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

A. Cvetkoska[1], E. Jovanovska[2], A. Francke[3], S. Tofilovska[4], H. Vogel[5], Z. Levkov[4], T. H. Donders[1], B. Wagner[3], and F. Wagner-Cremer[1]

[1]Utrecht University, Palaeoecology, Department of Physical Geography, Utrecht, the Netherlands
[2]Justus Liebig University, Department of Animal Ecology and Systematics, Giessen, Germany
[3]University of Cologne, Institute for Geology and Mineralogy, Cologne, Germany
[4]University Ss Cyril and Methodius, Institute of Biology, Skopje, Macedonia
[5]University of Bern, Institute of Geological Sciences, Bern, Switzerland

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Correspondence to: A. Cvetkoska (acvetkoska@yahoo.com)

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Abstract

In order to understand the panarchy and interactions since the last interglacial period in the oldest, most diverse and hydrologically connected European lake system, we assess changes in the diatom record and selected geochemistry data from Lake Ohrid's "DEEP site" core and compare it with the diatom and multi-proxy data from Lake Prespa core Co1215. Driven by climate forcing, tephra impact and/or human influence, the lakes experienced two adaptive cycles during the last 92 ka: "interglacial and interstadial-regime" and "glacial-regime". The patterns of regime shifts appear synchronous in both lakes, while differences occur in the inferred amplitudes of the variations. The deeper Lake Ohrid shifted between ultraoligo- and oligotrophic regimes in contrast to the more shallow Lake Prespa, which shifts from (oligo-) mesotrophic to eutrophic conditions. In response to external forcing, Lake Ohrid exhibits a high capacity to buffer disturbances, whereas Lake Prespa is much more resilient and "recovers" in relatively short time. This decoupling of the response is evident during the MIS 5/4 and 2/1 transitions, when Lake Ohrid displays prolonged and gradual changes.

The lakes' specific differences in the response and feedback mechanisms and their different physical and chemical properties, probably confine a direct influence of Lake Prespa's shallow/eutrophic regimes over the productivity regimes of Lake Ohrid. Regime shifts of Lake Ohrid due to the hydrological connectivity with Lake Prespa are not evident in the data presented here. Moreover, complete ecological collapse did not happened in both lakes for the period presented in the study.

1 Introduction

The structure and functions of the terrestrial ecosystems constantly evolved throughout the Quaternary, driven by a series of successive climate variations at different temporal scales. As dynamic and complex entities, the ecosystems developed through these fluctuations with a "panarchy", generated by a series of hierarchical adaptive cycles,

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each separated by critical thresholds of destabilization, followed by structural reorganization (Allen et al., 2014; Delcourt and Delcourt, 2004; Holling, 2001). Within these cycles, many ecosystems, especially lakes, experienced collapses of the structure and functions of their living communities, or the omega phase of release (Holling, 1986). Examples of such ecological collapses include many of the world's oldest lakes, like Baikal in Russia, Hövsgöl in Mongolia, Tanganyika and Malawi in East Africa (Burnet et al., 2011; Cohen et al., 2007; Karabanov et al., 2004; Scholz et al., 2011). Based on the intensity of the external forcing, the species communities in these lakes had different responses and capacities to restore and/or reorganize their structure and functions. Therefore, the aim to reconstruct their limnologic history has triggered extensive research on sediment records, as archives of past geological and biological dynamics of these ancient lakes.

In Europe, such important 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. Galicica (Anovski et al., 1997, 2001). The much shallower and nutrient rich Lake Prespa can thereby drive changes in Lake Ohrid (Matzinger et al., 2006, 2007). A primary force for co-evolution can be water level changes of Lake Prespa, where models predict that a 20 m lake level decrease can potentially trigger a regime shift in the physico-chemical and biological properties of Lake Ohrid by increasing the nutrient input through the karstic spring system (Matzinger et al., 2006, 2007). Parallel analysis of long-term temporal variations under changing climate boundary conditions from Quaternary sedimentary records of both lakes is thus important for identifying the potential interdependence between Lake Prespa and Lake Ohrid as potential internal drivers of shifts in lake levels and productivity.

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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 91.0 ka (Co1215, Prespa) (Damaschke et al., 2013; Vogel et al., 2009). Geochemical and biological records from these cores demonstrated the proxies' strength to infer the past ecological changes. The palaeoenvironmental reconstructions showed strong response of the lakes to the glacial–interglacial climate variability, their value as archives of the past volcanic activities across the Mediterranean, and the high potential for biodiversity and evolutionary studies (Aufgebauer et al., 2012; Cvetkoska et al., 2012, 2014, 2015; Panagiotpoulos et al., 2013, 2014; Reed et al., 2010; Vogel et al., 2010; Wagner et al., 2008, 2009). While environmental variations in Lake Prespa were resolved at high resolution for the last ca. 92.0 ka, the presence of hiatuses in cores from Lake Ohrid (e.g., Wagner et al., 2008; Vogel et al., 2010) hampered 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 Deep Drilling Program (ICDP) drilling campaign was carried at Lake Ohrid in 2013. A sediment sequence spanning > 1.2 Ma (Wagner et al., 2014) was recovered from the "DEEP site" in the central part of the lake. Multi-proxy analyses of this sequence currently proceed towards the ultimate aim of the project, which is to understand the influence of the past geological and environmental events on the biological evolution of the lake taxa.

