández, A., Giralt, S., Bao, R., Sáez, A., Leng, M., Barker, P., 2010. ENSO and solar activity signals from oxygen isotopes in diatom silica during late glacial-Holocene transition in Central Andes (18°S). Journal of Paleolimnology 44, 413-429.
Herrera, C., Pueyo, J.J., Sáez, A., Valero-Garcés, B.L., 2006. Relación de aguas superficiales y subterráneas en el área del lago Chungará y lagunas de Cotacotani, norte de Chile: un estudio isotópico. Revista Geológica de Chile 33, 299-325.
Hillyer, R., Valencia, B.G., Bush, M.B., Silman, M.R., Steinitz-Kannan, M., 2009. A 24,700-yr paleolimnological history from the Peruvian Andes. Quaternary Research 71, 71-82.
Hopkinson, B.M., Dupont, C.L., Allen, A.E., Morel, F.M.M., 2011. Efficiency of the CO_2-concentrating mechanism of diatoms. Proceedings of the National Academy of Sciences 108, 3830-3837.
Hora, J.M., Singer, B.S., Wörner, G., 2007. Volcano evolution and eruptive fl ux on the thick crust of the Andean Central Volcanic Zone: $^{40}Ar/^{39}Ar$ constraints from Volcán Parinacota, Chile. Geological Society of America Bulletin 119, 343-362.
Iltis, A., 1992. Phytoplankton. Quantitative aspects and populations, In: Dejoux, C., Iltis, A. (Eds.), Lake Titicaca. A Synthesis of Limnological Knowledge. Kluwer Academic Publishers, Dordrecht,

pp. 182-195.
Imboden, D.M., Wüest, A., 1995. Mixing mechanisms in lakes, In: Lerman, A., Imboden, D.M., Gat, J.R. (Eds.), Physics and Chemistry of Lakes. Springer-Verlag, Berlin, pp. 83-138.
Johnson, T.C., Brown, E.T., McManus, J., 2004. Diatom productivity in northern lake Malawi during the psat 25,000 years: implications for the position of the intertropical convergence zone at millenial and shrter time scales, In: Battarbee, R.W., Gasse, F., Stickley, C.E. (Eds.), Past Climate Variability through Europe and Africa. Springer, Dordrecht, pp. 932-116.
Jongman, R.H.G., ter Braak, C.J.F., van Tongeren, O.F.R., 1987. Data Analysis in Community and Landscape Ecology. Pudoc, Wageningen, p. 299.
Koutavas, A., Lynch-Stieglitz, J., Marchitto, T.M., Sachs, J.P., 2002. El Niño-Like Pattern in Ice Age Tropical Pacific Sea Surface Temperature. Science 297, 226-230.
Krammer, K., Lange-Bertalot, H., 1986-1991. Bacillariophyceae, In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora von Mitteleuropa. Fischer-Verlag, Stuttgart.
Lange-Bertalot, H., 2000-2005. Diatoms of the European Inland Waters and Comparable Habitats. Volumes 1, 2, 3, 4, 5. A. R. G. Gantner Verlag, Ruggell, Liechtenstein.
Leps, J., Smilauer, P., 2003. Multivariate Analysis of Ecological Data using CANOCO. Cambridge University Press, Cambridge.
Litchman, E., Klausmeier, C.A., Yoshiyama, K., 2009. Contrasting size evolution in marine and freshwater diatoms. Proceedings of the National Academy of Sciences 106, 2665-2670.
Lotter, A.F., Birks, H.J.B., Zolitschka, B., 1995. Late-glacial pollen and diatom changes in response to two different environmental perturbations: volcanic eruption and Younger Dryas cooling. Journal of Paleolimnology 14, 23-47.
Ma, T.S., Gutterson, M., 1970. Organic elemental analysis. Analytical Chemistry 42, 105-114.
Mackay, A.W., 2007. The paleoclimatology of Lake Baikal: A diatom synthesis and prospectus. Earth-Science Reviews 82, 181-215.
Margalef, R., 1978. Life forms of phytoplankton as survival alternatives in an unstable environment. Oceanologica Acta 1, 493-509.
Margalef, R., 1983. Limnología. Ediciones Omega, Barcelona.
Márquez-García, M., Vila, I., Hinojosa, L.F., Méndez, M.A., Carvajal, J.L., Sabando, M.C., 2009. Distribution and seasonal fluctuations in the aquatic biodiversity of the southern Altiplano. Limnologica - Ecology and Management of Inland Waters 39, 314-318.
Meyers, P.A., 1997. Organic geochemical proxies of paleoceanographic, paleolimnologic, and paleoclimatic processes. Organic Geochemistry 27, 213-250.
Meyers, P.A., 2003. Applications of organic geochemistry to paleolimnological reconstructions: a summary of examples from the Laurentian Great Lakes. Organic Geochemistry 34, 261-289.
Moreno, A., Giralt, S., Valero-Garcés, B.L., Sáez, A., Bao, R., Prego, R., Pueyo, J.J., González-Sampériz, P., Taberner, C., 2007. A 14 kyr record of the tropical Andes: The Lago Chungará sequence (18°S, northern Chilean Altiplano). Quaternary International 161, 4-21.
Mortlock, R.A., Froelich, P.N., 1989. A simple method for the rapid determination of biogenic opal in pelagic marine sediments. Deep-Sea Research 36, 1415-1426.
Mühlhauser, H.A., Hrepic, N., Mladinic, P., Montecino, V., Cabrera, S., 1995. Water quality and limnological features of the Andean Lake Chungará, northern Chile. Revista Chilena de Historia Natural 68, 341-349.
Placzek, C., Quade, J., Betancourt, J.L., Patchett, P.J., Rech, J.A., Latorre, C., Matmon, A., Holmgren, C., English, N.B., 2009. Climate in the dry central Andes over geologic, millennial, and interannual scales. Annals of the Missouri Botanical Garden 96, 386-397.
Polissar, P.J., Abbott, M.B., Wolfe, A.P., Vuille, M., Bezada, M., 2013. Synchronous interhemispheric Holocene climate trends in the tropical Andes. Proceedings of the National Academy of Sciences 110, 14551-14556.
Pueyo, J.J., Sáez, A., Giralt, S., Valero-Garcés, B.L., Moreno, A., Bao, R., Schwalb, A., Herrera, C., Klosowska, B., Taberner, C., 2011. Carbonate and organic matter sedimentation and isotopic signatures in Lake Chungará, Chilean altiplano, during the last 12.3 kyr. Palaeogeography, Palaeoclimatology, Palaeoecology 307, 339-355.
Quade, J., Rech, J.A., Betancourt, J.L., Latorre, C., Quade, B., Rylander, K.A., Fisher, T., 2008. Paleowetlands and regional climate change in the central Atacama Desert, northern Chile. Quaternary Research 69, 343-360.
Rawson, D.S., 1955. Morphometry as a dominant factor in the productivity of large lakes. Internationale Vereinigung fuer Theoretische und Angewandte Limnologie Verhandlungen 12, 164-175.
Renberg, I., 1990. A procedure for preparing large sets of diatom slides from sediment cores. Journal

