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Lateglacial and Holocene climate and environmental change in the northeastern Mediterranean region: diatom evidence from Lake Dojran (Republic of Macedonia/Greece)

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ABSTRACT

The juncture between the west–east and north–south contrasting Holocene climatic domains across the Mediterranean is complex and poorly understood. Diatom analysis of Lake Dojran (Republic of Macedonia/Greece) provides a new insight into lake levels and trophic status during the Lateglacial and Holocene periods in the northeastern Mediterranean. Following a very shallow or even desiccated state at the core base at ca. 12,500 cal yr BP, indicated by sedimentological and hydro-acoustic data, diatoms indicate lake infilling, from a shallow state with abundant benthos to a plankton-dominated relatively high lake level and eutrophic state thereafter. Diatom-inferred shallowing between ca. 12,400–12,000 cal yr BP and a very low lake level and eutrophic, oligosaline state between ca. 12,000–11,500 cal yr BP provide strong evidence for Younger Dryas aridity. The earliest Holocene (ca. 11,500–10,700 cal yr BP) was characterised by a high lake level, followed by a lake-level reduction and increased trophic level between ca. 10,700–8,500 cal yr BP. The lake was relatively deep and exhibited peak Holocene trophic level between ca. 8,500–3,000 cal yr BP, becoming shallow thereafter. The diatom data provide more robust evidence and strengthen previous lake-level interpretation based on sedimentological and geochemical data during the earliest, mid and late Holocene, and also clarify previous uncertainty in interpretation of Lateglacial and early-Holocene lake-level change. Our results are also important in disentangling regional climate effects from local catchment dynamics during the Holocene, and to this end we exploit extant regional palynological evidence for vegetation change in the highlands and lowlands. The importance of seasonality in driving Holocene climate change is assessed by reference to the summer and winter latitudinal temperature gradient (LTG) model of Davis and Brewer (2009). We suggest that increased precipitation drove the high lake level during the earliest Holocene. The early-Holocene low lake level and relatively high trophic state may result climatically from high seasonality of precipitation and locally from limited, nutrient-rich catchment runoff. We argue that the mid-Holocene relatively deep and eutrophic state was driven mainly by local vegetation succession and associated changes in catchment processes, rather than showing a close relationship to climate change. The late-Holocene shallow state may have been influenced by a temperature-induced increase in evaporative concentration, but was coupled with clear evidence for intensified human impact. This study improves understanding of Lateglacial and Holocene climate change in the northeastern Mediterranean, suggests the important role of the LTG on moisture availability during the Holocene, and clarifies the influence of catchment processes on palaeohydrology.

1. Introduction

The Mediterranean region is a primary global climate response hotspot (Giorgi, 2006) and a hotspot of biodiversity (Myers et al., 2000; Mittermeier et al., 2004). It is a transitional zone climatically influenced both by the mid-latitude westerlies and the Subtropical High pressure (anticyclone) belt, with the North Atlantic

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Oscillation (NAO) modulating winter precipitation and the migration of the Intertropical Convergence Zone (ITCZ) affecting summer drought (Lionello et al., 2006). It stretches longitudinally from the North Atlantic Ocean to continental Eurasia. It has a diversity of landscapes linked to spatial and altitudinal variation in climatic factors.

Palaeoenvironmental analysis offers potential to improve understanding of Mediterranean climate change, but the clear definition of regional contrasts is still elusive. An early review of lake-level reconstruction proposed an east–west contrast during the Holocene (Harrison and Digerfeldt, 1993). More recently, Roberts et al. (2008, 2011a) confirmed this, defining a marked contrast during the Holocene to the east and west of a line running through the Balkans, southern Italy and Tunisia, based on stable isotope data and model output; on a centennial-decadal timescale, the complexity of regional patterns was also demonstrated in an east–west contrast between the northern Iberian Peninsula and central Turkey (Roberts et al., 2012). In contrast, Magny et al. (2013) proposed a north–south divide around ca. 40°N during the Holocene in the central Mediterranean from carbonate-based lake-level reconstruction. Peyron et al. (2013) supported this from pollen-based quantitative reconstruction of summer precipitation, and also proposed a similar pattern in the Aegean Sea. This is coherent with a north–south contrast in fire activity in the western Mediterranean (Vannière et al., 2011).

From the foregoing, the southern Balkans is a key location for understanding Mediterranean climate change, being located at the juncture of the proposed boundaries between west–east and north–south contrasting climate and hydrological domains. The southern Balkans is particularly complex, and patterns and mechanisms of climate and environmental change are still poorly understood. The complexity of palaeoenvironments is indicated, for example, by discrepancies in vegetation reconstruction between adjacent sites such as Lake Ioannina (northwestern Greece) and Nisi Fen (northern Greece) (Lawson et al., 2004, 2005), and between Lake Gramousti at low altitude and Rezina Marsh at high altitude in northwestern Greece (Willis, 1992a).

Here, we build on previous multi-proxy palaeoclimate research in investigating the Lateglacial and Holocene record of Lake Dojran (Macedonia/Greece), by using diatom analysis as a strong proxy for lake levels and trophic status to strengthen interpretation based on sedimentological and geochemical data from the same core (Francke et al., 2013). In interpretation of Holocene limnological change in terms of palaeoclimate shifts *versus* the influence of local catchment dynamics, we exploit extant regional palynological data for vegetation change, comprising late-Holocene pollen data from a separate littoral Dojran sequence (Athanasiadis et al., 2000) and chronologically-robust Holocene pollen data from the highlands and lowlands in the southern Balkans (Kotthoff et al., 2008a; Tonkov et al., 2008, 2013). Adopting a novel approach, the importance of seasonality in driving Holocene climate change is assessed by reference to the summer and winter latitudinal temperature gradient (LTG) model (Davis and Brewer, 2009), which incorporates variation in the Subtropical High pressure and Arctic Oscillation (AO). For clarity, this is expanded upon in Section 2. We also compare with proxy data from the northeastern Mediterranean (the Balkans, Italy and Anatolia) (Fig. 1).

2. Review of Holocene climatic forcing

2.1. Summer climate mode and the Subtropical High pressure

The character and influence of the Holocene summer insolation maximum across the Mediterranean is a topic for vigorous ongoing debate (Tzedakis, 2007). In a major review, Tzedakis (2007) argued that the enhanced African monsoon did not extend to the

Fig. 1. Map of the northeastern Mediterranean showing the locations of the study site (*red*), relevant palynological records with robust chronologies (*purple*) and other palaeoenvironmental records (*black*) referred to in this paper. 1. Lake Dojran (this paper; Athanasiadis et al., 2000; Francke et al., 2013), 2. Lake Trilistnika (Tonkov et al., 2008), 3. Lake Ribno (Tonkov et al., 2013), 4. SL152 (Kotthoff et al., 2008a, 2008b, 2011; Dormoy et al., 2009), 5. Tenaghi Philippon (Müller et al., 2011), 6. Lake Ohrid (Wagner et al., 2009; Leng et al., 2010), 7. Lake Prespa (Aufgebauer et al., 2012; Panagiotopoulos et al., 2013; Leng et al., 2013; Cvetkoska et al., 2014), 8. Lake Maliq (Bordon et al., 2009), 9. Nisi Fen (Lawson et al., 2005), 10. Rezina Marsh (Willis, 1992a, 1992b), 11. Lake Gramousti (Willis, 1992a), 12. Lake Ioannina (Frogley et al., 2001; Lawson et al., 2004; Wilson et al., 2008; Jones et al., 2013), 13. Lake Xinias (Digerfeldt et al., 2007), 14. Lake Stymphalia (Heymann et al., 2013), 15. Lake Frassino (Baroni et al., 2006), 16. Lake Accesa (Drescher-Schneider et al., 2007; Peyron et al., 2011), 17. Valle di Castiglione (Di Rita et al., 2013), 18. Lake Albano (Guilizzoni et al., 2002), 19. Lago Grande di Monticchio (Allen et al., 2002), 20. MD90-917 (Combourieu-Nebout et al., 2013), 21. Lake Pergusa (Sadori and Narcisi, 2001; Sadori et al., 2008; Magny et al., 2012), 22. Lake Preola (Magny et al., 2011), 23. MD04-2797 (Desprat et al., 2013), 24. Lake Iznik (Roeser et al., 2012), 25. Lake Gölhisar (Eastwood et al., 2007), 26. Eski Acıgöl (Roberts et al., 2001; Turner et al., 2008), 27. Lake Van (Wick et al., 2003; Litt et al., 2009). The dashed-line rectangle shows the range of Fig. 2. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Mediterranean, and the monsoonal effect has been mainly indirect in terms of Nile discharge and runoff along the North African coast. On the other hand, the northward-migrated, strengthened North Atlantic Subtropical High pressure in response to high summer insolation blocked westerly moisture penetration into the Mediterranean (Desprat et al., 2013; Magny et al., 2013). Tzedakis (2007) also suggested that the enhanced Indian monsoon may have accentuated summer aridity in the eastern Mediterranean. Modelling experiments show little sign of summer precipitation in spite of high summer insolation (Brayshaw et al., 2011). Magny et al. (2013) discussed the influence of ice sheets in the Northern Hemisphere on humidity in the Mediterranean, and suggested that the rapid melting of ice sheets and associated fresh water forcing in the North Atlantic Ocean contribute to summer aridity during the earliest Holocene in the south-central Mediterranean.