Here, we present the past 92.0 ka of the DEEP site diatom record in combination with selected bio(geochemical) data. Trends in the dataset are used to infer Lake Ohrid's internal dynamics and to understand the external forces, which drive changes in the structure and productivity of its biological component, e.g. the diatoms. Lake Prespa's dynamics since the last interglacial, as inferred from the diatom, pollen, and geochemistry data from a 92.0 ka old sediment core from the northern part of the lake are used for a comparison between the lakes in order to assess the ecosystems panarchy, adaptability and response mechanisms to external disturbances at different spatial and temporal scales. At higher hierarchical level, revealing the past cross-scale inter-

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actions is a priority for testing the link between the lakes and recognizing the capacity of Lake Prespa as a driving force of co-evolutionary processes in the ancient sister lake system.

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. With a mean and maximum water depth of 155 and 293 m (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 $m^3 s^{-1}$ 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 yr. The average monthly air temperature of the surrounding area is 26 °C during summer and −1 °C in winter and the average precipitation is 750 mm yr^{-1}. Recent investigations reveal that the global warming and local anthropogenic impact have led to an increase in total phosphorus concentration to 4.5 mg P m^{-3} (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 less 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, shallow lake with only ~ 14 m mean and ~ 48 m maximum water depth. The estimated hydraulic residence time is ca. 11 yr (Matzinger et al., 2006). The water input, 534 Mio $m^3 yr^{-1}$, is via river inflow and catchment runoff (56 %), direct precipitation (35 %), inflow (9 %) from the nearby Lake Micri Prespa (Fig. 1), and groundwater input. The output is via evap-

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oration (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 yr^{-1} on the mountains (Hollis and Stevenson, 1997). The lake is highly sensitive to changes in the environment; 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, the human induced shift of the lake from nitrogen to phosphorus driven ecosystem has been stressed as a major threat to the ecosystem by the recent monitoring programs, which revealed TP concentrations in the lake of ca. 2.5 mg L^{-1}, and ca. 162 t 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 Scientific Collaboration on Past Speciation Conditions in Lake Ohrid (SCOPSCO) project deep drilling campaign in 2013 (Fig. 1). Six parallel holes (A to F) at ca. 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. (2014). An overview age model for the upper 247.8 m of the composite sequence of the DEEP site for the sediment core and downhole logging data bases on nine tephrostratigraphic tie points, and on tuning (bio-)geochemical proxy data to orbital parameters, and to the benthic isotope stack LR04 by Liesecky and Raymo (2005) (Baumgarten et al., 2015; Francke et al., 2015). According the age-depth model, the uppermost 37.5 m of the sequence represent the last ca. 92.0 ka. This period is well-constrained by the occurrence

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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; Francke et al., 2015; Leicher et al., 2015).

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 comprise non-destructive X-ray fluorescence scanning for potassium intensities (K), and measurements of total carbon (TC), total inorganic carbon (TIC), and biogenic silica (BSi). 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 cube, elementar Corp.) after combustion at 1150 °C and used to calculate the ratio between TOC and TN (abbreviated as C/N). The details of the bio(geochemical) analysis are described in more detail in Francke et al. (2015).

Diatom analysis of the 37.5 m sequence from 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^{-1} 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 1500× magnification with 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 Krammer and Lange-Bertalot (1986–1991), Levkov et al. (2007), and Cvetkoska et al. (2012). To assess the preservation quality in

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the sequence, the F index of Ryves et al. (2001) was calculated for *Cyclotella fottii* Hustedt, values of $F = 0$ indicate partial dissolution of all valves and $F = 1$ means ideal preservation.

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), Cvetkoska et al. (2014, 2015), Damaschke et al. (2013), Leng et al. (2013), Panagiotopoulos et al. (2014), and Wagner et al. (2012).

4 Diatom results and responses in the DEEP site sequence

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. Planktonic taxa from the genus *Cyclotella* (Kützing) Brébisson dominate the assemblages, while the facultative planktonic "FP" and benthic life habitat groups are represented with higher species numbers, but low overall relative proportions of species. The most abundant FP and benthic genera are *Amphora* Kützing, *Cocconeis* Ehrenberg, *Gomphonema* Ehrenberg, *Diploneis* Ehrenberg ex Cleve, *Navicula* Bory, *Staurosira* Ehrenberg and *Staurosirella* Williams et Round. Following previous studies of Cvetkoska et al. (2012), Reed et al. (2010), and Wagner et al. (2014), the dominant taxa were split in morphotypes, imperative to test the link between the long-term ecosystem dynamics and species evolution in the DEEP site record. *C. 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.

The species' indicative values have been already tested and temperature changes were determined as the main driving mechanisms of the diatom response in Lake Ohrid (Cvetkoska et al., 2012; Reed et al., 2010). A typical "glacial" indicator in the sediment record is *C. fottii*, an endemic species adapted to a hypolimnetic life habitat, which reaches maximum density in the contemporary planktonic communities between

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30 and 200 m water depth (Stanković, 1960). Increased abundance and/or dominance of the *C. ocellata* complex is indicative of temperature-related increase in productivity and/or increased light availability, while the small (5–7 µm) epilimnetic *C. minuscula* (Jurilj) Cvetkoska is primarily related to light and nutrient availability, with maximum peaks during low light conditions.

The low relative abundances, 5–15 %, of the FP and benthic species, resulting from the coring location, add little supporting evidence to the interpretation of the record. According to Reed et al. (2010), small Fragillariaceae in Lake Ohrid tend to peak at the onset of the warm season, in the ice free littoral zone. Therefore, periods of their increased abundances in the DEEP site record can indicate transport from the shallower parts of the lake due to wind induced wave activity and lake-internal currents.

The principal component ordination (Fig. 3, Table 2), PCA 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 is driven by *C. ocellata*, with high values of morphotypes with 4 and 5 ocelli, reflecting the "productivity" gradient 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. The diatom concentrations, DC in Fig. 2 reflect the overall diatom productivity in the record.