of Paleolimnology 4, 87-90.
Risacher, F., Alonso, H., Salazar, C., 1999. Geoquímica de las aguas en las cuencas de cerradas: I, II Regiones de Chile. Vol. II. Convenio de Cooperación DGA, UCN e IRD. Internal Report, p. 141.
Rowe, H.D., Dunbar, R.B., Mucciarone, D.A., Seltzer, G.O., Baker, P.A., Fritz, S., 2002. Insolation, Moisture Balance and Climate Change on the South American Altiplano Since the Last Glacial Maximum. Climatic Change 52, 175-199.
Rühland, K., Paterson, A.M., Smol, J.P., 2008. Hemispheric-scale patterns of climate-related shifts in planktonic diatoms from North American and European lakes. Global Change Biology 14, 2740-2754.
Rumrich, U., Lange-Bertalot, H., M., R., 2000. Diatomeen der Anden. Von Venezuela bis Patagonien/Tierra del Fuego. A. R. G. Gantner Verlag K. G., Ruggell.
Sáez, A., Valero-Garcés, B.L., Moreno, A., Bao, R., Pueyo, J.J., González-Sampériz, P., Giralt, S., Taberner, C., Herrera, C., Gibert, R.O., 2007. Lacustrine sedimentation in active volcanic settings: the Late Quaternary depositional evolution of Lake Chungará (northern Chile). Sedimentology 54, 1191-1222.
Saros, J.E., Anderson, N.J., 2014. The ecology of the planktonic diatom *Cyclotella* and its implications for global environmental change studies. Biological Reviews, http://doi.org/10.1111/brv.12120.
Sayer, C.D., Davidson, T.A., Jones, J.I., Langdon, P.G., 2010. Combining contemporary ecology and palaeolimnology to understand shallow lake ecosystem change. Freshwater Biology 55, 487-499.
Servant, M., Fournier, M., Argollo, J., Servant-Vildary, S., Sylvestre, F., Wirrmann, D., Ybert, J.P., 1995. La dernière transition glaciaire/interglaciaire des Andes tropicales sud (Bolivie) d'après l'etude des variations des niveaux lacustres et des fluctuations glaciaires. Comptes Rendus Académie des Sciences Paris 320, 729-736.
Servant-Vildary, S., 1992. Phytoplankton. The diatoms, In: Dejoux, C., Iltis, A. (Eds.), Lake Titicaca. A Synthesis of Limnological Knowledge. Kluwer Academic Publishers, Dordrecht, pp. 163-175.
Servant-Vildary, S., Roux, M., 1990. Multivariate analysis of diatoms and water chemistry in Bolivian saline lakes. Hydrobiologia 197, 267-290.
Smol, J.P., 2008. Pollution of Lakes an Rivers. A Palaeoenvironmental Perspective. Blackwell Publishing, Malden.
Sterner, R.W., 2008. On the Phosphorus Limitation Paradigm for Lakes. International Review of Hydrobiology 93, 433-445.
Stone, J.R., Fritz, S.C., 2004. Three-dimensional modeling of lacustrine diatom habitat areas: Improving paleolimnological interpretation of planktic : benthic ratios. Limnology and Oceanography 49, 1540-1548.
Sylvestre, F., Servant-Vildary, S., Roux, M., 2001. Diatom-based ionic concentration and salinity models from the south Bolivian Altiplano (15–23°S). Journal of Paleolimnology 25, 279-295.
Tapia, P.M., Fritz, S.C., Baker, P., Seltzer, G.O., Dunbar, R., 2003. A Late Quaternary diatom record of tropical climatic history from Lake Titicaca (Peru and Bolivia). Palaeogeography, Palaeoclimatology, Palaeoecology 194, 139-164.
Tapia, P.M., Theriot, E., Fritz, S.C., Cruces, F., Rivera, P., 2004. Distribution and morphometric analysis of *Cyclostephanos andinus* comb. nov., a planktonic diatom from the Central Andes. Diatom Research 19, 311-327.
Telford, R.J., Barker, P., Metcalfe, S.E., Newton, A., 2004. Lacustrine responses to tephra deposition: examples from Mexico. Quaternary Science Reviews 23, 2337-2353.
ter Braak, C.J.F., Smilauer, P., 1998. CANOCO reference manual and user's guide to CANOCO for Windows: Software for canonical community ordination (version 4). Microcomputer Power, Ithaca, New York.
Theriot, E., Carney, H.J., Richerson, P.J., 1985. Morphology, ecology and systematics of *Cyclotella andina* sp. nov. (Bacillariophyceae) from Lake Titicaca, Peru-Bolivia. Phycologia 24, 381-387.
Thompson, L.G., Davis, M.E., Mosley-Thompson, E., Sowers, T.A., Henderson, K.A., Zagorodnov, V.S., Lin, P.-N., Mikhalenko, V.N., Campen, R.K., Bolzan, J.F., Cole-Dai, J., Francou, B., 1998. A 25,000-Year Tropical Climate History from Bolivian Ice Cores. Science 282, 1858-1864.
Wetzel, R.G., 2001. Limnology. Academic Press, San Diego.
Wigdahl, C.R., Saros, J.E., Fritz, S.C., Stone, J.R., Engstrom, D.R., 2014. The influence of basin morphometry on the regional coherence of patterns of diatom-inferred salinity in lakes of the northern Great Plains (USA). The Holocene 24, 603-613.
Winder, M., Hunter, D., 2008. Temporal organization of phytoplankton communities linked to physical forcing. Oecologia 156, 179-192.
Wolfe, B.B., Aravena, R., Abbott, M.B., Seltzer, G.O., Gibson, J.J., 2001. Reconstruction of paleohydrology and paleohumidity from oxygen isotope records in the Bolivian Andes.