Davis and Brewer (2009) reconstructed Holocene changes in the latitudinal temperature gradient (LTG) based on differences in pollen-based area-average temperatures between northern (55–70°N) and southern Europe (35–45°N). The LTG reflects combined effects of the differential heating of insolation (the latitudinal insolation gradient, LIG) and the high-latitude cooling influence of remnant ice sheets (Davis and Brewer, 2009). The Subtropical High pressure is located at ca. 36°N when the summer LTG is zero (Davis and Brewer, 2009). A weaker (more positive) summer LTG drives a northern position of the Subtropical High pressure (Davis and Brewer, 2009), and the tendency would be towards much drier summers than today. The quantitative reconstruction of the Subtropical High pressure may be relevant to moisture change in the northeastern Mediterranean. The additional, area-average temperature reconstruction for southeastern Europe (Davis et al., 2003), supported by other regional syntheses (Finné et al., 2011; Abrantes et al., 2012), may be relevant in terms of evaporation and its effect on moisture balance.

2.2. Winter climate mode and the Arctic Oscillation (AO)

Modelling experiments show high winter precipitation during the early Holocene (Brayshaw et al., 2011), which is coherent with a southward-shifted storm track and responds to weak winter insolation (Desprat et al., 2013). Desprat et al. (2013) also suggested that the rapid melting of ice sheets in the Northern Hemisphere and associated reorganisation of atmospheric circulation contribute to high winter precipitation during the early Holocene in the south-central Mediterranean. Roberts et al. (2008, 2011a) and Magny et al. (2013) suggested that this is probably attributed to winter cyclogenesis and local precipitation. However, it is inconsistent with the positive AO/NAO and resultant aridity in the north-central Mediterranean (Magny et al., 2013). Data-model comparison shows that models underestimate the role of AO/NAO (Gladstone et al., 2005; Brewer et al., 2007; Mauri et al., 2013), and Davis and Brewer (2009) proposed that models overestimate low-latitude warming in summer and high-latitude warming in winter.

The Mediterranean exhibits a dry climate during the positive phase of AO/NAO and more precipitation during their negative phase (Martinson et al., 2000; Wanner et al., 2001). However, AO has a larger horizontal scale (Thompson and Wallace, 1998), and NAO alone cannot account for changes in winter precipitation in Turkey (Jones et al., 2006). In terms of precipitation, the northeastern Mediterranean is distinguished from the Levant and southeastern Mediterranean (Felis and Rimbu, 2010), and from the NAO-highly related Iberia and western Mediterranean (Roberts et al., 2012). The prominent role of AO/NAO in influencing Holocene hydroclimatic change across the Mediterranean is revealed not only at the centennial scale (e.g. Lamy et al., 2006) but also at the millennial scale (e.g. Davis and Stevenson, 2007; Fletcher et al., 2013). The AO index is zero when the winter LTG is zero (Davis and Brewer, 2009). A weaker (more positive) winter LTG drives a more positive AO, and the tendency would be towards dry winters. The AO quantitative reconstruction (Davis and Brewer, 2009) may be more relevant than the NAO in interpretation of northeastern Mediterranean climatic records.

3. Site description

Lake Dojran (41°12′N, 22°44′E, 144 m a.s.l.), a transboundary lake between Macedonia and Greece, sits within a karstic basin formed initially by a combination of Tertiary volcanic and tectonic activities, and the catchment sediments are largely composed of Quaternary alluvial and limnetic materials (Sotiria and Petkovski, 2004). In the catchment, the highland to the north is close to the Pirin and Rila Mountains in southwestern Bulgaria, and the lowland to the south is open to the Thessaloniki Plain and northern Aegean Sea (Fig. 2). The lake basin is surrounded by the Belasica (or Belles, Kerkini) Mountain (1847 m a.s.l.) to the north, the Kroussia (or Krusa, Dysoron) Mountain (766 m a.s.l.) to the east, the Boskija (or Boska) Mountain (714 m a.s.l.) to the northwest, and the Dab Mountain (689 m a.s.l.) to the southwest (Fig. 3; Sotiria and Petkovski, 2004). The lake is fed by small rivers, creeks and springs, with most of the runoff originating from the Belasica Mountain. Water loss is currently through evaporation and probably groundwater outflow, but during previous phases of high lake level, surface outflow was possible at the southern end of the lake through the Doirany (or Ayiak) River, which drained into the Vardar (or Axios) River and then into the Aegean Sea (Sotiria and Petkovski, 2004). The lake water is essentially fresh (see below), suggesting groundwater throughflow in karstic aquifers. This is supported by hydrogeological investigations (Sotiria and Petkovski, 2004).

The local climate regime is a hot and dry summer (June–September) and mild and humid winter (November–February) (Sotiria and Petkovski, 2004). In the lowlands of the catchment evergreen (*Quercus coccifera* L.) and deciduous oaks (*Quercus pubescens* Willd., *Quercus frainetto* Ten. and *Quercus dalechampii* Ten.) are the dominant trees, and at higher altitudes (>1000 m a.s.l.) beech forest (*Fagus moesiaca* Cz. and *Fagus orientalis* Lipsky) is dominant with a few scattered fir stands (*Abies borisii-regis* Mattf.) (Athanasiadis et al., 2000). Reed beds occupy the fringe of the lake, and submerged plants are common in the littoral zone. Recorded maximum lake level ranged from 7.9 to 10.0 m in 1951–1987, declined to 3.7 m in 2002 due to water abstraction practices and more intensive agriculture (Griffiths et al., 2002), and recovered to 6.7 m in 2010 due to an increase in rainfall, decrease in water use and additional water transfer from the Gjavato wells into the lake (Popovska and Bonacci, 2008; Stojov, 2012). Total phosphorus ranged from 15 to 130 μg l^{-1} in 1953–1960 (Sotiria and Petkovski, 2004), with consistently higher minimum values of >50 μg l^{-1} reported since 1996 and an occasional hypereutrophic state (Temponeras et al., 2000; Lokoska et al., 2006; Tasevska et al., 2010). Conductivity ranged from 0.4 to 0.6 mS cm^{-1} in 1974–1988, increased to 1.5 mS cm^{-1} in 2002 (Sotiria and Petkovski, 2004), and declined to 0.8 mS cm^{-1} in 2010 (Lešoski et al., 2010). This is within the freshwater range of eutrophic lake water. Ionic concentration may be influenced slightly by mineral-rich spring input; some springs are of high conductivity (Levkov, unpublished data), but others are extremely fresh (33 μS cm^{-1}; Griffiths et al., 2002). Dominance by fresh spring inflow is consistent with low $\delta^{13}C$ data of total dissolved inorganic carbon (−7.9 to −13.0‰ VPDB) in springs (Griffiths et al., 2002; Francke et al., 2013), suggesting that the effect of the karstic catchment is minor (Leng and Marshall, 2004) and the groundwater influence on

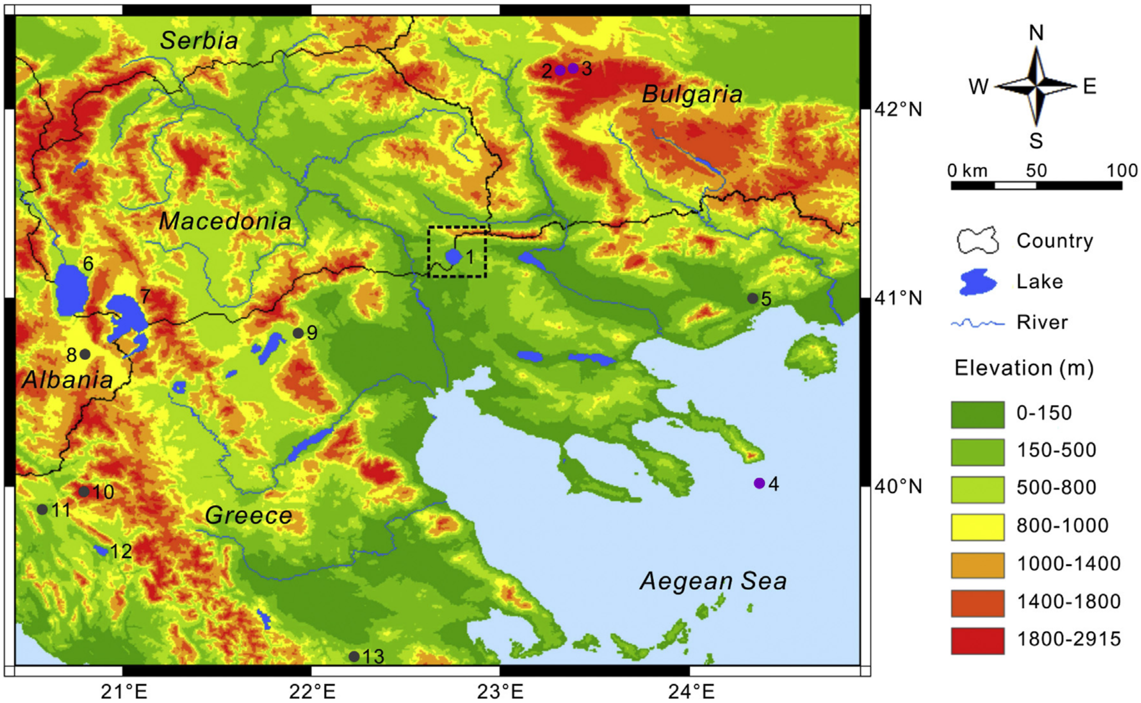

Fig. 2. Map of the adjacent region of Lake Dojran (Macedonia, northern Greece and southwestern Bulgaria) with the sites 1–13 in Fig. 1. The dashed-line rectangle shows the range of Fig. 3.

lake-water conductivity and salinity is insignificant. Lake Dojran is shallow and monomictic, and has a very simple, flat-bottomed morphometry (Francke et al., 2013), suggesting that moisture balance and water chemistry are sensitive to and possibly respond linearly to climate and environmental change (Gasse et al., 1997; Fritz, 2008).

