Ecosystem regimes and responses in a coupled ancient lake system from MIS 5b to present: the diatom record of lakes Ohrid and Prespa

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Abstract

We reconstruct the ecosystem interactions since the last interglacial period in the oldest, most diverse, hydrologically connected European lake system, by using palaeolimnological diatom and selected geochemistry data from Lake Ohrid “DEEP site” core and equivalent data from Lake Prespa core, Co1215. Driven by climate forcing, the lakes experienced two adaptive cycles during the last 92 ka: “interglacial and interstadial” and “glacial cycle”. The patterns of short-term ecosystems reorganizations, e.g. regime shifts within these cycles appear synchronous in both lakes, while differences occur in the inferred amplitudes of variation. The deeper Lake Ohrid shifted between ultra oligo- and oligotrophic regimes in contrast to the much shallower Lake Prespa, which shifted from (oligo-) mesotrophic to eutrophic conditions. Due to the high buffer capacity, Lake Ohrid appears relatively resistant to external forcing, such as climate change. Recovering in relatively short time from major climate change, Lake Prespa is a resilient ecosystem. At Lake Ohrid's DEEP site, this decoupling of the response is evident in the prolonged and gradual changes during the MIS 5/4 and 2/1 transitions. These response differences and the lakes' different physical and chemical properties may limit the influence of Lake Prespa over Lake Ohrid. Regime shifts of Lake Ohrid due to the hydrological connectivity with Lake Prespa are not evident in the data presented here. Moreover, a complete collapse of the ecosystems functionality and loss of their diatom communities did not happen in either lake for the period presented in the study.

Key words: Lake Ohrid, Lake Prespa, diatoms, regime shifts, resilience, ecosystems interactions

1 Introduction

The structure and functions of the continental ecosystems constantly changed throughout the Quaternary, driven by a series of successive climate variations at different temporal scales. As dynamic entities, the ecosystems developed through these fluctuations with a "panarchy", defined as a series of hierarchical adaptive cycles interacting across multiple scales of space and time (Holling, 2001; Delcourt and Delcourt, 2004; Allen et al., 2014). Four functional phases, controlled by top-down and bottom-up processes, have been identified within these cycles, growth (r), conservation (k), release (Ω), and reorganization (α). Change in the processes controlling the ecosystem's structure and functions can lead to regime change and creation of new self-organized structures (Holling, 1986). Regime shifts may occur within one adaptive cycle or between adaptive cycles at different scales, and cause reorganization or even sometimes a complete ecosystem collapse (Allen et al., 2014). Such catastrophic regime changes, marked by species communities loss and consequently, collapse of the ecosystem's functions have been recorded in many of the world's oldest lakes, like Baikal in Russia, Hövsgöl in Mongolia, Tanganyika and Malawi in East Africa (Karabanov et al., 2004; Cohen et al., 2007; Burnet et al., 2011; Scholz et al., 2011). Based on the intensity of forcing, and their physical, chemical and biological properties these lakes had different capacities to adapt, restore and/or reorganize their panarchy. The adaptive capacity of an ecosystem is intrinsically related to its resilience (Allen et al., 2005; Allen and Holling, 2008), and therefore, research on sediment records from ancient lakes is important for understanding the past adaptive capacities, regime changes, and resilience of these unique ecosystems.

In Europe, such Quaternary archives are neighboring lakes Ohrid and Prespa, located on the Balkan Peninsula. Since the Pliocene origin of their tectonic basins, more than 1 Ma co-existence and co-evolution (Stanković, 1960) resulted in the oldest and most diverse permanent lake systems in Europe (Albrecht and Wilke, 2008; Levkov and Williams, 2012). Understanding the external and internal drivers for these basins is critical for determining the high level of biological endemism of especially Lake Ohrid. At present, the lake system has unique spatial interaction due to hydrological connectivity via a karstic system in Mt. Galičica (Anovski et al., 1997, 2001). About 20% of the Lake Ohrid water inflow originates from Lake Prespa, and, therefore, the much shallower and nutrient rich Lake Prespa can potentially drive changes in Lake Ohrid (Matzinger et al., 2006). By applying a system analytical approach, Matzinger et al. (2006) assessed the anthropogenic influence on Lake Prespa, quantified the underground water and nutrient flow and developed linear phosphorus, P model. By using the 1960s' water-level high-stand of Lake Prespa (~855 m above sea level) as a baseline for the calculation, the model indicates that a 20 m water level decrease of Lake Prespa can cause a five-fold increase of its phosphorus concentration, which may lead to a 30% increase of the P load from Lake Prespa to Lake Ohrid (Matzinger et al., 2006). Such a scenario can potentially trigger a regime shift in the physico-chemical properties of Lake Ohrid and affect its fragile endemic community (Watzin et al., 2002; Matzinger et al., 2006, 2007). Therefore, parallel analysis of long-term temporal variations under changing climate boundary conditions from Quaternary sedimentary records of both lakes is important for identifying the potential interdependence between the lakes.

Between 2005 and 2012, multiple cores have been retrieved at different locations from lakes Ohrid and Prespa, the oldest dating to ca. 135.0 ka (Co1202, Ohrid) and 92.0 ka (Co1215, Prespa) (Vogel et al., 2010a; Damaschke et al., 2013). While environmental variations in Lake Prespa were resolved at high resolution for the last ca. 92.0 ka (Aufgebauer et al., 2012; Wagner et al., 2012; Panagiotpoulos et al., 2013, 2014; Cvetkoska et al., 2014a, 2015), the presence of hiatuses or the age of the retrieved cores from Lake Ohrid (Wagner et al., 2008; Vogel et al., 2010b; Lacey et al., 2014; Zhang et al., 2016) hampered a detailed palaeoenvironmental comparison between the two lakes until today.

As part of the project Scientific Collaboration on Past Speciation Conditions in Lake Ohrid (SCOPSCO), a successful International Continental Scientific Drilling Program (ICDP) drilling campaign was carried out at Lake Ohrid in 2013. A sediment sequence spanning >1.2 Ma (Wagner et al., 2014a) was recovered at the “DEEP site” in the central part of the lake. Multi-proxy analyses of this sequence currently proceed towards understanding the influence of the past geological and environmental events on the biological evolution of the lake taxa, as one of the main project objectives.

Aiming to assess the potential interactions between the lakes, we compare Lake Prespa’s dynamics, as already inferred from core Co1215 diatom, pollen, and geochemistry data with the diatom and selected bio(geochemical) data from the same age interval (ca. 92.0 ka to present) of the DEEP site sediment sequence. Here, we apply the concept of panarchy and consider lakes Ohrid and Prespa as lower-scale entities of the higher hierarchical, landscape scale, as justified by their hydrological connection. Trends in the multi-proxy dataset are used to reconstruct and compare the adaptive cycles, regime shifts and assess the response mechanisms to external disturbances on ecosystem scale (e.g. lakes Ohrid and Prespa). At higher hierarchical level, we aim to assess the potential interconnectivity between the lakes in order to understand the cross-scale linkages and recognize the capacity of Lake Prespa as a driving force of regime shifts in Lake Ohrid.

2 Environmental setting

Harboring more than 300 endemic faunal species (Föller et al., 2015), Lake Ohrid, Macedonia/Albania (41°01’N, 20°43’E, 693 m a.s.l., Fig. 1) has the highest index of endemism of all ancient lakes, when its surface area of 358 km^2 is taken into account (Albrecht and Wilke, 2008). With a mean and maximum water depth of 155 m and 293 m, respectively (Lindhorst et al., 2015), it is a deep, calcium-bicarbonate $Ca(HCO_3)_2$ dominated, oligotrophic lake. The hydrological balance of the lake is regulated by 37.9 $m^3 \times s^{-1}$ inflow, of which ~25 % derives from direct precipitation, ~25% from river input and ~50% from the karst aquifers, and the outflow through the river Crni Drim, (~60%) and evaporation (~40%, Matzinger et al., 2006). The estimated water residence time is ca. 70 years. The average monthly air temperature of the surrounding area is 26°C during summer and −1°C in winter and the annual precipitation averages to 750 mm/year. Recent investigations revealed that global warming and local anthropogenic impact led to an increase in total phosphorus concentration from ~1.3 mg P $\times m^{-3}$ in historic times (ca. 150 years ago) to 4.5 mg P $\times m^{-3}$ today (Matzinger et al., 2006, 2007).