Palaeogeography, Palaeoclimatology, Palaeoecology 176, 177-192.
Zech, J., Zech, R., May, J.-H., Kubik, P.W., Veit, H., 2010. Lateglacial and early Holocene glaciation in the tropical Andes caused by La Niña-like conditions. Palaeogeography, Palaeoclimatology, Palaeoecology 293, 248-254.
Zhou, J., Lau, K.M., 1998. Does a Monsoon climate exist over South America? Journal of Climate 11, 1020-1040.

TABLE CAPTIONS

Table 1.- Summarized description of diatom assemblage zones (DAZs) from Lake Chungará

FIGURE CAPTIONS

Figure 1.- A. Location of sites cited in this paper. B. Catchment and main topographical features of Lake Chungará. Star indicates position of the studied core CHUN11A. The black line correponds to the cross section (C) along the lake. C. Cross section of sediment infilling of the lake. The position of the studied core is indicated by the sketch of the coring platform. Lithological units according to Sáez et al. (2007).

Figure 2.- A. Digital DMT CoreScan (LRC, Minnesota) image of laminated sediments of core CHUN11A. B. Micrograph (X100) of a petrographical thin-section showing a couplet made up by a green (bottom) and a white lamina (top). C. Detail (X400) showing the white lamina exclusively formed by skeletons of *Cyclostephanos* cf. *andinus*. D. *Idem* green lamina dominantly made up by *Cyclostephanos andinus*, and some diatoms of the *Discostella stelligera* complex embedded in an organic matter matrix.

Figure 3.- Diatom percentage diagram for selected taxa (≥2% abundance in at least one sample) of Lake Chungará (core CHUN11A). Diatoms are grouped according to their habitat and salinity preferences. Sample scores of the first two axis of the Principal Component Analysis (PCA), and the diatom dissolution index *F* (Flower & Likhoshway, 1993), varying between 0 and 1, with values of *F*=1 indicating perfectly preserved valves, and *F*=0 indicating that all valves show dissolution, are also plotted. Diatom Assemblage Zones (DAZs) generated by a broken-stick model of the distribution of variance (Bennett, 1996)

and main lithological units and sedimentary facies according to Sáez et al. (2007) are also shown.

Figure 4.- Principal Component Analysis (PCA) ordination biplot of samples (numbers) and diatom taxa (acronyms) in Lake Chungará. Achcon=*Achnanthes conspicua,* Amplib=*Amphora libyca*, Cocpla=*Cocconeis placentula,* Cycand=*Cyclostephanos andinus*, Cyccfand=*Cyclostephanos* cf. *andinus,* Disste=*Discostella stelligera* complex*,* Fracap=*Fragilaria capucina* and varieties*,* Gommin=*Gomphonema minutum,* Navcry=*Navicula cryptotenella,* Navrad=*Navicula radiosa,* Navtri=*Navicula trivialis,* Navven=*Navicula veneta,* Navsem=*Naviculadicta seminulum,* Nittro=*Nitzschia tropica,* Opemut=*Opephora* sp. aff*. mutabilis,* Plalan=*Planothidium lanceolatum,* Staconv=*Staurosira construens* aff*. venter,* Staconc=*Staurosira construens* f*. construens,* Stacons=*Staurosira construens* f*. subsalina,* Stapin=*Staurosirella pinnata,* Ulnuln=*Ulnaria ulna*