5 Ecosystem dynamics

In the DEEP site sequence, four major diatom zones (DZ 1–4, Fig. 2), each divided in 4–6 subzones defined by CONISS (Grimm, 1987) 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 to the Marine Isotope Stages (MIS) according to Lisiecki and Raymo (2005).

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For a detailed overview of the diatom data and palaeoenvironmental interpretation of Lake Prespa core Co1215, the reader is referred to Cvetkoska et al. (2014, 2015).

Regarding the comparison between both sediment sequences, the age models of Ohrid's DEEP site core and Prespa's core Co1215 are independent age models and only few direct correlation points exist (e.g., the Y5 and Mercato tephra). Therefore, all correlations of the diatom assemblage occurrences (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 up to several thousand years (particularly as the lower part of Prespa misses an age control (tephra) at the base of the sequence).

5.1 The last interglacial, MIS 5 (92.0–71.0)

5.1.1 MIS 5b (92.0–85.0 ka)

The basal diatom zone, (DZ 4d) in Lake Ohrid's DEEP site core is marked by dominance of the *C. ocellata* complex until 88.5 ka, when *C. minuscula* peaks with ca. 80 % relative abundance, taking over a major part of the epilimnetic diatom productivity to the end of MIS 5b (Fig. 2). The autecology of *C. minuscula* indicates that its dominance was favored by the increased clastic input, rather than warmer temperatures, as it is also reflected by the corresponding increase of K content (Fig. 4) (Francke et al., 2015). Low DC (Fig. 2) and PCA Axis 2 values (Fig. 4), indicative of generally lower diatom productivity between 88.5 and 84.4 ka, match well with the low C/N ratio and TOC content (Fig. 4), which also suggest less productivity and/or preservation of the organic matter (Francke et al., 2015). Overall, the proxies indicate unstable climate with lower winter temperatures and increased wind activity during MIS 5b.

Unstable transitional phase of moderate, but variable moisture availability and temperatures was inferred during MIS 5b from the Co1215 diatom record. Low-lake-level phases during an oligo-mesotrophic trophic state in Lake Prespa occurred at 90.0, 88.4 and 85.6 ka (Cvetkoska et al., 2015).

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5.1.2 MIS 5a (85.0–71.0 ka)

The period between 84.4 and 78.3 ka is characterized by maximum PCA Axis 2 values in the DEEP site diatom record (Fig. 4), and high overall DC (Fig. 2), driven by the dominance of *C. ocellata* morphotypes with 4 and 5 ocelli (Fig. 2). Similar diversification and presence of different *C. ocellata* morphotypes during MIS 5, MIS 3 and the Holocene was observed by Cvetkoska et al. (2012), and Reed et al. (2010). Even though revealing the nature of this diversification requires more data from the earlier Quaternary, the hypothesis of climatically triggered evolution at sub-species level seems quite plausible at this stage. The increased diatom productivity in this part of the record is also reflected in the increased BSi content and high TOC values (Fig. 4). The diatom signal of warmer and/or drier climate is supported by the high TIC content, indicative of increased calcite precipitation and/or preservation and a higher primary productivity during spring and summer.

The return to dominance of *C. minuscula* from 78.3 ka onwards, along with a small peak of *Aulacoseira granulata* (Ehrenberg) Simonsen, points to decreased water transparency and increased mixing and suggests a colder climate. Small increase in the abundance of *C. fottii* at 76.0 ka, marks a return to dominance of the typical *C. ocellata* morphotypes, *sensu stricto*. Lake productivity values < 1 (PCA Axis 2) correspond to a TOC decline and glacial conditions at ca. 70.5 ka.

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 (Cvetkoska et al., 2015; Panagiotopoulos et al., 2014). A second lake level low-stand at Lake Prespa between 77.6 and 76.6 ka, related to decreased 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 and hydroacoustic data and bivalves indicate also a lake level low-stand around 74.0 ka (Wagner et al., 2014), but this is not reflected in the diatom data.

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5.2 The last glacial, MIS 4–2 (71.0–14 ka)

5.2.1 MIS 4 (71.0–59.0 ka)

At Lake Ohrid, the onset of MIS 4 is characteristic by a peak of the epilimnetic group in a zone of high relative proportion of *C. ocellata* and *C. minuscula*. Although the glacial climate signal between 70.5–65.3 ka might seem muted in the species data, the low DC and TOC content point to low productivity and/or enhanced decomposition during a regime of gradual transition. High *C. minuscula* abundance and K intensities (Fig. 4), indicative of decreased water transparency and enhanced clastic supply due to catchment erosion are a signal of glacial aridity and climate cooling. However, the high relative abundances of *C. ocellata* between ca. 70.5 and 65.3 ka (Fig. 2) indicate that the spring/summer temperatures and light availability were still favorable for its growth.

The dominance of *C. fottii* between 65.3 and 60.0 ka (Fig. 2) in a zone of low preservation quality indicates low lake productivity, mainly restricted to the hypoliminon, implying increased water transparency. In addition, the high proportions and/or dominance of *C. fottii* morphotypes > 30 µm are related to low nutrient availability, low competition and decreased grazing pressure, reflecting cold and/or arid glacial climate conditions.

In Lake Prespa, the glacial conditions during MIS 4 triggered a progressive opening of the landscape (Panagiotopoulos et al., 2014) and a 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).

