Complexity of diatom response to Lateglacial and Holocene climate and environmental change in ancient, deep, and oligotrophic Lake Ohrid (Macedonia/Albania)

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Abstract

Lake Ohrid (Macedonia/Albania) is a rare example of a deep, ancient Mediterranean lake and is a key site for palaeoclimate research in the northeastern Mediterranean region. This study conducts the analysis of diatoms as a proxy for Lateglacial and Holocene climate and environmental change in Lake Ohrid at higher resolution than in previous studies. While Lake Ohrid has potential to be sensitive to water temperature change, the data demonstrate a highly complex diatom response, probably comprising a direct response to temperature-induced lake productivity in some phases, and an indirect response to temperature-related lake stratification/mixing and epilimnetic nutrient availability in others. The data also demonstrate the possible influences of physical limnological (e.g. the influence of wind stress on stratification/mixing) and chemical processes (e.g. the influence of catchment dynamics on nutrient input) in mediating the complex response of diatoms. During the Lateglacial (ca. 12 300–11 800 cal yr BP), the low-diversity dominance of hypolimnetic *Cyclotella fottii* indicates low lake productivity, linked to low water temperature. Although the subsequent slight increase in small, epilimnetic *C. minuscula* during the earliest Holocene (ca. 11 800–10 600 cal yr BP) suggests climate warming and enhanced stratification, diatom concentration remains as low as during the Lateglacial, suggesting that water temperature increase was muted across this major transition. The early Holocene (ca. 10 600–8200 cal yr BP) marks a sustained increase in epilimnetic taxa, with mesotrophic *C. ocellata* indicating high water temperature-induced productivity between ca. 10 600–10 200 cal yr BP and between ca. 9500–8200 cal yr BP, and with *C. minuscula* in response to low nutrient availability in the epilimnion between ca. 10 200–9500 cal yr BP. During the mid Holocene (ca. 8200–2600 cal yr BP), when sedimentological and geochemical proxies provide evidence for maximum Holocene water temperature, anomalously low *C. ocellata* abundance is probably a response to epilimnetic nutrient limitation, almost mimicking the Lateglacial flora apart from the occurrence of mesotrophic *Stephanodiscus transylvanicus* in the hypolimnion. During the late Holocene (ca. 2600 cal yr BP–present), high abundance and fluctuating composition of epilimnetic taxa is probably a response more to enhanced anthropogenic nutrient input than to climate, and nitrogen enrichment in particular. Overall, the data indicate that previous assumptions concerning the linearity of diatom response in this deep, ancient lake are invalid, and multi-proxy analysis is essential to improve

understanding of palaeolimnological dynamics in future research on the long, Quaternary sequence.

1. Introduction

Deep, ancient lakes are of global importance for palaeoclimate research, and diatom records from these lakes can provide powerful insights into mechanisms of climate and environmental change over long timescales (Mackay et al., 2010). Lake Ohrid (Macedonia/Albania) is a rare example of a deep, ancient Mediterranean lake (Roberts and Reed, 2009). It is thought to be the oldest lake in Europe, and probably the most biodiverse lake in the world (Albrecht and Wilke, 2008; Levkov and Williams, 2012). It is therefore a key site for palaeoclimate research in the northeastern Mediterranean region (Wagner et al., 2014). As most Mediterranean lakes are relatively shallow and demonstrate a strong diatom response to shifts in moisture availability (Zhang et al., 2014), the diatom record in Lake Ohrid may provide an important means by which to disentangle temperature and precipitation effects in Mediterranean climate research.

Temperature reconstructions during the Lateglacial and Holocene in the northeastern Mediterranean region are rare and rely mainly on pollen data (e.g. Bordon et al., 2009; Dormoy et al., 2009; Pross et al., 2009). Using pollen as a temperature proxy in this region is controversial. Renssen et al. (2012) suggested that pollen-based temperature reconstruction may be unreliable since precipitation rather than temperature is the main climatic control on Mediterranean vegetation distribution, while Mauri et al. (2015) argued instead that pollen transfer functions can provide robust results for temperature reconstruction in this region. Quantitative climate reconstruction methods have their own stengths and weaknesses (Birks et al., 2010; Juggins and Birks, 2012), and pollen-based temperature reconstructions can show different patterns and amplitudes of change depending on the technique used (Dormoy et al., 2009; Peyron et al., 2013). Deep Lake Ohrid, wherein no major lake-level change during the Lateglacial and Holocene has been reported (Wagner et al., 2009; Reed et al., 2010), is arguably an ideal site for using palaeolimnological proxies such as diatoms to improve understanding of temperature change in this region.

To date, diatom-based palaeoclimate research in Lake Ohrid has focused on low-resolution analysis of response to the last glacial–interglacial cycle (Wagner et al., 2009; Reed et al., 2010; Cvetkoska et al., 2012). Fluctuations in diatom composition between glacial/stadial and interglacial/interstadial stages have suggested a strong and simple response to temperature-induced changes in lake productivity. Here, we focus on the analysis of diatom response to Lateglacial and Holocene limnological, climate and environmental change, testing the response of diatoms in greater detail than has been achieved previously. Core Co1262, in the western part of the lake, is chronologically well constrained and is the longest and most continuous Holocene sequence yet retrieved from the lake. Diatom results are compared with sedimentological and geochemical data from the same core (Wagner et al., 2012; Lacey et al., 2015). We also compare with low-resolution diatom data from core Lz1120 (southeastern Lake Ohrid; Wagner et al., 2009), core Co1202 (northeastern Lake Ohrid; Reed et al., 2010; Cvetkoska et al., 2012) and core 9 (north-central Lake Ohrid; Roelofs and Kilham, 1983), and with palynological data from the region (Wagner et al., 2009; Panagiotopoulos et al., 2013).

2. Site description

Lake Ohrid (40°54′–41°10′ N, 20°38′–20°48′ E, 693 m a.s.l.; Fig. 1) is an ancient graben lake with a continuous > 1.2 Ma sedimentary record (Wagner et al., 2014). The lake is about 30 km long, 15 km wide, and has a surface area of 358 km^2 and a maximum water depth of 293 m (Albrecht and Wilke, 2008; Wagner et al., 2012). The lake basin has a relatively simple tub-shaped morphometry with steep slopes along the western and eastern sides and less inclined shelves in the northern and southern parts. It is surrounded by the Galicica Mountain (2256 m a.s.l.) to the east, the Mali i Thate Mountain (2276 m a.s.l.) to the southeast, the Jablanica Mountain (2225 m a.s.l.) to the northwest, and the Mokra Mountain (1512 m a.s.l.) to the west. Geological formations around the lake comprise Palaeozoic metamorphics to the northeast, karstified Triassic limestones to the east, southeast and northwest, Jurassic ophiolites to the west, Tertiary molasse deposits to the southwest and south, and Quaternary fluvio-lacustrine deposits in the Struga, Ohrid and Starovo plains to the north, northeast and south, respectively (Hoffmann et al., 2010; Reicherter et al., 2011). The local climate belongs to the Mediterranean regime with minimum precipitation occurring in June–August, and it is also influenced by the continental regime as it is surrounded by high mountains (Watzin et al., 2002). North-south winds prevail in the lake basin (Stanković, 1960; Matzinger et al., 2006a). The catchment vegetation is distributed mainly in altitudinal belts as, in ascending order, mixed deciduous oak forest, beech forest, coniferous forest, and subalpine and alpine meadows (Lézine et al., 2010; Panagiotopoulos et al., 2013).