Lake Prespa, located at the border of Macedonia, Albania, and Greece (40° 46'–41° 00' N, 20° 54'–21° 07' E, Fig. 1) is situated at 849 m a.s.l. It is a tectonic lake which belongs to a former lake complex, called Dessarets (Stanković, 1960), but its age is still uncertain. Although it hosts fewer endemic species, it has been suggested that the endemic faunal species might be older than those in Lake Ohrid (Karaman, 1971). In terms of its physical properties, Lake Prespa is a large, 254 km^2, relatively shallow lake with ~14 m mean and ~48 m maximum water depth. At present, the estimated hydraulic residence time is ca. 11 years, but it varies highly with changing lake-levels; and for example, at ~19 m mean water depth during the 1980s, this number was ca.17 years (Matzinger et al., 2006). The water input, $16.92\ m^3 \times s^{-1}$, is via river inflow and catchment runoff (56%), direct precipitation (35%), inflow (9%) from the nearby Lake Micri Prespa (Fig. 1), and groundwater input (no data available). The output is via evaporation (52%), water abstraction for irrigation (2%) and subsurface outflow through the karstic aquifers of Galicica Mountain (46%, Matzinger et al., 2006). The average monthly temperature in the surrounding area is 21°C in summer and 1°C in winter, and the annual precipitation varies between 720 in the lowlands and $1200\ mm \times yr^{-1}$ on the mountains (Hollis and Stevenson, 1997). The lake is highly sensitive to external disturbances (e.g. climate change) and water loss; major lake-level fluctuations including a lake-level decline of almost 10 m have been documented between 1950 and 2009 (Popovska and Bonacci, 2007). In addition, recent monitoring programs of the lake revealed $\sim 31\ mg \times m^{-3}$ TP concentration (Matzinger et al., 2006), and $\sim 162\ t \times yr^{-1}$ TP input from the river tributaries (Krstić, 2012).

3 Methodology

3.1 Core recovery and chronology

Core "5045-1" was recovered at the DEEP site in the central part of Lake Ohrid within the scope of the SCOPSCO deep drilling campaign in 2013 (Fig. 1). Six parallel boreholes (A to F) at 243 m water depth were drilled down to a maximum sediment depth of 569 m below the lake floor (m blf) and a total 1526 m of sediment cores were recovered. Comprehensive details of the drilling procedure, sediment recovery and results from the preliminary analyses of core catcher samples are provided in Wagner et al. (2014a). The age model for the upper 247.8 m of the composite sequence of the DEEP site for the sediment core and downhole logging data is based on 11 tephrostratigraphic tie points (first order tie points), and on tuning (bio-)geochemical proxy data to orbital parameters (second order tie points) (Baumgarten et al., 2015; Francke et al., 2016). In order to compare the same age intervals in lakes Ohrid and Prespa, we analyzed the uppermost 37.5 m of the DEEP site sequence, which represent the last ca. 92.0 ka according the age-depth model. This period is well-constrained by the occurrence of the Y5 tephra layer at ca. 39 ka, the Y3 tephra layer at ca. 29 ka, and the Mercato tephra layer at 8.5 ka in the DEEP site sediment sequence (Baumgarten et al., 2015; Leicher et al., 2015; Francke et al., 2016).

The age-depth model of the 17.7 m long core Co1215 from Lake Prespa is based on 11 tephrochronological tie points, radiocarbon ^{14}C dating, electron spin resonance dating and comparison with the NGRIP ice core data. An age of ca. 92.0 cal ka BP was extrapolated for the base of the sequence; details are provided in Damaschke et al. (2013).

3.2 Analytical work

The core analysis of the 37.5 m sequence from the DEEP site comprises non-destructive X-ray fluorescence scanning (ITRAX core scanner, Cox Analytical, Sweden) for potassium intensities (K), and measurements of total carbon (TC), total inorganic carbon (TIC, DIMATOC 100 carbon analyzer, Dimatec Corp., Germany). The total organic carbon (TOC) content was calculated from the difference between TC and TIC. Total nitrogen (TN) was analyzed using an elemental analyzer (vario MICRO cube, Elementar Corp.) after combustion at 1150°C and used to calculate the ratio between TOC and TN (abbreviated as C/N). Biogenic silica concentrations (BSi) were inferred by means of Fourier Transform Infrared Spectroscopy at the University of Bern, Switzerland following the method outlined in Vogel et al. (2008) and the calibration after Meyer-Jacob et al. (2014). All bio(geochemical) analyses are described in more detail in Francke et al. (2016).

Diatom analysis on the DEEP site core was performed on 235 samples in total (resolution 16 cm, ca. 0.3−0.5 ka), prepared from freeze-dried sediment subsamples according the method of Cvetkoska et al. (2012). Known aliquots of cleaned samples were used to estimate the absolute diatom concentrations, “DC” ([n] valves * 10^7/g dry sediment), employing the sedimentation tray method of Battarbee (1986). Permanent diatom slides were prepared using Naphrax® as mounting medium. Around 350 diatom valves per slide were counted at 1500x magnification with an Olympus BX51 microscope. On exception, at least 100 valves per sample were counted in diatom assemblages with low species diversity and/or concentration. Species identification followed Levkov et al. (2007), Levkov and Williams (2011, 2012), Cvetkoska et al. (2012, 2014b), Jovanovska et al. (2013), and Pavlov et al. (2013). Diatom accumulation rates, "DAR" ([n] valves * 10^6 cm^{-2} ka^{-1}) were calculated by multiplying the dry sediment accumulation rates, "SAR" (g cm^{-2} ka^{-1}) and the DC, Anderson (1989). To assess the preservation quality in the sequence, the F index of Ryves et al. (2001) was calculated for *Cyclotella fottii* Hustedt as a proportion of the number of pristine valves and the total number of classifiable valves of the species. Values of F=0 indicate partial dissolution of all valves and F=1 means ideal preservation. The variation in the diatom data was explored by detrended correspondence analysis, "DCA", and with a gradient length of 2.2, principle component analysis, "PCA" was appropriate (Jongman et al., 1995). To maximize the apparent variance, PCA was run on species morphotypes at a sub-species level. The Spearman's rho rank-correlation test (‘‘stats’’ version 0.8-2; R Core Team, 2012) was used to analyze the correlation between the dominant diatom species abundance, the DAR, DC and the (bio)geochemistry data (Table 3). At both sites, the constrained stratigraphic diatom zones were defined by the incremental sum of squares distance metric of the CONISS program (Grimm, 1987).

The analytical approaches of the geochemistry, isotope, lithology, pollen, and diatom analyses of Lake Prespa core Co1215 have been extensively described in Aufgebauer et al. (2012), Wagner et al. (2012), Damaschke et al. (2013), Leng et al. (2013), Cvetkoska et al. (2014a, 2015), Panagiotopoulos et al. (2014). Diatom analysis on core Co1215 was carried out on 222 samples in total (resolution 8 cm, ca. 0.1−0.4 ka) and the variation in the diatom data was analyzed with DCA based on the >2.5 gradient length (Cvetkoska et al., 2015). Comparative details of the diatom analytical methods applied to both site cores, DEEP and Co1215, are presented in Table 1.

4 Principal diatom results and environmental controls

In total, 141 diatom species were identified for the past ca. 92.0 ka of the DEEP site core. The diatom diagram (Fig. 2) displays 31 species and morphotypes, present at >2% in the assemblages. The diatom assemblages are dominated by planktonic taxa, mainly from the genus *Cyclotella* (Kützing) Brébisson. The facultative planktonic "FP" and benthic life habitat groups are represented with higher species numbers, but low overall relative proportions due to the large depth of the coring location, which is beyond the optimal depth for their distribution in the lake. The most abundant FP and benthic genera are *Amphora* Kützing, *Cocconeis* Ehrenberg, *Gomphonema* Ehrenberg, *Diploneis* Ehrenberg ex Cleve, *Navicula* Bory, *Staurosira* Ehrenberg and *Staurosirella* D. M. Williams et F. E. Round. Following previous studies of Reed et al. (2010), Cvetkoska et al. (2012), and Wagner et al. (2014a), the dominant planktonic taxa were split in morphotypes, useful to test the link between the long-term ecosystem dynamics and species evolution in the DEEP site record. *Cyclotella fottii* was initially split in four morphotypes, based on valve size, and size and shape of the central area, while the *C. ocellata* Pantocsek complex was split in eight morphotypes based on valve size and number of ocelli in the central area.