5.2.2 The interstadial, MIS 3 (57.0–29.0 ka)

The start of the interstadial warming at the onset of MIS 3 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. Low TOC and DC suggest low productivity and/or enhanced decomposition in assemblages dominated by *C. minuscula* and *C. fottii* be-

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tween 57.5 and 35.0 ka. Overall, the data point to improved temperature/light availability during the spring and summer, favorable for the thermophilous epilimnetic species, but still insufficient to enhance the productivity.

The decline of *C. ocellata* to < 5 % and increased abundances of *C. minuscula* and *C. fottii* (Fig. 2) indicate the return to colder/and or dryer conditions after ca. 34.0 ka, culminating in the return to glacial climatic conditions in Lake Ohrid at ca. 28.3 ka.

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

The most notable features of MIS 3 in Lake Ohrid are two DC maxima 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 productivity, leading to 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., 2015), is compensated by its small valve size (3–7 µm) as superior adaptation enhancing its competitive strength during such conditions.

A shift 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 (Cvetkoska et al., 2015; Leng et al., 2013; Panagiotopoulos et al., 2014; Wagner et al., 2012).

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5.2.3 The last glacial maximum, MIS 2 (29.0–14.0 ka)

Minima in DC, low PCA Axis 1 values, and low BSi content in Lake Ohrid's diatom zones between 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) support this interpretation, also suggesting enhanced decomposition of the organic matter and dissolution, caused by cold/dry glacial regime (Francke et al., 2015; Wagner et al., 2009; Vogel et al., 2010). 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., 2010), and from the DEEP site pollen record as well (Sadori et al., 2015).

In terms of diatom response, the low DC during the LGM (Fig. 2) and a similar pattern of glacial assemblages dominated by large, robust valves of *C. fottii*, were also observed in the previous diatom records from Lake Ohrid (Cvetkoska et al., 2012; Reed et al., 2010; Wagner et al., 2009). 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.

Lake Prespa experienced low productivity and low lake levels during the LGM until 15.7 ka. Gradual lake level increase parallel with expansion of trees in the catchment area occurred during the Bølling/Allerød (B/A) interstadial (Cvetkoska et al., 2014; Panagiotopoulos et al., 2013). The signal in Lake Ohrid's diatom and bio(geochemical) data is too subtle to depict a synchronous response to the B/A climate warming.

5.3 Termination I and the Holocene, MIS 1 (14.0 ka to present)

Unlike the strong response of Lake Prespa to the wet-dry-wet phases between 15.7–12.3 ka due to the B/A and Younger Dryas (YD) (Cvetkoska et al., 2014; Panagiotopoluos et al., 2013), in Lake Ohrid, a first signal of enhanced productivity since the LGM derives from somewhat higher DC, TOC and BSi between 13.6 and 11.2 ka

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(Figs. 2 and 4). Unusual 15 % abundance of "Janus", e.g., heterovalvate cells of *C. ocellata* occurs at ca. 13.4 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 summer light and temperature conditions at the end of the LGM, as supported by declining K counts (Fig. 4). At the same time, low TIC implies to frequent mixing of the water column and dissolution of calcite during cold/dry winters (Francke et al., 2015; Vogel et al., 2010).

Indeed, Lacey et al. (2014) interpreted the changes between 12.4 and 11.9 ka in the multi-proxy 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 only provided incomplete or inconclusive results for this period (Cvetkoska et al., 2012; Reed et al., 2010; Vogel et al., 2009; Wagner et al., 2009, 2012), and we thus tentatively relate the weakness of response observed at the DEEP site to a combination of the depth at the coring location, low winter temperatures, improved light penetration and temperature regime and low nutrient availability prior to 11.2 ka.

Frequent shifts in the diatoms and the geochemistry proxies from 11.2 ka to present indicate that Lake Ohrid developed a more dynamic system during the Holocene. The presence of *Stephanodiscus* species (Kilham et al., 1986), indicative of increased nutrient availability, and slightly increased DC imply enhanced productivity between 11.2–9.0 ka. Peak (25 %) abundance of heterovalvate *C. ocellata* and higher DC at ca. 10.0 ka (Fig. 2) correspond to a peak in TOC (Fig. 4), implying to warmer temperatures and increased spring/summer light availability. A comparable trend of increased productivity was observed at the Lini site (Lacey et al., 2014), while in Lake Prespa, rapid wetting was inferred between 10.0 and 8.0 ka (Cvetkoska et al., 2014; Panagiotopoulos et al., 2013).

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In general, maximum BSi content and highest DC are observed between ca. 8.9–4.8 ka, in assemblages co-dominated by *C. ocellata* and *S. transylvanicus* (Figs. 2 and 4). Such high diatom productivity in the epi- and hypolimnetic zone is indicative of warm climate and high nutrient availability. This pattern is further supported by overall high TIC and TOC concentrations (Fig. 4).

The prevailing conditions between ca. 8.9 and 4.8 ka are 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 and 7.9 ka, respectively, co-occuring with peaks in K intensities (Figs. 2 and 4). These pronounced signals are related to the Mercato tephra layer in the DEEP site sequence (Francke et al., 2015; Leicher et al., 2015) and the "8.2 ka" cold event. A similar peak in K between ca. 8.2 and 7.9 ka can be also observed at the Co1202 and 1262 cores, which was interpreted as result of the 8.2 cooling event by Vogel et al. (2010) and Lacey et al. (2014), respectively. In the DEEP site diatom record, high DC at 8.5 ka is followed by increased TOC, indicating increased productivity due to increased silica availability from tephra influx. For the case of the 8.2 ka event, low productivity as evident in the low DC, indicates enhanced seasonality with cold winters and dry summers, accompanied by decreased transparency due to high clastic input. A regional pattern of climate aridification during the "8.2 ka" event has been suggested for Lake Dojran (Francke et al., 2013), Lake Maliq (Bordon et al., 2009) and Tenaghi Phillipon (Pross et al., 2007).

