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Diatom community responses to environmental change in Lake Ohrid (Balkan Peninsula) during the mid-Pleistocene Transition

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ABSTRACT

The Quaternary is characterized by a series of glacial-interglacial cycles and a shift in the Earth's climate state known as the mid-Pleistocene Transition (MPT, ca. 1200 ka to 720 ka). The progressive increase in glacial cycle length from approximately 41 ka to on average 100 ka affected marine and terrestrial life, but how it affected freshwater communities is far less known. Here, diatom and paleoenvironmental data between 1050 ka and 815 ka from a sediment succession of ancient Lake Ohrid are used to understand how the freshwater communities responded to environmental changes during key-periods of glacial intensification associated with the MPT. Based on stratigraphically constrained incremental sum of squares cluster (CONISS), a distinct diatom community turnover in Lake Ohrid was identified during the study period. The first community existed between 1050 and 955 ka MIS (Marine Isotope Stages) 30–25 and was mostly influenced by environmental parameters related to nutrient supply, mixing processes and primary productivity in the lake. The second community existed between 955 and 815 ka (MIS 25–21) and was largely driven by ontogenetic processes related to the ongoing deepening of the lake, changes in bottom water redox conditions and changes in mixing processes in the lake. The increased severity and duration of cold, glacial stages during the MPT shows only a weak impact on the diatom community in Lake Ohrid. Shifts in species phenotypes, abundance and composition are found in both communities, likely as adaptation in response to the changing environmental conditions. This study shows that the diatom communities were only weakly affected by the progressive intensification of the glacial intensity during the MPT, emphasizing the role of local environmental changes in regulating freshwater communities.

1. Introduction

The Quaternary is the most recent geological period spanning the last 2600 ka (thousand years; Pellans and Gibbard, 2012). It is characterized by a series of glacial-interglacial cycles caused by the cyclic growth and decay of continental ice sheets in the Northern Hemisphere (Head and Gibbard, 2015). The period between ca.1200 ka and ca. 720 ka ago, also known as the mid-Pleistocene transition (MPT) is one of the most pronounced transitions during the Quaternary because of the change in frequency (from 41 to 100 ka) and intensity of climate cycles (Head and Gibbard, 2015). The progressive increase in the amplitude of climate oscillations led to higher amplitude sea-level changes, a strong reduction in the North Atlantic thermohaline circulation and strong asymmetry in the glacial cycles, with a substantial increase in global ice volume occurring around 940 ka (Lisiecki and Raymo, 2007; Head and Gibbard, 2015).

The climatic oscillations, particularly during the MPT, affected species in life history traits associated with growth rates and survival (Hayward et al., 2007; Head and Gibbard, 2015). Species survival is largely dependent on species' ability to modify the phenotype to changes in environmental conditions or shift the distributional range to habitats where the environmental conditions are within species

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tolerance limits (Goldberger et al., 2007; Hetem et al., 2014). The phenotypic changes are usually facilitated through phenotypic plasticity and local adaptation (Ho and Zhang, 2018; Fox et al., 2019).

There is substantial information about the influence of the MPT climatic change on marine and terrestrial diversity (Tzedakis et al., 2004; Crundwell et al., 2008; Zhou et al., 2018). Comparably, much less is known about how freshwater communities responded to the Quaternary climate oscillations, particularly around the MPT. This is in part due to the lack of high-resolution freshwater microfossil data spanning a significant portion of the Quaternary.

Ancient lakes can be hundreds of thousands to several million years old and are home to exceptionally high species richness and endemism (Martens, 1997). Due to their age, these lakes hold long sedimentary records that allow detection of freshwater community responses to environmental change (Mackay et al., 2010; Cvetkoska et al., 2021). Lake Ohrid is located on the Balkan Peninsula and is the only ancient lake in the Mediterranean region, which provides a 1360 ka long sediment record (Wagner et al., 2019). The sediment succession retrieved through the International Continental Scientific Drilling Program (ICDP) has a well-constrained chronology (Wagner et al., 2014, 2019) and contains well-preserved diatoms (Cvetkoska et al., 2021). Previous studies have shown that these single-celled siliceous algae in Lake Ohrid responded strongly to climate and local environmental changes during the Quaternary (Reed et al., 2010; Cvetkoska et al., 2016, 2021). Moreover, it has been shown that diatom community composition and diversification rates shifted around 1000 ka (Wilke et al., 2020; Cvetkoska et al., 2021) when the ongoing deepening of Lake Ohrid may have passed a critical threshold. Although there is no evidence of major community shifts and changes in diversification rates to the effects of MPT (Wilke et al., 2020; Cvetkoska et al., 2021), we here use the Lake Ohrid diatom record at higher temporal resolution to capture a potential signal of climate-related species response, at least during key-periods of the MPT.

To do this, we combined diatom and paleoenvironmental data between 1050 ka and 815 ka (i.e. Marine Isotope Stages, MIS 30–21) from the sediment succession of ancient Lake Ohrid to assess the potential effects of climate change during the MPT on diatom community composition with a focus on peak glacial stages. This will help us to understand how freshwater communities responded to climate-driven environmental changes and use them to predict how they will react to such future climate change scenarios.

2. Regional settings

2.1. Site description

Lake Ohrid (North Macedonia/Albania; Fig. 1A) is the oldest and perhaps the most biodiversity rich lake in Europe (Albrecht and Wilke, 2008). It is located in a tectonically active graben that developed during the later stages of alpine orogeny (Lindhorst et al., 2015). Earlier studies have suggested that the lake originated between 2000 and 10 000 ka ago (Stankovic, 1960; Radoman, 1985), while more recent studies have shown that the lake established at 1360 ka (Wagner et al., 2019).