Two previous studies have been made of Holocene climate and environmental change in Lake Dojran. One is based on sedimentological and geochemical data (Francke et al., 2013) from the same core as our current study, and the other is based on pollen data from a separate littoral core Doirani-1/2 which covers the last 5,000 years (Athanasiadis et al., 2000). Francke et al. (2013) found that, during the Lateglacial period, high abundance of clay clasts, high mean grain size, an older shell fragment, and hydro-acoustic data indicated a low lake level and redeposition before ca. 12,100 cal yr BP. This was followed by a lake-level increase inferred from hydro-acoustic data, the absence of clay clasts, low mean grain size, and high potassium (K) concentration. During the earliest Holocene (ca. 11,500–10,700 cal yr BP), overall coarse sediment suggested high water inflow and high lake level, which led to high

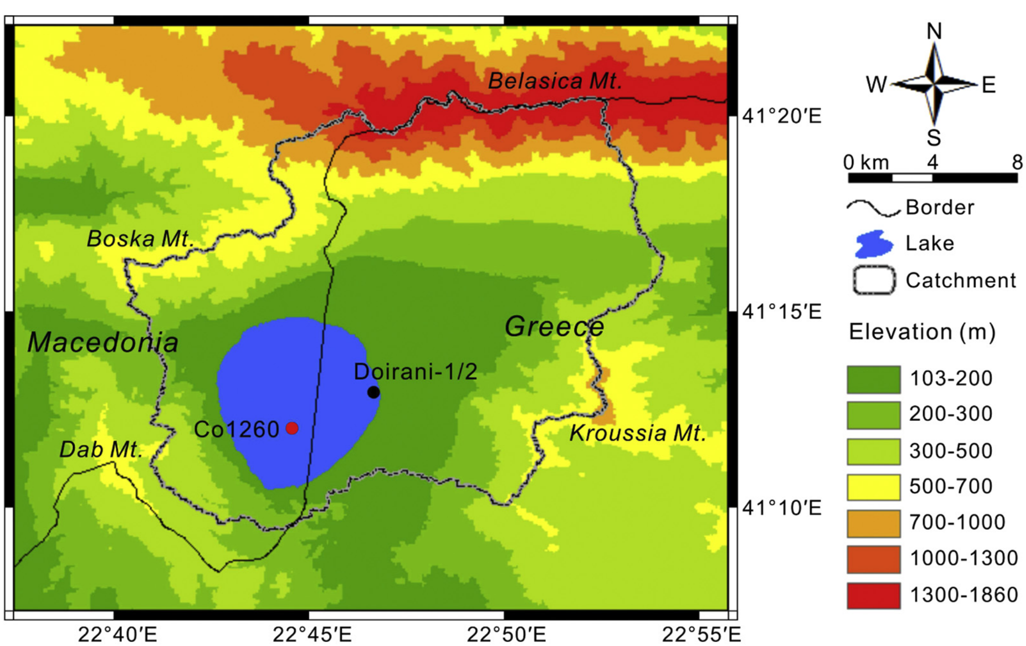

Fig. 3. Map of the catchment of Lake Dojran with the coring sites Co1260 (this paper; Francke et al., 2013) and Doirani-1/2 (Athanasiadis et al., 2000).

evaporation as indicated by high $\delta^{18}O_{carb}$ values; lower K concentration indicated lower erosion, and low organic matter content suggested low in-lake productivity. During the early Holocene (ca. 10,700–8,300 cal yr BP), decreasing $\delta^{18}O_{carb}$ values suggested increasing humidity; lower K concentration implied less clastic input while increasing organic matter content was from more allochthonous supply. During the mid Holocene, relatively high lake level was inferred from hydro-acoustic data and finer grain-size distribution. After ca. 2,800 cal yr BP, hydro-acoustic data and fine grain-size distribution suggested a lake-level lowstand apart from around 1,000 cal yr BP (Francke et al., 2013), while pollen data indicated changes in the catchment from a natural landscape to one modified by intensified human impact (Athanasiadis et al., 2000).

4. Material and methods

In June 2011, based on a hydro-acoustic survey, a 717 cm-long core Co1260 was recovered from the deepest (6.7 m water depth), south-central part of Lake Dojran using UWITEC gravity and piston coring equipments (www.uwitec.at). The age model was established by Francke et al. (2013) by polynomial interpolation between the calibrated radiocarbon ages of six terrestrial plant macrofossils, one charcoal fragment, two bulk organic matter samples, and a regionally-correlated point of a $CaCO_3$ minimum. Three carbonate shell dates and one dislocated terrestrial plant date were not included into the calculations, and Francke et al. (2013) provided more detailed discussion of each age-control point (Table 1). This age model indicates that core Co1260 covers the last 12,500 years (Fig. 4), spanning the Younger Dryas and Holocene periods.

Diatom analysis was carried out on 107 subsamples, taken at 8 cm intervals but at a higher resolution of 4 cm for important phases comprising the bottom 30 cm, the 50 cm between ca. 11,800–11,400 cal yr BP, the 20 cm around ca. 8,200 cal yr BP, and the top 60 cm. The age resolution is ca. 70–150 years, except the top and bottom sections (ca. 30–40 years) and the middle section (ca. 200–500 years). The low age resolution between ca. 8,000–4,000 cal yr BP is correlated with low sediment accumulation rate indicated by the age model, and with a stable environment indicated by sedimentological and geochemical data (Francke et al., 2013).

Techniques in Battarbee et al. (2001) were adopted for diatom preparation of ca. 0.1 g dry weight subsamples, using 30% H_2O_2 to oxidise organics and a few drops of concentrated HCl to remove carbonates. Known quantities of microspheres were added to allow calculation of absolute valve concentration. Slides were mounted using Naphrax™. Diatom valves were counted at × 1000 magnification under oil immersion on an OLYMPUS BX51 light microscope. More than 500 valves per slide were counted, and around 100 valves for some slides where preservation was very poor. Diatom identification was based on a range of published literature (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b; Lange-Bertalot, 2001; Krammer, 2002; Levkov et al., 2007; Levkov, 2009) and diatoms of Lake Dojran (Levkov, unpublished data), adopting the nomenclature of the Catalogue of Diatom Names (on-line version) (Fourtanier and Kociolek, 2011). Following current taxonomic principles, *Stephanodiscus minutulus* (Kützing) Cleve & Möller and *S. parvus* Stoermer & Håkansson are merged into *S. minutulus/parvus* (Scheffler and Morabito, 2003; Cruces et al., 2010; Hobbs et al., 2011; Bennion et al., 2012). Diatom percentages were displayed using Tilia version 1.7.16, and zone boundaries were defined according to Constrained Incremental Sum of Squares (CONISS) cluster analysis (Grimm, 2011). Unconstrained ordination techniques were used to explore the variance in the diatom data using Canoco for Windows 4.5 (Ter Braak and Šmilauer, 2002). Detrended correspondence analysis (DCA) gave the largest gradient length of 3.91 SD units, and thus this unimodal model is better than linear methods such as principal components analysis (PCA) (Ter Braak, 1995; Lepš and Šmilauer, 2003).

Quantitative diatom-inferred total phosphorus (DI-TP) and conductivity (DI-Cond) reconstructions were performed based on the Swiss TP and Combined Salinity training sets, respectively, available within the European Diatom Database (EDDI; Juggins, 2001), using classic weighted-averaging regression (WA-Cla) with bootstrapping cross-validation in C2 version 1.7.3 (Juggins, 2007). Both the Swiss TP and Combined Salinity training sets have higher determination coefficients (R^2) and lower maximum bias values in WA-Cla than weighted-averaging with inverse deshrinking (WA-Inv) and weighted-averaging partial least squares (WAPLS) component 2. WA-Cla also performs better than WAPLS component 2 in terms of root mean squared error of prediction (RMSEP), and has a slightly higher RMSEP than WA-Inv (bootstrapped RMSEP: 0.26 and 0.23, respectively, for $\log_{10}$-TP, and 0.48 and 0.47, respectively, for $\log_{10}$-conductivity). WA-Inv is susceptible to edge effects (bias at the gradient ends) (Juggins and Birks, 2012), and thus WA-Cla was chosen. Some potential problems have been identified with the application of DI-TP transfer functions (Bennion et al., 2001, 2010; Sayer, 2001; Hall and Smol, 2010; Juggins et al., 2013) and some have suggested there are some fundamental problems with underlying assumptions in the transfer function approach (Sayer et al., 2010; Juggins, 2013), but the species TP optimum and tolerance estimates, particularly of planktonic taxa, may still be useful for trophic reconstruction. Among the EDDI TP transfer functions, the Swiss training set is predominantly from mesotrophic and eutrophic lakes (mean TP: 41.9 $\mu g\ l^{-1}$), the Central European training set is mainly from oligotrophic and mesotrophic lakes (mean TP: 23.5 $\mu g\ l^{-1}$), and the Combined TP training set spans the gradient from oligotrophic to hypereutrophic (mean TP: 98.6 $\mu g\ l^{-1}$) but incorporates many non-karstic, hypereutrophic British and Danish lakes (Juggins, 2001). Although improving the likelihood of finding modern analogues, the merging in the Combined TP training set tends to extend the apparent distribution of species unevenly along the TP gradient, which not only affects species optimum estimates but also widens species tolerance ranges and makes them poor trophic indicators. Griffiths et al. (2002) suggested that Lake Dojran was mesotrophic in the recent past, and as shown above, it is currently eutrophic and occasionally hypereutrophic. Thus the Swiss training set was selected as more appropriate, although oligotrophic and hypereutrophic states are likely to be somewhat underestimated as they lie at the gradient

Table 1
Ages from core Co1260. The calibration of radiocarbon ages into calendar ages is based on Calib 7.0.2 (Stuiver and Reimer, 1993) and IntCal13 (Reimer et al., 2013) and on a 2σ uncertainty.