This interpretation sheds new light on previous tentative core Lz1120 results, in which the diatom response around the 8.2 ka event was inconclusive (Wagner et al., 2009), we now state that the earlier observed peak of *C. ocellata* and high DC in Lz1120 falls into the range of the Mercato deposition in Lake Ohrid. In Lake Prespa core Co1215, peaks in K correspond to a peak in *C. paraocellata* Cvetkoska, Hamilton, Ognjanova-Rumenova and Levkov at ca. 8.9 ka and *C. minuscula* at ca. 8.0 ka (Cvetkoska et al., 2014, 2015), similarly as in 5045-1. Thus, our results allow tying the earlier observed Lake Prespa signals to the Holocene short-term events evident in Lake Ohrid with high confidence.

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Lower DC and declining TOC from 4.8 ka onwards document lower productivity and decreased organic matter preservation, probably associated with lower temperatures. This interpretation is in contrast with increased calcite contents between ca. 5.0 and 2.5 in other Ohrid cores, which have been interpreted to be associated with warm and dry climate (Lacey et al., 2014; Vogel et al., 2010; Wagner et al., 2012). However, dry conditions are also in contrast to the sustained moisture availability and high lake levels prevailing in Prespa until 1.9 ka (Cvetkoska et al., 2014, 2015).

Previous interpretations from Lake Ohrid cores suggested enhanced erosion due to intensified human impact via forest clearance after 2.5 ka (Lacey et al., 2014; Wagner et al., 2009, 2012; Vogel et al., 2010). Low DC in an assemblage dominated by *C. ocellata* and *C. minuscula* at ca. 2.5 ka, along with low TIC, TOC indicate low primary productivity, despite the expected increased nutrient supply from the catchment as indicated by high K intensities. However, low TIC, TOC and BSi can also result from mutual dilution between the clastic and autigenic matter (Francke et al., 2015). Evidence for human-induced deforestation around Lake Prespa at ca. 2.0 ka was identified in the pollen record (Panagiotopoulos et al., 2013), but a diatom-inferred lake response was not recognized prior to 1.9 ka.

After 2.5 ka, the DC increase to a peak between 1.5–1.0 ka, coinciding with higher TOC and low K content (Fig. 4). The co-dominance of *C. ocellata* and *C. minuscula* reflects increased productivity in the epilimnion which can be related to combination of warm climate and/or anthropogenic influence between 1.5 and 1.0 ka. The peak TIC around 1.0 ka (Fig. 4) indicates high calcite preservation and just as in other Lake Ohrid cores, can also result from combination of increased evaporation and less water recharge (Lacey at al., 2014; Wagner et al., 2009; Vogel et al., 2010). Around the same time, 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 of almost 10 m at Lake Prespa (Cvetkoska et al., 2014 and references therein).

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6 Ecosystems internal dynamics and interactions

6.1 Adaptive cycles: thresholds, regimes, resistance and resilience

The presented diatom data improve the identification and interpretation of the types of disturbances, thresholds, regime shifts and patterns of response in both lakes since the last interglacial period to present days. From the diatom assemblages and the DC (Figs. 2 and 4), forward and backward shifts in the lakes' productivity regimes are triggered by critical thresholds at different scales of intensity and in different external and internal factors. As pointed out by Cvetkoska et al. (2015) and the multi-proxy approach in this study, regime shifts in Lake Ohrid are tipped by temperature thresholds, inducing changes in seasonality, wind activity, light and nutrient availability, while Lake Prespa is primarily driven by moisture availability. During the last ca. 2.5 ka, the climate signal is superimposed by the human influence in both lakes.

Apart from the encountered differences, two adaptive cycles at orbital scale can be identified in both lakes: "interglacial and interstadial-regime" and "glacial-regime". Lake Ohrid's glacial regime has much lower numbers of planktonic species and is characterized by a lower productivity than the interglacial/interstadial regimes (Fig. 2). Within these regimes, shifts of increased or decreased productivity occur at sub-orbital scale, but the lake remained ultra- to oligotrophic. Based on the proxy data, there is no indication for significant lake level changes throughout the entire studied period.

The glacial regime in Lake Prespa is also characterized by much lower productivity than the interglacial/interstadial regimes, however the glacial regime is dominated by facultative planktonic and benthic species (Cvetkoska et al., 2015). The lake also experienced multiple regime shifts on orbital and suborbital scale, resulting in low or high lake levels, changes in the trophic status, from (oligo-) meso- to eutrophic and associated productivity changes.

Apart from these lake specific differences, all diatom data show that during the last 92.0 ka both lakes did not underwent catastrophic ecosystem collapses leading to com-

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plete losses of the diatom communities, such as happened at lakes Baikal and Hovsgol during the LGM (Karabanov et al., 2004).

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 and feedback mechanisms. The feedback 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; Lake, 2013; Scheffer, 2001; Walker et al., 2004). Here, we consider the "resistance" and "resilience" as different components of the ecosystems response to disturbance; by interpreting the resistance 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 (Webster et al., 1983; Westman, 1978). As evident from the productivity data (DC in Fig. 2), and in the comparison of the lakes (Fig. 4), the critical thresholds for regime shifts occur with very similar temporal pattern. 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 (Fig. 2).

This implies a high capacity 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) and some abrupt disturbance pulses, such as the Y5 tephra impact (Jovanovska et al., 2015).

