

Quaternary climate change and Heinrich events in the southern Balkans: Lake Prespa diatom palaeolimnology from the last interglacial to present

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Abstract Lake Prespa, in the Balkans, contains an important palaeo-archive in a key location for understanding Quaternary climate variability in the transition between Mediterranean and central European climate zones. Previous palaeoenvironmental research on sediment cores indicates that the lake is highly sensitive to climate change and that diatoms are likely to be strong palaeohydrological proxies. Here, we present new results from diatom analysis of a *ca.* 91 ka sequence, core Co1215, which spans the time from the end of the last interglacial to the present. Fluctuations in the diatom data were driven primarily by changes in lake level, as a function of shifts in moisture availability. Warmer interglacial (MIS 5, MIS 1) and interstadial (MIS 3) phases exhibit higher lake levels in spite of enhanced evaporative concentration, underlining the

importance of changes in precipitation regimes over time. Low lake levels during glacial phases indicate extreme aridity, common to all Mediterranean lakes. Evidence for fluctuations in trophic status is linked, in part, to lake-level change, but also reflects nutrient enrichment from catchment processes. MIS 5a is characterized by the highest lake productivity in the sequence, but low lake levels, which are ascribed primarily to very low precipitation. On a suborbital timescale, the diatoms provide evidence for correlation to the millennial-scale variability recorded in the Greenland oxygen isotope records and clearly reflect the impact of the Heinrich H6, H5 and H3–1 ice-rafting events, suggesting the dominant influence of North Atlantic forcing in this region. Although the highest-amplitude shift in the diatom assemblages occurs

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during the time of H4 (40–38 ka), it may be superimposed upon the impact of the 39.28 cal ka BP Campanian Ignimbrite volcanic eruption. Diatoms from Lake Prespa core Co1215 display the first strong evidence for the impact of Italian volcanic activity on lacustrine biota in this region. Results emphasize the complexity of diatom response thresholds in different studies across the region. In the case of Lake Prespa, the results highlight the important role of precipitation for maintaining the hydrological balance of the lake, and indirectly, its biodiversity.

Keywords Lake Prespa · Diatoms · Lake-level change · Palaeoclimate · Tephra impact · Quaternary Heinrich events

Introduction

Quaternary researchers in the last few decades have made considerable efforts to understand spatial climate variability in the Mediterranean, but the main underlying mechanisms are still under debate (Magny et al. 2012). This is partly because of gaps in our understanding of spatial and temporal variability. Of the various palaeolimnological indicators studied, diatoms, in most cases, have been restricted to the late Glacial and Holocene epoch (Wilson et al. 2008; Jones et al. 2013). Diatom palaeoclimate records spanning multiple glacial-interglacial transitions are still very rare across the Mediterranean (Ampel et al. 2008, 2010), but demonstrate high sensitivity to climate change. A prime example is the diatom record from ancient Lake Ohrid (Reed et al. 2010; Cvetkoska et al. 2012), in which diatoms provide strong evidence for the lake's response to climate variability since the penultimate glacial-interglacial transition to the present.

Lake Prespa, in the Balkans, is an ancient lake that likely co-existed with its neighbour Lake Ohrid for more than 1 Ma (Stankovic 1960). Preliminary borehole data, core logging and geochemical data from a 569-m-long sediment sequence recovered during the Scientific Collaboration on Past Speciation Conditions (SCOPSCO) drilling campaign, indicate that Lake Ohrid is >1.2 Ma old (Wagner et al. 2014a, b). The exact age of Lake Prespa is still uncertain. The importance of both lakes, Ohrid and Prespa, as

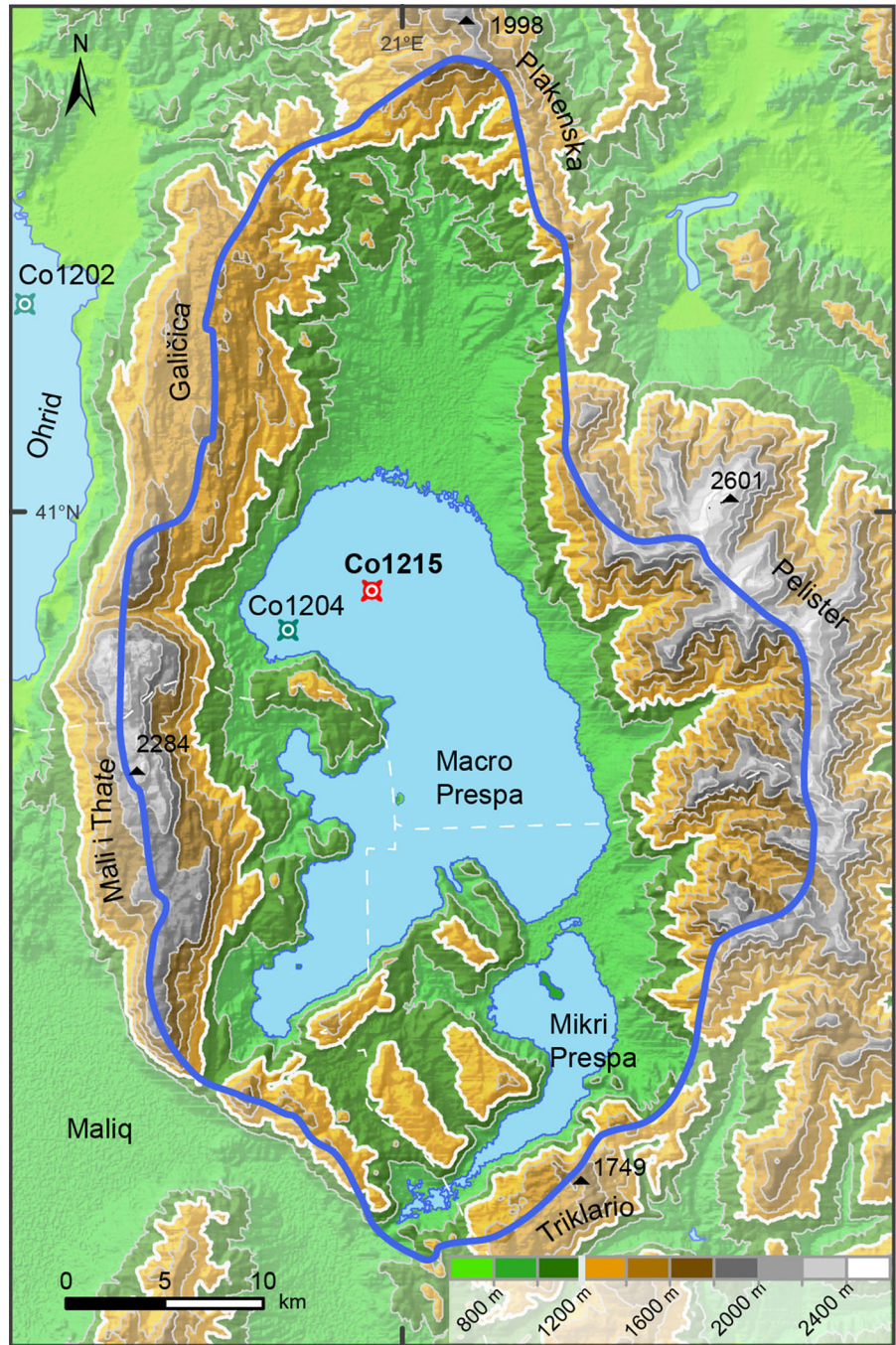
palaeoenvironmental archives for Mediterranean Quaternary climate research has been well documented (Wagner et al. 2008a). Multi-proxy geochemical analysis of a 10.5-m sequence from the northwestern part of Prespa demonstrates glacial-interglacial variability over the last *ca.* 48 ka (Leng et al. 2010; Wagner et al. 2010). A 17.76-m sequence, Co1215, spans the last ~91 ka (Damaschke et al. 2013). Multi-proxy analysis of the last glacial to Holocene sequence from ~17 ka to present in Co1215 (Aufgebauer et al. 2012; Wagner et al. 2012; Leng et al. 2013; Panagiotopoulos et al. 2013; Cvetkoska et al. 2014a) provides a useful interpretive tool for longer-term climate variability.