Core depth (cm)	Material	Radiocarbon age (^{14}C yr BP)	Calendar age (cal yr BP)
16.5	Bulk organic matter	140 ± 35	140 ± 140
53.3	Terrestrial plant remains	360 ± 70	410 ± 110
111.3	Terrestrial plant remains	840 ± 70	790 ± 120
253.0	Terrestrial plant remains	2,430 ± 30	2,520 ± 170
287.3	Terrestrial plant remains	3,080 ± 30	3,290 ± 80
309.1	Charcoal	3,560 ± 40	3,850 ± 130
404.9	Carbonate shell	6,410 ± 40	7,350 ± 80[a]
406.4	Terrestrial plant remains	8,020 ± 150	8,960 ± 440
460.9	Terrestrial plant remains	9,520 ± 160	10,820 ± 420[a]
502.9	Carbonate shell	9,840 ± 40	11,250 ± 60[a]
521.9	Terrestrial plant remains	9,330 ± 160	10,660 ± 440
635.0	Bulk organic matter	10,220 ± 70	11,920 ± 310
682.0	Carbonate shell	28,570 ± 170	32,830 ± 650[a]

[a] Indicating the dates excluded into the calculations of the age model.

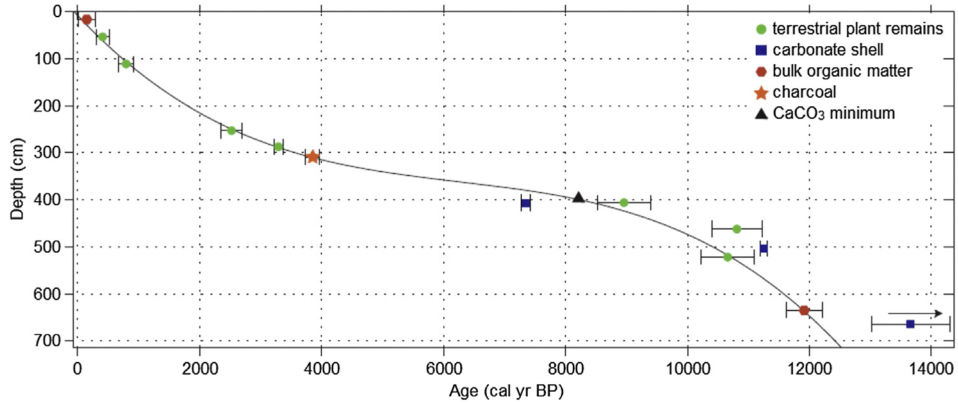

Fig. 4. Age-depth model of core Co1260 (modified from Francke et al., 2013).

ends. Importantly, the shifts between the dominance of centric (*Cyclotella ocellata* Pantocsek and *S. minutulus/parvus*) and fragilariod species in core Co1260 are well represented by their distributions along the TP gradient in the Swiss training set (Lotter et al., 1998).

5. Results and diatom interpretation

Six major diatom assemblage zones can be defined, which correlate clearly with lithostratigraphic boundaries from Francke et al. (2013) in Fig. 5. Diatom preservation quality is high with >500 valves counted and $>10^7$ g^{-1} concentration throughout until the late Holocene (Zone D-6). DI-TP log_{10} values range from 1.02 to 2.18 (equivalent to 10.6–149.8 μg l^{-1}), estimated standard error of prediction (eSEP) ranges from 0.26 to 0.29, and the error range (2 × eSEP) varies from 0.51 to 0.58 (calculated as 13.7–210.8 μg l^{-1}). DI-Cond log_{10} values range from 2.39 to 3.62 (equivalent to 0.2–4.2 mS cm^{-1}), eSEP ranges from 0.47 to 0.67, and the error range varies from 0.93 to 1.34 (calculated as 0.8–13.4 mS cm^{-1}). We treat the DI-TP and DI-Cond reconstructions with caution.

5.1. Zone D-1 (717–645 cm, ca. 12,500–12,000 cal yr BP)

In Subzone D-1a (717–696 cm, ca. 12,500–12,400 cal yr BP), the basal sample has relatively high abundance of benthic taxa (40%), possibly suggesting a lake-level lowstand at the base of the sequence, and this is followed at 713 cm depth by the dominance of planktonic taxa (50–70%), indicating relatively high lake level. Longer valves of *Fragilaria crotonensis* Kitton and *Asterionella formosa* Hassall have competitive advantages in deep waters for buoyancy and also prefer high nitrogen and silica concentrations (Bailey-Watts, 1986; Saros et al., 2005), and *S. minutulus/parvus* prefers high phosphorus concentration (Bennion, 1995; Kilham et al., 1996). Together, this also indicates a eutrophic state, presumably from high catchment runoff and nutrient erosion processes. The subsequent dominance of mesotrophic *Stephanodiscus medius* Håkansson and oligotrophic-mesotrophic *C. ocellata* suggests ongoing water inflow but declining nutrient enrichment, supported by declining DI-TP values. In Subzone D-1b (696–645 cm, ca. 12,400–12,000 cal yr BP), the increase in the relative abundance of facultative planktonic taxa, mainly comprising *Pseudostaurosira brevistriata* (Grunow) Williams & Round and *Staurosira construens* var. *venter* (Ehrenberg) Hamilton, and the clear increasing trend in benthic taxa from 667 cm depth suggest shallowing, starting with the peak concentration in the entire sequence at the 696 cm depth.

5.2. Zone D-2 (645–591 cm, ca. 12,000–11,500 cal yr BP)

Planktonic *C. ocellata* is at low abundance, and together with high relative abundance of benthos, this indicates a very low lake level. Facultative planktonic *Pseudostaurosira*, *Staurosira* and *Staurosirella* species are also rare. However, planktonic *Cyclotella meneghiniana* Kützing, *S. minutulus/parvus* and *Cyclostephanos dubius* (Fricke) Round (diameter <5 μm) are consistently present. *C. meneghiniana* lives in a wide range of habitats from shallow to deep waters (Gasse, 2002) and from fresh waters of high conductivity to saline conditions (Saros and Fritz, 2000). *S. minutulus/parvus* and *C. dubius* (small) are eutrophic freshwater taxa but tolerate oligosaline conditions (Fritz et al., 1993). Benthic taxa are remarkably diverse, most of which are eutrophic and halotolerant, such as *Nitzschia frustulum* (Kützing) Grunow, *Tryblionella constricta* (Kützing) Poulin, *Ctenophora pulchella* (Ralfs ex Kützing) Williams & Round, *Tabularia fasciculata* (Agardh) Williams & Round (Fritz et al., 1993; Reed, 1998a; Gasse, 2002; Reed et al., 2012). Importantly, the presence of rare obligate saline taxa such as *Biremis circumtexta* (Meister ex Hustedt) Lange-Bertalot & Witkowski and *Campylodiscus clypeus* (Ehrenberg) Kützing indicates aridity in a closed basin due to enhanced evaporative concentration, since the groundwater influence on lake-water conductivity and salinity is insignificant. Maximum DCA Axis 1 scores also make this zone distinctive. In Subzone D-2a (645–611 cm, ca. 12,000–11,700 cal yr BP), eutrophic, halotolerant benthic taxa are dominant, and the DI-Cond reconstruction indicates a peak concentration of total dissolved solids (>3 mS cm^{-1} conductivity). In Subzone D-2b (611–591 cm, ca. 11,700–11,500 cal yr BP), *S. minutulus/parvus* and *C. dubius* (small) increase distinctly. Since obligate saline taxa and eutrophic, halotolerant taxa indicate the maintenance of low lake level, enhanced nutrient input is inferred, supported by the peak in DI-TP.

5.3. Zone D-3 (591–525 cm, ca. 11,500–10,700 cal yr BP)

Zone D-3 exhibits a marked transition to the low-diversity dominance of planktonic oligotrophic-mesotrophic *C. ocellata* (70–90%), initially as a co-dominant with *P. brevistriata* (ca. 25%). The abundance of facultative planktonic taxa is <10% thereafter. Planktonic mesotrophic *S. medius* is consistently present at ca. 5% abundance. The abundance of benthic taxa is consistently <10%. A deep, oligotrophic to mesotrophic state can be inferred. A moderate, nearly stable nutrient level is shown by the DI-TP reconstruction. This zone is also clearly distinguished by stable, intermediate DCA Axis 1 scores.