Lake Ohrid is fed mainly by karstic springs (53 %, comprising 27 % surface springs and 26 % sublacustrine springs), with 24 % of water input from river inflow and 23 % from direct precipitation on the lake surface. Direct outflow is via the Crni Drim River (66 %), with 34 % evaporative loss (Matzinger et al., 2006a). The largest surface springs are those of Sveti Naum and Tushemisht at the southeastern edge of the lake, with smaller complexes comprising the Biljana spring in the northeastern part and the Dobra Voda spring in the northwest (Albrecht and Wilke, 2008). Sublacustrine springs are located mainly on the eastern shore of the lake, with one in the northwestern corner (Matter et al., 2010). An important source of karstic springs is the Lake Prespa underground outflow, which provides 21 % of total Lake Ohrid water input (Matzinger et al., 2006b). The karst aquifers are also charged by the infiltration of precipitation on the Galicica and Mali i Thate Mountains. There is no major inflow close to the Lini Peninsula in the western part of the lake. The top 150–200 m of the water column is mixed every winter, and a complete circulation of the entire water column occurs roughly every seventh winter (i.e. it is oligomictic) (Stanković, 1960; Matzinger et al., 2006a). Lake Ohrid is alkaline, with pelagic water pH 8.0–8.9 (measured in 2004–2006; Tasevska et al., 2012), and ionic composition dominated by bicarbonate and calcium (Stanković, 1960). It is highly oligotrophic, with total phosphorus and total nitrogen concentration throughout the water column at the lake centre of 4.6–6.8 µg l^{-1} and 171–512 µg l^{-1}, respectively (measured in 2000–2001; Watzin et al., 2002), and low dissolved silica concentration of < 0.2 mg l^{-1} in the trophogenic zone in summer (in 1957; Stanković, 1960). It is typically fresh and clear, with low water conductivity of 195–239 µS cm^{-1} in the littoral zone (in 2009–2010; Schneider et al., 2014), and high Secchi depth of 11–21 m (in 2000–2003; Petrova et al., 2008).

3. Material and methods

Following detailed hydro-acoustic surveys carried out between 2004 and 2009 on lake bathymetry and sediment architecture (Wagner et al., 2012; Lindhorst et al., 2015), a 1008 cm-long core Co1262 was recovered in June 2011 from 260 m water depth in front of the Lini Peninsula at the western margin of Lake Ohrid, using UWITEC gravity and piston coring equipment from a floating platform (www.uwitec.at). Excluding a 200 cm-thick mass wasting deposit and three smaller ones (< 20 cm) identified by coarse grain size and low water content (Wagner et al., 2012), the undisturbed composite sediment sequence is 785 cm long.

The age model of core Co1262 was described in detail by Lacey et al. (2015). Radiocarbon dating, tephrostratigraphy and cross correlation of calcite and organic matter content with other sediment cores from Lake Ohrid and the hydraulically-linked adjacent Lake Prespa were used to provide chronological control for core Co1262. The age model was calculated based on five calendar ages of terrestrial plant remains, three well-dated tephras (Somma-Vesuvius AD 472/512 tephra, Mount Etna FL tephra and Somma-Vesuvius Mercato tephra; Sulpizio et al., 2010; Damaschke et al., 2013) and five correlation points, using the smoothing spline method (smoothing = 0.1) with the software package Clam 2.2 (Blaauw, 2010). One radiocarbon age of fish remains is apparently too old and was excluded, as the fish remains are probably affected by a reservior effect or they are redeposited (Wagner et al., 2012). The radiocarbon and tephra chronologies are shown in Table 1, and the correlation of core Co1262 with other sediment cores was described in detail by Wagner et al. (2012). The age model shows that core Co1262 covers the past 12 300 years (Fig. 2), spanning the Lateglacial and Holocene period.

Diatom analysis was carried out on 104 samples in the 785 cm-long master sequence, taken every 8 cm but at a higher resolution of 4 cm around putative abrupt events at ca. 8200 and 4200 cal yr BP. The age resolution is ca. 80–110 years for the top 120 cm, ca. 40–70 years between 240–120 cm (ca. 2200–1400 cal yr BP), ca. 100–200 years between 350–240 cm (ca. 4400–2200 cal yr BP), ca. 270–350 years between 435–350 cm (ca. 7800–4400 cal yr BP), and ca. 90–120 years for the lower sequence. The relatively low age resolution in the mid core is a result of low sedimentation rate.

Standard techniques in Battarbee et al. (2001) were adopted for preparation of diatom slides. Approximately 0.1 g dry weight sediment samples were heated in 25–30 ml 30 % H_2O_2 to oxidise organic matter, and a few drops of concentrated HCl were added to remove carbonates and remaining H_2O_2. The residue was suspended in distilled water, centrifuged and washed 4–5 times to remove clay and remaining HCl. The suspension was diluted to an appropriate concentration, and known quantities of plastic microspheres were added to allow calculation of absolute diatom concentration. Diatom slides were mounted using Naphrax™. Diatoms were counted along transects at × 1000 magnification under oil immersion on an OLYMPUS BX51 light microscope. More than 500 valves per slide were counted. Diatom identification was based on a range of standard literature (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b; Lange-Bertalot, 2001; Krammer, 2002; Houk et al., 2010, 2014) and the dedicated Lake Ohrid works which reflect ongoing revision and improvement of diatom taxonomy (Levkov et al., 2007; Levkov and Williams, 2011; Cvetkoska et al., 2012, 2014a), adopting the nomenclature of the Catalogue of Diatom Names (on-line version) (Fourtanier and Kociolek, 2011). The endemics, *Cyclotella fottii* Hustedt and the smaller taxon *Cyclotella hustedtii* Jurilj were previously separated (Hustedt, 1945; Jurilj, 1954). They are now combined as *C. fottii* but we split morphotypes as size classes to investigate additional sub-species response (cf. Reed et al., 2010; Cvetkoska et al., 2012). *Cyclotella minuscula* (Jurilj) Cvetkoska is a new species identification (Cvetkoska et al., 2014a), which was previously identified as *Discostella stelligera* (Cleve & Grunow) Houk & Klee (Roelofs and Kilham, 1983; Wagner et al., 2009) or briefly combined with *Cyclotella ocellata* Pantocsek (Reed et al., 2010; Cvetkoska et al., 2012). *Cyclotella ocellata* morphotypes were split by number of ocelli. *Stephanodiscus transylvanicus* Pantocsek is another improvement of species identification (Cvetkoska et al., 2012), which was previously identified as *Stephanodiscus astraea* (Ehrenberg) Grunow (Roelofs and Kilham, 1983), *Stephanodiscus neoastraea* Håkansson & Hickel (Wagner et al., 2009) or *Stephanodiscus galileensis* Håkansson & Ehrlich (Reed et al., 2010). Diatom results were displayed using Tilia version 1.7.16, and zone boundaries were defined based on relative abundance data according to Constrained Incremental Sum of Squares (CONISS) cluster analysis (Grimm, 2011).

To assess the quality of diatom preservation, the *F* (fractional) index of Ryves et al. (2001) was used to calculate the dissolution of the dominant endemic taxon *C. fottii* which consists of a range of morphotypes in cell size. The *F* index is the ratio of pristine valves to all valves (sum of pristine and partially-dissolved valves), where $F = 1$ indicates perfect preservation (Ryves et al., 2001). Unconstrained ordination techniques were used to explore the variance in the diatom relative abundance data using Canoco for Windows 4.5 (Ter Braak and Šmilauer, 2002). Detrended correspondence analysis (DCA) gave the largest gradient length of 1.85 SD units, and thus the linear ordination method principal components analysis (PCA) was selected (Ter Braak, 1995; Lepš and Šmilauer, 2003). Diatom concentration data can be influenced both by differences in cell sizes of diatom species and by changes in sedimentation rates, and diatom biovolume accumulation rate (BVAR) data provide a more robust interpretive tool for productivity than concentration data (Battarbee et al., 2001; Rioual and Mackay, 2005). However, the necessary diatom cell biovolume data and dry sediment bulk density data were not available. Instead, we assessed qualitatively the potential influences of sedimentation rates and valve sizes of main planktonic taxa (including size classes of *C. fottii*) on diatom concentration.