Based on previous studies (Stanković 1960; Allen and Ocevski, 1976), the vertical distribution of the phytoplankton in Lake Ohrid is primarily driven by temperature, in combination with light, nutrient availability, and water mixing. The past 92.0 ka of the DEEP site diatom record are generally dominated by three planktonic species with different autecology, *C. fottii, C. ocellata* and *C. minuscula* (Jurilj) Cvetkoska. *Cyclotella fottii* is an oligotrophic, stenothermic species, adapted to low temperatures; viable populations of the species have been found at more than 100 m water depth, where the light availability is far below the optimal intensity for photosynthesis and temperature is permanently reduced (Stanković 1960). This indicates that low light availability is not limiting *C. fottii*, while temperature is likely more important factor for its vertical distribution and abundance in the phytoplankton. *Cyclotella ocellata* is an ecologically successful species of wide distribution, though, in Lake Ohrid, it dominates in the epilimnion during the spring and summer season (Stanković 1960; Zhang et al., 2016). This is the zone of warmer temperatures, higher light availability, but lower nutrients than the hypolimnion. However, in Lake Ohrid *C. ocellata* has been interpreted as mesotrophic and an indicator of increased productivity in comparison to *C. fottii* (Wagner et al., 2009; Lorenschat et al., 2014; Zhang et al., 2016). In lack of autecological data for *C. minuscula* we relied on previous study of Cvetkoska et al. (2014a), the findings of Winder et al. (2009), and the comparison with the geochemical proxies. At the DEEP site, maxima in the relative abundance of *C. minuscula* correspond to the Y5, Y3, and the Mercato tephra layers and peaks in K intensities. This is also shown by the high-resolution study of the diatom response to the Y5 tephra impact on lakes Ohrid and Prespa by Jovanovska et al. (2016). The tephra influx/deposition increases the silica availability, which is enhancing the diatom productivity, consequently leading to strong competition for nutrients and light resources.

At present, most of the FP and benthic species in Lake Ohrid are found between the shallow littoral zone and ~50 m water depth (Levkov et al., 2007). The overall low relative abundances, 5−15 %, of these species in the DEEP site record result from the coring location, and thus add little supporting evidence to the interpretation. However, the periods of their slightly increased abundances during the past ca. 92.0 ka can be interpreted as indication for intensified transport from the shallower parts of the lake due to wind-induced wave activity and lake-internal currents (Vogel et al., 2010c).

The PCA (Fig. 3, Table 2), displays *C. fottii*, *C. ocellata* (3 ocelli) and *C. minuscula* aligned along the low–high values range of PCA Axis 1, reflecting the overall trend of temperature-driven diatom response, due to over-dominance of *C. fottii*. PCA Axis 2 displays clustering of the *C. ocellata* morphotypes with 4 and 5 ocelli along the positive values, reflecting their dominance during the last interglacial. For both axes, the Holocene signal appears muted between ca. 7.0–2.0 ka due to presence of taxa, like *Stephanodiscus transylvanicus* Pantocsek and *S.* cf. *minutulus* (Kützing) Cleve et Möller, indicative of nutrient change per se (Kilham et al., 1986; Wagner et al., 2009; Cvetkoska et al. 2012; Zhang et al., 2016).

The DC and DAR (Figs 2, 4) show high positive correlation values with the other (bio)geochemistry proxies (BSi, TOC, TIC, C/N, see Table 3). In Lake Ohrid sediments, BSi and TOC are of mainly authigenic origin, indicating the primary productivity in the sediment record (Wagner at al., 2009; Vogel et al., 2010b; Francke et al., 2016). In addition, by adjusting the DC to the sedimentation rates, DAR can be used to qualitatively assess the overall, glacial-interglacial scale trends of diatom productivity in the record.

Regarding the interpretation of the C/N ratios, as an indication for the source of organic matter ‘OM’, we point to the study of Lacey et al. (2014) on the Lini sequence where it was demonstrated that in Lake Ohrid, the ‘OM’ is predominantly of pure algal source. The contribution of vascular vegetation to the OM at the DEEP site is also highly unlikely due to the coring location. Nonetheless, low C/N ratios (ca. 4) during the glacials can also result from enhanced supply of clay-bound ammonium following mineral soil erosion rather than algal OM, along with ongoing organic carbon degradation (Holtvoeth et al., 2016).

In nature, the biotic response to multiple environmental factors depends on the response to the single dominant (limiting) driver, and the chance of a driver of large effect being present increases with the number of drivers (Brennan and Collins, 2015). On a glacial-interglacial scale, multiple environmental drivers change synchronously with rising and/or declining temperatures, like the light and nutrient availability. In case of Lake Ohrid, the autecology of the species (e.g. alternations between *C. fottii* and *C. ocellata* dominance) and the significant correlation of their relative abundances with the other productivity related proxies (TOC, BSi, DC, DAR) allow to infer the orbital timescale trends in the diatom data as primarily driven by the large-scale temperature changes. Consistently with the interpretation of the diatom response at the Lini site (core Co1262; Zhang et al., 2016) we do not exclude the influence of other drivers, like nutrients, wind-induced water mixing, thermal stratification, light etc., but consider these factors as drivers that may play more important role during millennial timescale events.

5 Ecosystems dynamics

In the DEEP site sequence, four major, hierarchical diatom zones (DZ 1–4, Fig. 2), each divided in 4–6 subzones, were identified during the last ca. 92.0 ka. The diatoms are compared to selected geochemistry data, biogenic silica (BSi) and potassium (K) content in the record (Fig. 4). Diatom zones are compared and discussed according the Marine Isotope Stages (MIS) (Lisiecki and Raymo, 2005). For a detailed overview of the diatom data and palaeoenvironmental interpretation of Lake Prespa core Co1215, the reader is referred to Cvetkoska et al. (2014a, 2015).

The biological, chemical and physical components of the ecosystems constantly fluctuate, even sometimes at slow rates (Scheffer and Carpenter, 2003). Therefore, we apply the term regime, referring to the periods of diatom and bio(geochemistry) inferred ecosystems dynamics in terms of trophy and/or lake-levels. Changes in the diatom communities’ structure related to changes in the inferred lake’s dynamics are considered as regime shifts.

Regarding the comparison between both sediment sequences, the age models of Ohrid DEEP site core and Prespa core, Co1215 are independent and only few direct correlation points via the occurrences of well-known tephra layers exist (e.g., the Y5 and Mercato tephra). Therefore, the comparisons of the diatom data (and inferred temperature/trophic changes) need to be done carefully. This is especially the case of the single spikes, which may have easily an offset of several centuries to millennia, particularly in the lower portion of the Prespa core due to absence of absolute age control (tephra). However, the lack of similar abrupt peaks in the data is a good basis for comparing the overall trends and patterns in both records.

5. 1 The last interglacial, MIS 5 (92.0−71.0 ka; DZ 4d-b)

5.1.1 MIS 5b (92.0−85.0 ka; DZ 4d)

The MIS 5b period in Lake Prespa diatom record was interpreted as an unstable, transitional phase of moderate, but variable moisture availability and temperatures. Low-lake-level phases characterized by oligo-mesotrophy in Lake Prespa occurred at 90.0, 88.4 and 85.6 ka (Cvetkoska et al., 2015).