Low intensity disturbances in Lake Prespa, on the other hand, are occasionally already sufficient to trigger high amplitude changes in lake levels and productivity (DCA Axes 1 and 2 in Figs. 4–6), emphasizing a lower lake capacity to absorb disturbance. An example is the abrupt shift from oligo-mesotrophic to eutrophic state during MIS 5b (Fig. 5). Its ability to recover within relatively short periods of time, like the rapid lake-

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level increase after the LGM and the short recovery period from the Y5 tephra impact (Jovanovska et al., 2015) however, demonstrates that Lake Prespa is a much more resilient ecosystem than Lake Ohrid. This lake specific difference can be attributed to the lakes' different physical properties and hydrological balances.

6.2 Lake ecosystem interactions

For the past 92.0 ka, the panarchy within the "sister lake system" is explored by identifying possible cross-scale linkages between the adaptive regimes of both lakes as entities of the landscape dynamics. Shifts in productivity of Lake Ohrid are compared to Lake Prespa's eutrophic states at periods of low lake levels during MIS 5 (Fig. 5) and the MCA (Fig. 6). In fact, Prespa's decline of ~ 10 m at time of the MCA, as also evident in the position of the historic settlements around the lake (Sibinoviç, 1987), is close analogue to the modelled lake level decline of 20 m that can potentially increase the phosphorus load in Lake Ohrid by almost 30 % (Matzinger et al., 2006, 2007). However, Lake Ohrid's low DC, 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 does not support any interpretation of such a distinct influence from Lake Prespa. Apart from the general pattern of synchronously triggered regime shifts by climate change and/or human influence there is no clear indication in the presented multi-proxy datasets for a direct link between the lakes' cycles. The higher responsiveness of Lake Ohrid during glacial stages in terms of productivity imply that lowering water tables have a limited but detectable effect on the diatom assemblages.

While Lake Prespa shifted from shallow eutrophic to deep (oligo-)mesotrophic regimes, Ohrid remained a deep lake system, cycling between ultra- and oligotrophic regimes. Due to Lake Prespa's high resilience, changes in lake levels and trophic states were probably too short to affect Lake Ohrid's productivity. This decoupling results from the high capacity of Lake Ohrid, or at least the DEEP site, to absorb the disturbances which could have been introduced from Lake Prespa. Moreover, it can be argued that

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from MIS 5b to present, Lake Ohrid did not experience any stage of collapse and remained in the conservation phase, as defined by Holling (1986).

Although at this stage, the presented multi-proxy dataset does not provide conclusive evidence regarding the predictive models of Matzinger et al. (2006, 2007) we do not disregard the theory of Prespa-dependant regime shifts in Ohrid. In order to unravel the interactions and feedbacks, parallel documentation of the dynamics in these two ancient sister lakes beyond the temporal frame available to date is required.

Above all, future scenarios of a complete collapse of both ecosystems should not be neglected, given the fact that the continuing human impact can amplify the effects of global warming, and increase the rigidity while decreasing the resistance/resilience of the lakes. Such changes can potentially trigger regimes of structural reorganization that might lead to loss of the endemic diversity of both lakes.

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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	41°02′57″ N, 20°42′54″ E	40°57′50″ N, 20°58′41″ E
Water depth (m)	~ 250	14
Length of composite record (this study; m)	37.5	17.7
Age (ka BP)	91.8	90.8
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	DCA (SD > 2.5), R "stats" v. 0.8-2 (R Core Team, 2012)	PCA (SD = 2.2), Canoco 5 (ter Braak and Šmilauer, 1997–2014)

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Table 2. Summary results of the unconstrained PCA ordination of 235 diatom samples from Lake Ohrid DEEP core.

SD (PCA) = 2.2 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

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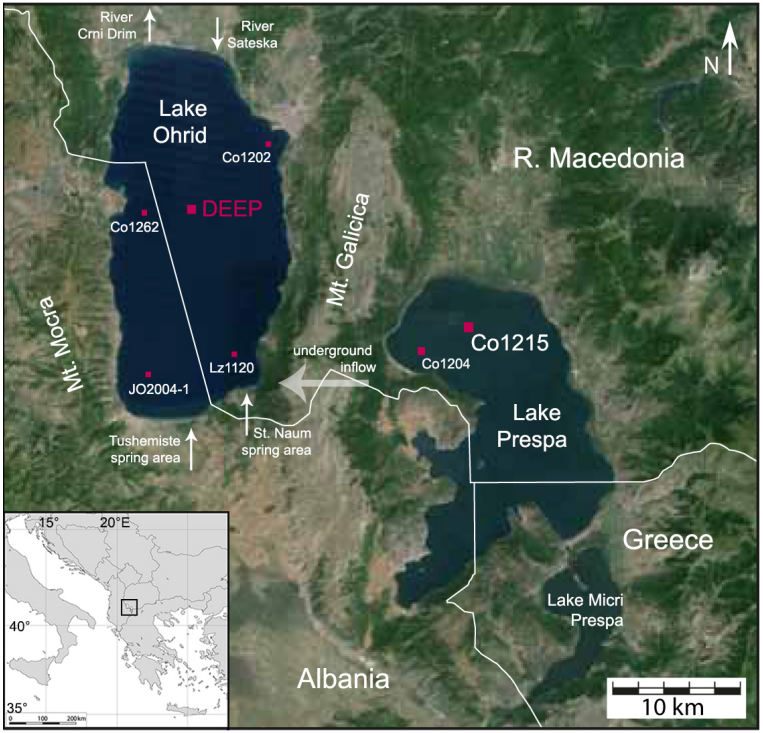

Figure 1. Map of the northern Mediterranean region showing the location of lakes Ohrid and Prespa. Marked in purple are the locations of the cores: Lz 1120, Co1202, Co1262 and JO2004 from former field campaigns at Lake Ohrid between 2005–2012, cores Co1204 and Co1215 recovered from Lake Prespa during field campaigns in 2009 and 2011 (Wagner et al., 2009, 2010, 2012) and the DEEP site core 5045-1, retrieved during the ICDP deep drilling campaign at Lake Ohrid in 2013 (Wagner et al., 2014). Modified from Francke et al. (2015).