Lake Ohrid is situated at an altitude of 693 m above sea level. It is about 30 km long, 15 km wide and covers an area of 360 km^2. The maximum water depth is 293 m and the total volume of the lake is 55.4 km^3 (Lindhorst et al., 2015). The total water inflow is 37.9 m^3 s^{-1}, accounting for ca. 25% direct precipitation, ca. 25% river input and ca. 50% karst aquifers charged from mountain range precipitation and water-fed springs from Lake Prespa (Wagner et al., 2010). The outflow is regulated through the river Crni Drim (60%) and evaporation (40%; Matzinger et al., 2006). The mean water residence time of Lake Ohrid is ca. 36 years (Lacey and Jones, 2018), which is a result of the dry climate and relatively small catchment area (1300 km^2). It is a calcium bicarbonate $Ca(HCO_3)_2$ dominated, oligotrophic and oligomictic lake with a weak density stratification and complete overturn of the water column every few years during strong winters (Allen and Ocevski, 1977). The average total phosphorus (TP) concentration is 4.5 mg m^{-3} (Matzinger et al., 2007), total nitrogen (TN) concentration is 171–512 mg m^{-3} (Watzin et al., 2002), and silica (Si) concentration is < 200 mg m^{-3} in the trophogenic zone during summer (Stankovic, 1960).

The study region is characterized by a sub-Mediterranean climate with hot and dry summers and cold and wet winters with a mean temperature of 26 °C and −1 °C, respectively. The mean annual precipitation varies from 720 to 1200 mm yr^{-1} in the lake's valley and the surrounding mountain ranges, respectively.

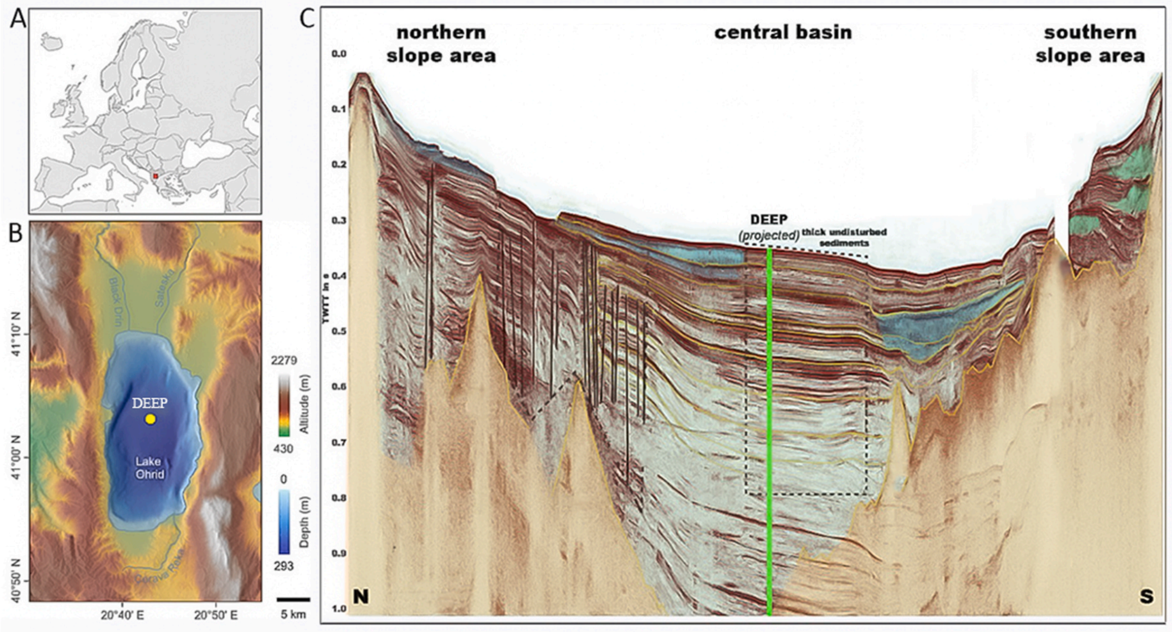

Fig. 1. Topographic and bathymetric map of Lake Ohrid with the DEEP drilling site. A) Location of Lake Ohrid on the Balkan Peninsula. B) Bathymetry of Lake Ohrid with the location of the DEEP drilling site. C). Seismic profile of Lake Ohrid showing undisturbed sediments at the DEEP drilled site.

2.2. Core recovery and geochronology

The sediment sucession (DEEP-5045-1) was retrieved from the central part of the Ohrid Basin at 243 m water depth (Wagner et al., 2014). The composite sediment record is based on six parallel boreholes (A– F), drilled down to 569 m beneath the lake floor (m blf) using Deep Lake Drilling System (DLDS) of Drilling, Observation and Sampling of the Earth's Continental Crust (DOSECC). For core recovery, a 3-m-long core barrel with different coring tools including a hydraulic piston corer, an extended nose and an and an inner diameter of 61 mm was used (Wagner et al., 2014). A total of 1525 m sediment cores were recovered with 99.8% of the succession spanning the continuous lacustrine phase of the lake (0–446.65 m composite depth (mcd)). Each core was sliced in a 1 m long segment and stored in darkness at 4 °C (for details see Wagner et al., 2014; Francke et al., 2016).

From the top to the bottom of the DEEP-5045-1 succession, the sediments varied in color and structure (massive, mottled) but lack of lamination (Francke et al., 2016; Wagner et al., 2019). The lower 447 m of the record consists of gravel and pebbles (Wagner et al., 2017; 2019), while the upper 447 m comprise finer sediments. During the study interval, the lithology consists of fine-grained hemipelagic sediments, pointing to deep-water conditions (Wagner et al., 2019). The lithological and sedimentological composition of DEEP-5045-1 indicates fairly stable sedimentation rates for the upper 447 m, averaging at 0.33 m x 1000 yr^{-1} (Wagner et al., 2019), possibly due to the lack of catastrophic ecosystem collapses (Francke et al., 2016; Wilke et al., 2020). The bioturbation is minimal as in the remaining sediments of the DEEP-5045-1 core (e.g. Wagner et al., 2008; Vogel et al., 2010a, 2010b; 2010c), possibly due to the massive and-or mottled nature of the sediments (Wagner et al., 2019).

