

Response of subfossil Cladocera in Gerzensee (Swiss Plateau) to early Late Glacial environmental change

K. Nováková^a, M. van Hardenbroek^{b,*}, W.O. van der Knaap^b

^a University of South Bohemia, Department of Botany, Branišovská 31, CZ-370 05 České Budějovice, Czech Republic

^b Institute of Plant Sciences and Oeschger Centre for Climate Change Research, University of Bern, Altenbergrain 21, CH-3013 Bern, Switzerland

ARTICLE INFO

Article history:

Received 18 April 2012

Received in revised form 11 October 2012

Accepted 18 October 2012

Available online 26 October 2012

Keywords:

Palaeolimnology

Cladocera

Late-glacial

Bølling

Climatic change

Biotic response

Switzerland

ABSTRACT

Sub-fossil Cladocera were studied in a core from Gerzensee (Swiss Plateau) for the late-glacial periods of Oldest Dryas, Bølling, and Allerød. Cladocera assemblages were dominated by cold-tolerant littoral taxa *Chydorus sphaericus*, *Acroperus harpae*, *Alonella nana*, *Alona affinis*, and *Alonella excisa*. The rapid warming at the beginning of the Bølling (GI-1e) ca. 14,650 yr before present (BP: before AD 1950) was indicated by an abrupt 2‰ shift in carbonate $\delta^{18}\text{O}$ and a clear change in pollen assemblages. Cladocera assemblages, in contrast, changed more gradually. *C. sphaericus* and *A. harpae* are the most cold-tolerant, and their abundance was highest in the earliest part of the record. Only 150–200 years after the beginning of the Bølling warming we observed an increase in less cold-tolerant *A. excisa* and *A. affinis*. The establishment of *Alona guttata*, *A. guttata* var. *tuberculata*, and *Pleuroxus unicatus* was delayed by ca. 350, 770, and 800 years respectively after the onset of the Bølling. The development of the Cladocera assemblages suggests increasing water temperatures during the Bølling/Allerød, which agrees with the interpretation by von Grafenstein et al. (2013-this issue) that decreasing $\delta^{18}\text{O}$ values in carbonates in this period reflect increasing summer water temperatures at the sediment–water interface. Other processes also affected the Cladocera community, including the development and diversification of aquatic vegetation favourable for Cladocera. The record is clearly dominated by Chydoridae, as expected for a littoral core. Yet, the planktonic *Eubosmina*-group occurred throughout the core, with the exception of a period at ca. 13,760–13,420 yr BP. Lake levels reconstructed for this period are relatively low, indicating that the littoral location might have become too shallow for *Eubosmina* in that period.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Cladocera (Crustacea: Branchiopoda; water fleas) play an important role in freshwater ecosystems because of their central position in the food web, between bottom-up factors (phytoplankton availability and quality) and top-down regulators (fish and invertebrate predators). The intermediary position of Cladocera in lacustrine food webs underlies their significance as sensitive indicators for environmental change (Korhola and Rautio, 2001). Since the pioneer work of Frey (1955, 1958), Cladocera have been recognised as a valuable palaeoecological indicator group in lakes, because their skeletal parts (including head shields, carapaces, and postabdominal claws), and ephippia (resting eggs) are well preserved in lake sediments (Frey, 1988). Fossil Cladocera assemblages can provide information about various environmental factors, including temperature (Lotter et al., 1997, 2012; Kattel et al., 2008), trophic state (Lotter et al., 1998; Davidson et al., 2007), predation by fish (Jeppesen et al., 1996), acidification (Korhola, 1992; Jeziorski et al., 2008), and water level (Sarmaja-Korjonen and Hyvärinen, 1999; Korhola et al., 2005).

The aim of this study is to understand better the responses of Cladocera communities in Gerzensee (Switzerland) to the rapidly rising temperatures at the transition from the Oldest Dryas to the Bølling. We therefore studied the lake sediments for this interval at a high sampling resolution and a well-constrained timescale based on the ice core age scale GICC-05 from NGRIP (van Raden et al., 2013-this issue). Changes in the Cladocera assemblage were compared with oxygen-isotope ratios of sedimentary carbonates and a lake-level reconstruction based on carbonate morphotypes (Magny, 2013-this issue) from the same core. These relationships have rarely been investigated, although they can provide new insights into late-glacial ecological dynamics in this lake. Furthermore, we compared our results to changes in Cladocera assemblages in Gerzensee during the later phase of rapid warming at the Younger Dryas–Holocene transition (Hofmann, 2000; Lotter et al., 2000).