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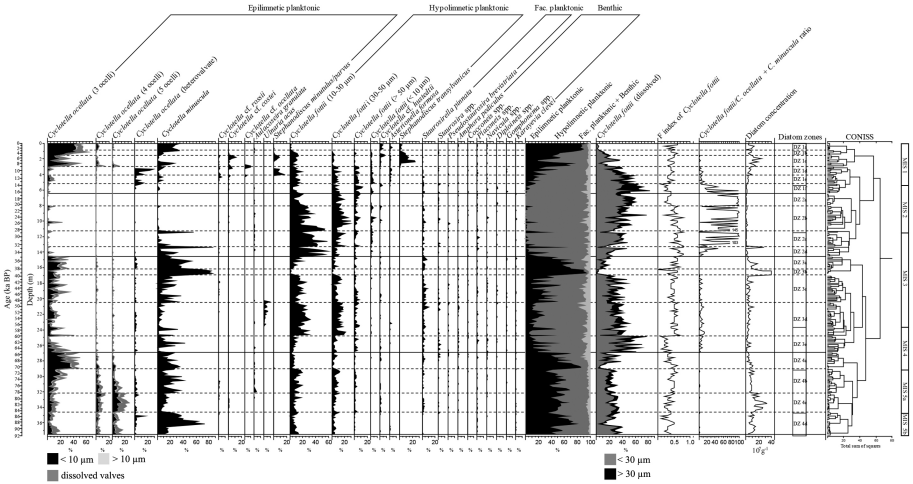

Figure 2. Stratigraphic diatom diagram showing species with > 2 % abundance in Lake Ohrid DEEP site core 5045-1, *F* index of *Cyclotella fottii* and diatom concentrations ([*n*] valves × 10^7 g^{-1} dry sediment). Diatom zone boundaries are defined by CONISS, Marine Isotope Stages (MIS) boundaries after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

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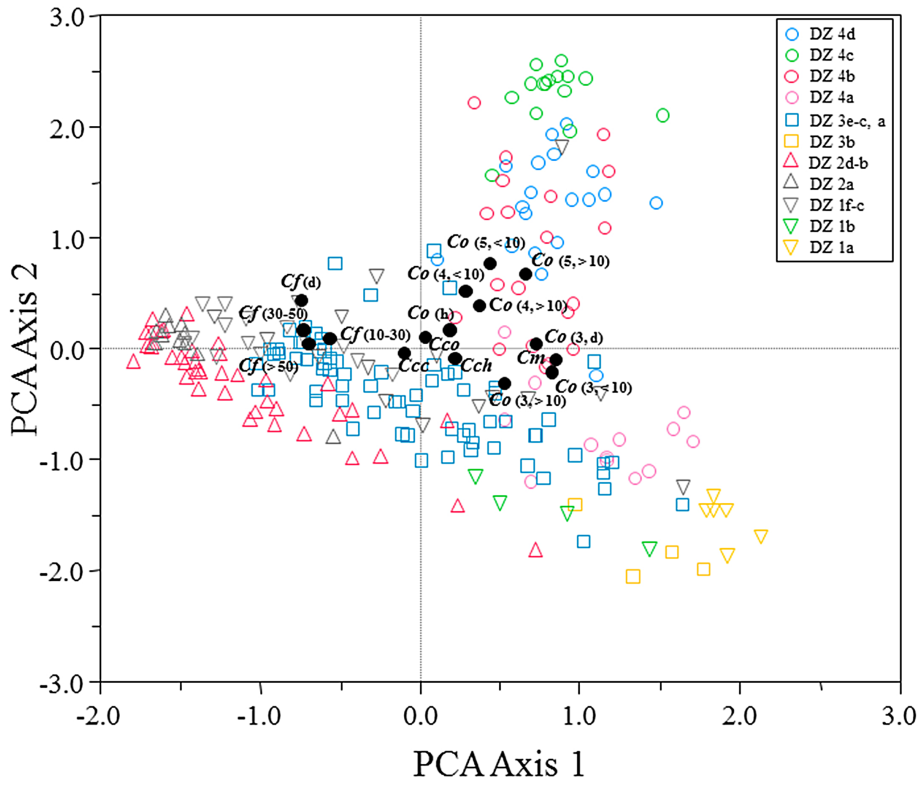

Figure 3. Biplot of PCA Axis 1 vs. PCA Axis 2 sample and species scores from Lake Ohrid DEEP site core (5045-1). Symbol keys for diatom zones and sub-zones in top right corner. Selected diatom taxa and morphological splits of *Cyclotella fottii* (*Cf*, size in µm) and *Cyclotella ocellata* (*Co*) are 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.