The basal diatom zone, (DZ 4d) in Lake Ohrid DEEP site core is marked by dominance of the *C. ocellata* complex until 88.7 ka, when *C. minuscula* peaks with ca. 65% relative abundance, taking over a major part of the epilimnetic diatom productivity to the end of MIS 5b (Figs 2, 4). The autecology of *C. minuscula* indicates that its dominance was favored by the increased clastic input in this part of the record, rather than warmer temperatures, as it is also reflected by the corresponding increase of K content (Fig. 4) (Francke et al., 2016). The low DAR match well with low BSi, TOC and C/N ratio, suggesting less productivity and/or preservation of the organic matter (Francke et al., 2016). The overall comparison between both records indicates that both lakes responded to the similar, transitional phase of moderate temperatures, but lake-level fluctuations in Lake Prespa do not find an equivalent in Lake Ohrid DEEP site.

5.1.2 MIS 5a (85.0−71.0; DZ 4c, b)

In Lake Prespa, a signal of climatic drought between 85.0 and 83.0 ka causing a lake-level decline and a shift to a regime of highest productivity in the record was interpreted from the diatom and pollen data (Panagiotopoulos et al., 2014; Cvetkoska et al., 2015). A second lake-level low-stand at Lake Prespa between 77.6 and 76.6 ka, related to decreased effective precipitation, occurred before the end of the last interglacial, which is marked at 70.2 ka in the diatom record (Cvetkoska et al., 2015). Sedimentological, hydroacoustic data and bivalves indicate another lake-level low-stand around 74.0 ka (Wagner et al., 2014b), but this is not reflected in the Co1215 diatom data.

In Lake Ohrid DEEP site diatom record, the period between ca. 85.0 and 78.0 ka is characterized by the dominance of *C. ocellata* morphotypes with 4 and 5 ocelli (Fig. 2) and high overall DC and DAR (Figs 2, 4). Similar diversification and presence of different *C. ocellata* morphotypes during MIS 5, MIS 3 and the Holocene was observed by Reed et al. (2010) and Cvetkoska et al. (2012). To this point, the hypothesis of climatically triggered species evolution seems quite plausible, even though revealing the nature of this diversification requires more data from the earlier Quaternary. The higher productivity inferred from the diatom data in this part of the record is also seen in the increased BSi content, high TOC values and C/N ratio (Fig. 4). In a phase of constant SAR, this implies a temperature-related increase in the diatom productivity. The diatom signal of warmer climate is also supported by the high TIC content, indicative of increased endogenic calcite precipitation and/or preservation. Small increase in the abundance of *C. fottii* at ca. 76.5 ka, marks a return to dominance of the typical *C. ocellata* morphotypes.

The diatom and geochemistry data show that the overall dynamics of Lake Ohrid’ DEEP site during MIS 5b and 5a are primarily related to climate change. The absence of mesotrophic species and the lack of bio(geochemical) evidence for a lake-level decline in core 5045-1 support the notion that the periods of low lake-levels and highest productivity in Prespa between 85.0 and 71.0 ka did not affect Lake Ohrid, at least in its deepest and central parts. This notion can be further supported by the seismic data, indicating a stepwise regression of Lake Ohrid water level from a prominent low-stand of ~60 m bellow the modern lake-level that occurred during MIS 6, but had only minor effects on the lake surface area, coastline, and habitat (Lindhorst et al., 2010).

5.2 The last glacial, MIS 4–2 (71.0–14.0 ka; DZ 4−1f)

5.2.1 MIS 4 (71.0−57.0; DZ 4a, 3e, part of DZ 3d)

In Lake Prespa, the glacial conditions during MIS 4 triggered a progressive opening of the landscape (Panagiotopoulos et al., 2014) and a regime shift to low lake-levels, evident by low plankton abundances and diatom growth restricted to the shallow littoral habitats in a low productive lake (Cvetkoska et al., 2015).

Contrary, the glacial climate signal in Lake Ohrid DEEP site diatom record appears muted between 70.5−65.3 ka due to the high relative proportions, 30−50 %, of the epilimnetic, thermophilous, spring/summer species *C. ocellata* (Fig. 2, DZ 4a). At the same time, the low DAR, BSi and TOC point to low diatom productivity and/or enhanced OM decomposition. High *C. minuscula* abundance and K intensities in this period (Fig. 4), indicative of enhanced clastic supply due to catchment erosion are consistent with climate cooling. Nonetheless, the high relative abundances of *C. ocellata* between ca. 70.5 and 65.3 ka indicate that probably the spring/summer temperatures of the epilimnetic zone were still favorable for its growth implying a gradual transition of Lake Ohrid towards the glacial, unlike Lake Prespa, where the MIS 5/4 transition is marked with a sharp boundary ca. 70.2 ka.

The dominance of *C. fottii* between 65.3 and 60.0 ka (Fig. 2) in a zone of low preservation quality indicates that the diatom productivity was mainly restricted to the hypoliminon. In addition, the high proportions and/or dominance of *C. fottii* morphotypes >30 µm can be related to ultra(-oligotrophic) conditions, and consequently low competition and decreased grazing pressure, reflecting the cold glacial climate conditions. Similarly, large-celled diatom populations have been noted in other ancient lakes (e.g. Baikal, Hövsgöl) and it is supposed that they reflect oligotrophy, in contrast to smaller-celled diatoms which are more competitive in conditions of limiting nutrients and light (Stoermer et al., 1989; Edlund et al., 2003).

5.2.2 The interstadial, MIS 3 (57.0−29.0 ka; part of DZ 3d, DZ 3c-a, DZ 2d, c)

In Lake Prespa, the increased moisture availability at the interstadial onset prompted an increasing lake-level, but the productivity remained low until 38.2 ka. Aridification and/or cooling were inferred from the diatom and pollen data at ca. 29.0 ka (Panagiotopoulos et al., 2014; Cvetkoska et al., 2015).

The start of the interstadial warming in the DEEP site diatom record is documented between ca. 57.5 and 52.0 ka by a successive increase in the relative proportions of *C. ocellata* (25−35%, Fig. 2) and BSi concentrations (Fig. 4), as well as decreasing K content. However, low BSi, TOC, DAR and DC in assemblages dominated by *C. fottii* and *C. minuscula* between 57.5 ka and 35.0 ka suggest low productivity and/or enhanced decomposition, and similarly, as in Prespa indicate that the interstadial warming was insufficient to enhance the dominance of the epilimnetic, thermophilous species. The decline of *C. ocellata* to <5% and increased abundances of *C. fottii* (Fig. 2) indicate the return to colder conditions after ca. 33.0 ka, culminating in the return to glacial climatic conditions in Lake Ohrid at ca. 28.3 ka.

During MIS 3, a change in the structure and productivity of the diatom assemblages in Lake Prespa core Co1215 was related to the joined effect of the CI/Y5 tephra and the inferred climate aridity/cooling at ca. 39.3 ka (Wagner et al., 2012; Leng et al., 2013; Panagiotopulos et al., 2014; Cvetkoska et al., 2015).

Similarly, the most notable features of MIS 3 in Lake Ohrid are two maxima in DAR and DC between 39.2–38.8 ka and at ca. 29.0 ka, prompted by ca. 85% and ca. 55% relative abundance of *C. minuscula*, respectively (Fig. 2). Both events coincide with high K intensities (Fig. 4), and correspond to the Y5 and Y3 tephra layers in the DEEP site sequence (Leicher et al., 2015). The diatoms indicate that the Y5 and Y3 tephra deposition disturbed the diatom communities by creating conditions of low transparency and high silica availability that enhanced the dominance of small celled *Cyclotella* species, due to the strong competition for nutrients and light resources. In a case study with leaching experiments on fresh ash samples from Popocatépetl and Etna eruptions, D'Addabbo et al. (2015) showed that there is only a little impact of tephra on Lake Ohrid water, except for Si and F saturation. Here, for example, the over-dominance of *C. minuscula* after the Y5 tephra impact in both lakes (this study, Cvetkoska et al., 2015; Jovanovska et al., 2016), is compensated by its small valve size (3−7 μm) as superior adaptation enhancing its competitive strength during such conditions.

5.2.3 The last glacial maximum, MIS 2 (29.0−14.0 ka; DZ 2b, a, 1f)

During the LGM, Lake Prespa experienced low productivity and low lake-levels until 15.7 ka, and the diatom communities were dominated by facultative planktonic and benthic species (Cvetkoska et al., 2014a, 2015).