Here, we build on previous palynological and geochemical studies (Panagiotopoulos et al. 2014) of the longer sequence, using diatoms to infer hydrological and productivity shifts since Marine Isotope Stage (MIS) 5b to present. Diatoms of Lake Prespa are highly sensitive to lake-level variation and are important in elucidating hydrological variability (Cvetkoska et al. 2014a). Trends in the extended multi-proxy dataset are assessed to explore the links between limnological and catchment change. The diatom-inferred palaeoclimate data are compared to other Mediterranean and global records to improve understanding of the nature of glacial-interglacial climate variability in this region.

Site description

A detailed description of the geographical, physical and chemical properties of Lake Prespa is provided in Hollis and Stevenson (1997). Lake Prespa (Fig. 1), also known as Macro Prespa, Macedonia/Albania/Greece, is located at an altitude of 849 m a.s.l., has a surface area of 254 km², a mean water depth of ~14 m, a maximum water depth of ~48 m and a total volume of 3.6 km³ (Wagner et al. 2012). The water balance is controlled by inputs from river inflow, catchment runoff, direct precipitation, inflow from Lake Mikri Prespa and groundwater. Output is via surface evaporation, water abstraction for irrigation and subsurface outflow through the karstic aquifers of Galicica Mountain into Lake Ohrid (Matzinger et al. 2006). Climate in the catchment is described as Mediterranean in the southern part and continental in the northern part, with a sub-alpine character below 1,650 m in elevation and alpine character above (Krstić 2012). Mean

Fig. 1 Topographic map of Lake Prespa showing lake catchment (blue line) and location of cores Co1215 (this study) and Co1204 recovered from Lake Prespa (Wagner et al. 2010). NASA Shuttle Radar Topographic Mission (SRTM) Data: Jarvis et al. 2008 (modified from Panagiotopoulos et al. 2013). (Color figure online)



temperature fluctuates from +1 °C in winter to +21 °C in summer, and mean annual precipitation varies between 750 and 1,200 mm/a in the lake valley and the surrounding mountain ranges, respectively (Hollis and Stevenson 1997).

Overall, the hydrology of Lake Prespa is controlled by a complex interplay of factors, including the geomorphology of the area, catchment vegetation, hydrology of the watershed area, climate, and its relatively large but shallow bathymetry, which lacks a

surface outflow. This makes Lake Prespa highly sensitive to environmental forcing and especially susceptible to lake level change.

Materials and methods

Core Co1215 was recovered in the north-central part of Lake Prespa at a water depth of 14 m, during two field campaigns, in November 2009 and June 2011 (Wagner et al. 2012; Damaschke et al. 2013). Coring was performed from a floating platform equipped with gravity corers for surface sediments and a 3-m-long percussion piston corer for deeper sediments (UWI-TEC Corp. Austria). Correlation of the individual core sections resulted in a 1,776-cm-long composite sequence.

Analytical core analysis, described in detail in Aufgebauer et al. (2012), Wagner et al. (2012), Leng et al. (2013) and Panagiotopoulos et al. (2014) consisted of non-destructive X-ray fluorescence (XRF) scanning, total carbon (TC) and total inorganic carbon (TIC) measurements, stable isotope ratios, X-ray diffraction (XRD) mineralogy and palynological analysis. The final age-depth model for the sequence was presented in detail by Damaschke et al. (2013).

Diatoms were analyzed in 222 samples, taken at ~8-cm intervals (resolution = ~0.1–0.4 ka), spanning the 1,760-cm section, or the last 91.0 cal ka. Samples were cleaned using cold H₂O₂ and 10 % HCl to oxidize organics and remove carbonates, respectively (Cvetkoska et al. 2012). Permanent diatom slides were prepared using Naphrax[®] as a mountant and ~400 diatom valves per slide (Battarbee 1986) were counted under oil immersion at 1,500× magnification using a Nikon Eclipse 80i microscope. Identification of diatom taxa followed Krammer and Lange-Bertalot (1986–1991) and the dedicated Ohrid and Prespa work of Levkov et al. (2007b) and Cvetkoska et al. (2012, 2014b). Diatom counts were converted to percentage data and displayed using Tilia and TGView v. 2.0.2. (Grimm 1991). Stratigraphic zone boundaries were defined using Constrained Incremental Sum of Squares cluster analysis (Grimm 1987) for diatom taxa present at >2 % abundance. Multi-proxy stratigraphic diagrams were prepared using C2 (Juggins 1991–2007). Correlation between diatom relative abundance data and geochemical

proxies was tested using Spearman's rho correlation test, in the statistical package "stats," version 0.8-2 (R Core Team 2012). Variation in the diatom data was explored by ordination, and with a gradient length of >2.5, detrended correspondence analysis, ('DCA') was appropriate (Jongman et al. 1995).

Results

Core chronology

The core chronology (Fig. 2) was developed using accelerator mass spectrometry (AMS) ¹⁴C dating, tephra analysis, electron spin resonance (ESR) and correlation with NGRIP ice core data (Damaschke et al. 2013). Calibration of the radiocarbon ages to calendar years (cal ka BP) was accomplished using the INTCAL09 calibration curve (Reimer et al. 2009), except for the uppermost sample, which was calibrated using the Levin¹⁴C dataset (Levin and Kromer 2004). At a core depth of 1,463–1,458 cm, a layer of shells of the mollusk *Dreissena* was dated by electron spin resonance (ESR) and was discussed in Damaschke et al. (2013) and Wagner et al. (2014c). Ages presented here are calendar years before present (cal ka BP) with 2σ ranges. The detailed tephrostratigraphic record and sedimentation rates for the 1,776-cm composite sequence are presented in Damaschke et al. (2013). The calculated sediment accumulation rate (mm/a; SAR) is between 0.09 and 1.36 mm/a, with the exception of a peak of 190 mm/a at the time of deposition of tephra PT0915–7, correlated to the Campanian Ignimbrite (CI) eruption from the Campi Flegrei volcanic field (Damaschke et al. 2013).