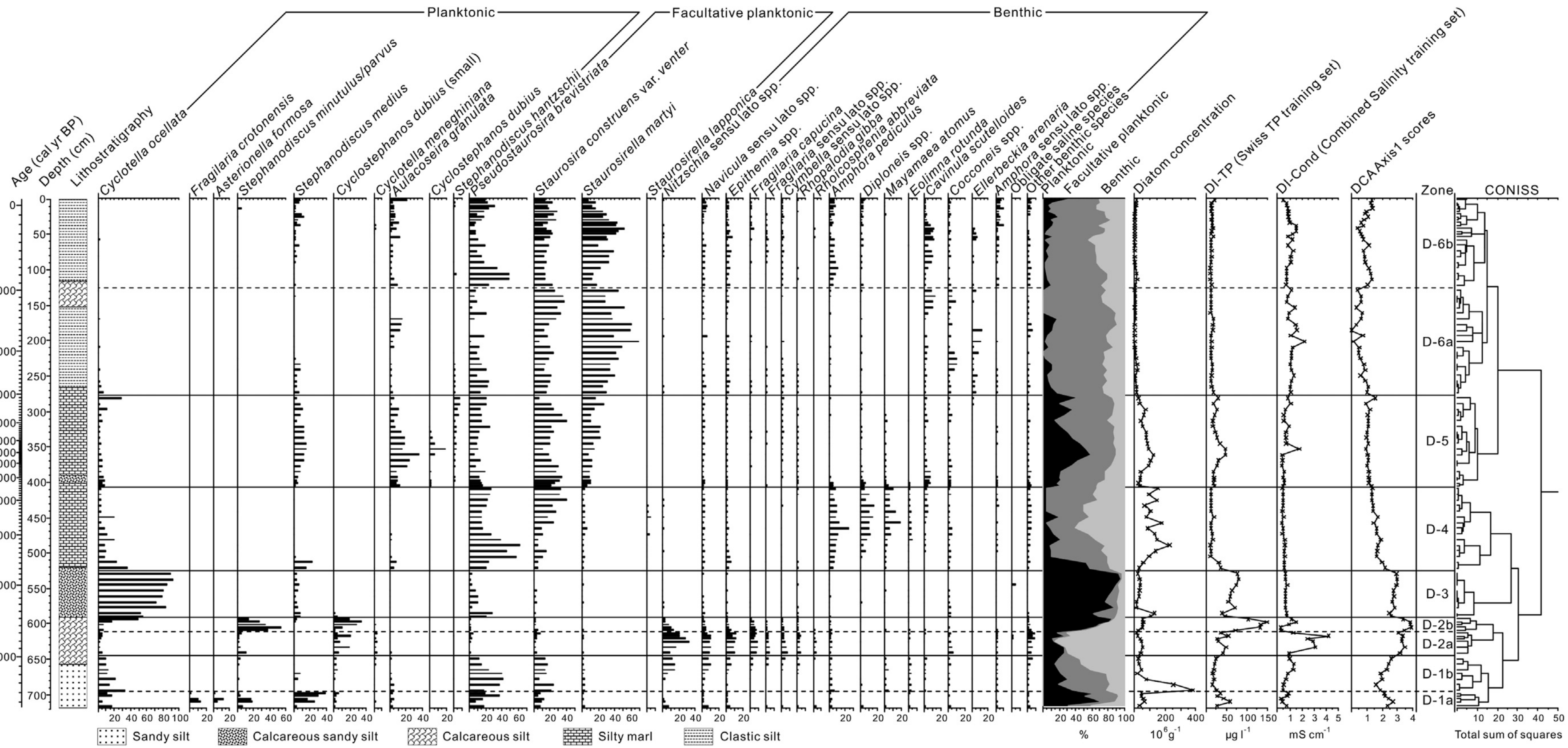

Fig. 5. Lithostratigraphy (modified from Francke et al., 2013) and summary diatom diagram of core Co1260, showing diatom-inferred total phosphorus (DI-TP) and conductivity (DI-Cond) reconstructions based on the Swiss TP and Combined Salinity training sets (EDDI; Juggins, 2001), respectively, and Axis 1 scores from detrended correspondence analysis (DCA). The calibrated radiocarbon chronology is marked at 1000-year intervals, with an estimated age of 12,500 cal yr BP at the base of the sequence.

5.4. Zone D-4 (525–407 cm, ca. 10,700–8,500 cal yr BP)

A shallow condition prevails in Zone D-4, clearly indicated by a transition to the co-dominance of *C. ocellata*, *S. medius* and *F. brevistriata* (ca. 20% each), to the dominance of *F. brevistriata* (up to 60%) and then to the relatively high abundance of *S. construens* var. *venter* (30–40%). Heavily-silicified facultative planktonic *Staurosirella martyi* (Héribaud) Morales & Manoylov and *S. lapponica* (Grunow) Williams & Round are consistently present. Benthic taxa are at higher abundance, including smaller *Amphora pediculus* (Kützing) Grunow and *Mayamaea atomus* (Kützing) Lange-Bertalot, and heavier *Diploneis mauleri* (Brun) Cleve and *Eolimna rotunda* (Hustedt) Lange-Bertalot, Kulikovskiy & Witkowski. *A. pediculus* is tolerant of oligotrophic to eutrophic conditions, *D. mauleri* and *E. rotunda* live mostly in mesotrophic waters, and *M. atomus* is a eutrophic species. A relatively high trophic level can also be inferred; this is not clear in the DI-TP reconstruction but is supported by high diatom concentration in this phase.

5.5. Zone D-5 (407–277 cm, ca. 8,500–3,000 cal yr BP)

The relatively high abundance of planktonic eutrophic *Aulacoseira granulata* (Ehrenberg) Simonsen and mesotrophic *S. medius*, the consistent presence of eutrophic *Stephanodiscus hantzschii* Grunow, and the short-lived peak of eutrophic *C. dubius* around 353 cm depth (ca. 5,700 cal yr BP), indicate a relatively deep and turbid state. It is supported by relatively high DI-TP and diatom concentration, particularly between 377 and 329 cm depth (ca. 7,200–4,500 cal yr BP), where it correlates with a broad peak of plankton and high in-lake productivity. Low light availability in the deeper water would reduce the growth of benthic diatoms, while tychoplanktonic *Pseudostaurosira*, *Staurosira* and *Staurosirella* species (maintained at 40–60%) are commonly transported into the water column (Battarbee et al., 2001) and are tolerant of disturbed environments (Anderson, 2000). Larger and heavily-silicified planktonic diatoms sink rapidly in the absence of mixing, even in a deep lake with a long settling distance (Bennion et al., 2010; Wolin and Stone, 2010), and in a shallow lake there is insufficient mixing to suspend these taxa for long growth periods (Bennion, 1995). Thus it is relatively high lake level and mixing that make robust planktonic *A. granulata*, *C. dubius*, *S. hantzschii* and *S. medius* and tychoplanktonic *S. martyi* remain in the photic zone. This supports an interpretation of the planktonic abundance both in terms of productivity and increased lake level.

5.6. Zone D-6 (277–0 cm, ca. 3,000 cal yr BP-present)

Diatom concentration is low, with high dissolution, particularly between 209 and 177 cm depth (ca. 1,900–1,500 cal yr BP) and between 81 and 21 cm depth (ca. 600–100 cal yr BP), where the diatom count is < 300 valves and assemblages are dominated by poorly-preserved valves of robust taxa. More fragile taxa such as *P. brevistriata* and *A. pediculus* are possibly dissolved. Despite the dissolution, the dominance of facultative planktonic taxa and low abundance of planktonic taxa indicate a shallow environment, possibly with the expansion of emergent vegetation, because the base of emergent macrophytes is a major habitat for small fragilaroid species (Sayer, 2001). After ca. 1,000 cal yr BP (in Subzone D-6b) there is a slight increase in *Amphora* species, but no major ecological shift occurs in the recent past. The topmost sample is distinguished by the relatively high abundance of *A. granulata*, which is probably a reflection of the incorporation of living diatoms rather than an indication of recent accelerated eutrophication. In the light of the lake's modern eutrophic to hypereutrophic state, the ecologically-consistent diatom assemblages suggest that high trophic level possibly prevails in this zone, although nutrient reconstruction is not particularly sensitive here. There are several possible reasons for lack of diatom evidence for accelerated eutrophication in the recent past: 1) eurytopic diatoms with broad tolerance ranges tend to dominate at a high trophic state as an adaptation to wide fluctuations in water chemistry, compounding the aforementioned potential for poor reconstruction at the upper end of the nutrient gradient; 2) non-planktonic diatoms respond to water-column nutrient additions less directly than phytoplankton, and they are more sensitive to habitat availability as they can derive nutrients from sediments and macrophytes (Bennion et al., 2010; Hall and Smol, 2010); 3) other algae (chlorophytes, cyanobacteria and dinoflagellates) are the most important primary producers rather than diatoms in this lake at a high trophic level; and 4) a more turbid state due to increased phytoplankton growth in turn reduces diatom growth, while chlorophytes and cyanobacteria are better competitors for light (Tilman et al., 1986).

6. Multi-proxy, regional- and catchment-scale interpretation

The diatoms provide strong proxy data for Lateglacial and Holocene changes in lake levels and trophic status in Lake Dojran, and strengthen previous lake-level and palaeoclimate interpretation by comparison with extant sedimentological and geochemical data from the same core in Fig. 6. The diatom data are also important in disentangling regional climate effects from the influence of local catchment processes on Holocene hydrological variability, and we exploit extant regional pollen data with robust chronologies for vegetation change in the highlands and lowlands in Fig. 7. We compare with various proxy data from the northeastern Mediterranean, and assess the importance of seasonality in driving Holocene moisture availability by using the summer and winter latitudinal temperature gradient (LTG) to disentangle precipitation from temperature effects (Fig. 7).

6.1. Younger Dryas (ca. 12,400–11,500 cal yr BP)

Francke et al. (2013) suggested that the presence of clay clasts, the occurrence of a 32,830 cal yr BP old shell fragment, and an undulated reflector in the hydro-acoustic data probably indicate a low lake level and redeposition between ca. 12,500–12,100 cal yr BP. This interpretation of a shallow state may be consistent with the relatively high abundance of benthic diatoms at the base of the sequence at ca. 12,500 cal yr BP. Subsequently in Subzone D-1a, even if the presence of eutrophic plankton may relate more to high productivity than lake level, the well-preserved diatom flora are important in indicating the presence of permanent water. A viable interpretation is that redeposition may occur, but that diatoms indicate lake refilling after desiccation, from a shallow state with the relatively high abundance of benthos to a relatively high lake level and eutrophic state with the dominance of plankton just above the core base. In Subzone D-1b (ca. 12,400–12,000 cal yr BP), diatom-inferred shallowing appears inconsistent with redeposition, since diatoms are well preserved, with a clear shift from the dominance of facultative planktonic taxa (50–65%) to increasing abundance of benthos, and peak concentration at the base of this subzone. Diatoms can be preserved during redeposition, as in the mass wasting deposit from Lake Ohrid (Zhang, unpublished data), but they would be present at extremely low concentration and with enhanced dissolution.