4. Results

A total of 99 diatom species was identified, consisting of nine planktonic species, five facultative planktonic species and 85 benthic species. In spite of low diversity of plankton, its relative abundance is > 90 % throughout the record. Six major diatom assemblage zones can be defined based on diatom relative abundance data, which match well with changes in absolute diatom concentration (Fig. 3). *F* index values for endemic *Cyclotella fottii* are > 0.75 throughout the record with > 500 valves counted each slide and > 2×10^7 valves g^{-1} concentration per sample, and diatom preservation quality is high.

In Zone D-1 (785–639 cm, ca. 12 300–10 600 cal yr BP), planktonic *C. fottii* is dominant at > 80 % abundance, diatom PCA Axis 1 scores are low, and diatom concentration is very low. In Subzone

D-1a (785–743 cm, ca. 12 300–11 800 cal yr BP), facultative planktonic taxa, mainly comprising *Staurosirella pinnata* (Ehrenberg) Williams & Round and *Pseudostaurosira brevistriata* (Grunow) Williams & Round, are present at ca. 8 % abundance. Subzone D-1b (743–639 cm, ca. 11 800–10 600 cal yr BP) is marked by a slight increase in the abundance of planktonic *C. minuscula*, and facultative planktonic taxa decreases slightly to < 5 %.

Zone D-2 (639–551 cm, ca. 10 600–9500 cal yr BP) shows a decline in the abundance of *C. fottii* (and its large morphotypes in particular), and a shift to relatively high diatom PCA Axis 1 scores. *Cyclotella ocellata* increases to ca. 10–30 % in Subzone D-2a (639–607 cm, ca. 10 600–10 200 cal yr BP), and *Stephanodiscus transylvanicus* appears, with a peak in diatom concentration. In Subzone D-2b (607–551 cm, ca. 10 200–9500 cal yr BP), *C. minuscula* increases to ca. 20–40 % at the expense of *C. ocellata* and *S. transylvanicus*, while diatom concentration is relatively low.

In Zone D-3 (551–449 cm, ca. 9500–8200 cal yr BP), *C. ocellata* is abundant throughout (ca. 20–60 %), with high diatom PCA Axis 1 scores and diatom concentration. In Subzone D-3a (551–511 cm, ca. 9500–9000 cal yr BP), *C. ocellata* shows sustained peak abundance (ca. 30–60 %), including non-classic morphotypes with ≥ 4 ocelli in valve centre. Subzone D-3b (511–449 cm, ca. 9000–8200 cal yr BP) is characterised by an increased abundance of *S. transylvanicus*, and *C. ocellata* consists mainly of the classic morphotype (three ocelli).

In Zone D-4 (449–269 cm, ca. 8200–2600 cal yr BP), *C. fottii* is at high abundance (ca. 60–85 %), *S. transylvanicus* is consistently present at ca. 5–10 % abundance, and *C. ocellata* is at relatively low abundance (ca. 10–20 %), with a decline in diatom PCA Axis 1 scores and diatom concentration.

In Zone D-5 (269–214 cm, ca. 2600–2000 cal yr BP), *C. ocellata* shows renewed high abundance (ca. 50–60 %), with an increase in diatom PCA Axis 1 scores. Diatom concentration is relatively high.

In Zone D-6 (214–0 cm, ca. 2000 cal yr BP–present), *C. ocellata* is abundant (ca. 25–60 %), and there is increased but fluctuating abundance of *C. minuscula*, showing a sharp peak (ca. 35 % abundance) at the lower zone boundary. Diatom PCA Axis 1 scores are high, but diatom concentration is low.

5. Interpretation

The limnological interpretation of diatoms rests in part on previous studies (Stanković, 1960; Allen and Ocevski, 1976; Ocevski and Allen, 1977), which found that endemic *C. fottii* occupies the hypolimnion throughout the year in Lake Ohrid. *Cyclotella fottii* is described as oligothermic and oligophotic, and is thought to be an opportunistic species which extends its growth into the epilimnion during periods of low temperature in winter and early spring (Stanković, 1960). *Stephanodiscus transylvanicus* probably has similar ecological preferences to other intermediate- to large-sized *Stephanodiscus* species by virtue of their morphological similarity (Bradbury, 1991), and has been described as hypolimnetic (Stanković, 1960; Allen and Ocevski, 1976) and mesotrophic (Wagner et al., 2009). *Cyclotella ocellata* (and by inference *C. minuscula*) adopts an epilimnetic life habit in Lake Ohrid, thrives mainly in late spring and summer, and is described as eurythermic (Stanković, 1960). It has been described as mesotrophic (Wagner et al., 2009), and is taken as an indicator of nutrient enrichment in this highly oligotrophic lake compared to *C. fottii* (Lorenschat et al., 2014). *Cyclotella ocellata* is also found to be favoured by high nitrogen concentration in shallower, mesotrophic Lake Prespa, the sister lake of Lake Ohrid (Kocev et al., 2010). *Cyclotella minuscula* is very small (3–5 µm diameter), and probably has a similar ecological niche as other small-celled *Cyclotella sensu lato* species (Saros and Anderson, 2015), which have low nutrient and light requirements, high growth rates and low sinking rates, owing to their high surface area to volume ratio (Winder et al., 2009; Finkel et al., 2009).

In contrast to previous, preliminary, and low-resolution diatom studies (Roelofs and Kilham, 1983; Wagner et al., 2009; Reed et al., 2010; Cvetkoska et al., 2012), variations in the relative abundance of these taxa may be a direct response to shifts in temperature-induced lake productivity, and we should also consider the possible influences of temperature-related stratification/mixing regime, wind forcing, catchment mediation, light limitation, and/or spring inflow. It should be noted that temperature here is mean annual epilimnetic water temperature ("water temperature" hereafter). Lake Ohrid is still highly oligotrophic and exceptionally transparent (Matzinger et al., 2006a, 2007) and hypolimnetic diatoms can be found at > 200 m water depth (Stanković, 1960), so light limitation can be assumed insignificant. Although Lorenschat et al. (2014) suggested that karstic springs from Lake Prespa have a strong influence on the nutrient budget of Lake Ohrid, it is apparent that spring inflow and associated nutrient transport do not reach the site of core Co1262 in the westernmost part of the lake (Matzinger et al., 2006a), and thus the direct influence of springs is probably negligible.

From the results of this study, the complacency in *C. fottii F* index values and high quality of diatom preservation (Fig. 3) indicate that major shifts in diatom composition are not related to the taphonomic effects of dissolution, but represent real ecological shifts. Diatom PCA Axis 1 scores clearly vary according to the relative abundance of the epilimnetic taxa, with high positive scores associated with the dominance of epilimnetic taxa and high negative scores in zones of low-diversity *C. fottii* dominance. To strengthen interpretation, the diatom results of core Co1262 are compared with calcite ($CaCO_3$) and organic matter (i.e. total organic carbon, TOC) content and Rock Eval pyrolysis data (hydrogen index, HI; oxygen index, OI) from the same core (Fig. 4; Wagner et al., 2012; Lacey et al., 2015). Calcite content in particular has proved to be a strong proxy for temperature-induced productivity in this lake (Vogel et al., 2010; Wagner et al., 2010). Diatom shifts in core Co1262 are well correlated with those of core Lz1120 (Fig. 5; Wagner et al., 2009), validating diatom interpretation of core Co1262 as representative of basin-wide response. The possible influence of catchment dynamics and nutrient delivery is assessed through comparison with sedimentological potassium (K) intensity and sedimentation rate data from the same core (Fig. 4, Wagner et al., 2012; Lacey et al, 2015), with palynological data from previous lake sediment cores in Lake Ohrid (Fig. 5, Wagner et al., 2009) and Lake Prespa (Panagiotopoulos et al., 2013), and with calcite $\delta^{18}O$ data from existing sediment cores in Lake Ohrid (Leng et al., 2010; Lacey et al., 2015).