Diatom analysis

Two hundred and seventy diatom taxa were identified in Lake Prespa core Co1215 and the summary diatom diagram (Fig. 3) displays the 40 taxa present at >2 % relative abundance. Six major diatom assemblage zones (D1–6), each divided into 2–4 subzones, were identified with CONISS. The DCA results (Fig. 4; Table 1) clearly support the stratigraphic zone delineation. Planktonic taxa, i.e. the *Cyclotella* complex and *Aulacoseira* spp., have high scores on Axis 1 (eigenvalue = 0.47), and benthic taxa have low

Fig. 4 Scatter plot of DCA Axis 1 versus DCA Axis 2 scores of diatom samples and species from core Co1215. The symbol key in the top right hand corner represents the diatom zones. Diatom zone D1 is split into two subzones because of the marked difference in Axis 2 scores. Only selected diatom taxa are displayed

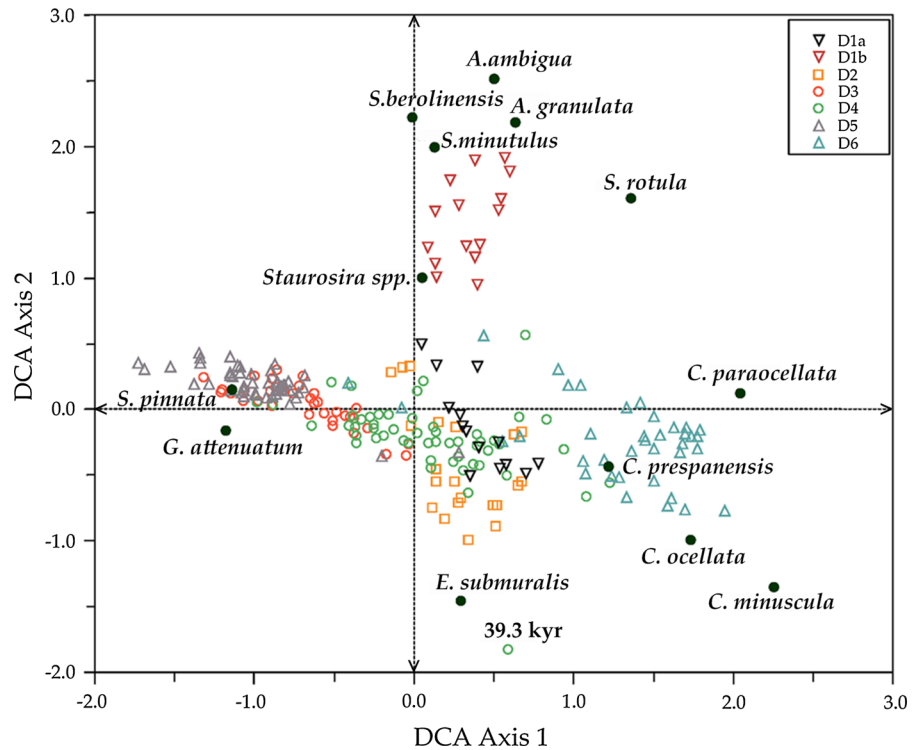


Table 1 Summary of the DCA ordination of the diatom assemblages found in Lake Prespa core Co1215 (222 samples) and Spearman’s rho (ρ) coefficient values for the correlations between selected diatom data and geochemical proxies and DCA score

Axes	DCA 1	DCA 2	DCA 3	DCA 4	
Eigenvalues	0.47	0.23	0.17	0.14	
Axis lengths	3.48	2.95	2.10	1.75	
Decorana values	0.50	0.32	0.12	0.08	
Spearman’s correlation	<i>Cyclotella group</i>	<i>Fac. Plankton</i>	<i>S. pinnata</i>	<i>Benthic</i>	<i>E. submuralis</i>
TOC (%)	0.63	−0.49	−0.76	−0.62	0.11
TN (%)	0.62	−0.54	−0.77	−0.63	−0.06
TOC/TN	0.52	−0.38	−0.66	−0.53	0.16
Ca (counts)	/	/	−0.53	−0.38	−0.05
K (counts)	−0.63	0.54	0.69	0.63	0.14
Ti (counts)	−0.57	0.55	0.64	0.56	0.20
Fe/Ti	0.39	−0.38	−0.41	−0.50	−0.35
DCA Axis 1	0.87	−0.73	−0.89	−0.58	0.10
DCA Axis 2	−0.58	0.48	0.39	/	−0.51

Values in bold are significant at $p < 0.0001$

“/” no significant correlation

scores, indicating that Axis 1 reflects lake-level variation. The Spearman’s test results (Table 1) display a positive correlation between the *Cyclotella* group and DCA Axis 1 ($\rho = 0.87, p < 0.0001$), and a

negative correlation between the facultative planktonic and benthic group and DCA Axis 1 ($\rho = -0.73$ and $-0.58, p < 0.0001$, respectively), emphasizing the influence of lake level in the data. Axis 2 scores

(eigenvalue = 0.23) reflect a clear trophic gradient between oligo-mesotrophic taxa, which include the *Cyclotella* complex and *Eolimna submuralis* (Hustedt) Lange-Bertalot et Kulikovskiy that have relatively low scores on Axis 2, and meso-eutrophic species *Aulacoseira granulata* (Ehrenberg) Simonsen, *Aulacoseira ambigua* (Grunow) Simonsen, *Staurosirella berolinensis* (Lemmermann) Bukhtiyarova, *Stephanodiscus minutulus* (Kützing) Cleve et Möller and *Stephanodiscus rotula* (Kützing) Hendeby, which have high scores. Based on the hypothesized resource relationships among the planktonic diatoms (Kilham et al. 1986), increased abundance and/or dominance of *A. granulata* in core Co1215, is indicative of eutrophic, low-light and turbid-water conditions, whereas *A. ambigua* stages reflect more stable lake stratification, higher light availability and a meso-eutrophic state. From the Spearman test, the trophic gradient is supported by the negative correlation between the *Cyclotella* group and *E. submuralis* to DCA Axis 2

($\rho = -0.58$ and -0.51 , $p < 0.0001$, respectively). *E. submuralis* has been described as an epiphytic species from the littoral and sub-littoral zone of Lake Ohrid (Hustedt 1945). Diatoms are compared in Fig. 5 to selected geochemical, isotope and pollen data from the core according to the chronology of MIS boundaries (Lisiecki and Raymo 2005). Description of the diatom zones (D):

D1: 1,760–1,530 cm depth, 91.0–78.0 cal ka BP

D1a (1,760–1,652 cm depth, 91.0–85.5 cal ka BP)

Planktonic, facultative planktonic (FP) and benthic taxa are present in approximately equal proportions at the base of the sequence, with minor fluctuations between groups, until an increasing trend in FP at the expense of benthic taxa occurs at 90.0 cal ka BP, reaching a maximum of >80 % at 85.5 cal ka BP. Planktonic *Cyclotella ocellata* Pantocsek and *C. paraocellata*