Figure 5.- Diatom and geochemical productivity-related proxies from core CHUN11A with indication of defined productivity stages and water level phases/events according to the constructed lake-level curve. Data are compared with the water availability curve of Giralt et al. (2008) and the insolation curve in austral summer at 18ºS for the studied period (Berger & Loutre, 1991). Proxies include sample scores for axis 1 (PC1) and axis 2 (PC2) of Principal Component Analysis on the diatom assemblages, percent of benthic diatoms, total biogenic silica (TBSi), total organic carbon (TOC), the TOC/total nitrogen atomic ratio (TOC/TN), and total inorganic carbon (TIC). TBSi and TOC are expressed as percent contents and mass accumulation rates (MARs). The figure also plots values of carbon and nitrogen isotopes on organic matter ($\delta^{13}C_{org}$, $\delta^{15}N_{org}$) and carbonates ($\delta^{18}O_{carbonate}$, $\delta^{13}C_{carbonate}$) (Pueyo et al., 2011), diatom frustules ($\delta^{18}O_{diat}$, $\delta^{13}C_{diat}$) (Hernández et al., 2013), as well as abundances of the chlorophycean *Botryococcus braunii* (Saéz et al., 2007). All data are plotted against age (cal yr BP).

1029 **Figure 6.-** Sedimentary and paleoecological model for Lake Chungará evolution in the period 12,400
1030 to 1,300 cal yr BP, with description of the defined paleoproductivity stages. See detailed
1031 explanation in text.

Table

DIATOM ASSEMBLAGE ZONE Depth (cm) Age (cal yr BP)	MAIN TAXA	OVERALL TRENDS
CHUN11-01 860.7 - 835.2 12,400 – 12,100	Dominated by *Cyclostephanos andinus* and *Staurosira construens* aff. *venter*. Other tychoplanktonic (mainly *Fragilaria capucina* and varieties) and benthic (mainly *Nitzschia tropica*, *Cocconeis placentula* and *Opephora* sp. aff *mutabilis*) taxa appear in the record	Codominance of benthic and planktonic diatoms in a oligosaline waterbody of shallow but open waters
CHUN11-02 835.2 – 729.5 12,100 – 11,100	The assemblage is dominated by fluctuating numbers of diatoms of the *Discostella stelligera* complex (26.3 – 87.4%) with *Cyclostephanos andinus*, *Cyclostephanos* cf. *andinus* and the tychopelagic *Staurosira construens* aff. *venter* as subdominant taxa	Shift to deeper and predominantly low mixing water conditions
CHUN11-03 729.5 – 627.9 11,100 – 10,450	*Cyclostephanos andinus* is the dominant taxa, reaching its maximum value (89.2%). The *Discostella stelligera* complex dissapears, except in the interval 693.9 – 683.8 cm. *Cyclostephanos* cf. *andinus* shows episodic peaks. Moderate increase of the subdominant *Staurosira construens* aff. *venter* and the benthic *Cocconeis placentula*. Decline of *Nitzschia tropica*	Water shallowing with episodes of a strong turbulent regime
CHUN11-04 627.9 – 587.2 10,450 – 10,000	Marked increase of the *Discostella stelligera* complex, dominating almost the entire assemblage (82.6 – 94.2 %). *Cyclostephanos andinus* and *Cocconeis placentula* are a minor component of the zone	Deeper and stable water conditions
CHUN11-05 587.2 – 540.3 10,000 - -9,500	Starts with a sharp increase in *Cyclostephanos andinus*, decreasing afterwards. This decrease is paralleled by an increase in *Cyclostephanos* cf. *andinus*, which dominates the assemblage, and by *Staurosira construens* aff. *venter* and *Cocconeis placentula*. The *Discostella stelligera* complex acquire low percentages. Reappearance of *Nitzschia tropica*	Shift to a turbulent regime accompanied by a decrease in water level. Slight salinization
CHUN11-06 540.3 – 344.0 9,500 – 7,400	The *Discostella stelligera* complex dominates almost the entire assemblage (67.1 – 95.3%) reaching a maximum in the whole record. *Cyclostephanos andinus* shows low values (5.0 – 23.4%), and *Cyclostephanos* cf. *andinus* dissapears in the record. *Cocconeis placentula* decreases	Lake deepening with a predominantly non-turbulent regime. The reduction in the oligosaline diatoms points to a salt dilution
CHUN11-07 344.0 – 61.8 7,400 – 2,600	*Cyclostephanos andinus* and the diatoms of the *Discostella stelligera* complex show fluctuating values codominating the assemblage. The epiphytic *Cocconeis placentula* increases	Moderate lake shallowing allowing macrophytic development. Shift to moderate mixing conditions
CHUN11-08 61.8 – 14.3 2,600 – 1,300	Sharp increase in the *Discostella stelligera* complex (74.2 – 87.0%) followed by a decline in *Cyclostephanos andinus*. *Cocconeis placentula* becomes a minor component of the assemblage	Maximum lake level situation, with the development of a predominantly stable water column