The diatom-inferred shallowing culminates in an extremely low lake level and eutrophic, oligosaline condition in the endorheic lake between ca. 12,000–11,500 cal yr BP (Zone D-2), indisputably interpreted as peak aridity of the Younger Dryas due to enhanced evaporative concentration. Based on strong evidence for the

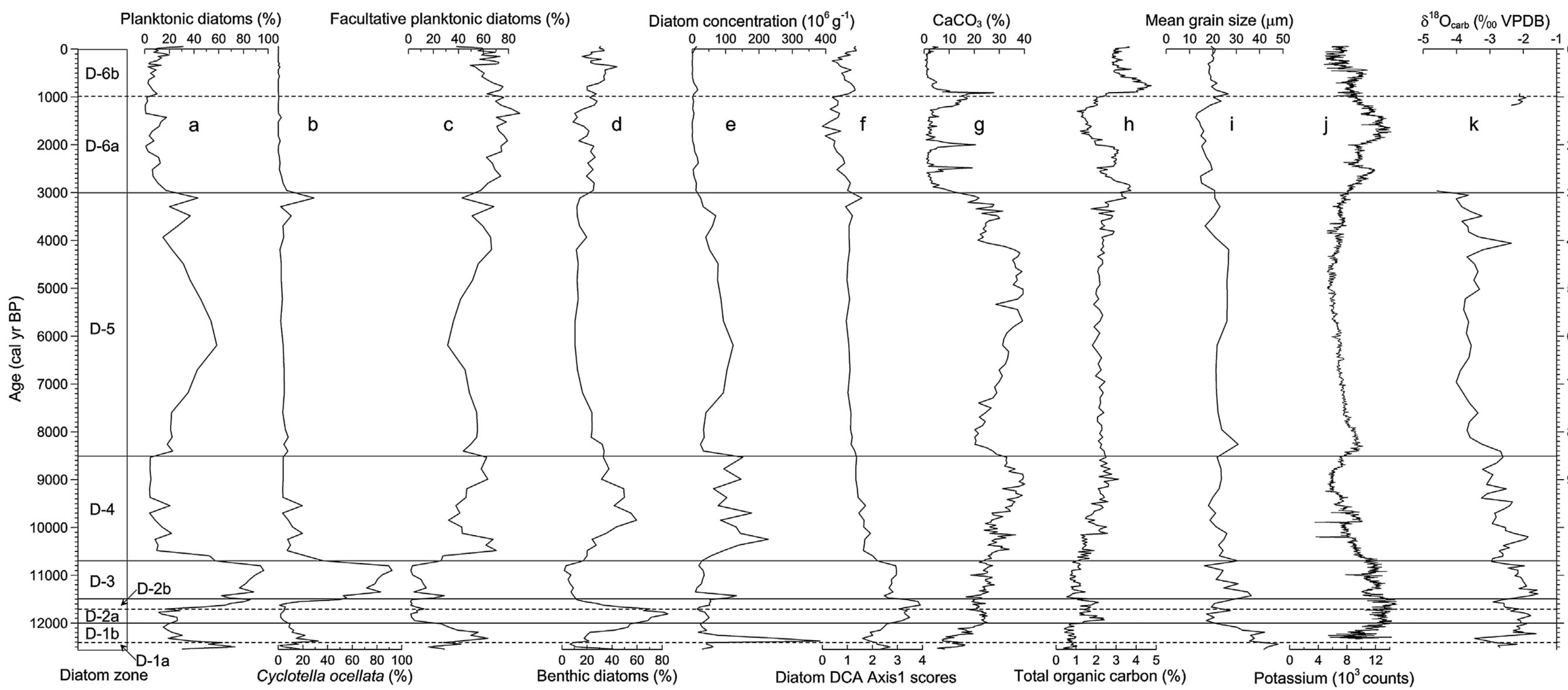

Fig. 6. Comparison of diatom data with selected sedimentological and geochemical data (Francke et al., 2013) in Lake Dojran. (a)–(d) the relative abundance of planktonic diatoms, *C. ocellata*, facultative planktonic diatoms and benthic diatoms; (e) absolute diatom concentration; (f) diatom DCA Axis 1 scores; (g) and (h) carbonate and organic matter contents; (i) mean grain size; (j) K concentration; (k) carbonate oxygen stable isotope data.

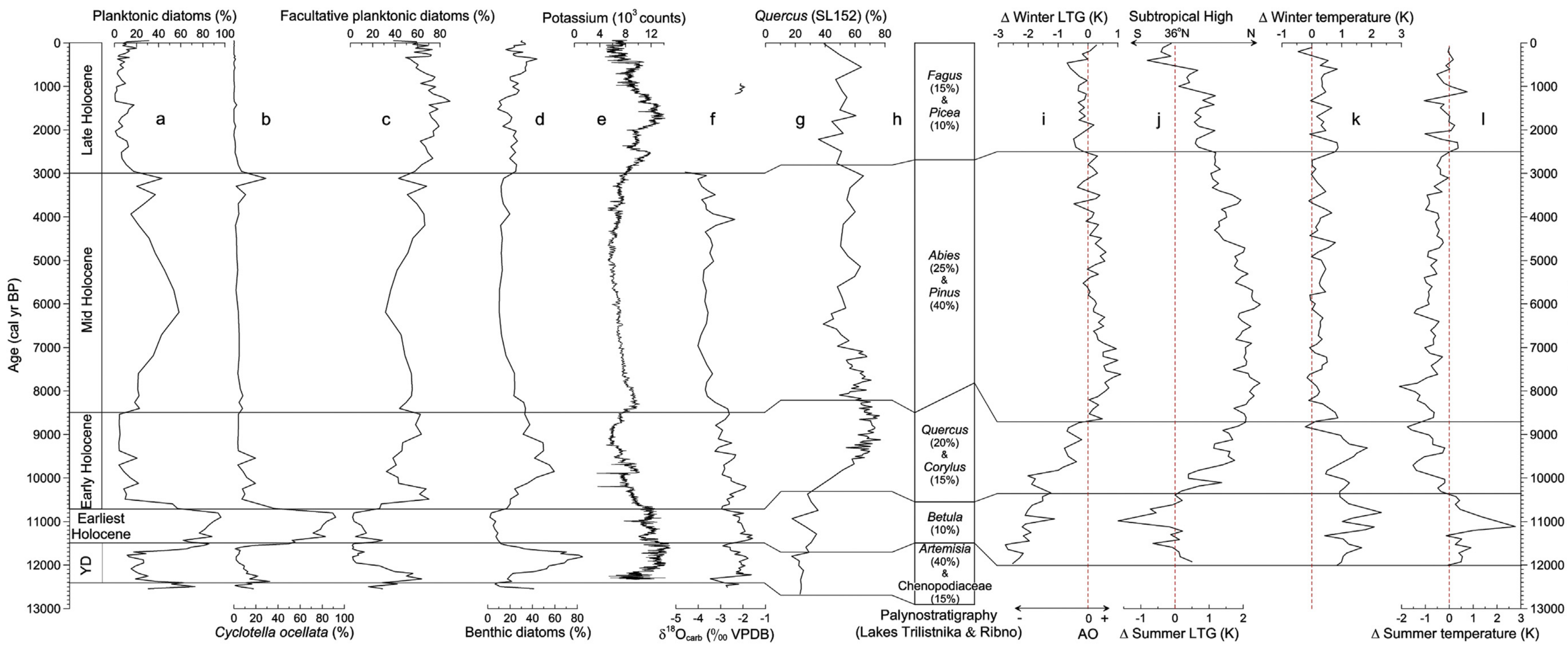

Fig. 7. Comparison of Lake Dojran diatom data with key palaeoclimate data. (a)–(d) the relative abundance of planktonic diatoms, *C. ocellata*, facultative planktonic diatoms and benthic diatoms; (e) K concentration (Francke et al., 2013); (f) carbonate oxygen stable isotope data (Francke et al., 2013); (g) percentage of *Quercus* pollen in SL152 (northern Aegean Sea) (Kotthoff et al., 2008a, 2008b); (h) palynostratigraphy with key pollen taxa and approximate average percentages from Lakes Trilistnika and Ribno (the Rila Mountain, southwestern Bulgaria) (Tonkov et al., 2008, 2013); (i) and (j) the Holocene winter and summer latitudinal temperature gradient (LTG) between northern and southern Europe (Davis and Brewer, 2009); (k) and (l) the Holocene winter and summer temperature anomalies in southeastern Europe (Davis et al., 2003).

presence of permanent water derived from hydro-acoustic data, grain-size composition and the absence of clay clasts, Francke et al. (2013) interpreted this zone as one of higher lake level than the shallow or even desiccated state at the base of the sequence. Since extremely shallow or even ephemeral lakes may be characterised by 'lacustrine' sediment (Reed, 1998a, 1998b), the data in conjunction indicate that this later phase (Zone D-2) can be interpreted as a stable and lacustrine state, but with the classic enhanced aridity of the Younger Dryas.

In the northeastern Mediterranean, there is growing palynological evidence for aridity during the Younger Dryas, commonly marked by a peak in steppic pollen taxa *Artemisia* and Chenopodiaceae throughout the altitudinal range (e.g. Lake Ribno, 2184 m a.s.l., Tonkov et al., 2013; Lake Prespa, 849 m a.s.l., Panagiotopoulos et al., 2013; Valle di Castiglione, central Italy, 44 m a.s.l., Di Rita et al., 2013), and including a peak in *Ephedra* in marine records (e.g. Kotthoff et al., 2008a; Desprat et al., 2013). Pollen-based biome reconstructions (Allen et al., 2002; Bordon et al., 2009) and quantitative temperature and/or precipitation reconstructions (e.g. Bordon et al., 2009; Dormoy et al., 2009) also provide evidence of a cold, arid steppe environment. Our results are important in strengthening the sparse regional palaeohydrological dataset, which to date only comprises a distinct decrease in planktonic diatoms (particularly *C. ocellata*) in Lake Ioannina (Wilson et al., 2008), a peak of the eutrophic diatom species *A. granulata* and facultative planktonic *Staurosirella pinnata* (Ehrenberg) Williams & Round in Lake Prespa, Macedonia/Albania/Greece (Cvetkoska et al., 2014), a decrease in rubidium (Rb)/strontium (Sr) ratio in Lake Stymphalia, southern Greece (Heymann et al., 2013), and an increase in $\delta^{18}O_{carb}$ values and magnesium (Mg)/calcium (Ca) ratio in Lake Van, eastern Turkey (Wick et al., 2003; Litt et al., 2009).