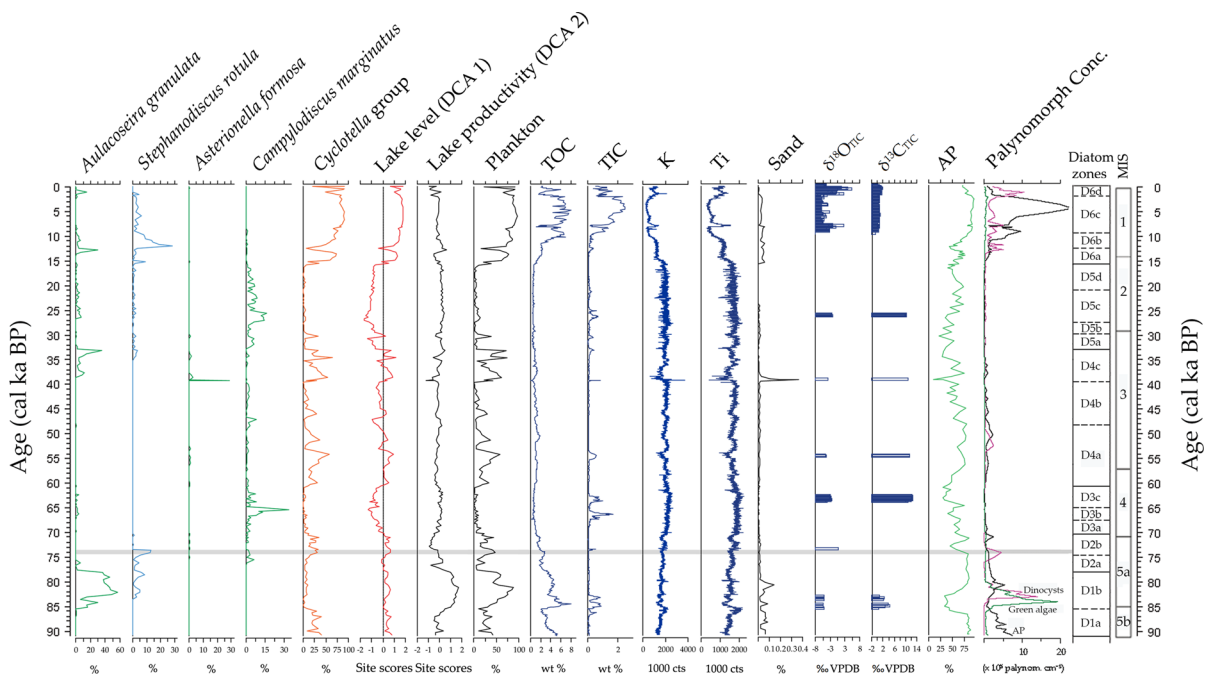


Fig. 5 Diagram of Lake Prespa core Co1215 displaying: abundance (%) of selected diatom taxa, DCA Axis 1 (lake-level) and DCA Axis 2 (lake productivity) scores and diatom plankton (%) abundance. Previously published data include total organic carbon (TOC; wt%), total inorganic carbon (TIC; wt%), potassium (K; 1,000 cts), titanium (Ti; 1,000 cts), sand (%) (Wagner et al. 2012), $\delta^{18}\text{O}_{\text{TIC}}$ (‰ VPDB), $\delta^{13}\text{C}_{\text{TIC}}$ (‰ VPDB) (Leng et al. 2013), arboreal pollen (%) and concentrations

($\times 10^5$) of arboreal pollen (AP; black), green algae (green) and dinoflagellates (purple) (Panagiotopoulos et al. 2014). Light gray band marks the *Dreissena* shell horizon between 14.58 and 14.63 m depth, ca. 73.57 ± 7.74 ka (Damaschke et al. 2013). CONISS-delineated diatom zones are marked. Marine Isotope Stage (MIS) boundaries are from Lisiecki and Raymo (2005). (Color figure online)

Cvetkoska, Hamilton, Ognjanova-Rumenova et Levkov are each present at >20 %, while *C. prespanensis* Cvetkoska, Hamilton, Ognjanova-Rumenova et Levkov is rare, at <5 % relative abundance. *E. submuralis* is the most abundant benthic species, exhibiting a peak of 22 % at 88.0 cal ka BP. Other common benthic taxa are *Amphora* spp., *Diploneis* spp., *Navicula hastata* Jurilj and *Navicula* spp.

D1b (1,652–1,530 cm depth, 85.5–78.0 cal ka BP)

Zone D1b is marked by a shift to dominance of planktonic *Aulacoseira* Thwaites taxa, increasing to >50 % at 84.2 cal ka BP. *A. granulata* and *A. ambigua* co-dominate initially, with *A. granulata* dominating thereafter (>35 %) until 78.0 cal ka BP. *A. ambigua* is at low abundance except for two peaks of >35 % at 83.0 cal ka BP and 81.2 cal ka BP. FP and benthic taxa increase to >30 and 10 %, respectively, from 81.0 cal ka BP.

D2: 1,530–1,364 cm depth, 78.0–70.2 cal ka BP

D2a (1,530–1,474, 78.0–74.5 cal ka BP)

Subzone D2a marks a sharp decline in the abundance of *A. granulata* and renewed dominance of small Fragilariaceae. Benthic species dominate in a single sample at 76.7 cal ka BP, at 70 % abundance, a consequence of peak abundance (~60 %) of *E. submuralis*.

D2b (1,474–1,364 cm depth, 74.5–70.2 cal ka BP)

Plankton increases in D2b, but stays below 50 %. In two assemblages, at 73.4 cal ka BP and 70.9 cal ka BP, all habitat groups are present at similar abundance. Small Fragilariaceae reach a maximum of 38 % at the upper zone boundary. Benthic species are diverse and dominate from 73.0 to 71.5 cal ka BP, with a peak of 71 % at 72.8 cal ka BP. *Amphora* spp., *Campylodiscus* spp., *Diploneis* cf. *krammeri* Lange-Bertalot et Reichardt, *Diploneis* sp., *Fallacia ohridana* (Hustedt) Levkov et Krstic, *Gyrosigma attenuatum* (Kützing) Cleve, *E. submuralis*, *Navicula* spp., *Nitzschia* spp. Hassall and *Surirella* spp. Turpin are most abundant within the group.

D3: 1,364–1,086 cm depth, 70.2–60.7 cal ka BP

D3a (1,364–1,284 cm depth, 70.2–67.5 cal ka BP)

Small Fragilariaceae exhibit a consistent increasing trend to ~60 % abundance, driven by *S. pinnata*. Plankton is at <15 % abundance. Benthic taxa decline to ~35 % at the upper zone boundary, with *E. submuralis* and *G. attenuatum* being most common, peaking at 34 % abundance at 70.0 cal ka BP and 27 % at 68.7 cal ka BP, respectively.

D3b (1,284–1,212 cm depth, 67.5–65.0 cal ka BP)

Plankton continues to decrease and is mainly represented by *Cyclotella* spp. (<8 %) and *A. granulata* (<5 %). High *Staurosira* spp. and *S. pinnata* abundance at the base of the subzone is replaced by increasing benthic species abundance to ~80 % at 65.5 cal ka BP, marked by a distinct peak (34 %) of *Campylodiscus marginatus* Jurilj.

D3c (1,212–1,086 cm depth, 65.0–60.7 cal ka BP)

Low plankton abundance (<8 %) is maintained in subzone D3c. Small Fragilariaceae are present at 45–70 % throughout. The benthic group increases to 25–50 % abundance throughout the zone. A single peak (6 %) in the record of the aerophilous *Ellerbeckia arenaria* (Moore ex Ralfs) Crawford occurs at 62.5 cal ka BP. The benthic group is represented by species similar to those in zone D2b.

D4: 1,086–667 cm depth, 60.7–33.0 cal ka BP

D4a (1,086–904 cm depth, 60.7–48.1 cal ka BP)

Subzone D4a is marked by fluctuating abundance of all species groups. *Cyclotella* species increase from the base of the zone, to 60 % at 54.3 cal ka BP, at the expense of FP, while benthic taxa maintain 40–50 % abundance. Among them, *E. submuralis* is most abundant (10–20 %), while *Amphora* spp. reach maximum abundance of 9 % at 58.4 cal ka BP. At 53.4 cal ka BP small FP start to increase towards the upper zone boundary, reaching >50 % at 49.6 cal ka BP, while at same time, the benthic group decreases to 35 %.

D4b (904–776 cm depth, 48.1–39.3 cal ka BP)

Plankton remains below 10 % in subzone D4b, apart from the peak at 46.0 cal ka BP when *C. prespanensis* peaks at 20 %. The zone exhibits high diversity and co-dominance of FP and benthic taxa. *E. submuralis* is present throughout, at up to 25 % abundance. Other abundant benthic species in this subzone are *Cocconeis* spp., *Cavinula scutelloides* (Smith) Lange-Bertalot, *Cavinula* cf. *cocconeiformis* var. *elliptica* (Hustedt) Lange-Bertalot, *D. krammeri*, *Diploneis* sp. and *Pinnularia subrupestris* Krammer.