5.1 The Lateglacial (ca. 12 300–11 800 cal yr BP)

During the Lateglacial or Younger Dryas (Subzone D-1a; ca. 12 300–11 800 cal yr BP), the low-diversity dominance of hypolimnetic, oligothermic and oligophotic *C. fottii* indicates low lake productivity in relation to low water temperature, as during marine isotope stage 2 (MIS 2) in core 9 (Roelofs and Kilham, 1983) and core Co1202 (Reed et al., 2010). This corresponds to low calcite content, and is also consistent with low organic matter content, low HI and high OI which suggest low algal organic matter contribution and/or high organic matter degradation (Lacey et al., 2015). The regularly-distributed (ca. 8 % relative abundance) pioneering, facultative planktonic fragilaroid taxa *S. pinnata* and *P. brevistriata* are probably related to cold water and winter lake ice cover (Mackay et al., 2003; Schmidt et al., 2004), which is consistent with the deposition of ice-rafted debris inferred from the occurrence of gravel grains ("silt with dropstones" in "lithostratigraphy" in Fig. 3; Wagner et al., 2012). These taxa are also probably related to physical disturbance (Anderson, 2000), which is consistent with intense lake circulation as a result of low water temperature and strong winds (see below). Low water temperature would have resulted in the high frequency and long duration of complete lake circulation which usually occurs in severe winters or following intense wind action in less severe winters in this lake today (Stanković, 1960). If subject to winter lake ice cover, this lake would have been dimictic or monomictic rather than currently oligomictic. Low water temperature during the Younger Dryas in this lake is consistent with pollen-based air temperature reconstruction in Lake Maliq, Albania (Bordon et al., 2009) and SL152, northern Aegean Sea (Kotthoff et al., 2011), with alkenone- and foram-inferred low sea surface temperature (SST) in MNB3, northern Aegean Sea (Gogou et al., 2007; Geraga et al., 2010), and with the globally-stacked proxy surface temperature record (Shakun et al., 2012). Intense wind action may have occurred during this cold period (Vogel et al., 2010), in accord with the observation that average wind speed in winter is higher than in summer today (Stanković, 1960). Thus, the capacity for mixing-induced upward nutrient supply would have been high. High sedimentation rate, high K intensity (i.e. high clastic content), and low calcite and organic matter content (i.e. low authigenic matter content) suggest high catchment erosion. This is supported by sparse vegetation and unsettled soils in the catchment during the Younger Dryas (Panagiotopoulos et al., 2013). Thus, erosion-induced external nutrient input would also have been high. However, Younger Dryas water temperature must have been low enough to prevent nutrient-induced productivity increase.

5.2 The earliest Holocene (ca. 11 800–10 600 cal yr BP)

After the Lateglacial, the slight increase in the relative abundance of small, epilimnetic *C. minuscula* during the earliest Holocene (Subzone D-1b; ca. 11 800–10 600 cal yr BP) is surprisingly subtle. It is consistent with the inherent response of small planktonic diatoms to climate warming and enhanced thermal stratification with reduced epilimnetic nutrient availability and/or increased sinking velocities in a deep, oligotrophic lake (Winder et al., 2009; Finkel et al., 2009; Jewson et al., 2015). Less intense winds and prolonged calm periods may be another factor contributing to the increase in *C. minuscula* in this deep, oligomictic lake. The rarity (< 5 % relative abundance) of facultative planktonic taxa suggests either a shorter, less intense period of lake circulation, in accord with the increase in *C. minuscula*, or a more prolonged ice-free period, in accord with the disappearance of ice-rafted debris deposition after ca. 11 300 cal yr BP (Wagner et al., 2012). The increase in the abundance of epilimnetic *Cyclotella* species is also possibly related to a longer ice-free season (Smol et al., 2005; Rühland et al., 2008). There is a gradual rather than abrupt change in increasing organic matter content, increasing HI and decreasing OI which indicate relatively subtle increases in algal organic matter contribution and/or organic matter preservation (Lacey et al., 2015). However, diatom concentration remains as low as during the Lateglacial. Sedimentation rate remains constant (Fig. 4), and in terms of the possible influence of diatom cell size, an increase in the abundance of large *C. fottii* morphotypes (> 20 µm) may compensate for the increase in small *C. minuscula* (Fig. 3). In combination with low calcite content, low diatom concentration thus indicates that water temperature is still very low during this period, possibly with only intermittent stratification. Although the diatom signature of the Lateglacial–Holocene transition is more pronounced here than in core Co1202 (Reed et al., 2010), the transition is remarkably muted compared to the marked diatom shifts observed in shallower southern Balkan lakes. The distinct transition in Lake Ioannina, northwestern Greece (Wilson et al., 2008; Jones et al., 2013), Lake Prespa, Macedonia/Albania/Greece (Cvetkoska et al., 2014b) and Lake Dojran, Macedonia/Greece (Zhang et al., 2014), for example, is instead a response driven by a major increase in lake level and moisture availability. The temperature shift was insufficient to cause major productivity increase in this deep lake, although high sedimentation rate, high K intensity and low authigenic matter content probably indicate high catchment erosion and associated nutrient delivery similar to the Lateglacial environment. The results also confirm the potential of Lake Ohrid's contrasting response thresholds to contribute to separation of temperature and precipitation change in regional palaeoclimate reconstruction. However, muted water temperature increase in this lake is not consistent with a distinctly increasing trend for the globally-stacked proxy mean annual surface temperature (Shakun et al., 2012; Marcott et al., 2013).

5.3 The early Holocene (ca. 10 600–8200 cal yr BP)

The early Holocene (Zones D-2 and D-3; ca. 10 600–8200 cal yr BP) marks a sustained increase in the abundance of epilimnetic taxa, with an alternation between *C. ocellata* and *C. minuscula* in Zone D-2 (ca. 10 600–9500 cal yr BP) and dominance by *C. ocellata* in Zone D-3 (ca. 9500–8200 cal yr BP). Diatom PCA Axis 1 scores are correspondingly high. Since sedimentation rate is nearly unchanged compared to Zone D-1 (Fig. 4), high diatom concentration in Subzone D-2a and Zone D-3 might be attributed to declined abundance of large *C. fottii* morphotypes and increased abundance of relatively small *C. ocellata*, but high abundance of very small *C. minuscula* in Subzone D-2b is correlated with low rather than high diatom concentration (Fig. 3). Thus, diatom concentration could still indicate a real change in lake productivity during the early Holocene. High abundance of eurythermic, mesotrophic *C. ocellata* between ca. 10 600–10 200 cal yr BP (Subzone D-2a) and between ca. 9500–8200 cal yr BP (Zone D-3) corresponds to high diatom concentration and high organic matter content, supporting an interpretation of *C. ocellata* as indicative of high water temperature-induced lake productivity, as in core Co1202 (Reed et al., 2010). This is also consistent with generally high HI and slightly low OI, reflecting high algal organic matter contribution and/or better organic matter preservation (Lacey et al., 2015). High water temperature clearly implies high air temperature, although the converse does not necessarily apply since low water temperature occurred during the earliest Holocene. High temperature and possibly associated low winter wind stress would have reduced the frequency, duration and strength of lake circulation, and thus restrained nutrient availability in the epilimnion. Nearly constant sedimentation rate (compared to Zone D-1), generally low K intensity and high organic matter content in the diatom zones D-2a and D-3 probably represent a decline in catchment erosion and associated nutrient delivery, rather than dilution effects. This is consistent with dense forest and stable soils in the catchment (Wagner et al., 2009; Panagiotopoulos et al., 2013). However, nutrient concentration must have been insufficiently low to prevent temperature-induced productivity increase.