Figure
Click here to download high resolution image

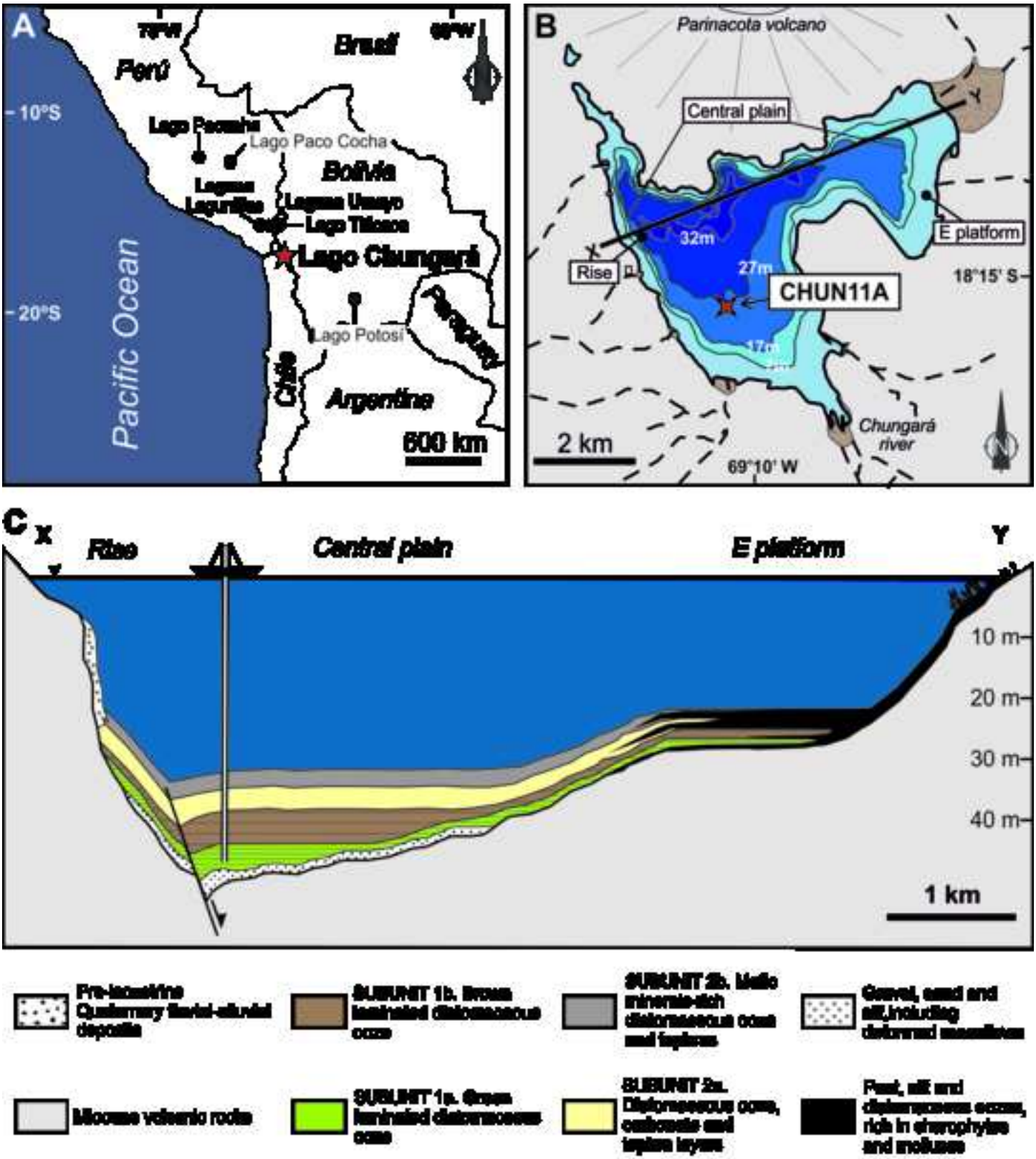

Figure 1

Figure