D4c (776–667 cm depth, 39.3–33.0 cal ka BP)

The only peak of *Asterionella formosa* Hassall (~30 %) in the record occurs at 39.3 cal ka BP, accompanied by peak abundance (22 %) of *Nitzschia palea* (Kützing) Smith. The planktonic *C. ocellata*, *Stephanodiscus hantzschii* Grunow, facultative planktonic *Pseudostaurosira brevistriata* (Grunow) Williams et Round, *S. pinnata* and the benthic species *Fallacia helensis* (Schulz) Mann, *G. attenuatum* and *Navicula* spp. compose the diatom assemblage at 39.3 cal ka BP, all of them present at similar abundance. At 38.6 cal ka BP, *C. ocellata* is present at 32 %, accompanied by a 17 % peak of *Cyclotella minuscula* (Jurilj) Cvetkoska.

After a minimum of <10 % at 35.2 cal ka BP, plankton increases again, a consequence of a peak in *Cyclotella* abundance (~65 %). At 34.3 cal ka BP *Cyclotella* spp. decline again and are replaced by increasing *A. granulata*, which becomes dominant in the plankton at the upper zone boundary. FP dominate only at 35.2 cal ka BP. The benthic group is dominant from 39.0 to 34.2 cal ka BP. From 36.2 cal ka BP, *E. submuralis* declines to <5 %.

D5: 667–293 cm depth, 33.0–15.7 cal ka BP

D5a (667–611 cm depth, 33.0–29.7 cal ka BP)

Subzone D5a is co-dominated by benthic and FP species. *C. ocellata* displays a single peak of 30 % at 30.4 cal ka BP. *G. attenuatum* is the dominant benthic species (12–23 % abundance) until 30.9 cal ka BP, when it declines and *Diploneis alpina* Meister peaks at 22 %. *Amphora* spp., *C. marginatus*, *Cocconeis* spp.,

Diploneis mauleri (Brun) Cleve and *Gyrosigma macdonicum* Levkov, Krstic et Nakov are common.

D5b (611–556 cm depth, 29.7–27.3 cal ka BP)

Subzone D5b maintains low plankton abundance (<5 %). Small FP species prevail until 27.8 cal ka BP, when benthic taxa increase to >55 %. The benthic group is of similar composition to that in D5a.

D5c (556–405 cm depth, 27.3–21.0 cal ka BP)

Low plankton abundance (<15 %) is maintained throughout D5c, with *Aulacoseira granulata* present at <10 %. At 27.1 cal ka BP, the maximum benthic abundance of 75 % is dominated by *D. alpina* (35 %) and *C. marginatus* (15 %). Benthic domination is replaced by small Fragilariaceae, from 25.4 cal ka BP, mainly because of increased abundance of *S. pinnata*.

D5d (405–293 cm depth, 21.0–15.7 cal ka BP)

In subzone D5d small Fragilariaceae continue to increase as benthic taxa decrease, with *S. pinnata* being dominant at >40 % abundance throughout. Plankton remains at low abundance, with a maximum of 10 % at the upper zone boundary. Among the benthic species, *D. alpina* declines to <10 %, while *Diploneis* sp. increases to 10 % at 17.7 cal ka BP.

D6: 293–2 cm depth, 15.7 cal ka BP–present

D6a (293–220 cm depth, 15.7–12.3 cal ka BP)

Subzone D6a incorporates a shift at 15.7 cal ka BP to increased abundance of *Cyclotella* taxa (>25 %). At 15.2 cal ka BP, *S. rotula* exhibits a minor peak of ~9 %, which is followed by an increase in the relative proportion of *S. pinnata* (~35 %). From 14.8 cal ka BP, small Fragilariaceae decline and planktonic *Cyclotella* taxa dominate up to the upper zone boundary. The benthic group declines to <20 %, and is similar to D5d. The 13.1–12.3 cal ka BP interval comprises only two samples, but is distinct because of a peak of 30 % in *A. granulata* at 12.9 cal ka BP, and of *S. pinnata* at the upper zone boundary.

D6b (220–164 cm depth, 12.3–9.3 cal ka BP)

D6b is delineated by a peak in *S. rotula* (~30 %) at the base of the zone and a sharp increase in planktonic taxa to >70 %. After the initial peak, *S. rotula* declines towards the upper zone boundary, while the *C. ocellata* and *C. paraocellata* sum abundance increases to ~70 % at 10.5 cal ka BP. The FP decline from ~20 % at the base to <5 % at the upper zone boundary. The benthic group is present at ~10–20 % abundance throughout.

D6c (164–70 cm depth, 9.3–1.9 cal ka BP)

Subzone D6c is delineated by the highest plankton abundance, >90 % relative abundance, between 7.9 and 4.2 cal ka BP. *C. paraocellata* dominates the planktonic group. *C. minuscula* peaks with 10 % at 8.0 cal ka BP. Benthic taxa decline to <10 % after 7.9 cal ka BP.

D6d (70–2 cm depth, 1.9 cal ka BP-present)

C. ocellata becomes dominant at the expense of *C. paraocellata*, which declines sharply to <10 % abundance. *C. minuscula* peaks between 1.7 and 1.5 cal ka BP and at 0.5 cal ka BP. *A. granulata* and *Staurosira* spp. peak at 15 and 25 % relative abundance, respectively, at 1.0 cal ka BP, while from 0.3 cal ka BP (seventeenth century AD), there is a marked trend towards increasing dominance, for the first time, of the benthic species *C. scutelloides*. It reaches a maximum of ~40 % at 0.05 cal ka BP (ca. AD 1900), when benthic taxa dominate at >60 %. The surface sediment sample is dominated by *C. ocellata* (>80 %), accompanied by the benthic *N. subacicularis* Husted.

Discussion

Diatom response

Shifts in relative abundance of *C. ocellata*, *C. paraocellata* and *C. prespanensis* were interpreted in the late glacial to Holocene record as a response to shifts in trophic status within waters of low to medium productivity (Cvetkoska et al. 2014a). In the longer record, this is supported in part by the absence of more eutrophic taxa such as *A. granulata* in *Cyclotella*-

dominated zones. Across a range of diatoms with contrasting P-availability and light-intensity preferences, Kilham et al. (1986) placed *A. ambigua* as intermediate between the oligotrophic, high-light-demanding *Aulacoseira distans* (Ehrenberg) Simonson, and the eutrophic, low-light *A. granulata*.

Dominance of small Fragilariaceae and the benthic *E. submuralis* likely reflect a shallow, low-productivity lake. *S. pinnata* is considered a typical glacial-type species, based on inferences for its high sensitivity to the climate-related variables “duration of ice cover” and “mean July water temperature” (Schmidt et al. 2004) and also its presence in glacial phases of other Mediterranean lakes such as Ioannina (Wilson et al. 2008; Jones et al. 2013). During interglacials, small Fragilariaceae tend to occur in marginal open lake waters at the start of the warming season and are often regarded as pioneering taxa with broad ecological preferences (Smol 1988).

The highly diverse benthic group is mainly represented by species with large, heavily silicified valves such as *C. marginatus*, *D. alpina*, *G. attenuatum* and *Surirella* spp., without major species turnover from the last interglacial to the present. Modern ecological studies (Levkov et al. 2007a, b) demonstrate that these species dominate as epipelagic taxa in deeper waters (4–18 m) and the physico-chemical properties of the lake (substrate, light intensity, dissolved oxygen, Si) are the main factors that determine the structure of these communities.