In Lake Ohrid, minima in DAR, DC, and low BSi content between ca. 29.0 and 13.6 ka (Fig. 2) indicate low productivity and low temperatures during the last glacial maximum. The low TOC and TIC (Fig. 4) additionally support this interpretation, suggesting enhanced decomposition of the organic matter and dissolution, caused by cold/dry glacial regime (Wagner et al., 2009; Vogel et al., 2010b; Francke et al., 2016). Similar conditions with winter-ice cover at least in the littoral zone, frequent complete overturn of the lake and substantial opening of the landscape and lowering of vegetation belts were interpreted from multi-proxy analyses of other Lake Ohrid cores Lz1120 and Co1202 (Wagner et al., 2009; Vogel et al., 2010b), and from the DEEP site pollen record as well (Sadori et al., 2015).

In terms of diatom response, the similar pattern of glacial assemblages dominated by large, robust valves of *C. fottii*, were also observed in the previous diatom records from Lake Ohrid (Wagner et al., 2009; Reed et al., 2010; Cvetkoska et al., 2012). Such similarity indicates that this is a "glacial-climate" driven regime of low productivity and diversity, and not just an artifact of taphonomic bias due to weak preservation. In general, both lakes seem to have buffered climate change during the LGM, since no major changes of the diatom communities, and/or species extinctions have been observed in the diatom records.

5.3 Termination I and the Holocene, MIS 1 (14.0 ka to present; DZ 1e-a)

Unlike the strong response of Lake Prespa to the wet-dry-wet phases between 15.7–12.3 ka due to the Bølling/Allerød (B/A) interstadial and Younger Dryas (YD) (Panagiotopoluos et al., 2013; Cvetkoska et al., 2014a), a first signal of climate warming subsequent to the LGM in Lake Ohrid derives from somewhat higher DAR, DC, TOC and BSi between 13.6 and 11.2 ka (Figs 2, 4). Unusual 15% abundance of "Janus", e.g., heterovalvate cells of *C. ocellata* occurs at ca. 14.0 ka (Fig. 2). The formation of heterovalvate cells is a phenomenon observed in many diatoms and often related to variation in nutrients, pH or temperatures (McBride and Edgar, 1998; Stoermer, 1967; Teubner, 1995). Their increased abundances in core 5045-1 can be tentatively related to improved temperature and light conditions at the end of the LGM, as supported by declining K counts (Fig. 4). At the same time, low TIC implies frequent mixing of the water column and dissolution of calcite during cold/dry winters (Vogel et al., 2010b; Francke et al., 2016).

Indeed, Lacey et al. (2014) and Zhang et al. (2016) interpreted the changes between 12.3 and 11.8 ka in the bio(geochemical) and diatom dataset of the "Lini" core Co1262 as reflection of the YD climate reversal. However, this record dates only back to 12.4 ka and does not provide complete insights into the MIS 2/1 transition. Due to the sampling resolution and presence of hiatuses, cores Lz1120 and Co1202 from Lake Ohrid (Fig. 1) only provided incomplete or inconclusive results for this period (Wagner et al., 2009, 2012; Reed et al., 2010; Vogel et al., 2010a; Cvetkoska et al., 2012). We thus tentatively relate the weakness of response observed at the DEEP site to a combination of the depth at the coring location, low temperatures, and low nutrient availability prior to 11.2 ka.

While rapid water level increase in Lake Prespa was inferred between 10.0 and 8.0 ka (Panagiotopulos et al., 2013; Cvetkoska et al., 2014a), in Lake Ohrid DEEP site record, the presence of *Stephanodiscus* species, indicative of increased nutrient availability, and slightly increased DC and DAR during low SAR imply enhanced productivity between 11.2–9.0 ka. A comparable trend of increased productivity was observed at the Lini site (Lacey et al., 2014), while Zhang et al. (2016) found similar trends of water temperature-induced lake productivity with an interruption between 10.2 and 9.5 ka.

Based on core Co1215 diatom data, sustained moisture availability, high lake-levels and oligo-mesotrophic state prevailed in Lake Prespa between 7.9 and 1.9 ka (Cvetkoska et al., 2014a, 2015). Comparably, at Lake Ohrid DEEP site, maximum BSi content, high TIC and TOC concentrations and diatom assemblages co-dominated by *C. ocellata* and *S. transylvanicus* are observed between ca. 8.9–4.8 ka (Figs 2, 4). The presence of mesotrophic species (e.g. *S. transylvanicus*) in the hypolimnetic zone is rather indicative of warm mid-Holocene climate and high nutrient availability than any influence from Lake Prespa. Although the underground outflow increases with rising water levels at Prespa, the subsequent decrease of the nutrient concentrations in the lake will decrease the nutrient load to Lake Ohrid (Matzinger et al., 2006). Thus, the mid-Holocene inferred oligo-mesotrophy at Prespa, and by inference low nutrients were most likely insufficient to enhance the nutrient load and productivity at Lake Ohrid.

The mid-Holocene at Lake Ohrid is punctuated by two synchronous peaks of *C. ocellata* (ca. 5−7 µm) and *C. minuscula*, with sum abundances of ca. 50% and 75% at ca. 8.5 ka and 7.9 ka, respectively, co-occuring with peaks in K intensities (Figs 2, 4). These pronounced signals are related to the Mercato tephra layer in the DEEP site sequence (Leicher et al., 2015; Francke et al., 2016) and the “8.2 ka” cold event. At this moment we can relate the diatom response to these events - a high-resolution study is necessary to delineate the exact mechanisms of the response during both events.

Around 1.0 ka, the combination of human impact, climate aridification and decreased summer precipitation during the “Medieval Climate Anomaly”, MCA was considered as the tipping point that led to significant lake-level decline at Lake Prespa (Cvetkoska et al., 2014a and references therein). In fact, Prespa’s decline of ~20 m at time of the MCA, as also evident in the position of the historic settlements around the lake (Sibinoviç, 1987), is a close analogue to the modelled lake-level decline of 20 m that can potentially increase the phosphorus load in Lake Ohrid by almost 30% (see Fig. 11 in Matzinger et al., 2006). However, the lack of meso-eutrophic species and low TOC, in combination with the high water depth at the DEEP site coring location and the sample resolution do not support enhanced nutrient levels and, by extension, significant influence from Lake Prespa. Moreover, the co-dominance of *C. ocellata* and *C. minuscula* between 1.5 ka and present at the DEEP site can be related to a combination of warm climate and/or anthropogenic influence, as also shown from the diatom study of core Co1262 from the Lini site (Zhang et al., 2016).

6 Ecosystems internal dynamics and interactions

6.1 Adaptive cycles: thresholds, regimes, resistance and resilience

From the above interpretation and comparison between the lakes, shifts in the diatom communities, and by inference the lakes’ response, are triggered by critical thresholds at different scales of intensity and by different external factors. As pointed out by Cvetkoska et al. (2015) while the diatom response in Lake Prespa is primarily driven by moisture availability, the multi-proxy approach in this study shows that regime shifts in Lake Ohrid are tipped by temperature thresholds, inducing changes in wind activity, light and nutrient availability.

Apart from the encountered differences, two lake’s adaptive cycles can be identified at orbital scale: “interglacial and interstadial” and “glacial cycle”. The glacial cycle of Lake Prespa is characterized by much lower productivity than the interglacial/interstadial cycle, and dominated by facultative planktonic and benthic species (Cvetkoska et al., 2015). The lake experienced multiple regime shifts on sub-orbital time scale, resulting in low or high lake-levels, changes in the trophic status, from (oligo-) meso- to eutrophic and associated productivity changes. Lake Ohrid’s glacial cycle is mainly dominated by the hypolimnetic planktonic *C. fottii* and is characterized by a lower productivity than the interglacial/interstadial cycles (Fig. 2). Within these cycles, short-term regime shifts in the diatom communities occur at sub-orbital time scale, but the lake remained ultra- to oligotrophic. Based on the presented proxy data, there is no indication for lake-level changes throughout the entire studied period.