The age model of the DEEP-5045-1 core is based on tephrochronological information as first-order tie points supplemented by second-order tie points derived from tuning of climate-sensitive proxy data against orbital parameters. The age model was calculated using Bacon 2.2 (Blaauw and Christen, 2011) and resulted in estimated age of ca. 1360 ka for the upper 447.12 m of the core. An age error of ±2000 years was applied to the second-order tie points and an age uncertainty of the tephra layer between ±5500 years and ±10 680 years for the first-order tie points (Wagner et al., 2019). Two tephra layers (OH-DP-3144 at 888 ka) and (OH-DP-3443 at 979 ka), are encountered within the study interval with an origin from the Italian volcanic provinces (Leicher et al., 2021). MIS boundaries were estimated based on LR04 global benthic isotope stack (Lisiecki and Raymo, 2005; Wang et al., 2010).

3. Materials and methods

3.1. Data collection and analyses

For this study, 110 sediment samples were taken at 64 cm intervals (ca. 2000 years) between 366 and 296 mcd from the core DEEP-5045-1. Wet sediment samples of ca. 0.1 g were acid-cleaned using a modification of Ranberg's technique (Cvetkoska et al., 2012). All cleaned samples were mounted on glass microscope slides using Naphrax™ (Brunel Microscopes Ltd). In each sample, random transects were selected and up to 400 diatom valves per slide were identified and counted at 1,000× magnification with a Nikon Eclipse 80i light microscope, equipped with Nikon Coolpix P6000 digital camera. High intraspecific morphological variability was observed within species of the genus *Cyclotella*. For separating different morphologies of *Cyclotella cavitata* species complex that encompasses morphologies from *Cyclotella praecavitata* nom. prov. and *C. cavitata*, the most variable traits like valve diameter, valve shape, shape of the central area, stria density, position of rimoportulae, valve ornamentations and valve face undulation were used. In order to fully cover the level of community change, taxa variations are assigned to distinct morphotypes and used for the analysis. Species identification followed Krammer (2003), Levkov et al. (2007) and Hofmann et al. (2018). For each taxon, ecological preferences were determined using both, the effect of important environmental influence (see Table 1) and species with known ecology (Levkov et al., 2007; Cvetkoska et al., 2012). All microscopic slides are stored at the Macedonian National Diatom Collection (MKNDC) at the Institute of Biology at the Faculty of Natural Sciences and Mathematics in Skopje.

Community compositions were displayed as relative abundances over time using the software Tilia (Grimm, 1987). Major community structures were defined for taxa above 2% abundance by using the Constrained Incremental Sum of Squares cluster analysis, CONNIS (Grimm, 1987).

3.2. Paleoenvironmental variables

To asses diatom community response to MPT-induced environmental changes, the relative abundance data of most dominant diatoms was plotted against selected paleoenvironmental data using the C2 software (Juggins, 1991-2007). A set of previously published data was selected for this purpose (i.e. Lisiecki and Raymo, 2005; Wang et al., 2010; Francke et al., 2016; Wagner et al., 2019; Wilke et al., 2020), which represents local and global paleoenvironmental change (see Table 1 for details). In additioan, unpublished data of biogenic silica (bSi), and manganese/iron ratio Mn/Fe was included. The biogenic silica (bSi), an indicator for past diatom productivity (Vogel et al., 2008), was quantified using Fourier Transform Infrared Spectroscopy (FTIRS). Prior to analysis 11 ± 0.05 mg powdered and dried sediment was homogenized along with 500 ± 0.05 mg spectroscopic grade and oven-dried (12 h at 200 °C) KBr (Uvasol©, Merck). Sample preparation and the measurement set up are described in detail in Vogel et al. (2016). The independent calibration introduced in Meyer-Jacob et al. (2014) was used for bSi quantification from FTIR spectra. For calculating the Mn/Fe ratios, XRF scanning was carried out at 2.5 mm resolution and with an integration time of 10 s using an ITRAX core scanner (Cox Analytical, Sweden). The ITRAX core scanner was equipped with a chromium (Cr) X-ray source and was run at 30 kV and 30 mA (Francke et al., 2016).

Table 1

Selected global and local paleoenvironmental variables used for exploring diatom community response to MPT.

Paleoenvironmental variables	Interpretation	References
TIC (total inorganic carbon)	calcite precipitation controlled by temperature, productivity and ion supply from karst aquifer activity	(Francke et al., 2016; Wagner et al., 2019)
TOC (total organic carbon)	temperature, productivity and lake mixis	(Francke et al., 2016; Wagner et al., 2009; 2019)
K (potassium)	catchment erosion and clastic sediment supply	(Francke et al., 2016; Wagner et al., 2019)
Mn/Fe (manganese/ iron ratio)	changes in lake mixis and thus the redox conditions of the bottom waters and surface sediments	(Francke et al., 2016., Gächter and Müller, 2003)
Grain size	transport energy or the distance of the coring location to inlets	Wilke et al. (2020)
Deciduous oaks	catchment vegetation, which is mainly controlled by temperature and precipitation	(Wagner et al., 2019., Donders et al., 2021)
Herbs	catchment vegetation, which is mainly controlled by temperature and precipitation	(Wagner et al., 2019., Donders et al., 2021)
LR04 δ18O	global ice volume and glacial-interglacial intensity	Lisiecki and Raymo (2005)
Medstack δ18O	Mediterranean evaporation and temperature.	Wang et al. (2010)

4. Results

In total, 147 species and morphotypes were identified in the core DEEP-5045-1 for the period between 1050 and 815 ka. Of these, the planktonic diatom genera *Cyclotella*, *Stephanodiscus*, *Aulacoseira*, *Pantocsekiella* and *Asterionella* dominated the fossil assemblages. High intraspecific diversity was observed in the dominant plankton *Cyclotella cavitata* species complex, which encompasses morphologies from *Cyclotella praecavitata* and *Cyclotella cavitata*. Based on the changes in valve morphology eleven different morphotypes were identified. Facultative planktonic and benthic species of the genera *Staurosira*, *Pseudostaurosira*, *Amphora*, *Cocconeis*, *Navicula* and *Sellaphora* and other littoral are represented with higher species richness but lower relative abundance. Based on the CONISS cluster analysis (Fig. 2) two distinct diatom zones with several subzones (ODAZs) are identified.