MIS 5 (91.0–71.0 cal ka BP; D1, D2)

MIS 5b (91.0–85.0 cal ka BP; D1a)

Rapidly fluctuating lake levels during MIS 5b are inferred from the shifts in *Cyclotella* abundance (10–45 %) in the basal diatom zone (Fig. 3) and positive, but low DCA Axis 1 scores (Fig. 4), overall representative of an intermediate, moderately deep lake. Minima at 90.0, 88.4 and 85.6 cal ka BP indicate low-lake-level phases. The dominant *Staurosira* spp., *S. construens* and *E. submuralis*, reflect diatom growth restricted to the sandy, shallow and nutrient-depleted littoral zone.

Panagiotopoulos et al. (2014) suggest MIS 5b was a period of rather high lake productivity based on high AP % and green algae concentration, TOC and C/N values. However, the diatoms indicate an oligo-

mesotrophic state (Cvetkoska et al. 2014a), correlating with a decreasing trend in TOC values from the base of the sequence. The higher SAR (Fig. 2) and sand content (Fig. 5) indicate catchment erosion, supported by a gradual increase in Ti and K, but apparently insufficient nutrients to generate high productivity.

Diatom-inferred intermediate moisture availability and possible (based on low productivity) relatively low temperatures in MIS 5b, are indicated more strongly by the absence of warm, sclerophyllous Mediterranean taxa in the pollen record between 91.0 and 85.0 cal ka BP, which suggests unfavorable winter temperatures for such vegetation around Lake Prespa (Panagiotopoulos et al. 2014). Overall, the data suggest a phase of unstable climate with moderate, but fluctuating moisture availability and temperature, which may reflect a transitional phase towards the end of the previous interglacial.

MIS 5a (85.0–71.0 cal ka BP; D1b, D2)

Initial dominance of a eutrophic diatom flora and high DCA Axis 2 scores indicative of high productivity, support inferences from rising Ti and K counts (Fig. 5) for increased allochthonous input and/or nutrient upwelling from the sediment. The peak in *A. granulata* correlates with high TOC at ca. 85.0–84.0 cal ka BP, a double peak in TIC between 85.0 and 83.0 cal ka BP and maximum concentration of green algae and dinocysts. Although diatom response is dominated by a productivity shift, low DCA Axis 1 scores also indicate low lake levels between 85.0 and 83.0 cal ka BP, correlated with peaks of *Artemisia* (32 %) and *Chenopodiaceae* (12 %), indicative of drought (Panagiotopoulos et al. 2014). As in the upper record, productivity may be high in low-lake-level phases, in particular when wind-induced mixing causes nutrient re-suspension from bottom sediments. This is at odds with inferences for low evaporative concentration based on relatively low $\delta^{18}\text{O}$ (–5 to –4 ‰) values.

A second lake low-stand is inferred between 77.6 and 76.6 cal ka BP from diatoms and low DCA Axis 1 scores. The occurrence of ice rafted debris (IRD) for the first time in the sediment record of Lake Prespa (Damaschke et al. 2013) provides strong evidence that the lake was ice-covered during the winter season, and along with the decline in *Quercus* pollen (Panagiotopoulos et al. 2014), supports the lake low-stand being triggered by decreased precipitation during cold/dry

‘glacial’ climate conditions. A diatom-inferred moderate increase in lake level and moisture availability after 76.6 cal ka BP is clear from *Cyclotella* abundance and DCA Axis 1 scores; the lack of sensitivity of other proxy indicators suggests high diatom sensitivity to a phase of subtle climate change at the end of the last interglacial, until 70.2 cal ka BP.

The most distinct horizon in the core is the *Dreissena presbensis* shell layer, at 73.6 ± 7.7 ka (Damaschke et al. 2013), and a lake level low-stand in Lake Prespa (and potentially Lake Ohrid) has been inferred from a combination of seismic, isotope and pollen data (Wagner et al. 2012; Leng et al. 2013; Panagiotopoulos et al. 2014). Wagner et al. (2014c) recognize tectonic events or karst processes as a possible cause of this low-stand, but also note its intriguing chronological correspondence to the 74 ka BP eruption of the Toba volcano. A peak in abundance of mesotrophic *S. rotula* (~15 %), in an assemblage dominated by the *Cyclotella* group, occurs at 73.6 cal ka BP. This can indicate a mixed diatom assemblage, not correlated completely with the shell horizon, or increasing lake levels immediately after its deposition. Higher-resolution analysis is needed to test these scenarios.

MIS 4 (71.0–57.0 cal ka BP; D3, part of D4a)

The diatoms and low DCA Axis 2 scores in zone D3 reflect low lake productivity and match well with the silty sediments and low organic content of lithofacies 1 (Damaschke et al. 2013), reflecting glacial onset. Dominance of small Fragilariaceae, *E. submuralis* and *Cocconeis* spp. implies that diatom growth was mainly restricted to ice-free, shallow littoral habitats, most likely during a short growing season. *S. pinnata*, at 30 % abundance, points to prolonged ice cover and low mean summer temperatures. The high abundance of large, heavily silicified benthic species throughout the zone, such as *G. attenuatum*, *Campylodiscus* spp. and *D. mauleri*, does not reflect increased productivity, because growth was probably facilitated by high water transparency, resulting from low plankton concentration in the epilimnion during the glacial, and points to a sufficient Si supply, necessary for formation of their large, complex frustules. Relatively high Ti and K values and SAR between 70.0 and 60.0 cal ka BP indicate high catchment erosion, most likely caused by greater input of ice-melt water during

the spring/summer season, in agreement with the simultaneous opening of the landscape (Panagiotopoulos et al. 2014).

The low DCA Axis 1 scores and *Cyclotella* group at <10 % provide strong evidence for lake-level decline since MIS 5, indicative of glacial aridity in MIS 4. The maximum benthic abundance (85 %) at 65.5 cal ka BP is synchronous with distinct minima in the AP percentages in the pollen record, indicative of low moisture availability.

MIS 3 (57.0–29.0 cal ka BP; D4, D5a)

Positive DCA Axis 1 scores and *Cyclotella* (>10 %) suggest increased lake level as a rapid response to increased moisture availability at the start of MIS 3. Phases of low lake level within the time period are indicated by peaks in small Fragilariaceae and *E. submuralis* between 49.0–46.6 and 45.0–39.5 cal ka BP and correlate with high erosion inferred from high Ti and K values (Wagner et al. 2012). Although the interstadial climate was relatively warm, the diatoms, low DCA Axis 2 scores and the relatively low TOC and TIC, suggest low productivity and/or higher decomposition of the organic matter until 38.2 cal ka BP.

An unusual shift at 39.28 cal ka BP, to a species richness of < 10 in a diatom assemblage co-dominated by *A. formosa* (~30 %) and *N. palea* (~20 %), can be ascribed to the influence of the PT0915-7/Y-5 tephra deposition, fingerprinted to the CI eruption of the Campi Flegrei caldera, considered the most explosive eruption in Europe over the last ca. 200 ka (Barberi et al. 1978; Fitzsimmons et al. 2013). Tephra influx increases the silica content in the water (Barker et al. 2000) and in the case of Lake Prespa, both dominant species require a high Si:P ratio and have maximum growth rates at temperatures below 20 °C (Holm and Armstrong 1981). The tephra deposition most likely altered the lake water chemistry and the benthic habitats, and caused a shift in conditions that reduced the diversity of ecological niches and favored only a few species. The diatom data, the high SAR, spike in TIC, low TOC (Wagner et al. 2012; Damaschke et al. 2013), low C/N and $\delta^{18}\text{O}$ (–2.8 ‰; Leng et al. 2013), and extremely low AP (~10 %; Panagiotopoulos et al. 2014), suggest that the CI eruption enhanced climate aridity and/or cooling, which affected both the lake and its catchment area.