High *C. minuscula* abundance between ca. 10 200–9500 cal yr BP (Subzone D-2b), at the expense of *C. ocellata*, corresponds to a major peak in calcite content. Given primarily photosynthesis-induced calcite precipitation in this lake with negligible detrital calcite and minor contribution of calcite precipitated around spring areas, the peak calcite content indicates high lake productivity and, by inference, high water temperature (Vogel et al., 2010; Wagner et al., 2010). However, a contrasting diatom ecological response is shown in this subzone, with high *C. minuscula* abundance and low diatom concentration. Although, as suggested above, strong stratification would support the bloom of small-sized planktonic diatom species, low diatom concentration is not consistent with the inferred high water temperature-induced productivity. Sedimentation rate is nearly unchanged compared to Subzone D-2a, and, under a densely-vegetated catchment (Panagiotopoulos et al., 2013), high K intensity in Subzone D-2b, along with low organic matter content and relatively high calcite content, does not necessarily imply high catchment erosion, possibly due to dilution effects. In contrast to Subzone D-2a and Zone D-3, it is most likely in Subzone D-2b that, corresponding to the peak calcite content, more nutrients such as phosphorus are lost from the epilimnion through being absorbed onto the surface of precipitating calcite particles (Allen and Ocevski, 1976). Epilimnetic nutrient availability in Subzone D-2b must have been low enough to prevent high water temperature-induced productivity increase. The significance of this shift was not highlighted in previous study (Reed et al., 2010), wherein *C. minuscula* was separated only as a morphotype of *C. ocellata*.

An increase in the abundance of hypolimnetic, mesotrophic *S. transylvanicus* in Subzone D-3b (ca. 9000–8200 cal yr BP) corresponds to renewed calcite accumulation, and the lower boundary of this subzone is also coincident with an extreme, abrupt peak in K intensity, which originates from volcanic glass shards and corresponds to the Mercato tephra (Wagner et al., 2012). The tephra input would increase epilimnetic silica availability and reduce phosphorus release from the sediment (Barker et al., 2000; Telford et al., 2004), resulting in either an increase in diatom concentration (Lotter et al., 1995; Eastwood et al., 2002) or a shift of diatom composition to the dominance of taxa that require high Si/P ratio (Abella, 1988; Cruces et al., 2006). The tephra impact would also be short-lived, with a recovery of diatom composition towards the pre-tephra state (Telford et al., 2004; Cruces et al., 2006). It is apparent that the Mercato tephra has no impact on diatoms here, since *S. transylvanicus* maintains its abundance over the long term and diatom concentration maintains its maximum level. Moreover, most *Stephanodiscus* species prefer low Si/P ratio (Kilham et al., 1986), which also suggests that the tephra has no impact. It is possible that *S. transylvanicus* is favoured by phosphorus release in the hypolimnion due to the dissolution of precipitating calcite and the mineralisation of settling organic matter from the upper layer (Stanković, 1960; Allen and Ocevski, 1976; Matzinger et al., 2006a, 2007). In all, during the early Holocene, high water temperature in this lake is in accord with the globally-stacked proxy mean annual surface temperature record (Marcott et al., 2013), and diatom species appear to respond to high water temperature in different ways: the response of *C.*

ocellata is direct in relation to high water temperature-induced epilimnetic productivity, while the response of *C. minuscula* is indirect in relation to nutrient limitation in the epilimnion. Lacey et al. (2015) interpreted the phase between ca. 8600–8000 cal yr BP (ca. 600 years) as a response to the abrupt 8.2 ka cooling event based on sedimentological and geochemical data. However, based on ca. 100-year resolution diatom data, there is no apparent diatom reversal to an oligothermic-type flora, and the decline in diatom concentration is more a long-term change associated with reduced sedimentation rate.

5.4 The mid Holocene (ca. 8200–2600 cal yr BP)

The mid Holocene (Zone D-4; ca. 8200–2600 cal yr BP) was a phase of maximum Holocene water temperature and lake productivity, as indicated strongly by high calcite and organic matter content, high HI and low OI (Vogel et al., 2010; Wagner et al., 2010; Lacey et al., 2015). This is in accord with the globally-stacked proxy mean annual surface temperature record (Marcott et al., 2013). However, diatom response is complex. *Cyclotella ocellata* is anomalously at low abundance, with reduced diatom PCA Axis 1 scores. As in Subzone D-2b, this may be attributed to epilimnetic nutrient limitation, but to the extent that *C. minuscula* is also constrained. Mixing-induced upward nutrient supply is probably low, as a result of strong thermal stratification and probably weak winds associated with high temperature. Erosion-induced external nutrient input is also probably low, as indicated by low sedimentation rate and K intensity (i.e. clastic content). Low catchment erosion is also supported by dense vegetation and stable soils in the catchment (Fig. 5; Wagner et al., 2009) and by a drying trend and reducing water inflow from rising calcite δ^{18}O values (Leng et al., 2010; Lacey et al., 2015). The effect of high phosphorus precipitation linked to the calcite-scavenging effect (Allen and Ocevski, 1976), and exacerbated by low internal and external nutrient supply, could be sufficient to limit the development of *C. ocellata* during the mid Holocene in spite of high water temperature. The only predictable aspect of the diatom data is the relatively high abundance of mesotrophic *S. transylvanicus*, which may benefit from high water temperature-induced productivity in the hypolimnion and/or high nutrient availability in the hypolimnion under strong stratification. The flora is similar to that of the mid Holocene in core Lz1120 (Fig. 5; Wagner et al., 2009). Compared to Zone D-1, although *C. fottii* is similarly at high abundance, the abundance of large *C. fottii* forms is much lower (Fig. 3) and fewer cells can complete their full life cycle with sexual reproduction (Stoermer et al., 1989) possibly linked to strong stratification during this period. Since high calcite and organic matter content indicates high algal production, the discrepancy between low abundance of epilimnetic diatom taxa and high algal production suggests that Chlorophyceae, the other dominant algae in this lake (Stanković, 1960; Miho and Lange-Bertalot, 2003), may outcompete diatoms in the epilimnion and contribute more to algal production. Diatom concentration is relatively high, correlating with low rather than high abundance of smaller valves of *C. ocellata* and *C. minuscula*, but this may be largely an artefact of the consistently low sedimentation rate. As in other Lake Ohrid sediment cores (Wagner et al., 2009; Vogel et al., 2010), there is no evidence for an abrupt event at ca. 4200 cal yr BP. Overall, in contrast to Zone D-1, low abundance of epilimnetic diatom taxa here is the response to high rather than low water temperature; in contrast to Zones D-2 and D-3, the diatom response here is to limited epilimnetic nutrient availability rather than high water temperature-induced productivity.

5.5 The late Holocene (ca. 2600 cal yr BP–present)

Between ca. 2600–2000 cal yr BP (Zone D-5), high *C. ocellata* abundance, along with high diatom PCA Axis 1 scores, is consistent with that of core Lz1120 (Fig. 5; Wagner et al., 2009). There is surprisingly little change in other limnological proxies during this phase, but high *C. ocellata* abundance correlates with palynological evidence for anthropogenic catchment deforestation in core Lz1120 (Fig. 5; Wagner et al., 2009). Relatively high diatom concentration probably represents a response to epilimnetic productivity increase, caused at least in part by human activity such as forest clearance and agricultural development. At ca. 2000/1900 cal yr BP, the abrupt peak in *C. minuscula* abundance is correlated with peak sedimentation rate and K intensity, abrupt reductions in calcite, organic matter and HI, and a peak in OI. The peak is consistent with previous interpretations, suggesting that this is related to intensified human activity in the catchment during the Roman Period, and that enhanced erosion causes increased delivery of nutrients, clastic material and organic matter that is extensively oxidised (Wagner et al., 2009; Vogel et al., 2010; Lacey et al., 2015). It is a complex diatom response to high nutrient availability, however. While very small *Cyclotella sensu lato* species have low nutrient preferences, they may respond to nitrogen enrichment when N/P supply ratio is low (Saros and Anderson, 2015). There is no abiotic mechanism for the removal of nitrogen from the epilimnion, and phosphorus precipitation linked to the calcite-scavenging effect is low at this time (Allen and Ocevski, 1976).