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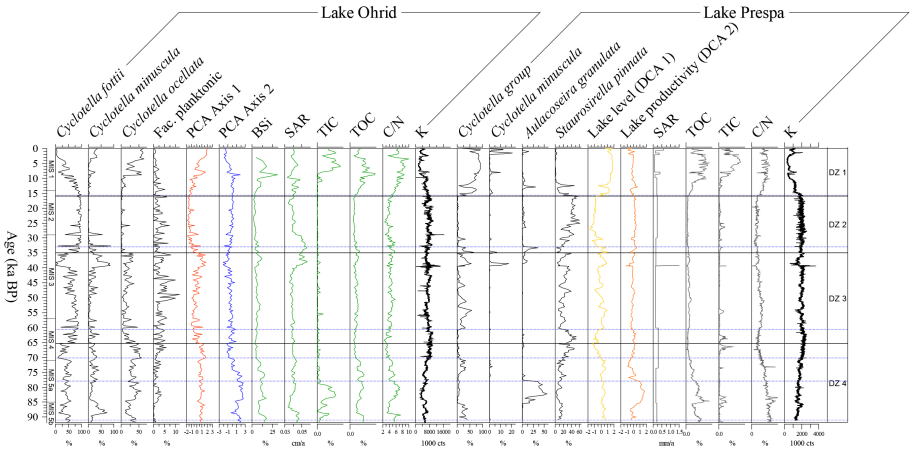

Figure 4. Comparison diagram between Lake Ohrid core 5045-1and Lake Prespa core Co1215 showing the relative abundance data of selected diatom species, the PCA 1 and 2 sample scores; the sediment accumulation rates (SAR) and the biogenic silica content (BSi, % weight) of Lake Ohrid core DEEP. Prespa DCA 1 and 2 sample scores represent lake level and productivity. Displayed are the diatom zones (DZ 1–4) of Lake Ohrid core DEEP; the blue 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. (2015); 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).

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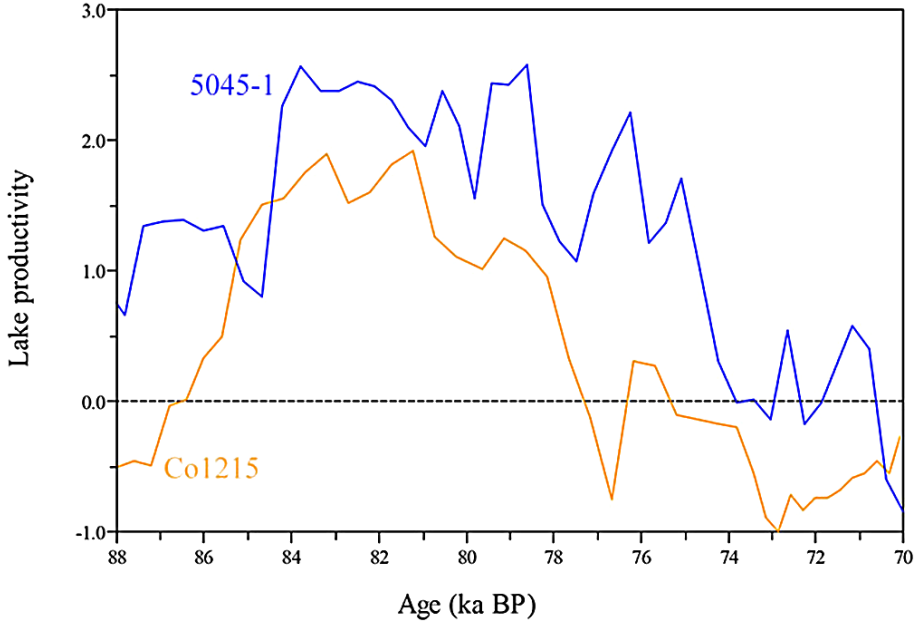

Figure 5. Comparison of the ecosystems dynamic regimes during MIS 5. Lake productivity inferred from PCA Axis 2 for Lake Ohrid (blue) and from DCA Axis 2 for Lake Prespa (orange).

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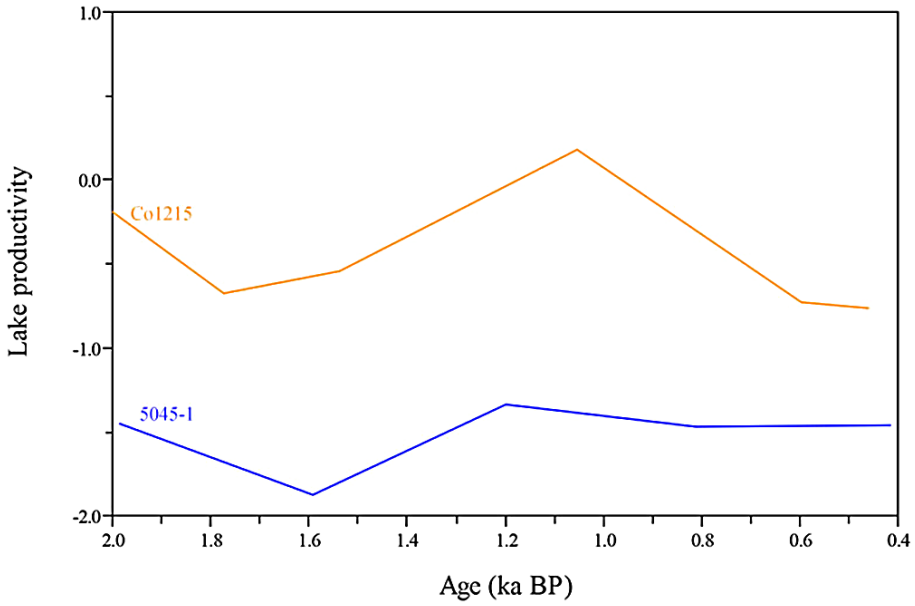

Figure 6. Comparison of the ecosystems dynamic regimes during the Medieval Climate Anomaly. Lake productivity inferred from PCA Axis 2 for Lake Ohrid (blue) and from DCA Axis 2 for Lake Prespa (orange).

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