4.1. Diatom zone ODAZ 1 (1050–954 ka; MIS 30–25)

4.1.1. Diatom subzone ODAZ 1a (1050–992 ka; MIS 30–28)

Cyclotella praecavitata dominates the subzone (<70%), interrupted briefly in thin zones of increased abundance of the small-sized *C. praecavitata* MT *irregularis* and *C. praecavitata* MT *intermedia* (Fig. 4A–V) at ca. 1020, 1015, 1010 and 1005 ka. *Cyclotella praecavitata* MT *magniaretata* appeared in this subzone with 20% abundance at 993 ka. The small *C. minuscula* (<5 μm) is present throughout the subzone, reaching a maximum of ca. 20% during 1037 ka (MIS 30) and 1005 ka (MIS 28). *Stephanodiscus carsonensis* and *S. carsonenis* var. *pusila* are present throughout the subzone at a relative abundance between 5 and 15%, while *S. transylvanicus* and *S. vestibulis* occur only sporadically with <5%. The planktonic species *Asterionela formosa* is constantly present throughout the subzone reaching a maximum of ca. 8% at 1042 ka and 1012 ka. *Aulacoseira* spp. dominated the assemblage (ca. 55%) at 1038 ka (MIS 30).

The most pronounced minimum in the relative abundance of planktonic species occurs at 1043 ka (ca. 50%) when facultative planktonic and benthic species, belonging to the genera *Staurosira*, *Staurosirella*, *Navicula*, *Cymbella*, and *Amphora*, increased to ca. 40% in abundance.

4.1.2. Diatom subzone ODAZ 1 b (992–9534 ka; MIS 28–25)

Cyclotella praecavitata morphotypes maintained dominance in this subzone. The small-sized *C. praecavitata* MT *praecavitata*, *C. praecavitata* MT *irregularis* and *C. praecavitata* MT *intermedia* decreased but remained >40%, while the larger in size *Cyclotella praecavitata* MT *magniaretata* (Fig. 4 W–AC) increased but remained <70% abundance. *Cyclotella cavitata* s.s (Fig. 4 AD–AH) appear for the first time with abundance of 20% at 968 ka. *Stephanodiscus* with *S. carsonensis* and *S. carconenis* var. *pusila* range from 25 to 40%, peaking at high abundance during the glacial periods. *Asterionella formosa* maintained relative abundance of up to ca. 10% at 965 ka.

Facultative planktonic and benthic species also maintained low abundance. *Diatoma* spp. appears for the first time in this subzone and exhibits a minor peak of 5% at 976 ka (MIS 27).

4.2. Diatom zone ODAZ 2 (954–815 ka; MIS 25–21)

4.2.1. Diatom subzone ODAZ 2a (954–943 ka; MIS 25)

This subzone is marked by a rapid change in dominance from *C. praecavitata* morphologies to *Cyclotella cavitata* morphologies. *Cyclotella praecavitata* MT *magniaretata* and *C. praecavitata* MT *irregularis* decreased rapidly to <2% at the lower subzone boundary and shortly after disappeared, while *C. cavitata* s.s. and *C. cavitata* MT *fragilis* increased to >60% and ca. 25%, respectively (Fig. 4 AI–AM). Also, notable in this subzone is the appearance of *Cyclotella cavitata* MT *crasa* (Fig. 4 AZ–BE) and *C. cavitata* MT *minuscula* (Fig. 4 AN–AY) with ca. 15% relative abundance.

The planktonic *Aulacoseira* spp., *C. minuscula*, *A. formosa, S. carsonensis* and *S. carconenis* var. *pusila* declined to <5% in the abundance. Facultative planktonic and benthic remain at low abundance (<4%).

4.2.2. Diatom subzone ODAZ 2 b (943–885 ka; MIS 25–22)

Cyclotella cavitata morphotypes remain dominant in this subzone, with *C. cavitata* MT *crasa* increasing to <80% abundance. *Cyclotella cavitata* MT *fragilis*, C. *cavitata* s.s and *C. cavitata* MT *minuscula* gradually decreased to ca. 2% abundance towards the upper subzone boundary. Notable in this subzone is the appearance of *C. cavitata* MT *magna* (Fig. BF) and *C. cavitata* MT *maxima* (Fig. BG) at 921 ka and 900 ka, each present at >5%, respectively. *Aulacoseira* spp. peak with 10% at 900 ka and *A. formosa* with 17% abundance at 940 ka.

Benthic and facultative planktonic taxa remain at low abundance and only slightly peak at 10% around 938 ka and 910 ka. They are mainly represented by species similar to those in subzone ODAZ 2a.