More importantly, all diatom data show that during the last 92.0 ka both lakes did not underwent catastrophic ecosystem collapses imprinted by loss of the diatom communities, and/or ecosystems functionality, such as happened at other ancient lakes during the LGM, like Baikal and Hövsgöl (Karabanov et al., 2004; Khurshevic et al., 2006).

Assessing the capacity of both ecosystems to absorb disturbances and reorganize in order to retain their functional and structural characteristics implies that both lakes have different response mechanisms. The concept of the "ecosystems resilience" (Holling, 1973) is widely accepted, but also controversial because of its definition of mechanisms and components (Carpenter et al., 2001; Scheffer, 2001; Walker et al., 2004; Lake, 2013). Here, we consider the "resistance" and "resilience" as different components of the ecosystems response to disturbance; by interpreting the resistance in this case as the capacity of the ecosystem to absorb and withstand the disturbance and the resilience as the capacity to reorganize and/or restore or "recover" from the disturbance (Westman, 1978; Webster et al. 1983). As evident from the diatom and bio(geochemical) data, and the comparison of the lakes (Fig. 4), the amplitude of Lake Ohrid's response, though, appears smaller and in some cases more gradually shifting into the new regime, like for example the MIS 5/4 transition (Figs 2, 4).

This implies a high capacity of Lake Ohrid to absorb the disturbances and retain, and/or reorganize its structure, in order to maintain its functionality. Similarly, once pushed into a new regime, a tipping point of much higher intensity is required so the system can reorganize and/or restore a similar dynamic regime. In the DEEP site record, this pattern is evident from the gradual, prolonged "recovery" periods after climate disturbances, as the gradual transition and muted response to the two-step deglaciation pattern of Termination I (cf. Lowe et al., 2008).

Low intensity disturbances in Lake Prespa, however, are occasionally already sufficient to trigger high-amplitude changes in lake-levels and productivity (DCA Axes 1 and 2 in Fig. 4), emphasizing a lower lake capacity to absorb disturbance. An example is the abrupt shift from oligo-mesotrophic to eutrophic state during MIS 5b (Fig. 4). Interestingly, the relatively short periods of “recovery” after these climate-induced disturbances, like for example the rapid lake-level increase after the LGM, demonstrates that Lake Prespa is a resilient ecosystem. These lakes’ specific differences can be attributed to their different physical properties and hydrological balances.

6.2 Lake ecosystem interactions

Understanding the interactions between lakes Prespa and Ohrid requires assessment of several parameters which influence the dynamics of their hydrological connection through the karst system of Mt. Galičica: i) Lake Prespa water balance, ii) the phosphorus P load and TP concentration in the lake, iii) the underground outflow from Lake Prespa, and iv) the P load from Lake Prespa to Lake Ohrid. Matzinger et al. (2006) assessed these parameters, demonstrating that currently, about 20% of Lake Ohrid water inflow and 7% of the TP load originate from Lake Prespa. However, a large part, ~ 65%, of the P load from Lake Prespa is retained in the karst aquifers. Lake Prespa is highly sensitive to water loss, a 5 m lake-level decrease corresponds to a ~25% loss of the total lake volume, which directly affects its water quality by increasing the concentration of dissolved nutrients (Matzinger et al., 2006).

In order to understand the role of Lake Prespa as possible driver of lake-level and/or nutrient shifts in Lake Ohrid over the past 92.0 ka, we explored the panarchy within the “sister lake system” by identifying possible cross-scale linkages between the adaptive cycles and regime changes of both lakes as lower-scale entities of the landscape dynamics.

From the comparison of the multi-proxy inferred lake-levels and productivity of both lakes, (see Ecosystem dynamics, Fig. 4), it is evident that the low lake-levels and eutrophic regimes at Prespa that have occurred during the interglacials, like the MIS 5a and the MCA, do not counterpart similar regimes at Lake Ohrid DEEP site. On the contrary, the glacial, low lake-levels at Prespa can potentially affect Ohrid due to reduced underground outflow and consequently, decreased recharge through the spring area. A glacial inactivity of Ohrid’s karst springs due to permafrost formation in large parts of the lake’s watershed was considered as the main factor inhibiting the calcite precipitation and ostracod preservation in a 10 m core, JO2004-1, recovered from a 100 m water depth in south-western part of the lake (Belmecheri et al., 2009). Such extreme interruption of the underground connection between the lakes can substantially reduce the water input in Lake Ohrid through the spring area and lead to a lake-level decline. However, a diatom-inferred low lake-levels are not evident in the DEEP site data presented here, nor in any of the previous diatom records from cores Lz1120 (Wagner et al., 2009), Co1202 (Reed et al., 2010, Cvetkoska et al., 2012) and Co1262 (Zhang et al., 2016). Indeed, Lacey et al. (2014) already discussed the potential scenario for reduced water input from Prespa during the glacials resulting in lower lake-water $\delta^{18}O$. In addition, carbonates are not completely absent in the glacials, and carbonate (siderite) spikes have been observed in the MIS 4−2 period (Lacey et al., 2015; Francke et al., 2016). Similar spikes during the last glacial were recorded also in Lake Prespa and those comprise siderite (Leng et al., 2013). The palynological analyses of the last ca. 0.5 Ma from the DEEP site sequence support the notion that the lake has been a refugium area for both, temperate and montane trees during glacials (Sadori et al., 2015). Most likely, the moraines shown in Belmecheri et al. (2009) are of older age then the LGM, as also indicated in the pollen based reconstructed LGM temperatures (T annual anomaly of -5 to -10 °C; see Peyron et al., 1998) which may not cause permanent permafrost at the altitudes of Prespa and Ohrid.

As pointed by Matzinger et al. (2006) the P load to Lake Ohrid changes with decreasing Lake Prespa water level, but it highly depends on the following factors: (i) a smaller subterranean outflow is reducing the P input, (ii) declining volumes of Lake Prespa lead to increase in P concentration in the lake and (iii) shorter hydraulic residence time of Lake Prespa decreases its P concentration.

On a Quaternary scale, it can be argued that climate disturbances leading to changes in lake-levels and trophic states in Lake Prespa were probably insufficient to affect Lake Ohrid’s productivity. This decoupling results from the high resistance of Lake Ohrid, or at least the DEEP site, against the disturbances which could have been introduced from Lake Prespa. Moreover, the data shows that from MIS 5b to present, Lake Ohrid did not undergo regime changes introduced by Lake Prespa and did not experienced a phase of collapse, or release (Ω) as defined by Holling (1986).

7 Conclusions

From the presented data, it is evident that apart from the general pattern of synchronously triggered regime shifts by climate change, the lack of similar abrupt peaks in the lake-levels and/or productivity in the sediment records of lakes Ohrid and Prespa, there is no clear indication for a direct link between the lakes' regime changes. While Lake Prespa shifted from shallow eutrophic to deep (oligo-)mesotrophic regimes, Lake Ohrid remained an (ultra-)oligotrophic deep lake system over the last glacial-interglacial period.

In general, both lakes display different response mechanisms to external disturbances. While Lake Ohrid is more resistant to climate change, Lake Prespa is very sensitive, but a resilient ecosystem, and recovers in relatively short time. Nonetheless, both lakes buffered the climate change during the glacials and did not experience loss of the diatom communities and/or catastrophic ecosystem collapses. The overall comparison provides sufficient evidence to disregard the theory of Prespa-dependent regime shifts in Ohrid.

Productivity and/or lake-level changes at Lake Ohrid forced by Lake Prespa are not evident at the DEEP site, which allows the future research on Lake Ohrid a more confident interpretation of the earlier parts of the DEEP site sediment sequence in terms of climate change.

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Table 1. Locations, sediment recovery and summary of methods used for the diatom analyses of cores 5045-1 from Lake Ohrid and Co1215 from Lake Prespa.

