Reconciling diverse lacustrine and terrestrial system response to penultimate deglacial warming in southern Europe

Graham P. Wilson1*, Jane M. Reed2, Michael R. Frogley3, Philip D. Hughes4, and Polychronis C. Tzedakis5

1Department of Geography and International Development, University of Chester, Chester CH1 4BJ, UK
2Department of Geography, Environment and Earth Sciences, University of Hull, Hull HU6 7RX, UK
3Department of Geography, University of Sussex, Brighton BN1 9QJ, UK
4Department of Geography, School of Environment, Education and Development, University of Manchester, Manchester M13 9PL, UK
5Department of Geography, University College London, London WC1E 6BT, UK

ABSTRACT

Unlike the most recent deglaciation, the regional expression of climate changes during the penultimate deglaciation remains understudied, even though it led into a period of excess warmth with estimates of global average temperature 1–2 °C and sea level ~6 m above pre-industrial values. We present the first complete high-resolution southern European diatom record capturing the penultimate glacial-interglacial transition, from Lake Ioannina (northwest Greece). It forms part of a suite of proxies selected to assess the character and phase relationships of terrestrial and aquatic ecosystem response to rapid climate warming, and to resolve apparent conflicts in proxy evidence for regional paleohydrology. The diatom data suggest a complex penultimate deglaciation driven primarily by multiple oscillations in lake level, and provide firm evidence for the regional influence of abrupt changes in North Atlantic conditions. There is diachrony in lake and terrestrial ecosystem response to warming at the onset of the last interglacial, with an abrupt increase in lake level occurring ~2.7 k.y. prior to sustained forest expansion with peak precipitation. We identify the potentially important role of direct input of snow melt and glacial meltwater transfer to the subterranean karst system in response to warming, which would cause rising regional groundwater levels. This explanation, and the greater sensitivity of diatoms to subtle changes in temperature, reconciles the divergent lacustrine and terrestrial proxy evidence and highlights the sensitivity of lakes situated in mountainous karstic environments to past climate warming.

INTRODUCTION

During the penultimate deglaciation (ca. 136–129 ka, the Marine Isotope Stage 6 [MIS 6] to MIS 5 transition, Termination II) global climate shifted from one of the most extreme glaciations to one of the warmest interglacials. Recent high-resolution marine sediment records from the Iberian margin reveal a complex multiple-step climate transition in response to deglacial meltwater pulses into the North Atlantic associated with Heinrich Stadial 11 (HS11; ca. 136–130 ka; Martrat et al., 2014; Marino et al., 2015) to deglacial meltwater pulses into the North Atlantic associated with Heinrich margin reveal a complex multiple-step climate transition in response to deglacial meltwater pulses into the North Atlantic associated with Heinrich Stadial 11 (HS11; ca. 136–130 ka; Martrat et al., 2014; Marino et al., 2015), a pattern also seen in regional speleothem δ18O records (Drysdale et al., 2009; Grant et al., 2012). Episodes of low sea-surface temperatures (SSTs) and aridity at this time may have been caused by the expansion of North Atlantic cold water masses into lower latitudes (Martrat et al., 2014). Few data from this period are available from continental lake and peat bog archives. In Lago Grande di Monticchio, southern Italy, expansion of forests started at 130.6 ka; a short-lived (~250 yr) reduction in tree populations is apparent at 128.2–127.9 ka (Brauer et al., 2007). In Lake Ohrid (Albania-Macedonia), the absence of ice-rafted debris and rising calcite from ca. 130 ka indicate a transition to interstadial conditions, with onset of full interglacial conditions from ca. 127 ka (Vogel et al., 2010), during which limnological shifts in productivity predated forest expansion (Lézine et al., 2010). The Soreq Cave (Israel) δ18O speleothem data (Grant et al., 2012) suggest an overall gradual and moderate increase in regional precipitation from ca. 139.5 ka. Sedimentological data and climate simulations indicate increasing seasonality through the penultimate late glacial (Brauer et al., 2007; Kutzbach et al., 2014). In this study, we return to Lake Ioannina (Epirus, northwest Greece; see the GSA Data Repository1 for site details), a reference site for paleoclimate research in southern Europe (e.g., Frogley et al., 1999; Tzedakis et al., 2002, 2003; Wilson et al., 2008; Roucoux et al., 2011) to improve understanding of paleohydrology and terrestrial and aquatic responses to abrupt climate change during the penultimate deglaciation.