4.2.3. Diatom subzone ODAZ 2c (885–815 ka; MIS 22–21/20)

Cyclotella cavitata MT *crasa* remain at high abundance throughout the ODAZ 2c. *Cyclotella cavitata* MT *magna* and *C. cavitata* MT *maxima* increased in abundance to <10% at ca. 875 ka, the former decreasing to <2% and the latter increasing to <20% at ca. 830. The increase of *C. cavitata* MT *maxima* was accompanied by increased abundance (<6%) of a novel morphology *C. cavitata* MT *distincta* (Fig. BH) that emerged at 875 ka. The other *C. cavitata* morphotypes (*C. cavitata* s.s, *C. cavitata* MT *fragilis*, *C. cavitata* MT *minuscula* and *C. cavitata* MT *magna*) gradually decreased and almost disappeared towards the upper subzone boundary. *Pantocsekiella ocellata* sharply increased to 33% at 885 ka. *Stephanodiscus*

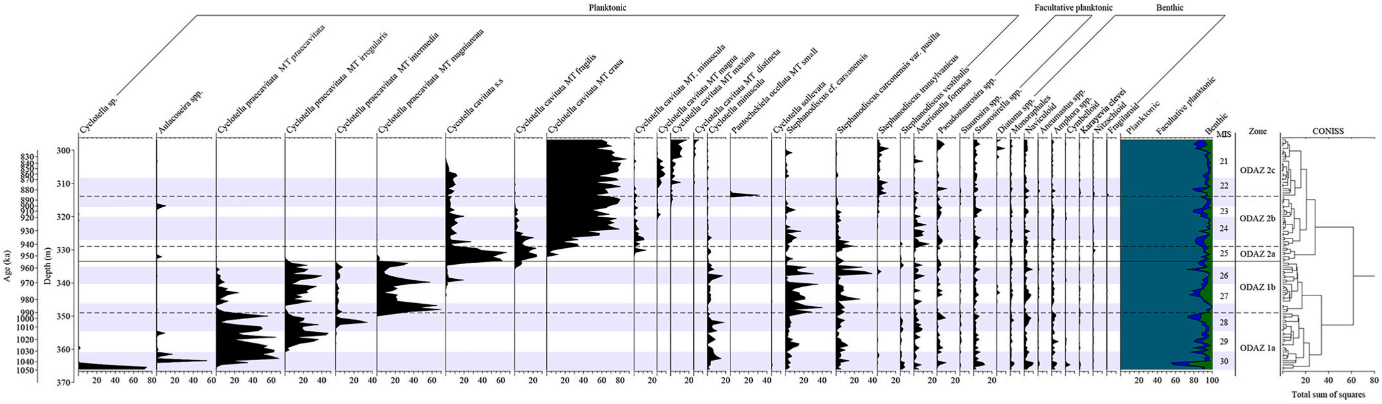

Fig. 2. Stratigraphic CONISS diagram showing the diatom taxa presented at >2% abundance in the core DEEP-5045-1. A sum of planktonic, facultative planktonic and benthic taxa is shown. Chronological timescale and MIS boundaries following Wagner et al. (2019) and Lisiecki and Raymo (2005), respectively.

transylvanicus peaks in abundance (10%) three times in the record at 882 ka, 872 ka and 820 ka. *Asterionella formosa* peaks to 10% at 836 ka.

Facultative planktonic taxa remain at low abundance in this subzone, except for two peaks of 17% at ca. 879 ka and 15% at ca.815 ka, represented mostly by *Pseudostaurosira* spp. At same time, benthic species increase to 15%, marked by a distinct peak of *Diatoma* spp.

5. Discussion

5.1. Community responses to environmental change during the MPT

5.1.1. *MIS 30–25 (1050–954 ka, ODAZ 1)*

The high relative abundance of planktonic species and the fine grain size (ca. 80% silt and ca. 20% clay, Wagner et al., 2019) point to a fairly deep-water conditions at Lake Ohrid between MIS 30–25 (1050 and 955 ka; Wilke et al., 2020; Cvetkoska et al., 2021). The dominance of the small (5–20 μm) planktonic taxon *C. praecavitata* between MIS 30–29 (1040 and 1005 ka) corresponds to periods of relatively high primary productivity, less oxidation of organic matter (OM) and/or less mixing conditions as implied by the high TOC and bSi contents and lower Mn/Fe values (e.g. Francke et al., 2016). This is in line with findings that high nutrient availability promotes dominance of small-sized planktonic species (Saros and Anderson, 2015; Spanbauer et al., 2016). The extremely high population sizes that *C. praecavitata* exerted in community 1 are probably because of its relatively high nutrient affinity and ability to consume the highest proportion of resources at the expense of the other species, whose relative abundances significantly decreased (Fig. 4 A–AC). Changes in morphology of *C. praecavitata* are apparently also related to environmental changes (Fig. 3). For example, the dominance of *C. praecavitata* MT *praecavitata* (Fig. 4 A–G) at MIS 30/29 boundary (1035–1025 ka), and peak abundance (>50%) of its morphotype *magniareata* (Fig. 4 W–AC) during MIS 28 (990–985 ka) correspond with high overall values of TOC and bSi that indicate relatively high nutrient availability and productivity levels in the lake (Francke et al., 2016; Wagner et al., 2019). In contrast, relatively cold/dry periods characterized by enhanced catchment erosion and low productivity i.e. high K values, low TOC and bSi values (Francke et al., 2016) fostered the morphotype *C. cavitata* MT *irregularis* (Fig. 4 H–O) to increase its relative abundances, particularly around MIS 29 (1015 ka) and MIS 26 (965 ka). Similarly, the high relative abundance of *C. praecavitata* MT *intermedia* (Fig. 4 P–V) at MIS 28, (ca. 1005 ka) was most likely promoted by low water temperatures and nutrients and/or high clastic input from catchment erosion (i.e. minima in TIC, TOC, and bSi and high K counts; Fig. 3).

The replacement of *C. praecavitata* morphologies with species belonging to the genus *Stephanodiscus* (Fig. 2) between 990–985 ka and 970–960 ka could be associated with the better competitive abilities of the later taxa to low nutrient contents during the cold/dry MIS 28 and 26 glacials. For example, high relative abundances of *S. carconensis* were also recorded in the fossil assemblages of Lake Baikal during periods of colder climate conditions (Mackay et al., 2010).