	Lake Ohrid ‘5011-1’	**Lake Prespa Co1215**
Drill site location	N 41°02’57’’, E 020°42’54’’	N 40° 57’ 50”, E 20° 58’ 41”
Water depth (m)	243	14 m
Length of composite record (this study; m)	37.5	17.7 m
Age (ka BP)	92.0	92.0
Sample resolution for diatom analysis (cm, ka)	16, ca. 0.3−0.5	8, ca. 0.1–0.4
Total number of slides	235	222
Stratigraphic plots of relative diatom abundances	Tilia/TGView v. 1.7.16. (Grimm, 1987)	
Diatom assemblages zonation	CONISS (Grimm 1987)	
Multi-proxy stratigraphic diagrams	C2(Juggins 1991–2007)	
Ordination	PCA (SD = 2.2), Canoco 5 (ter Braak and Šmilauer (1997–2014)	DCA (SD > 2.5), R “stats” v. 0.8-2 (R Core Team 2012)

Table 2. Summary results of the unconstrained PCA ordination of 235 diatom samples from Lake Ohrid DEEP core and the DCA ordination of the 222 samples from Lake Prespa core Co1215 (modified from Cvetkoska et al., 2015).

SD (PCA) = 2.2, SD (DCA) > 2.5

Lake Ohrid, PCA Axes	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.44	0.13	0.09	0.06
Explained variation (cumulative)	44.46	57.08	66.30	72.24
Lake Prespa, DCA Axes	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.47	0.23	0.17	0.14
Decorana values	0.50	0.32	0.12	0.08

Table 3. Spearman's rho (q) coefficient values for the correlations between selected diatom data, and geochemical proxies from Lake Ohrid DEEP site core.

Spearman's correlation	***Cyclotella fottii***	***C. ocellata***	***C. minuscula***	**DC**	**DAR**
TIC (%)	−0.48	0.47	0.32	0.45	0.35
TOC (%)	−0.36	0.50	/	**0.64**	**0.50**
BSi	−0.45	**0.53**	0.30	**0.75**	**0.7**
C/N	−0.40	**0.53**	/	**0.63**	0.47
K	0.38	−0.41	/	**−0.60**	**−0.43**

All presented values are significant at $p < 0.05$

"/" low values and/or no significant correlation

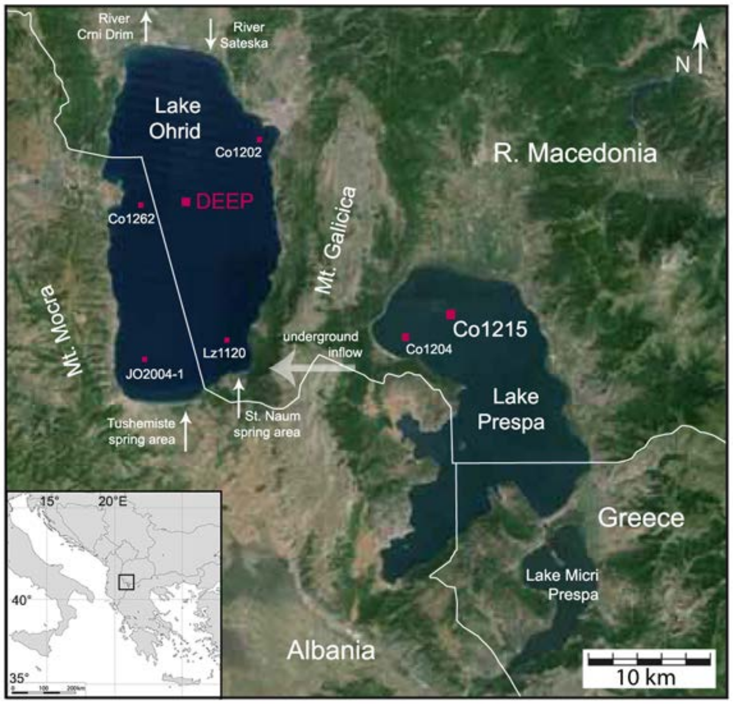

Fig. 1. Map of the northern Mediterranean region showing the location of lakes Ohrid and Prespa. Marked in purple are the locations of the cores: Lz 1120, Co1202, Co1262 and JO2004 from field campaigns at Lake Ohrid between 2005−2012, cores Co1204 and Co1215 recovered from Lake Prespa during field campaigns in 2009 and 2011 (Wagner et al., 2009, 2010, 2012) and the DEEP site core 5045-1, retrieved during the SCOPSCO deep drilling campaign at Lake Ohrid in 2013 (Wagner et al., 2014a). Modified from Francke et al. (2016).

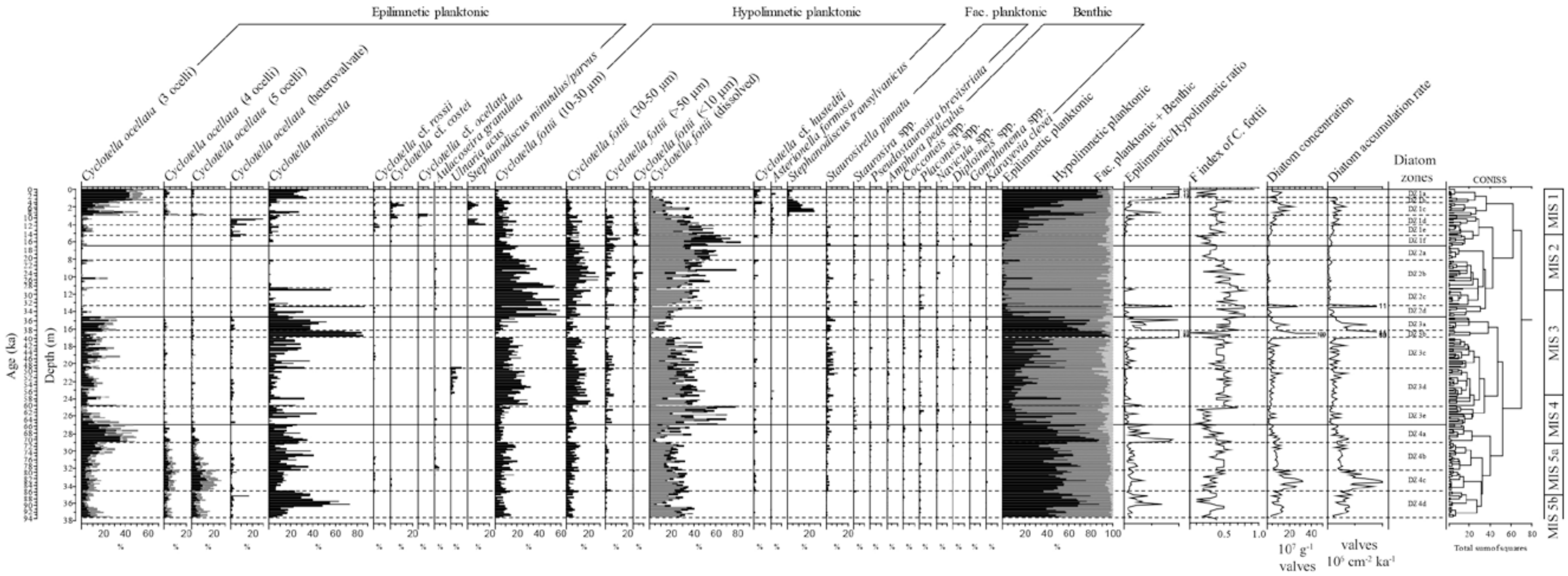

Fig 2. Stratigraphic diatom diagram showing species with >2 % abundance in Lake Ohrid DEEP site core 5045-1, F index of *Cyclotella fottii*, diatom concentrations ([n] valves * 10^7/g dry sediment) and diatom accumulation rates ([n] valves * 10^6 cm^{-2} ka^{-1}). Diatom zone boundaries are defined by CONISS, Marine Isotope Stages (MIS) boundaries after Lisiecki and Raymo (2005).