CORE I-284 DIATOM RECORD

The penultimate late glacial and last interglacial sections of sediment core I-284 (Fig. 1) from the Ioannina basin have previously been the focus of multiproxy analysis (pollen, ostracod, calcite δ18O, and δ13C; Frogley et al., 1999; Tzedakis et al., 2003). The I-284 time scale used here is constructed by aligning the percentage of temperate tree pollen to Corchia speleothem δ18O (Drysdale et al., 2009), on the premise that the amount of precipitation in southern Europe exerts a dominant control over both the composition of vegetation and the δ18O of speleothems (Tzedakis et al., 2002; Drysdale et al., 2009; see the Data Repository). Between 101.97 and 94.80 m (ca. 140.3 and 125.9 ka), 70 samples for diatom analysis were taken at 10 cm intervals (~200 yr resolution) or greater, sufficient to span the glacial-interglacial transition as determined from changes in arboreal pollen frequency and concentration (Tzedakis et al., 2003). Sample preparation for diatom analysis followed standard techniques (Battarbee, 1986; see the Data Repository).

Two major biostratigraphic zones can be defined: diatom assemblage zone (DAZ) 1 (101.97–98.25 m, ca. 140.3–131.3 ka) and DAZ 2 (98.23–94.80 m, ca. 131.3–125.9 ka) (Fig. 2). Diatom concentrations are generally low during DAZ 1, which contains relatively high frequencies of bentic (particularly Navicula rotundata Hustedt) and facultative planktonic species (small Fragilariaceae: Staurosirella pinnata [Ehrenberg] Williams and Round, and Pseudostaurosira brevistriata [Grunow] Williams and Round), but with distinct peaks (to >80% abundance) in planktonic taxa, dominated by classic forms (with three ocelli) of Cyclotella ocellata Pansocek, and accompanied by large, non-classic forms with complex central area structure. Five subzones (DAZ 1a–DAZ 1e) can be defined based on the interchanging dominance of these taxa. DAZ 1b (101.62–101.12 m, ca. 139.4–138.1 ka) is notable in the consistent dominance of C. ocellata. A marked increase in relative abundance of C. ocellata occurs at the DAZ 1–DAZ 2 boundary ca. 131.3 ka at the expense of liitoral taxa. Diatom concentrations in DAZ 2 are typically higher than in DAZ 1. Cyclotella ocellata is dominant throughout. The transition from DAZ 2a to DAZ 2b is marked by a slight increase in facultative planktonic and benthic taxa (e.g., Cocconeis placentula Ehrenberg and N. rotunda). From previous research on the glacial diatom flora of Ioannina (e.g., Wilson et al., 2008, 2013) and other Mediterranean, relatively shallow, aquifer-fed, alkaline

1GSA Data Repository item 2015277, site details, methods, chronology, and diatom data, is available online at www.geosociety.org/pubs/ft2015.htm, or on request from editing@geosociety.org or Documents Secretary, GSA, P.O. Box 9140, Boulder, CO 80301, USA.
lakes, including Lake Dojran (Macedonia-Greece; Zhang et al., 2014) and Lake Prespa (Macedonia-Greece; Cvetkoska et al., 2014a), the small Fragilariaceae are indicative of shallow lake conditions with extended seasonal ice cover in a cold, arid glacial climate. *C. ocellata* has broad ecological preferences (in part because it is likely to represent a species complex), but in these systems, appears to indicate oligotrophic-mesotrophic conditions, particularly when accompanied by large, non-classic forms (Cvetkoska et al., 2014a). The large Ioannina morphotypes await taxonomic description, but show affinities with recently described Mediterranean taxa separated from the *C. ocellata* complex, comprising *C. prespanensis* Cvetkoska, Hamilton, Ognjanova-Rumenova and Levkov, *C. paraocellata* Cvetkoska (Cvetkoska et al., 2014b), and *C. paleo-ocellata* Vossel and Van de Vijver (Vossel et al., 2015).