After ca. 1900 cal yr BP (Zone D-6), Lake Ohrid essentially reached its modern state with high abundance of epilimnetic taxa, dominated by smaller valves of *C. ocellata* and *C. minuscula*. As suggested in the previous zones, the autecology of *C. ocellata* and *C. minuscula* is probably divergent in relation to nutrient availability and mixing depth, which is supported by other observational and experimental studies (e.g. Saros et al., 2012); on the other hand, *C. ocellata* is relatively small, and may also show synchronous change with very small *Cyclotella sensu lato* species (e.g. Rühland et al., 2008). Moreover, high nitrogen concentration may favour both *C. ocellata* and *C. minuscula* (Kocev et al., 2010; Saros and Anderson, 2015). Thus, it is not surprising that *C. ocellata* and *C. minuscula* concur to respond to enhanced anthropogenic nutrient input during this period. There is strong palynological evidence for catchment deforestation after ca. 1900 cal yr BP from core Lz1120 and Lake Prespa core Co1215 (Wagner et al., 2009; Panagiotopoulos et al., 2013). There is no definitive evidence for diatom response to known late-Holocene climatic events such as the Medieval Climate Anomaly (MCA) or the Little Ice Age (LIA). If a stong MCA did occur, anthropogenic nutrient input to the modern lake was sufficient to override temperature-induced nutrient limitation in the epilimnion. With maintained external nutrient input, the implications for future climate warming are that loss of epilimnetic diversity would not occur. Instead, the main threat to Lake Ohrid is probably eutrophication, resulting in the invasion of non-native taxa (Levkov and Williams, 2012).

6. Conclusions

This study provides a detailed picture of diatom response to Lateglacial and Holocene climate and environmental change in Lake Ohrid, based on diatom analysis of core Co1262 and comparison with sedimentological and geochemical data from the same core, with extant low-resolution diatom data from cores Lz1120 and Co1202 and with palynological evidence for catchment vegetation change. Since most Mediterranean lakes are relatively shallow, with a strong diatom response to lake-level change linked to moisture availability rather than temperature, this study is important in improving understanding of the strength and complexity of diatom response to water temperature change in deep, oligotrophic Lake Ohrid. Our multi-proxy analysis reveals that water temperature was low during the Lateglacial and even the earliest Holocene, was high during the early Holocene and reached the maximum during the mid Holocene, but that the diatom response is strongly non-linear and coherent interpretation requires consideration of the influence of multiple limnological parameters which vary in their importance over time. There is probably a direct response of diatoms to temperature-induced lake productivity in some phases, but an indirect response to temperature-related lake stratification/mixing and epilimnetic nutrient availability in others. We demonstrate the possible additional influences of physical limnological (e.g. the influence of wind stress on stratification/mixing) and chemical processes (e.g. the influence of catchment dynamics on nutrient input).

During the Lateglacial (ca. 12 300–11 800 cal yr BP), the low-diversity dominance of hypolimnetic *C. fottii* indicates low lake productivity in relation to low water temperature. During the earliest Holocene (ca. 11 800–10 600 cal yr BP), although the slight increase in small, epilimnetic *C. minuscula* probably represents climate warming and enhanced stratification, diatom concentration is as low as during the Lateglacial, indicating that water temperature increase was muted. The early Holocene (ca. 10 600–8200 cal yr BP) marks a sustained increase in epilimnetic taxa, with mesotrophic *C. ocellata* indicating high water temperature-induced lake productivity between ca. 10 600–10 200 cal yr BP and between ca. 9500–8200 cal yr BP, and with *C. minuscula* in response to low nutrient availability in the epilimnion between ca. 10 200–9500 cal yr BP. During the mid Holocene (ca. 8200–2600 cal yr BP), in spite of maximum Holocene water temperature, anomalously low *C. ocellata* abundance is probably a response to epilimnetic nutrient limitation, as a result of high temperature-related stratification (i.e. low internal nutrient upward supply), low catchment erosion (i.e. low external nutrient input) and the calcite-scavenging effect (i.e. high phosphorus precipitation). However, mesotrophic *S. transylvanicus* may benefit from high water temperature-induced productivity in the hypolimnion and/or high nutrient availability in the hypolimnion under strong stratification. During the late Holocene (ca. 2600 cal yr BP–present), high abundance and fluctuating composition of epilimnetic taxa is largely a response to enhanced anthropogenic nutrient input, particularly nitrogen enrichment.

Author contributions

B. Wagner, M. J. Leng and J. M. Reed designed this research in the SCOPSCO project. X. S. Zhang performed diatom analysis. X. S. Zhang and J. M. Reed interpretated diatom data by comparison with other proxy data. A. Francke and B. Wagner developed the age model. A. Francke and B. Wagner generated and interpretated sedimentological and geochemical data (sedimentation rate, potassium concentration, and calcite content). J. H. Lacey and M. J. Leng generated and interpretated geochemical data (total organic carbon content, hydrogen index, and oxygen index). Z. Levkov informed on developments in diatom taxonomy. X. S. Zhang wrote the paper under the supervision of J. M. Reed with editorial comments from all co-authors.

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Table 1. Age estimates for core Co1262. The calibration of radiocarbon ages into calendar ages is based on Calib 7.0.2 (Stuiver and Reimer, 1993) and IntCal13 (Reimer et al., 2013) and on a 2σ uncertainty.

Core depth (cm)	Lab code	Material	Radiocarbon age (^{14}C yr BP)	Calendar age (cal yr BP)
17	COL 1251.1.1	terrestrial plant remains	164±20	140±145
122		the AD 472/512 tephra		1478/1438
240	COL 1735.1.1	terrestrial plant remains	2176±46	2190±140
315		the FL tephra		3370±70
318	COL 1736.1.1	terrestrial plant remains	3280±45	3510±110
335	COL 1737.1.1	terrestrial plant remains	3581±40	3850±130
368	COL 1738.1.1	terrestrial plant remains	4370±44	5030±190
503		the Mercato tephra		8890±90
548	COL 1243.1.1	fish remains	10 492±37	12 400±190 (rejected)