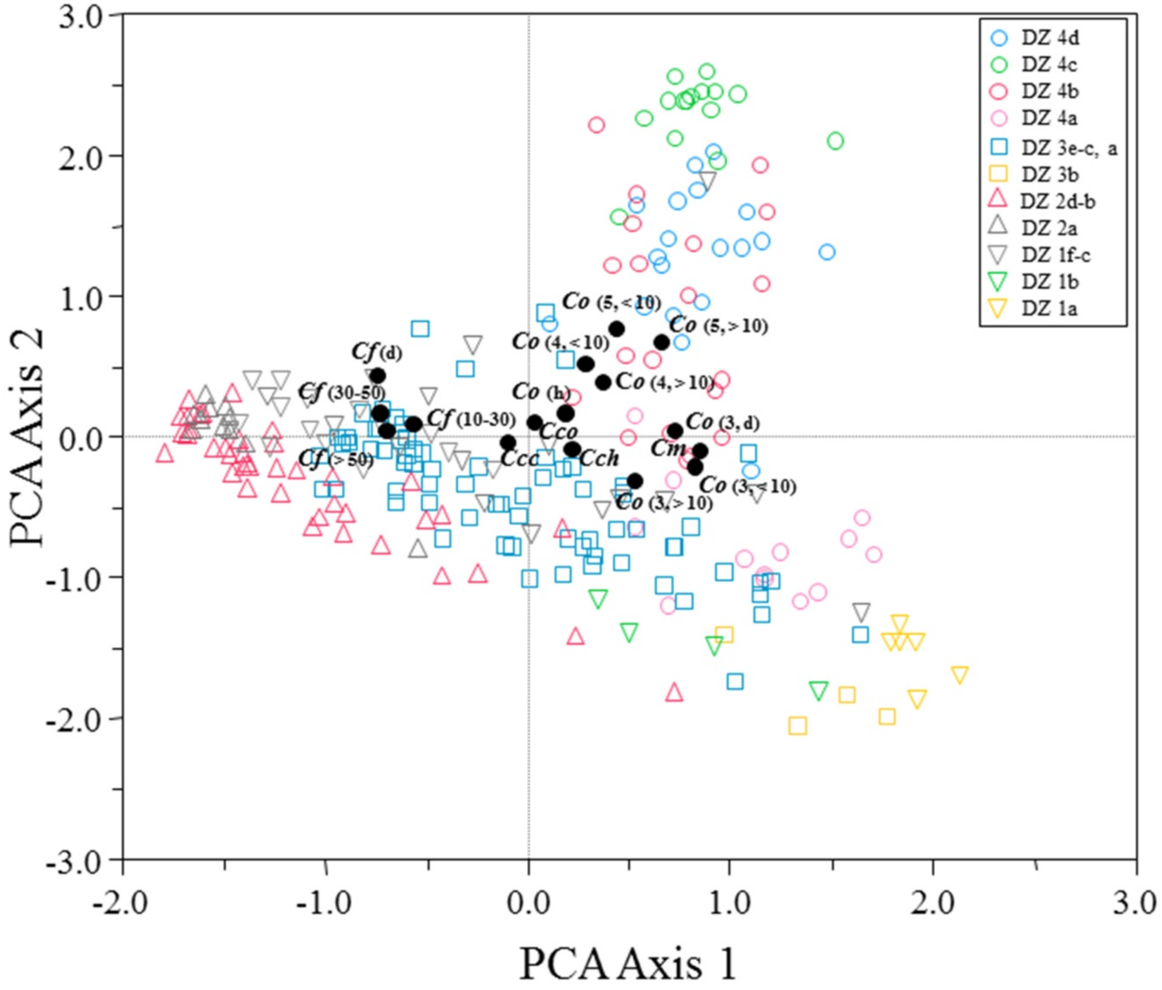

Fig. 3. Biplot of PCA Axis 1 vs. PCA Axis 2 sample and species scores from Lake Ohrid DEEP site core (5045-1). Symbol keys for diatom zones and sub-zones in top right corner. Selected diatom taxa and morphological splits of *Cyclotella fottii* (*Cf*, size in µm*)* and *Cyclotella ocellata* (*Co*) are plotted, where numbers in brackets refer to size splits (µm) and ocelli number in *C. ocellata*. Explanation: *Cm* = *Cyclotella minuscula*, *Cch* = *Cyclotella* cf. *hustedtii*, *Ccc* = *Cyclotella* cf. *costei*, *Cco* = *Cyclotella* cf. *ocellata*, (d)=dissolved.

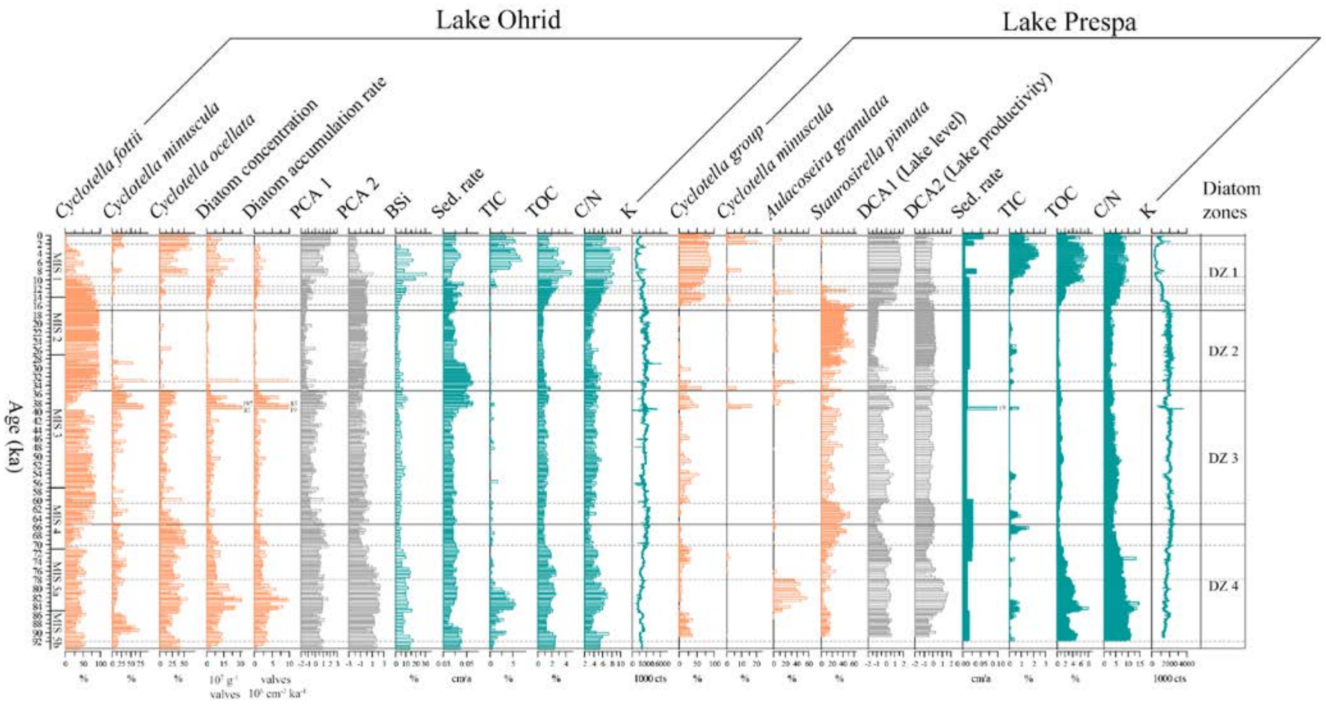

Fig. 4. Comparison diagram between Lake Ohrid core 5045-1and Lake Prespa core Co1215 showing the relative abundance data of selected diatom species, the PCA 1 and 2 sample scores; DC and DAR, the sediment accumulation rates (SAR) and the biogenic silica content (BSi, % weight) of Lake Ohrid core DEEP. Prespa DCA 1 and 2 sample scores represent lake level and productivity. Displayed are the diatom zones (DZ 1–4) of Lake Ohrid core DEEP; the dotted lines mark the six major diatom zones of Lake Prespa core Co1215 (Cvetkoska et al., 2015). Selected geochemical proxies from Lake Ohrid core DEEP: total organic carbon (TOC), total inorganic carbon (TIC), C/N ratio and potassium (K); data from Francke et al. (2016); Lake Prespa core Co1215: TOC, TIC, C/N ratio, K; data from Wagner et al. (2012) and *S. pinnata* (%), data from Cvetkoska et al. (2015); The MIS boundaries are from Lisiecki and Raymo (2005).