**PENULTIMATE DEGLACIATION**

The high frequency of benthic and facultative planktonic taxa between ca. 140.3 and 131.3 ka (DAZ 1) suggests that the water depth at the core site was relatively shallow, in a cold, arid climate. However, *C. ocellata* dominance suggests sustained higher lake levels between 139.4 and 138.1 ka (DAZ 1b). This interval coincides with a marked initial expansion in arboreal pollen from ~17% to 37% (Fig. 3), indicating an initial phase of forest expansion coeval with an inferred increase in regional precipitation (Grant et al., 2012) marking the start of the late glacial. During a period of reduced tree populations at Ioannina (ca. 137–132.5 ka), the high abundance of small Fragilariaceae and slight increase in benthic taxa suggest a return to shallow lake conditions with greater seasonal ice cover in a cold, arid climate. This is coeval with an interval of minimum SSTs in the Alboran Sea and Portuguese margin ca. 136–132 ka (Martrat et al., 2014; Fig. 3). Therefore, there is strong evidence for both terrestrial and aquatic ecosystem response at Ioannina to cooler and drier conditions associated with changes in the North Atlantic during HS11. Warming events

---

Figure 1. A: Location of Ioannina (northwest Greece) and sites mentioned in the text. LdGM—Lago Grande di Monticchio; ODP-976—Ocean Drilling Program Site 976. B: Sediment core site I-284 (39°45′N, 20°51′E) in relation to the present lake (470 m asl, above sea level) and surrounding topography. Areas of land >1850 m asl (dashed line) correspond to the estimated equilibrium line altitude of glaciers in this area during the penultimate glacial. Snow cover would have been permanent in the stippled areas. Glaciers would have been larger than these stippled areas but with variable hypsometries depending on local topoclimatic factors. Adapted from Wilson et al. (2013).

---

Figure 2. Summary diatom diagram of taxa present with relative frequencies of ≥2%. Diatom assemblage zones (DAZ), as determined by CONISS (constrained incremental sum of square cluster analysis), and DAZ boundary ages are also shown. Plank.—plankton; F.—facultative; conc.—concentration; sed.—sediment.
may have punctuated stadials associated with Heinrich events, including HS11 (Martrat et al., 2014). The diatom record at Ioannina also shows short-lived peaks in *C. ocellata* at the expense of small Fragilariaceae. This may suggest short-lived episodes of higher lake levels (Wilson et al., 2008; Jones et al., 2013; Cvetkoska et al., 2014a), possibly accompanied by a longer open-water season with earlier spring ice melt (cf. Wilson et al., 2013). Lower resolution δ¹⁸O data in this section of the core prevents a robust and detailed comparison with the diatom record, but the tendency is for plankton peaks to be matched with lower δ¹⁸O values indicative of increased lake levels. Reduced forest populations and the increase in steppe elements during this interval (ca. 137–133 ka) indicate that these episodes were probably not related to increases in regional precipitation. Instead, the source of hydrological input may be from late winter pulses of groundwater flow from meltwater flooding.

The rapid transition to prolonged dominance of *C. ocellata* at the DAZ 1–DAZ 2 boundary (ca. 131.3 ka) indicates water column stability in a sustained phase of high lake level (Cvetkoska et al., 2014a). A concomitant rapid decrease in δ¹⁸O values from ca. 131.7 ka provides independent evidence of rapid lake-level rise (Fig. 3). Only a moderate increase in regional precipitation (Grant et al., 2012) and an associated intermediate expansion in tree populations at Ioannina are apparent from 132.5 ka (Fig. 3). A sharp rise in Alboran SSTs from ca. 129.5 ka (Martrat et al., 2014) is closely followed by a contemporaneous marked increase in regional precipitation (Drysdale et al., 2009; Grant et al., 2012) and in southern European tree populations between 129 ka and 128 ka (Tzedakis et al., 2003; Brauer et al., 2007). This marked increase in regional precipitation occurs 2.7 k.y. after the rapid rise in Ioannina lake level. Therefore, there is an apparent inconsistency in the timing of the main increase in regional precipitation as inferred from Ioannina lake-level changes and from changes in vegetation during the penultimate late glacial.