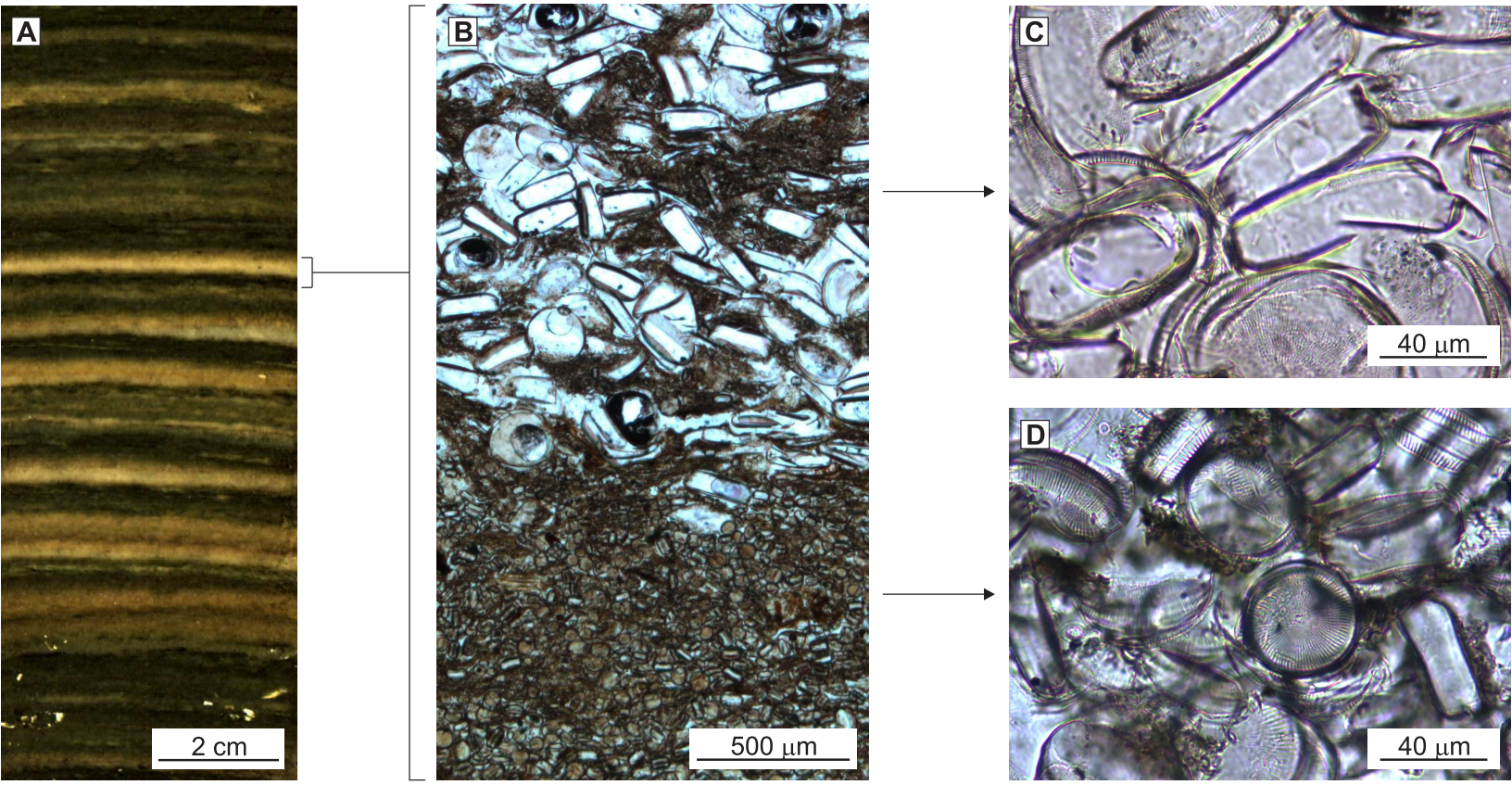

Figure 2

Figure

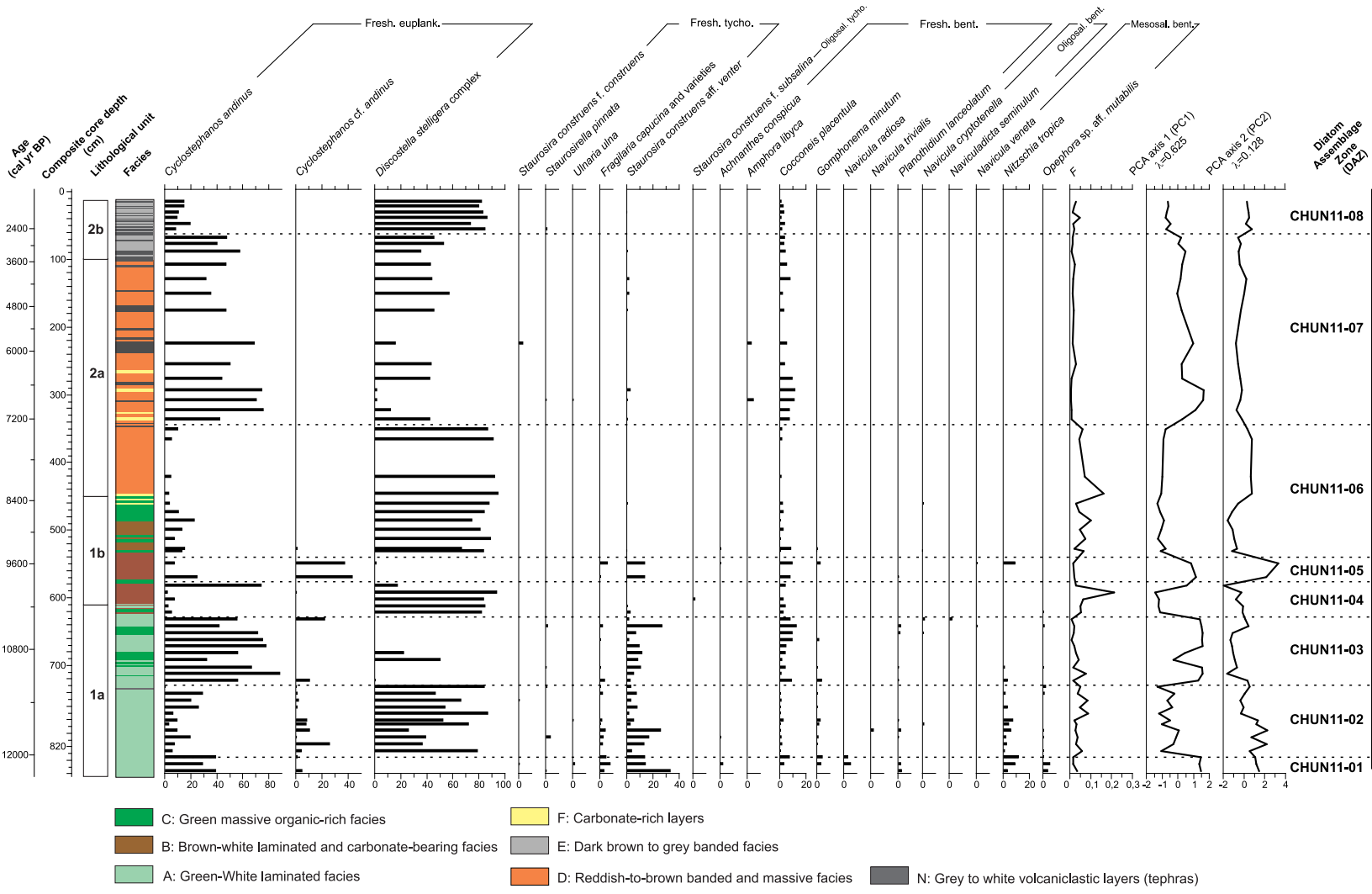

Figure 3