Furthermore, the high relative abundance (ca. 40%) of facultative planktonic and benthic species (Fig. 2) at MIS 30 (1045 ka) corresponds to peaks in K. This could be possibly associated with catchment erosion and clastic sediment supply during cold/dry glacial climate (e.g. Vogel et al., 2010b) and/or ontogenetic processes associated to the basin deepening (Wilke et al., 2020; Cvetkoska et al., 2021).

5.1.2. *MIS 25–21 (954–815 ka, ODAZ 2)*

Planktonic species increased their population densities between MIS 25 and 21 (Fig. 2) likely in response to ontogenetic processes related to the ongoing deepening of the lake during this period (Wilke et al., 2020; Cvetkoska et al., 2021). This may have enhanced increased frequency and duration of lake mixies and/or improved oxygenation of the water column (i.e higher Mn/Fe values), particularly between 955 and 940 ka (MIS 25) and 870–815 ka (MIS 21) (Fig. 3). Such changes probably caused a shift in the diatom community at the onset of MIS 25, characterized by replacement of the C. *praecavitata* morphotypes with a novel, large sized morphologies belonging to *C. cavitata* (Fig. 4 AD–BH). This is likely because of the limited survival strategies of the earlier morphological entities. The ongoing deepening of the lake and associated change to more oligotrophic conditions (Cvetkoska et al., 2021) have most probably supported the establishment and overdominance of *C. cavitata* sensu lato (s.l) (Fig. 4 AD–BH), a seemingly highly adaptable and morphologically variable planktonic taxon. Specific morphotypes of *C. cavitata* s.l., namely *C. cavitata* sensu stricto (s.s) (Fig. 4 AD–AH). and *C. cavitata* MT *fragilis* (Fig. 4 AI–AM), were co-dominant in the community during MIS 25, when higher Mn/Fe values point to a higher

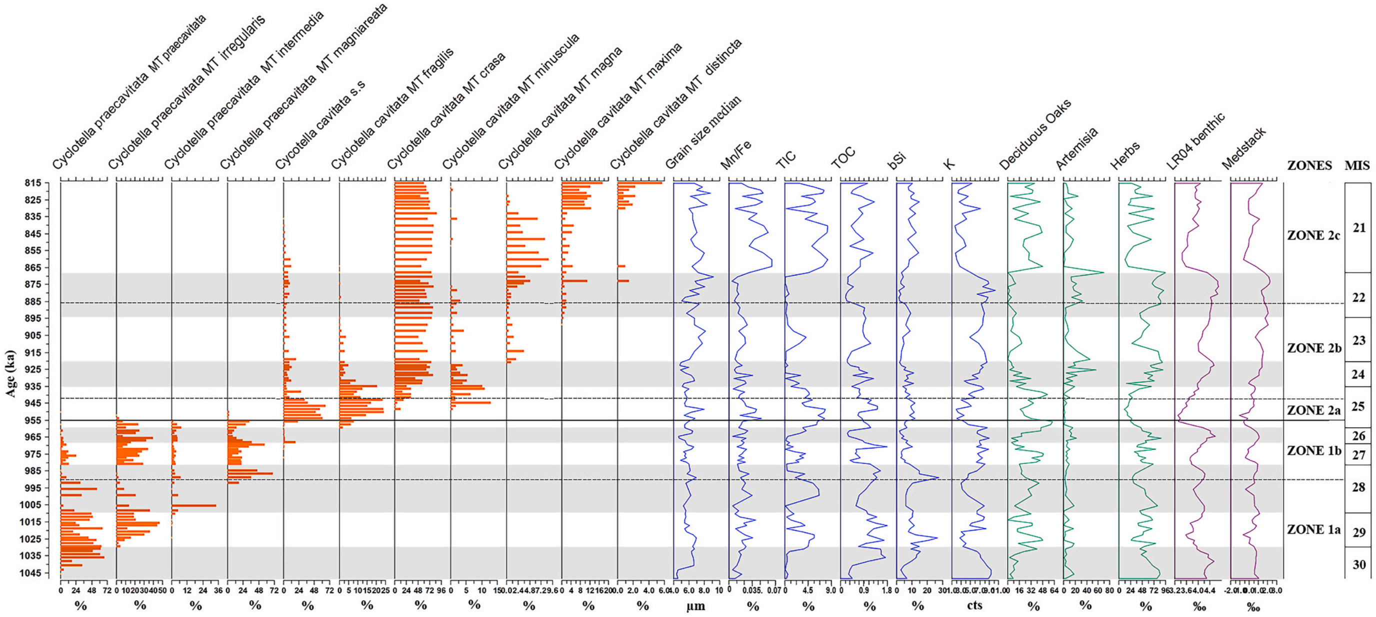

Fig. 3. Comparison of selected diatom taxa with selected pollen and geochemical data: TIC – total inorganic carbon, TOC – total organic carbon, bSi – biogenic silica, K – potassium, Mn/Fe – manganese/iron ratio, Deciduous oaks, *Arthemisia*, Herbs, LR04 benthic $\delta^{18}O$ stack isotope ratios, and Medstack $\delta^{18}O$ planktonic isotope ratios. Chronological timescale following Wagner et al. (2019).