To explain this divergence, we suggest that regional groundwater levels may have risen during the penultimate late glacial as a result of the transfer of Pindus mountain glacial meltwater to the subterranean karst system, which is well developed in this area (see the Data Repository), and by input from snow melt. During the penultimate glacial, large glaciers existed on Mount Tymphi, with frontal moraines on the southern slopes situated ~25–30 km north of Ioannina (Hughes et al., 2007). A total of 14 glaciers covered an area of 21.3 km² on Mount Tymphi, with an average equilibrium line altitude of 1862 m asl (above sea level). Similar-sized glaciers would have also formed on Mount Lakmos/Peristeri (2295 m asl), <15 km east of Ioannina, and the neighboring Tzoumerka/ Athanamnias massif (2429 m asl), both of which have a glacial geomorphology similar to that of Mount Tymphi. These massifs currently record the largest precipitation totals in Greece (Fotiadi et al., 1999) and, if precipitation distribution was similar in glacial stages, these would have been favorable for the formation of some of the largest glaciers in Greece (Fig. 1). Permanent snow fields and possibly small niche glaciers are likely to have formed on the slopes of Mount Mitsikeli (1813 m asl), the most immediate mountain catchment to Lake Ioannina. An increase in lake sediment calcite content at Lakes Ioannina and Ohrid ca. 132 ka and ca. 130 ka, respectively (Frogley, 1997; Vogel et al., 2010), and an absence of ice-rafter debris in Ohrid from ca. 130 ka (Vogel et al., 2010) indicate regional climate warming, even though freshwater flux from ice sheets may have prolonged stadial conditions in the North Atlantic.

A warming climate would increase snow and ice melt rates, resulting in glaciers retreating upvalley to higher elevations. Moraine calcite cements in the mountains of both Greece and Montenegro yield corrected U-series ages dating to the last interglacial, with the earliest and most precise ages yielding a tight range (n = 5) ca. 124.6–120.2 ka (maximum error at 2σ = 5.3%) (Hughes et al., 2007, 2010, 2011). This indicates that glaciers had retreated from their most extensive MIS 6 positions by this time and that the moraines had stabilized, with their surfaces developing respiring soils, promoting the formation of secondary carbonate cements. Glacier retreat in response to rising temperatures during the penultimate late glacial would have led to karst reactivation and the release of significant amounts of meltwater discharge to surface waters and groundwater aquifers through the karst (cf. Adamson et al., 2014). The combination of accelerated subterranean and surface water input would account for the rapid rise in lake level at Ioannina ca. 131.7 ka. In this context, lacustrine and terrestrial proxies would not be responding to a common driving mechanism. If local conditions are playing an important role in modulating lake response to climate change at Ioannina,
then no apparent conflict between the lacustrine and terrestrial proxy evidence remains. According to the pollen record, the onset of the last interglacial at Ioanna-
nina is placed ca. 128.6 ka, in line with a rapid shift in climate conditions from a number of Mediterranean records for that time (Fig. 3). From ca. 128.3 ka (DAZ 2b), the diatoms suggest minor lake-level reduction. This is in agreement with overall higher δ18O values, perhaps reflecting increased summer aridity and evaporation and a reduction or cessation in snowmelt and glacial meltwater input, coeval with an expansion in sclerophyllous woodland (Tzedakis et al., 2003). Taken together, these indicators of sum-
mer conditions are in line with the general framework of accentuated sea-
sonality of precipitation during the early interglacial (Milner et al., 2012).

CONCLUSIONS

Diatom evidence for multiple oscillations in lake level, and possibly thermal regime, at Lake Ioannina (northwest Greece) provide firm evi-
dence for the regional influence of abrupt changes in the North Atlantic during the HS11 stadial, and add to growing regional evidence for a com-
plex penultimate deglacial. Snowmelt and glacial meltwater transfer are
during the HS11 stadial, and add to growing regional evidence for a com-
plex penultimate deglacial. Snowmelt and glacial meltwater input, coeval with an expansion in sclerophyllous woodland (Tzedakis et al., 2003). Taken together, these indicators of sum-
mer conditions are in line with the general framework of accentuated sea-
sonality of precipitation during the early interglacial (Milner et al., 2012).

ACKNOWLEDGMENTS

This research was supported by Natural Environment Research Council (NERC) awards NE/C507210/1 (Reed) and NER/A/S2/2000/0946 (Tzedakis), with Open Access publication kindly funded by the University of Hull, UK. Isotope analyses were undertaken at the NERC Isotope Geosciences Laboratory (UK), supervised by T. Heaton. We thank B. Martrat and R. Drysdale for providing data; B. Wagner, H. Vogel, and M. Leng for constructive discussions on Ohirid; Z. Levkov, H. Yos-
sel, and A. Cvetkosva for discussion of recent taxonomic revisions; R. Drysdale for discussion of the Corchia cave chronology; and four anonymous reviewers for helpful comments.

REFERENCES CITED

Adamson, K.R., Woodward, J.C., and Hughes, P.D., 2014, Glaciers and rivers:

Pliocene uncoupling in a Mediterranean mountain karst: Quaternary Sci-