Figure

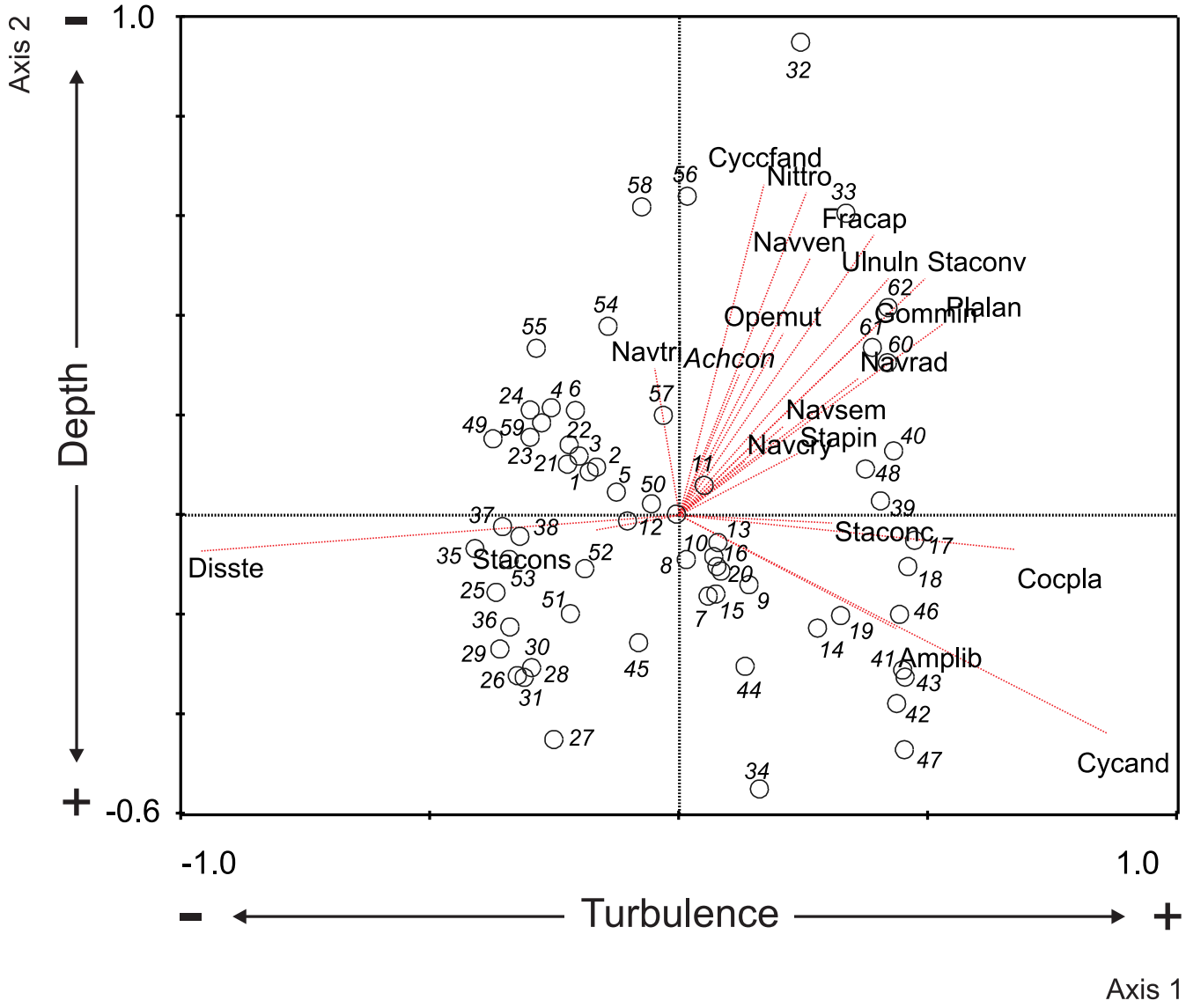

Figure 4

Figure

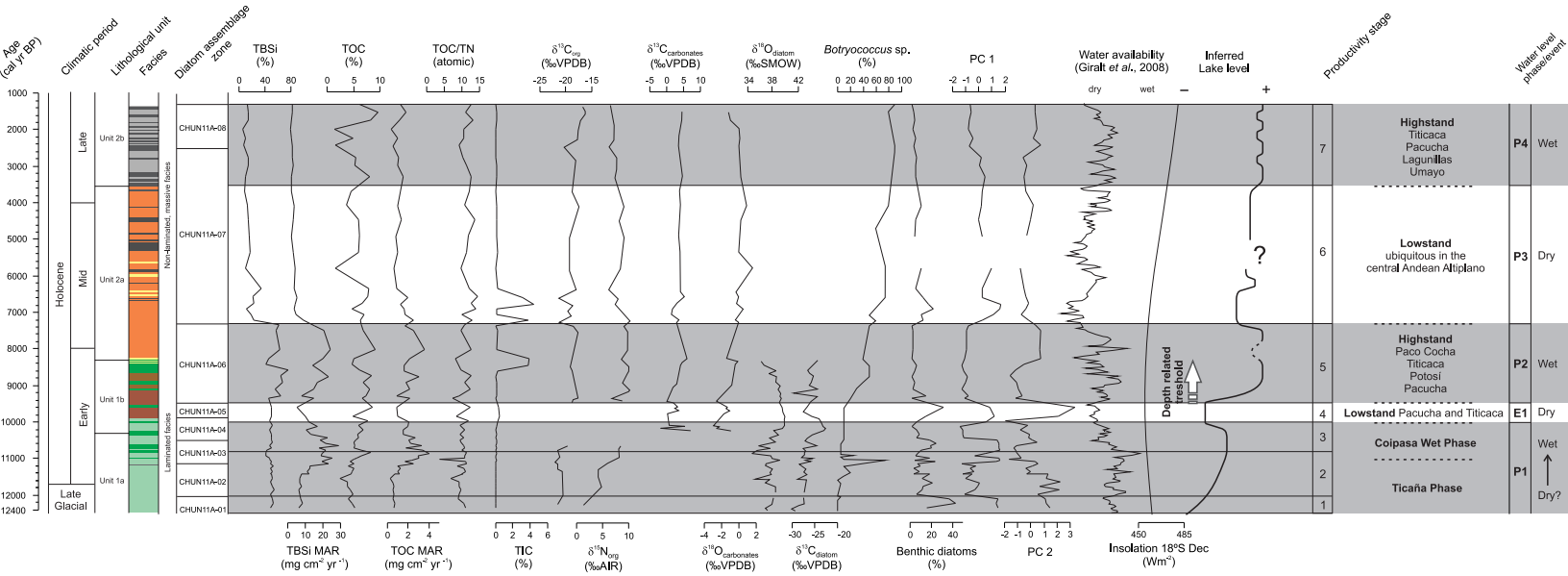