6.2. The earliest Holocene (ca. 11,500–10,700 cal yr BP) (corresponding to the Preboreal period)

Diatom-inferred high lake level and relatively low trophic state during the earliest Holocene (Zone D-3) strengthens the previously tentative interpretation of high $\delta^{18}O_{carb}$ values. Francke et al. (2013) suggested that evaporation was promoted during this period by large lake surface area that was accompanied by lake-level increase in such a flat-bottomed basin. The high lake level in Lake Dojran is in accord with abrupt isotopic depletion at the Younger Dryas–Holocene transition in Lake Ioannina, Lake Van and Eski Acıgöl (central Turkey) (Roberts et al., 2008 and references therein). It is also in accord with the inference of high humidity from increased Rb/Sr ratio in Lake Stymphalia (Heymann et al., 2013). However, it is not in complete agreement with vegetation development in the northeastern Mediterranean during the earliest Holocene. Non-steppic herb pollen increased rather than *Quercus* pollen in SL152 in the northern Aegean region at this time (Kotthoff et al., 2008a). Non-steppic herb pollen were abundant during this period although *Quercus* pollen increased rapidly at the onset of the Holocene in Nisi Fen (Lawson et al., 2005) and Lake Accesa (central Italy) (Drescher-Schneider et al., 2007). Non-steppic herb and steppe pollen were replaced by *Quercus* pollen gradually until its maximum around 10,500 cal yr BP in Lake Prespa (Panagiotopoulos et al., 2013) and Tenaghi Philippon (northeastern Greece) (Müller et al., 2011). Non-steppic herb pollen was dominant, with a gradual increase of *Quercus* pollen until ca. 10,500 cal yr BP in Eski Acıgöl (Roberts et al., 2001; Turner et al., 2008) and MD04-2797 (Siculo-Tunisian Strait) (Desprat et al., 2013). Non-steppic herb pollen replaced steppe pollen gradually during this period, along with a slightly increasing trend in *Quercus* pollen in Lake Van (Litt et al., 2009). Non-steppic herb taxa were more important in these records than the percentage data implied, because they are mostly lower pollen producers than *Quercus* (Broström et al., 2008).

The high lake level in Lake Dojran and isotopic depletion in the northeastern Mediterranean suggest that the increase in humidity during the earliest Holocene would be attributed to increased precipitation, since Younger Dryas mountain glaciations did not develop widely in this region (Hughes et al., 2006; Hughes, 2012) and meltwater input is an unlikely forcing function. However, the wide distribution of non-steppic herb taxa suggest that increased moisture availability was insufficient to support extensive forest development, since afforestation linked to soil development was asynchronous in this region. The limited increase in humidity is possibly the effect of high evaporation, corresponding to high pollen-inferred area-average summer and winter temperature in southeastern Europe (Davis et al., 2003) and high alkenone-inferred sea surface temperature (SST) at the beginning of the Holocene in the Mediterranean Sea (Abrantes et al., 2012). The comparison with the summer and winter LTG supports increased precipitation during the earliest Holocene. The negative (strong) winter LTG resulted in the negative phase of AO (Davis and Brewer, 2009), and promoted the penetration of more westerly moisture of North Atlantic origin in winter. The summer LTG suggests that the Subtropical High pressure was not strengthened and displaced northward (Davis and Brewer, 2009), and summer moisture was not scarce at this time. Thus the LTG and atmospheric moisture availability would contribute to the increase in precipitation during the earliest Holocene, modulated by high temperature-induced evaporation.

Changes in catchment vegetation and erosion can have a major influence on lake hydrology and nutrient input and hence diatom composition (Fritz and Anderson, 2013). At the catchment scale, the steppe vegetation was replaced by birch forest at high altitudes (Lakes Ribno and Trilistnika, the Rila Mountain, southwestern Bulgaria) (Tonkov et al., 2008, 2013) and by non-steppic herbs in the lowlands (SL152, northern Aegean Sea) (Kotthoff et al., 2008a). Despite increased precipitation and water inflow, the vegetation development restrained catchment erosion and nutrient input, which is supported by lower clastic input indicated by decreased K concentration (Francke et al., 2013). Together with the dilution effect of increased freshwater input, lower nutrient input resulted in the relatively low trophic level and in-lake productivity, which is supported by low organic matter content (Francke et al., 2013). In the northeastern Mediterranean, low trophic levels during the earliest Holocene were also indicated by pigment and diatom data in Lake Albano, central Italy (Guilizzoni et al., 2002). In all, increased precipitation was a major contributor to the high lake level in Lake Dojran and increased humidity in the northeastern Mediterranean during the earliest Holocene, although high evaporation reduced the effect of increased precipitation.

6.3. The early Holocene (ca. 10,700–8,500 cal yr BP)

The diatom data show a low lake level and relatively high trophic state during the early Holocene (Zone D-4), which is not in accord with decreasing $\delta^{18}O_{carb}$ values in Lake Dojran. Francke et al. (2013) suggested that the littoral zone might extend during this phase. If valid, epiphytic and epipelic diatoms can be similarly facilitated, and they could reach the coring site through water mixing and/or sediment redistribution. However, water mixing would cause nutrients to become well distributed in the water column as well as in the pelagic zone, conflicting with the rather low relative abundance of planktonic taxa at the coring site; sediment disturbance would be unfavourable to the settlement and preservation of smaller, fragile valves, conflicting with the relatively high percentages of *A. pediculus* and *M. atomus*.

The diatom-inferred low lake level is also inconsistent with low bulk carbonate $\delta^{18}O$ values in Lake Pergusa (Sicily) (Sadori et al., 2008), authigenic carbonate $\delta^{18}O$ values in Lake Gölhisar (southwestern Turkey) (Eastwood et al., 2007) and ostracod $\delta^{18}O$ values in Lake Ioannina (Frogley et al., 2001). Roberts et al. (2008) suggested that the freshening of surface water in the eastern Mediterranean Sea in parallel with sapropel formation would affect the isotopic composition of precipitation during the early Holocene. However, the low lake level in Lake Dojran is in line with relatively high $\delta^{18}O$ values of authigenic carbonates in Lake Ohrid (Macedonia/Albania) (Leng et al., 2010), Lake Prespa (Leng et al., 2013) and Lake Van (Litt et al., 2009), and mollusc $\delta^{18}O$ values in Lake Frassino (northern Italy) (Baroni et al., 2006). The apparent discrepancy in isotope proxy data is probably due to the control of different hydroclimatic parameters (Jones and Roberts, 2008) and the influence of catchment factors on the specific hydrology of each lake (Leng and Marshall, 2004). The diatom-based inferences in Lake Dojran are also in accord with the inference of low lake levels from low Rb/Sr ratio in Lake Stymphalia (Heymann et al., 2013) and high Ca/titanium (Ti) ratio in Lake Iznik, northwest Turkey (Roeser et al., 2012) at this time.

Palynological data are also complex, with the occurrence of different ecological pollen groups in this region (e.g. Roberts et al., 2011b; Sadori, 2013) and even in the same record (e.g. Peyron et al., 2011; Panagiotopoulos et al., 2013), which have been interpreted in different ways. The apparent discrepancy in the regional vegetation distribution was attributed to spatial and altitudinal variation in climatic factors (De Beaulieu et al., 2005; Sadori, 2013), and Roberts et al. (2011b) suggested that increased seasonality of climatic factors is an important factor. Willis (1992a) invoked the distance from mountain refugia of different taxa, and Sadori et al. (2011) linked this to edaphic conditions and water retention capacity suitable for different plant growth. With respect to the combination of ecologically-incompatible pollen groups in the same record, Panagiotopoulos et al. (2013) attributed this to a more even distribution of annual precipitation, while Magny et al. (2013) invoked high seasonality of precipitation. Roberts et al. (2011b) cautioned against interpreting this pollen flora too closely in terms of modern climate analogues. Despite this complexity, the Lake Dojran diatom data are supported by pollen-based quantitative reconstructions of higher winter precipitation and lower or consistently low summer precipitation in SL152 (Dormoy et al., 2009), Lake Accesa (Peyron et al., 2011), Lake Pergusa (Magny et al., 2012; Peyron et al., 2013) and MD04-2797 (Desprat et al., 2013). The low lake level and relatively high trophic state in Lake Dojran are probably driven by strong seasonal hydrological contrasts, and extreme summer aridity offset the effect of winter precipitation recharge. This is consistent with the wide distribution of *Quercus ilex* in the northern Aegean region rather than *Quercus* deciduous type (Kotthoff et al., 2008b), although moisture availability was sufficient to support tree growth.

The comparison with the summer and winter LTG supports this climatic interpretation as high seasonality. The negative (strong) winter LTG suggests that AO was in the negative phase (Davis and Brewer, 2009), the storm track was in a southerly path and moisture availability in winter was high during the early Holocene. The positive (weak) and increasing summer LTG suggests that the Subtropical High pressure was migrating northward (Davis and Brewer, 2009), blocking westerly moisture penetration in summer and leading to much drier summers than today. It is associated with the intensified African monsoon and the large number of lake records in the Sahara and Sahel (Lézine et al., 2011), and with sapropel formation in the eastern Mediterranean Sea since 10,800 cal yr BP (De Lange et al., 2008). Thus the LTG and high seasonality of moisture availability would contribute to the reduced lake level and increased nutrient level in Lake Dojran during the early Holocene.