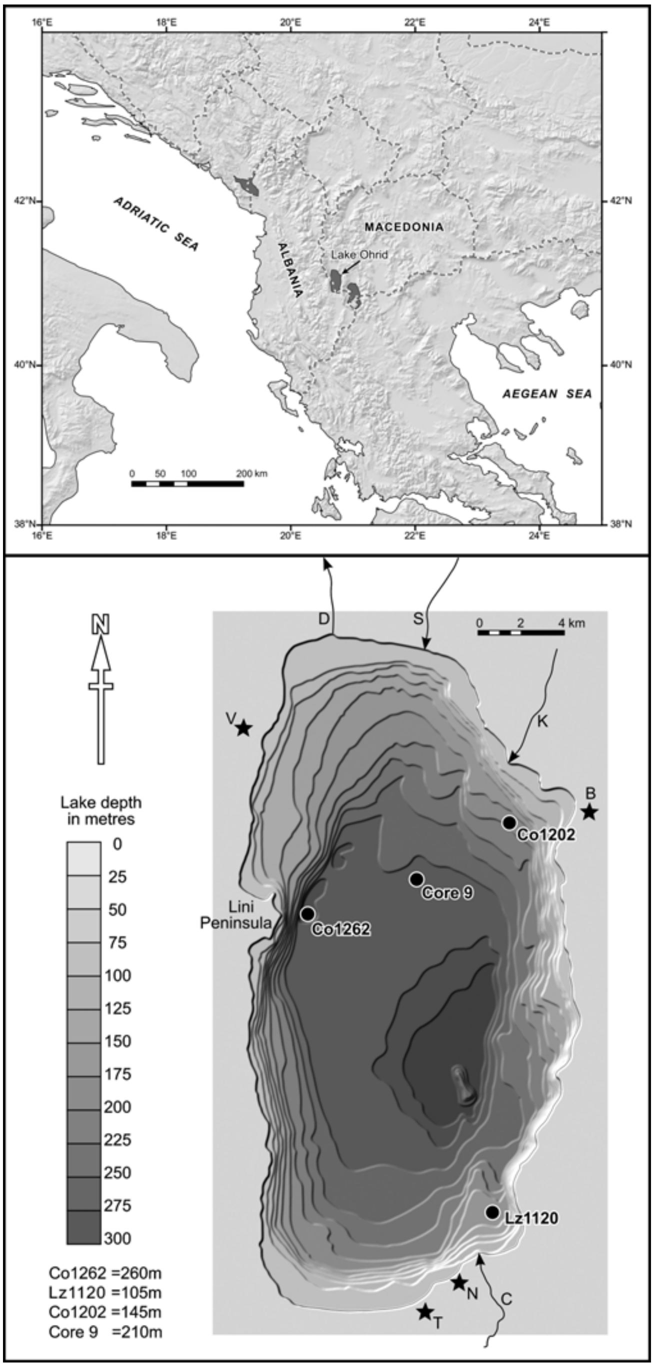

Figure 1. Map showing the location of Lake Ohrid (Macedonia/Albania) and the coring sites Co1262 (this study; Wagner et al., 2012; Lacey et al., 2015), Lz1120 (Wagner et al., 2009), Co1202 (Vogel et al., 2010; Reed et al., 2010; Cvetkoska et al., 2012), and Core 9 (Roelofs and Kilham, 1983). *Arrows* indicate main river flows (C=Cerava River, K=Koselska River, S=Sateska River, D=Crni Drim River) and *asterisks* indicate major springs (N=Sveti Naum, T=Tushemisht, B=Biljana, V=Dobra Voda). Modified from Reed et al. (2010).

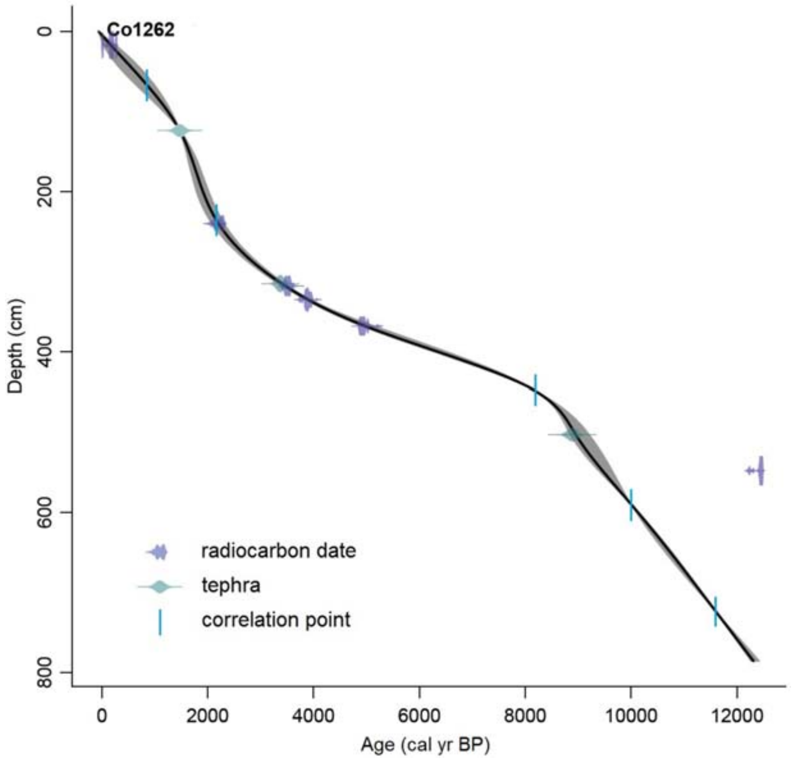

Figure 2. Age-depth model of core Co1262 (modified from Lacey et al., 2015).

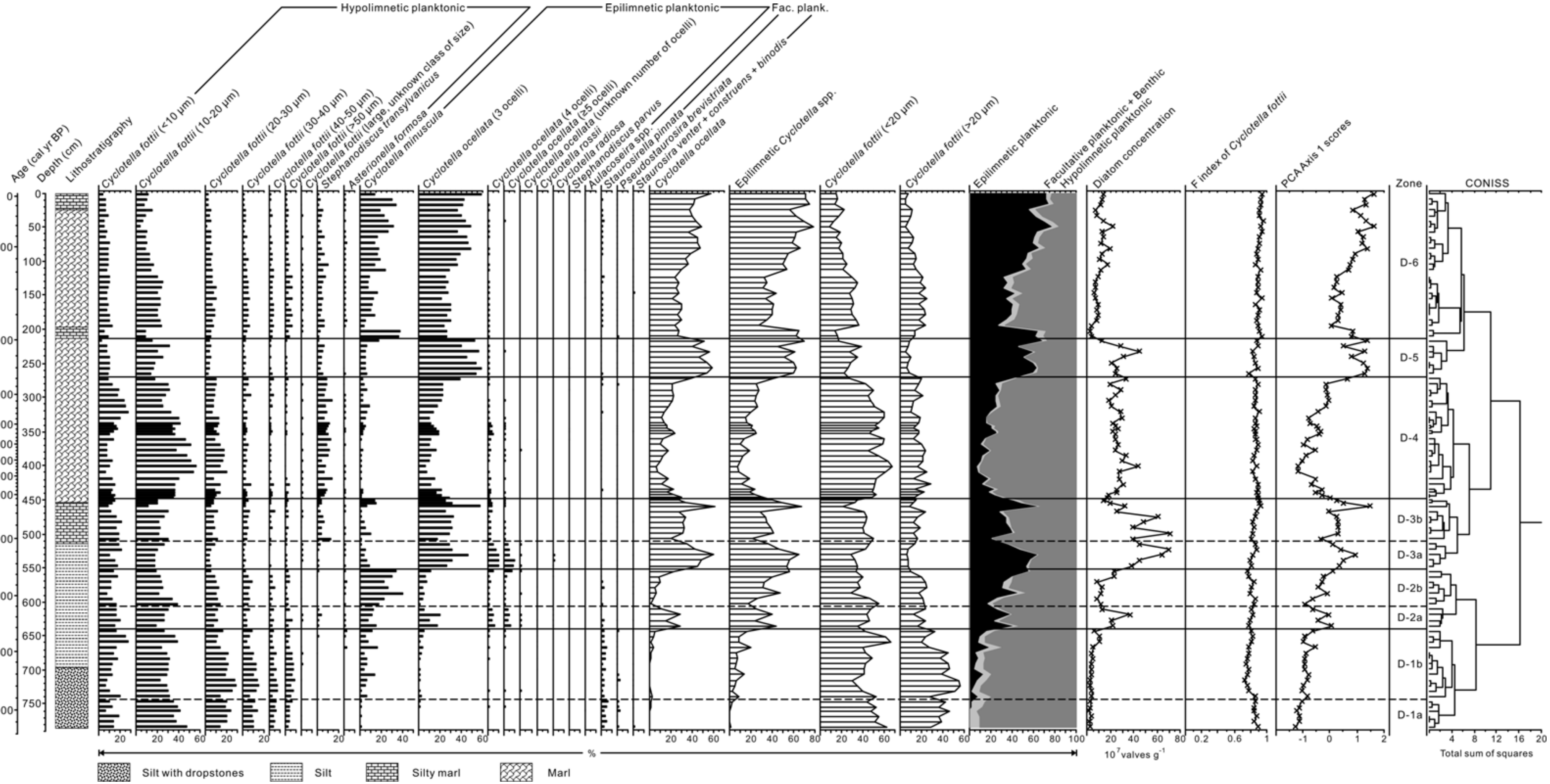

Figure 3. Summary diatom diagram of relative abundance of planktonic and facultative planktonic species from core Co1262, showing lithostratigraphy (modified from Wagner et al., 2012), diatom concentration, *C. fottii F* index values, and principal component analysis (PCA) Axis 1 scores.