Figure 5

Figure
Click here to download high resolution image

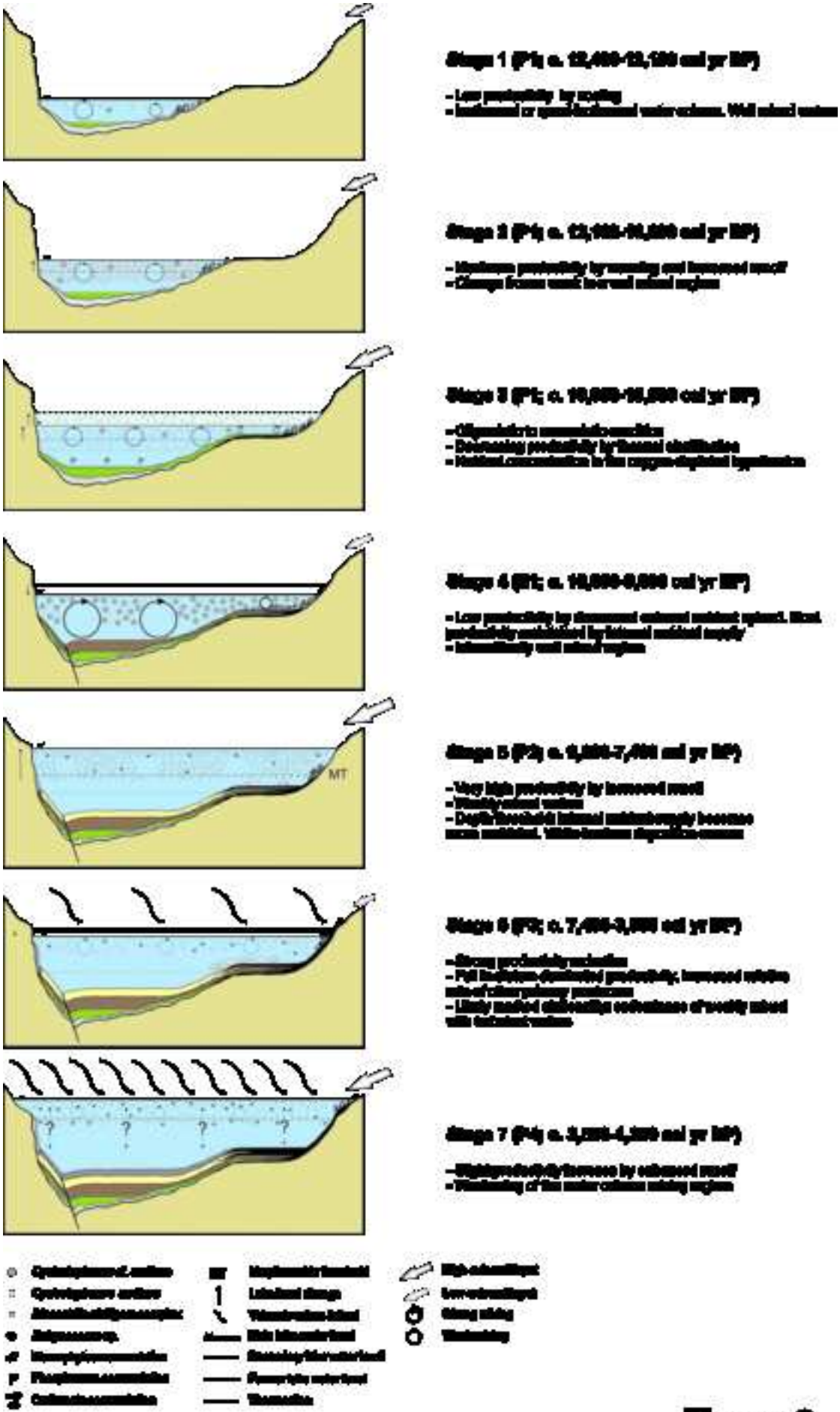

Figure 6