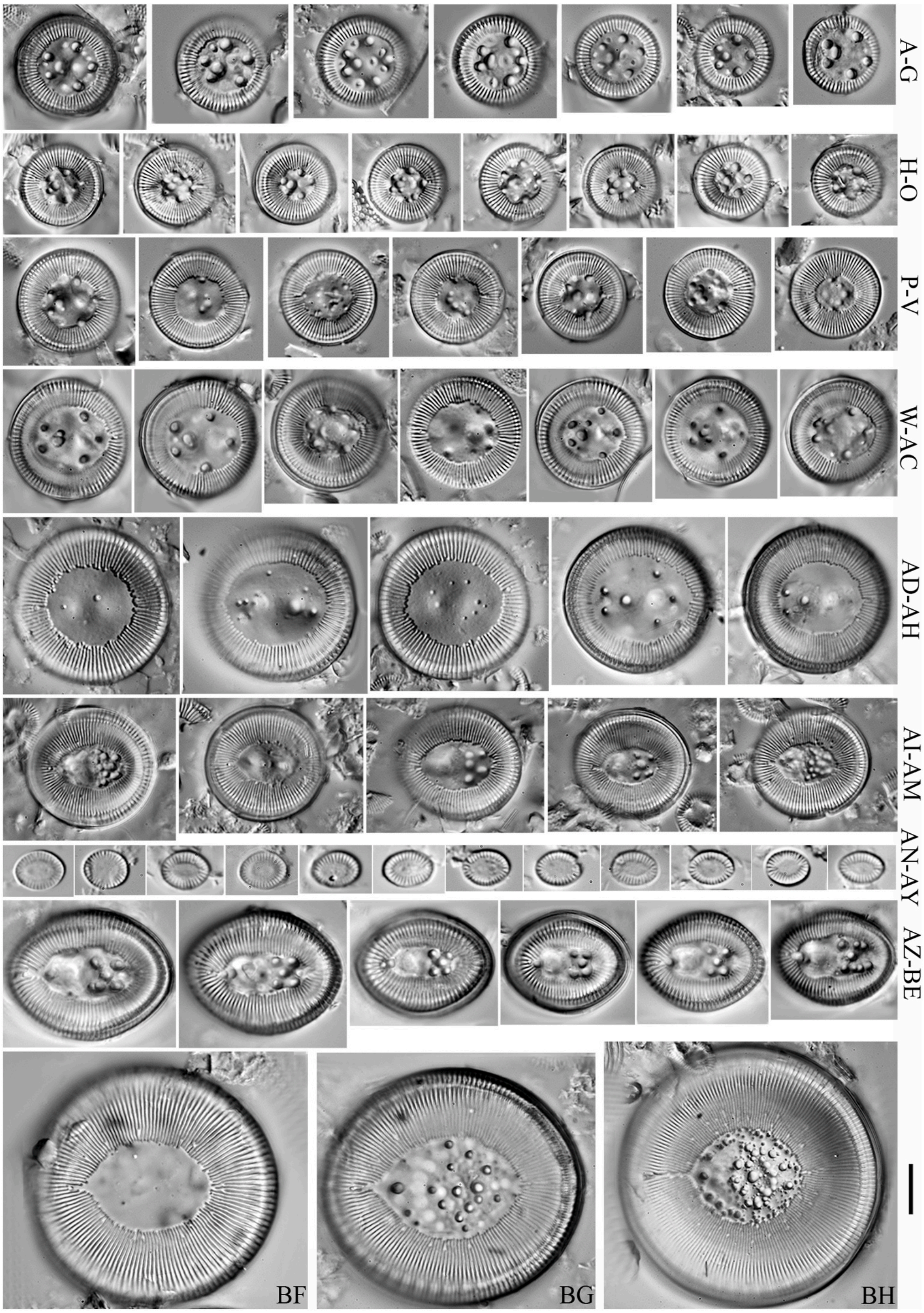

Fig. 4. Illustration of different morphologies of *Cyclotella cavitata* species complex: A–G: *Cyclotella praecavitata* MT *praecavitata*, H–O: *Cyclotella praecavitata* MT *irregularis*, P–V: *Cyclotella praecavitata* MT *intermedia*, W-AC: *Cyclotella praecavitata* MT *magniaretata*, AD–AH: *Cyclotella cavitata s.s*, AI–AM: *Cyclotella cavitata* MT *fragilis,* AN–AY: *Cyclotella cavitata* MT *minuscula,* AZ–BE: *Cyclotella cavitata MT crasa*, BF: *Cyclotella cavitata* MT *magna,* BG: *Cyclotella cavitata* MT *maxima*, and BH: *Cyclotella cavitata* MT *distincta.*

frequency and/or duration of lake mixis. High TIC values during this period, indicate higher photosynthesis due to increased lake water temperature and/or nutrient supply from the catchment (Fig. 3).

The decline in abundance of the two morphotypes and their replacement with a novel one, *C. cavitata* MT *crassa* (Fig. 4 AZ–BE) corresponds with the onset of MIS 24. The MIS 24–22 interval is also known as the '900 ka event' (Clark et al., 2006). It is the first Pleistocene glaciation with extended duration, interrupted by the relatively weak MIS 23 interglacial period (Head and Gibbard, 2015). The '900 ka event' event is characterized by a major expansion of the continental ice sheets and exceptionally reduced thermohaline circulation in the North Atlantic (Pena and Goldstein, 2014; Head and Gibbard, 2015). The low TIC, TOC and bSi content imply low primary productivity and/or enhanced OM degradation, and thus, probably to low local temperatures at Lake Ohrid during the MIS 24–22 interval (Fig. 3). The cold and dry climate conditions, as also inferred from the high abundance of herb pollen (Fig. 3, Sadori et al., 2016), have probably contributed to a further decline of the nutrient concentrations in the already deep lake, and facilitated the dominance of *C. cavitata* MT *crassa*. The later morphotype appears to perform well across a broad range of environmental conditions, such as temperature, light and nutrients, as it retained its dominance over multiple glacial-interglacial periods. Such tolerance could have been promoted by lower variations in the environment here probably caused by the deep and stable conditions and the longer glacial-interglacial periods.