At the catchment scale, the Lake Dojran diatom data coincide with extensive forest development, mainly comprising deciduous oak forest (*Quercus robur* and *Quercus cerris*) at high altitudes (Lakes Ribno and Trilistnika, southwestern Bulgaria) (Tonkov et al., 2008, 2013) and evergreen oak forest (*Q. ilex*) in the lowlands (SL152, northern Aegean Sea) (Kotthoff et al., 2008a, 2008b). According to the contrasting growth requirements of deciduous and evergreen oaks (Roberts et al., 2011b), it can be posited that the dense, thick vegetation would reduce runoff and erosion in the catchment throughout the year through soil absorption and retention, which may contribute to the low lake level, high shell abundance and lower K concentration during this phase (Francke et al., 2013). However, forest vegetation would enhance chemical weathering and nutrient supply through soil development, which may contribute to the relatively high trophic level in spite of the limited water inflow. This is supported by high diatom concentration, as well as higher organic matter and carbonate content (Francke et al., 2013), indicating high in-lake productivity. In all, the low lake level and relatively high trophic state in Lake Dojran may result climatically from high seasonality of precipitation and locally from dense forest development and limited, nutrient-rich catchment runoff.

6.4. The mid Holocene (ca. 8,500–3,000 cal yr BP)

A relatively high lake level and maximum Holocene trophic level are inferred during the mid Holocene (Zone D-5). This is supported by decreased $\delta^{18}O_{carb}$ values. Francke et al. (2013) also discussed a relatively high lake level during this phase based on sedimentological data. The relatively high lake level in Lake Dojran is consistent with low $\delta^{18}O_{carb}$ values in Lake Prespa (Leng et al., 2013) and Lake Van (Litt et al., 2009), low mollusc $\delta^{18}O$ values in Lake Frassino (Baroni et al., 2006), and high lake levels in Lake Xinias, central Greece (Digerfeldt et al., 2007). However, in the northeastern Mediterranean, an aridification trend was shown by isotopic enrichment in Eski Acıgöl (Roberts and Jones, 2002), diatom succession in Lake Ioannina (Wilson et al., 2008; Jones et al., 2013), and lithological changes in Lake Pergusa (Sadori and Narcisi, 2001). Sadori et al. (2011) and Roberts et al. (2011b) improved understanding of this aridification process after ca. 8,000 cal yr BP based on a regional synthesis of pollen and isotope data, respectively. The comparison with the summer and winter LTG does not give support to increased humidity during the mid Holocene. Both the summer and winter LTG were more positive (weaker) during this period (Davis and Brewer, 2009), and the positive phase of AO and the northern position of the Subtropical High pressure suggest that winter was not influenced by the northward-shifted storm track and summer was controlled mostly by the downdraught of dry air, respectively. This would lead to low winter precipitation and much drier summers than today, although several regional syntheses of temperature (Davis et al., 2003; Finné et al., 2011; Abrantes et al., 2012) suggested cooling and decreased evaporation during the mid Holocene.

At the catchment scale, the relatively high lake level and high trophic state in Lake Dojran coincide with the dominance of coniferous forest (mainly firs) at high altitudes at ca. 8,500–7,800 cal yr BP (Lakes Ribno and Trilistnika, southwestern Bulgaria) (Tonkov et al., 2008, 2013) and the opening of the oak forest with an increase in non-steppic herbs in the lowlands (SL152, northern Aegean Sea) (Kotthoff et al., 2008a, 2008b). The reduction of forest density in the lowlands, most probably corresponding to the aridification process discussed above, was also clearly indicated by a distinct decrease in *Quercus* pollen concentration at ca. 8,400 cal yr BP (Kotthoff et al., 2008a), which would cause an increase in nutrient mobility. The expansion of firs at high altitudes is a regional signal across the southern Balkans, including Rezina Marsh (1800 m a.s.l.) at ca. 8,600 cal yr BP (Willis, 1992b). Fir trees developed in more humid and organic soils (Sadori et al., 2011), and the wetting of the highlands and forest development enhanced runoff and nutrient supply. In all, the wetting of the highlands and the drying of the lowlands and associated local vegetation succession enhanced catchment runoff and nutrient erosion, and resulted in the relatively high lake level and eutrophic state in Lake Dojran.

6.5. *The late Holocene (ca. 3,000–0 cal yr BP)*

Despite low diatom concentration and high dissolution, a low lake level and high trophic state can be inferred during the late Holocene (Zone D-6). Late-Holocene aridity prevailed in the northeastern Mediterranean, indicated by isotope data (e.g. Roberts et al., 2008, 2011b; Leng et al., 2013) and lake-level reconstructions (e.g. Harrison and Digerfeldt, 1993; Digerfeldt et al., 2007; Magny et al., 2011). The comparison with the summer and winter LTG suggests that atmospheric moisture availability is not a determining factor, because the Subtropical High pressure regressed and AO index was slightly negative, which would not result in the obvious moisture deficit in this region. In contrast, the increase in regional temperature (Davis et al., 2003; Finné et al., 2011) and high evaporation may contribute to the aridity during the late Holocene, although one model simulation suggests that anthropogenic deforestation may itself have caused a decrease in summer and winter temperature in southern Europe due to increased albedo effect (Strandberg et al., 2014).

A previous late-Holocene palynological study in the littoral zone of Lake Dojran revealed that the oak forest in the lowlands and the conifer and beech forests in the mountain region were replaced by herb vegetation and secondary trees at ca. 2,800 cal yr BP as a result of intensified human impact (Athanasiadis et al., 2000). At the catchment scale, beech and spruce forests expanded widely at high altitudes, and beech trees were favoured by human agricultural and stock-breeding activities and resultant soil deterioration (Marinova et al., 2012; Tonkov et al., 2013). Non-steppic herbs expanded in the lowlands along with the further decline of the oak forest, and human disturbance was an important factor (Kotthoff et al., 2008a). Deforestation at mid-low altitudes during the late Holocene was also a regional event, for example, in Nisi Fen (475 m a.s.l.) the temperate forest declined at ca. 3,500 cal yr BP (Lawson et al., 2005; Kotthoff et al., 2008a), and in Lake Ohrid (693 m a.s.l.) it was reflected by the reduction of the coniferous forest at ca. 2,500 cal yr BP (Wagner et al., 2009). Thus human impact is possibly an important factor not only leading to the high trophic state during the late Holocene by deforestation and enhanced nutrient erosion, but also contributing to the low lake level through agriculture and irrigation.

7. Conclusions

The Lake Dojran diatom data, supported by extant sedimentological and geochemical data from the same core and late-Holocene palynological data from a separate littoral core, give a new insight into Younger Dryas and Holocene changes in lake levels and trophic status in the northeastern Mediterranean. The Lake Dojran diatom data provide more robust evidence and strengthen previous lake-level interpretation based on sedimentological and geochemical data during the earliest, mid and late Holocene, and also clarify previous uncertainty in interpretation of Younger Dryas and early-Holocene lake-level change. Following a very shallow or even desiccated state at the core base at ca. 12,500 cal yr BP, indicated by sedimentological and hydro-acoustic data, diatoms indicate lake infilling, from a shallow state with abundant benthos to a plankton-dominated relatively high lake level and eutrophic state thereafter. Diatom-inferred shallowing between ca. 12,400–12,000 cal yr BP and a very low lake level and eutrophic, oligosaline state between ca. 12,000–11,500 cal yr BP provide clear evidence for aridity during the Younger Dryas. Although a slightly higher lake level was previously inferred during the second part of this period, the lacustrine state with permanent water does not conflict with the diatom-inferred salinity shift. Lake Dojran's water level increased markedly during the earliest Holocene (ca. 11,500–10,700 cal yr BP). A low lake level and relatively high trophic state are inferred during the early Holocene (ca. 10,700–8,500 cal yr BP), conflicting with the previous inference of increased humidity from decreasing $\delta^{18}O_{carb}$ values and sedimentological data. Lake Dojran was relatively deep and exhibited the maximum Holocene trophic level during the mid Holocene (ca. 8,500–3,000 cal yr BP), and it became shallow during the late Holocene (ca. 3,000–0 cal yr BP). Our results indicate that, being located at the juncture of the proposed boundaries between the west–east and north–south contrasting Holocene climatic domains, Lake Dojran cannot be classified simply into the western or eastern sector, or the northern or southern sector in the Mediterranean.

Our results are also important in disentangling regional climate effects from local catchment dynamics during the Holocene, and to this end we exploit extant regional palynological data for vegetation change in the highlands and lowlands. The importance of seasonality in driving Holocene climate change is assessed by reference to the summer and winter LTG model, linked to the Subtropical High pressure and AO, respectively. We suggest that diatom-inferred high lake level during the earliest Holocene was attributed to the increase in precipitation, in spite of high pollen-inferred, temperature-induced evaporation, and is coherent with high winter and summer atmospheric moisture availability inferred from the LTG. The relatively low trophic state at this time was possibly driven in part by vegetation development and reduced catchment erosion. The diatom-inferred early-Holocene lake-level reduction and increased trophic level may result climatically from high seasonality of precipitation, coherent with the contrasting summer and winter LTG, and locally from limited, nutrient-rich runoff in a densely-forested catchment. The relatively deep, eutrophic state in Lake Dojran during the mid Holocene shows strong affinity with palaeolimnological data from central Greece, northern Italy and eastern Turkey, but not with other records in the northeastern Mediterranean, where aridification is recognised. It is also not coherent with the LTG-inferred low atmospheric moisture availability. This may reflect local complexity of climate variability, but may also indicate that changes were driven more by local vegetation succession and associated changes in catchment processes than by climate change. During the late Holocene, diatom-inferred shallow and high trophic state is consistent with strong regional evidence for temperature-induced aridity, coupled with the influence of intensified human land use.

Overall, our study is important in strengthening existing multi-proxy interpretation of Lateglacial and Holocene palaeohydrology and associated shifts in nutrient status. This study improves understanding of Younger Dryas and Holocene climate change in the northeastern Mediterranean, providing a coherent interpretation which suggests the important role of the LTG on moisture availability during the Holocene and clarifies the influence of catchment processes on Holocene hydrological variability.

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