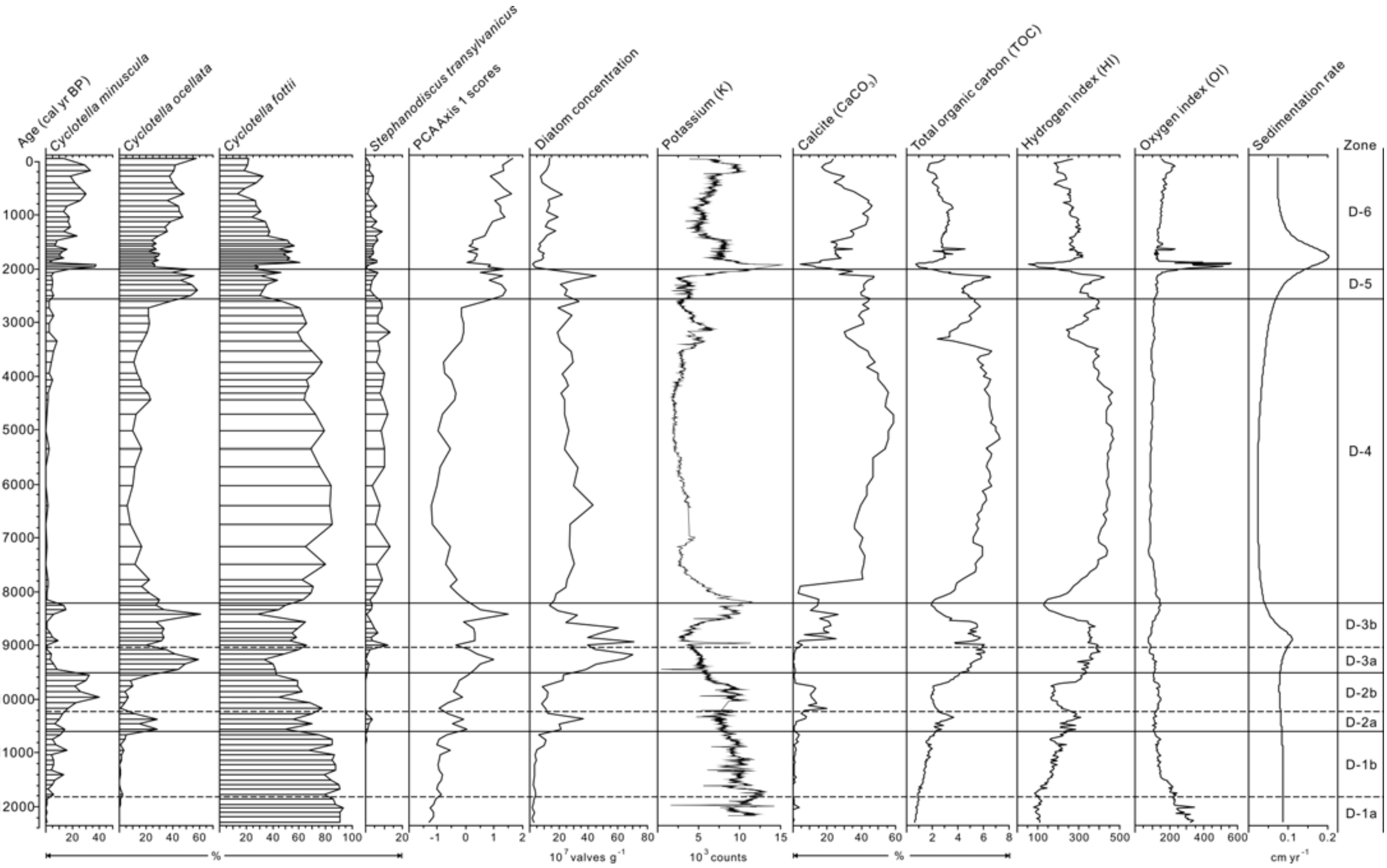

Figure 4. Comparison of diatoms in core Co1262 with sedimentological and geochemical data from the same core. Calcite (CaCO$_3$) content and potassium (K) concentration are from Wagner et al. (2012), and total organic carbon (TOC) content, hydrogen index (HI) and oxygen index (OI) are from Lacey et al. (2015).

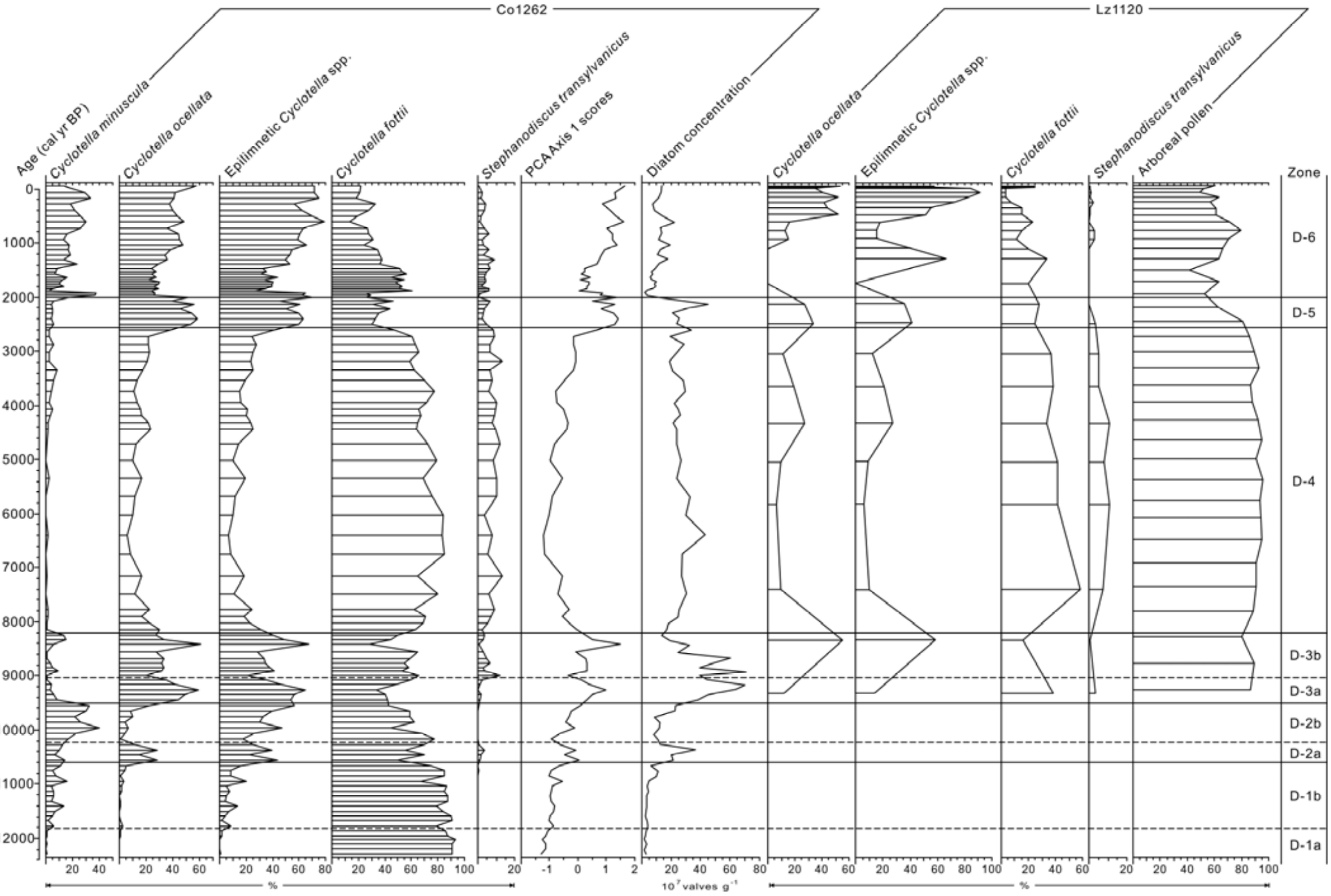

Figure 5. Comparison of diatoms in core Co1262 with diatom and palynological data from core Lz1120, southeastern Lake Ohrid (Wagner et al., 2009).