The subsequent peak of *C. minuscula* at 38.7 cal ka BP indicates nutrient enrichment, possibly representing a lag response to the tephra deposition, as in the appearance of small-sized species and the single appearance of *S. minutulus* in Lake Ohrid core Co1202 (Cvetkoska et al. 2012) after tephra deposition associated with the FL eruption of Etna at 3.4 cal ka BP (Wagner et al. 2008b; Vogel et al. 2010). The increasing abundance of *A. granulata* thereafter, suggests relatively high trophic status was maintained until 33.0 cal ka BP. Similar shifts in the structure and productivity of the diatom assemblages caused by volcanic disturbance were also noted in other parts of the world, for example Lake Galletué in the Chilean Andes (Cruces et al. 2006). The subsequent return to dominance of small Fragilariaceae and benthic taxa indicates renewed aridification and/or cooling, supporting palynological inferences that define the end of MIS 3 at 29.0 cal ka BP.

MIS 2 (29.0–14.0 cal ka BP; D5b-d, part of D6a)

The diatoms and low DCA Axis 1 scores at the base of zone D5c point to low lake levels and mark the onset of the Last Glacial Maximum (LGM) in Lake Prespa (Clark et al. 2009). The concurrent TIC spike, siderite precipitation and high $\delta^{13}\text{C}$ imply within-sediment reducing conditions and methanogenesis (Leng et al. 2013). The overall high facultative planktonic and benthic abundance between 29.0 and 15.7 cal ka BP reflects a shift in the hydrological balance, most likely triggered by reduced moisture availability and low temperatures at the time of the LGM, as also indicated by the domination of open vegetation in the catchment (Panagiotopoulos et al. 2014). The low DCA Axis 2 scores reflect low productivity of the lake, as indicated by low TOC and TIC values, and may be assigned to the lower biomass available in the catchment, as suggested by the pollen concentration curve (Panagiotopoulos et al. 2014).

The onset of late glacial warming and increased moisture availability is indicated from 15.7 cal ka BP by a diatom-inferred increase in lake level, correlating with rising TOC values. The shift in dominance of *A. granulata* and *S. pinnata* between 13.1 and 12.3 cal ka BP has been interpreted as strong evidence for the Younger Dryas climate reversal. According to the age model presented in Aufgebauer et al. (2012), the “YD” event in Lake Prespa has an earlier onset than in

most sites, where it tends to occur from 12.8 to 11.7 ka (cf. Alley 2000). The diatoms support previous inferences derived from the pollen record (Panagiotopoulos et al. 2013) and probably represent a nutrient pulse linked to enhanced catchment erosion caused by a combination of lake-level reduction and wind stress (Cvetkoska et al. 2014a).

The Holocene (14.0 cal ka BP-present, part of D6a, D6b-D6d)

The gradual transition to the Holocene, and diatom response to Holocene climate change and human impact in Lake Prespa, was discussed in detail by Cvetkoska et al. (2014a). A middle Holocene (7.9–1.9 cal ka BP) phase of high diatom-inferred lake levels and humidity, peaking from 7.9 to 6.0 cal ka BP, is the most important feature. After 1.9 cal ka BP, intensified human impact and associated increases in nutrient status occur, along with two lake-level declines at 1.0 and 0.1 cal ka BP. The prominent climatic aridity at 1.0 cal ka BP is also noted in sediment records from Lake Ohrid (Wagner et al. 2009; Vogel et al. 2010; Lacey et al. 2014).

Comparison with other records

Diatom response thresholds

Few long-term diatom studies have been carried out in the Mediterranean, but there are two relevant studies in close proximity to Lake Prespa. Published data from the Co1202 diatom record from Prespa's sister lake, Lake Ohrid (Fig. 6) span the last ca. 140 cal ka BP (Vogel et al. 2010). Published data from ancient Lake Ioannina, Greece, is currently restricted to MIS 4 to present (Fig. 6) and the earlier interglacial-glacial transition at ca. 189–170 ka (Wilson et al. 2013). Lakes Prespa, Ohrid and Ioannina all show strong diatom responses to orbital and suborbital climate variability, but the results of this study confirm clear contrasts in response mechanisms. A good example is the evidence for climate warming and wetting during MIS 3. As a deep lake system, Ohrid's strong diatom response appears to be driven by temperature-induced productivity change (Reed et al. 2010; Cvetkoska et al. 2012), whereas the Prespa signal is one of increasing moisture availability, underlining the importance of changes in precipitation in spite of increased

temperature-induced evaporation. This is evident in MIS 5a when the low lake levels induced by drought accelerated the eutrophication of Lake Prespa. This suggests that in Lake Prespa, the hydrological balance is crucial, and future drought would cause serious consequences to the lake and its biota.

Comparison of glacial and interglacial taxonomic shifts also highlights contrasting drivers of ecological response in groups of diatom taxa, indicating that a 'transfer-function' approach incorporating simple response to climate variables is invalid. All the lakes were dominated by the *Cyclotella ocellata* complex during interglacials, but, as in MIS 3, with a contrast in productivity (Ohrid) versus moisture availability (Prespa, Ioannina) as drivers. Preservation of diatoms during glacial phases also differs between deep Lake Ohrid, which exhibits monospecific dominance by the planktonic *C. fottii/hustedtii* complex, and the shallower lakes, where small Fragilariaceae dominate in glacial phases and are thus taken as indicators of a cold, arid climate. In contrast, Reed et al. (2010) note that in Ohrid these taxa are strongly indicative of initial glacial-interstadial warming, as productivity increased in the littoral zone. The similarity in response mechanisms between Prespa and Ioannina supports the validity of direct comparison. There is evidence for a strong response to the YD climate reversal and initial warming/wetting at the Holocene transition in both sites, based on a switch from small Fragilariales to *Cyclotella ocellata*, but a major divergence in the timing of middle Holocene humidity. Whereas in Lake Prespa high lake levels are maintained until 1.9 cal ka BP (Cvetkoska et al. 2014a), lake-level decline in Ioannina started at 7.0 cal ka BP (Jones et al. 2013). In terms of climate change, this would suggest disparity in moisture availability at both sites, but nevertheless, the lake low-stand at Ioannina might be the culmination of a longer-term trend toward natural lake infilling (Jones et al. 2013) rather than a simple climate response. Future research on longer records is required to test this.

Sub-orbital climate variability

During the last glacial, six episodes of massive iceberg discharges, named Heinrich (H) events, reduced ocean deep-water formation and caused cooling of the North Atlantic (Bond et al. 1993). Potential correlations with