The prolonged dominance of specific taxa in community 2 is in contrast to the much shorter dominance periods of certain morphotypes in the first community, possibly because of the more frequent environmental fluctuations during the 41 ka world and likely promoted by somewhat shallower water levels and lower lake volume (Fig. 3). Nonetheless, high trait variation in both communities is observed, which is likely related to the species ability to better tolerate the changing environmental conditions (Pacala and Tilman, 1994; Funk et al., 2017).

With the establishment of the warm interglacial period MIS 21, some of the morphotypes, such as *C. cavitata* MT *crassa* (Fig. AZ–BE), *C. cavitata* MT *magna* (Fig. 4 BF), *C. cavitata* MT *maxima* (Fig. 4 BG) and *C. cavitata* MT *distincta* (Fig. 4 BH) increased in cell size and/or population densities. Larger and heavier cells allow species to more easily sink into deeper waters, where nutrients can be provided by upwelling and/or grazing by zooplankton predators is restricted (e.g. Geider et al., 1986). Under stratified conditions, larger and heavier diatoms such as the endemic *Cyclotella fottii* inhabit the deep waters of Lake Ohrid today (Mitic and Patceva, 2004). An increase in cell size during warm interglacials has also been observed in *Pantocsekiella elgygytgynensis* from Lake El'gygytgyn as a result of longer lake-mixing period and increased nutrient availability (Luethje and Snyder, 2021).

5.2. *Causes for diatom community turnover and species abundance shifts*

Multi-proxy comparison indicated that the diatom communities in Lake Ohrid between MIS 30 and 21 were mostly influenced by changes in nutrient availability, lake depth, water column mixis, as well as local temperatures (Fig. 3). In contrast, the diatom communities were only weakly affected by the intensification of the glacial intensity associated with the MPT. This finding contradicts our prediction that diatom communities will respond to the increased severity and duration of cold, glacial stages during the MPT. Similar weak effects of the MPT have been observed on plants and mammals in the Mediterranean region (Suc and Popescu, 2005; Madurell-Malapeira et al., 2010; Kahlke et al., 2011; Magri and Palombo, 2013; Strani et al., 2019). Likewise, a weak effect of MPT has been detected on the vegetation in the catchment of Tenaghi Philippon (Tzedakis et al., 2004). This is opposite to the Lake Ohrid catchment where no signal of MPT on the vegetation has been observed (Fig. 3; Donders et al., 2021).

The major community shift that took place at the beginning of a warm interglacial period, at MIS 25, is in line with the previously observed community turnover (Cvetkoska et al., 2021). The exact causes for this major shift remain inconclusive due to the lack of major changes in the lake and its catchment and/or lack of support from other local and global proxy data related to nutrients, light, pH, which are most critical growth limiting factors for diatoms. The correspondence of the diatom community turnover with the peak in Mn/Fe–a change in the lake mixis, could have triggered the change in community structure. The ongoing deepening of the lake around MIS 25 probably led to restricted mixis of the water column, for example from a polymictic or dimictic lake to a monomictic or oligomictic lake. Changes in species composition and abundance are highly related to increased nutrient content, lake mixis and lacustrine primary productivity (Wagner et al., 2014; Wilke et al., 2020; Cvetkoska et al., 2021). Therefore, a period of increased bottom water oxygenation, as indicated in high Mn/Fe, could have caused a change in nutrient recycling (Gächter and Müller, 2003), sufficient to cause a collapse of community 1 and establishment of a new diatom community.

Moreover, although some of the morphotypes tend to increase their abundances during specific glacial/interglacial stages, their high population densities during multiple MIS stages point to a weak effect of the major global climate change during the MPT. This adaptive potential of species to survive the changing conditions during MPT coincidence with the period of a shift in macroevolutionary tread-off when long-lived endemic species began proliferating in the lake (Wilke et al., 2020). Although the reconfiguration of the climate system to 100 ka cycles has greatly affected many marine (Hoegh-Guldberg and Bruno, 2010) and terrestrial organisms (Tzedakis et al., 2004; Tylianakis et al., 2008), these findings show that the planktonic diatom communities in Lake Ohrid are primarily triggered by local environmental changes, which were superimposed by regional and global changes.

6. Conclusions

Two distinct diatom communities were observed in Lake Ohrid between 1050 and 815 ka. The first community existed between 1050 and 955 ka (MIS30–25) and was mostly influenced by environmental parameters related to nutrient availability, lake mixis, primary productivity and local temperatures. The subsequent community, 955–815 ka (MIS 25–21) was mostly affected by the ongoing deepening of the lake, and related changes in lake mixis and bottom water redox conditions. In contrast, only a weak correlation of this shift with the glacial-interglacial cyclicity was found, as well as with the prolonged duration and intensification of glacials during the mid-Pleistocene Transition.

In both communities, shifts in phenotypes, species abundances and composition were observed, likely as survival and fineness strategies to promote adaptation to different environmental conditions. Abrupt changes in the environment, like short-term enhanced mixis, probably triggerred species replacements and caused complete community turnover, demonstrating the high diatom sensitivity to local environmental alterations. The combination of different proxy data in this study allowed us to obtain evidence that the progressive intensification of the glacial intensity during the MPT only weakly affected freshwater communities compared to marine and terrestrial communities.

Author contributions

D.Z. and Z.L. conceived the research, with E.J. and A.C. contributing to the study design. D.Z. generated the diatom fossil data and conducted the community analyses in collaboration with Z. L and A.C. B.W. and A. F. provided the paleoenvironmental variables in collaboration with the SCOPSCO Science Team. H.V. provided FTIR-bSi data. D.Z. and E.J. wrote the manuscript with contributions of all authors.

Data availability

All study data are included in the article. Previously published geochemical data that was used for this work is available from PANGAEA repository: https://doi.org/10.1594/PANGAEA.934402.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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