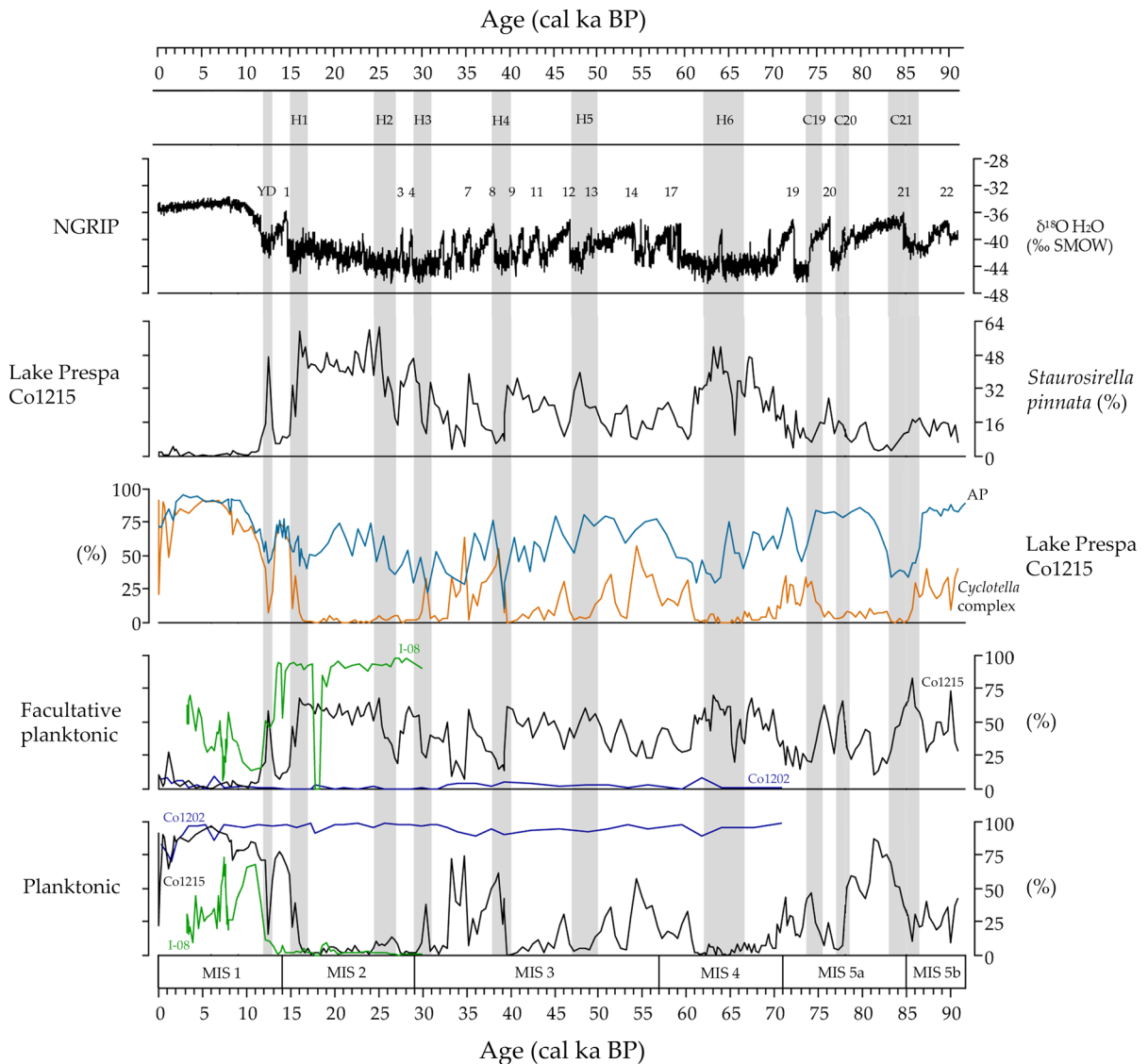


Fig. 6 Relative abundance (%) of planktonic and facultative planktonic taxa compared between Lake Prespa core Co1215 (black; this study), Lake Ohrid core Co1202 (blue; Reed et al. 2010) and Lake Ioannina core I-08 (green; data from Jones et al. 2013). The relative abundance (%) of the *Cyclotella* complex (orange, this study), interpreted as a proxy record of lake-level variations in Lake Prespa, is compared to arboreal pollen (AP, blue) percentages from core Co1215 (Panagiotopoulos et al.

2014) and relative abundance of *S. pinnata* (%; this study) and $\delta^{18}\text{O H}_2\text{O}$ (‰ SMOW) of the NGRIP ice core record (GICC05); the Dansgaard/Oeschger (D/O) warming events/Greenland interstadials (GI) are numbered. Explanation: MIS (Marine Isotope Stages) from Lisiecki and Raymo (2005), gray bands mark the H1–6 (Heinrich events) and the Younger Dryas (YD) as in Panagiotopoulos et al. (2014) and the C19–21 ice-rafting events (Chapman and Shackleton 1999). (Color figure online)

and differences between H events and several short-term hydrological changes at Lake Prespa, are defined by distinct peaks in Mn and TIC from core Co1204 (Wagner et al. 2010). By interpreting several distinct minima in the AP percentages in core Co1215 as reflecting the influence of Heinrich events on Lake Prespa catchment vegetation, and comparing existing

proxy data from lakes Ohrid and Prespa with the ages of the H events, Panagiotopoulos et al. (2014) hypothesized that the northern Mediterranean was influenced by rapid climate change in the North Atlantic. It is possible to test this hypothesis further using the strong proxy data for hydrological shifts. As noted, *S. pinnata* is typical of glacial environments in

Lake Prespa and its abundance curve displays a very close match to the GICC05 $\delta^{18}\text{O}$ record (GICC05modelext 2010) by increased values during the GS (Greenland Stadial) and distinct declines at the beginning of the GI (Greenland Interstadial). For example, the diatom-inferred low lake stand at 85.6 cal ka BP coincides with GS 22 (~88–85 ka; NGRIP members 2004) and the minimum in benthic $\delta^{13}\text{C}$ during the C21 ice-rafting episode at ~86 ka (Chapman and Shackleton 1999). The lake low stand from 77.6 to 76.6 cal ka BP correlates to the GS 21 (77.8–76.4 ka; Wolff et al. 2010).

Peaks of *S. pinnata*, coincident with distinct declines in the *Cyclotella* complex abundance at 65.5; 29.0; 25.0 and 16.0 cal ka BP are correlated to the AP minima in the pollen record, implying a well synchronized response between the catchment vegetation and the lake to the potential impact of the H6, H3–1 events. The impact of the H5 event (48.0 cal ka BP) was described as less severe on the arboreal catchment vegetation (Panagiotopoulos et al. 2014), however, the *Cyclotella* complex abundance (<8 %) between 49.0 and 46.6 cal ka BP implies that the H5 event had a more severe influence on the lake. The H4 event has been described as most severe on the catchment vegetation, enhanced by the Campanian Ignimbrite volcanic eruption at 39.3 cal ka BP (Panagiotopoulos et al. 2014). The diatoms also prove the severity of the H4 event and the Y5 tephra deposition, but disentangling their respective influences is difficult, because it appears that the diatom record primarily reflects the tephra impact. The distinct minimum in the *Cyclotella* complex at 25.0 cal ka BP is approximately comparable to the H2 event in the diatom record from Les Echets (Ampel et al. 2008). Overall, we infer that North Atlantic forcing has had a major influence on climate variability in Lake Prespa on a variety of timescales since MIS 5.

Conclusions

The diatom record of Lake Prespa core Co1215 and the multi-proxy approach in the interpretation demonstrate an outstanding potential for inferring past climate change in this area at orbital and sub-orbital scales. The glacial-interglacial shifts in species assemblage composition support the notion that precipitation drives the diatom response, enabling

confident interpretation of changes in moisture availability. The sensitivity of the lake and its biota to changes in the hydrological balance, and hence shifts in nutrient status, are the most notable elements of variation since MIS 5 to the present.

The imprint of rapid climate variations in the diatom record is readily apparent, implying that North Atlantic forcing was the prime factor driving changes in Lake Prespa over the last 91.0 cal ka. Indeed, variations in the relative abundances of *S. pinnata* and the *Cyclotella* complex can be regarded as indicative of differences in the intensity of the impact of glacial Heinrich events on the lake, implying that the H2, H5 and H6 events were probably more severe than H1 and H3. The imprint of H4 needs future clarification, to disentangle the effects of climate and tephra influx on the diatom flora. Still, more diatom data from longer regional records are required to test temporal and spatial variation of moisture availability in the northern Mediterranean.

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