2. Material and methods

2.1. Site location

The core GEJK studied for Cladocera analysis was collected from Gerzensee, located on the Swiss Plateau (46° 49' 56.95" N, 7° 33'

* Corresponding author. Tel.: +41 31 631 3868; fax: +41 31 631 4942.

E-mail address: maarten.vanhardenbroek@ips.unibe.ch (M. van Hardenbroek).

00.63° E, 603 m a.s.l. (Fig. 1)), at the interfluvium between the rivers Aare and Gürbe, where till of the Aare glacier was deposited during the Last Glaciation. The lake surface today has an area of 25.16 ha, but it was probably twice that size during the Late-Glacial (Eicher, 1979). The maximum water depth at present is 10.7 m, and the lake has no major in- or outflow. The coring site lies in the reed belt (*Phragmites australis*) of the present-day littoral zone near the eastern shore of the lake. This is very close (<20 m) to the coring sites used by Eicher and Siegenthaler (1976) and Hofmann (2000). Two adjacent cores GEJ and GEK were taken in September 2000 with a Streif-modification of a Livingston corer of 8 cm diameter (Merkt and Streif, 1970). Cores GEJ and GEK are horizontally less than 50 cm apart and are vertically shifted by 50 cm in their core sections. The parallel cores were correlated on the basis of oxygen isotopes (van Raden et al., 2013–this issue), and a detailed site description and stratigraphy of the combined GEJK core profile are provided by Ammann et al. (2013a–this issue).

2.2. Chronology

The chronology (expressed in yr BP, equivalent to yr before AD 1950) is based on the oxygen-isotope stratigraphy established in core GEJK and other cores in Lake Gerzensee and a comparison with oxygen isotopes in the NGRIP ice core, using the GICC-05 time scale anchored at 1950 AD in order to correlate events with those based on radiocarbon dates in terrestrial, marine, and archaeological sites, assuming that changes in oxygen isotopes were synchronous in Greenland and Europe. van Raden et al. (2013–this issue) provide a detailed discussion of the age–depth relationship in the core. For the nomenclature of the different late-glacial climatic phases and biozones we refer to Ammann and Lotter (1989) and Lotter et al. (1992). The terminology of Björck et al. (1998) was used for the late-glacial stable oxygen-isotope stages in the Greenland ice cores. The sediment sequence starts ca. 15,675 yr BP and includes the end of Greenland Stadial 2a (GS-2a) and Greenland Interstadial 1 (GI-1e to GI-1b) up to the Laachersee tephra at 272 cm dated to 13,035 yr BP. The temporal resolution is 18.2 ± 6.7 yr cm^{-1} on average (\pm standard deviation) for the section of the core analysed in this study.

2.3. Sample preparation

We focussed on the period of rapid climatic warming during Oldest Dryas/Bølling transition (Termination 1a). The core was sampled every 2 cm in the sections 414–392, 358–320, and 293–273 cm and every 1 cm in the sections 390–361 and 319–295 cm. For sample preparation, standard methods developed by Frey (1986) were slightly modified, as follows; samples of 4 cm^3 volume were taken from 1 cm thick slices. The fresh sediment was soaked in distilled water for a few hours, heated at 80 °C for 5 min in 5% HCl to dissolve the calcium carbonates, centrifuged, and washed. Next, samples were heated at 80 °C for 5 min in 10% KOH to remove the non-chitinous organic content, centrifuged and washed, and decanted to remove sand. The material was then sieved with Nitex-screens of 55 and 37 μm , and the two fractions were analysed separately. A known quantity of *Lycopodium* spores was added to each sample to determine the concentration of Cladocera remains (Stockmarr, 1971). 96% alcohol was used for dehydration, and finally the samples were heated at 70 °C for 4 min in 85% glycerine to evaporate the alcohol. Lactic blue was used for staining during slide preparation, since this colourant only adheres to chitinous fragments.

At least 250–300 remains of Cladocera were counted in each sample (3–5 slides). This is considered sufficient to get a reliable representation of the fossil assemblage (Kurek et al., 2010). For identification the descriptions by Frey (1958, 1959) and Flössner (1972) were used. The nomenclature follows Flössner (1972). For each taxon a minimum number of individuals was calculated from the different exoskeletal remains (head shields, carapaces, postabdomens, claws) and ephippia according to Frey (1986). These numbers were used to calculate relative abundances and concentrations, which were plotted stratigraphically using

Tilia software (Grimm, 1991). Zonation methods follow the recommendations of Bennett (1996). Numerical zonation was carried out by optimal sum of squares partition, and the number of statistically significant splits was determined with the broken-stick model (MacArthur, 1957).

3. Results

The subfossil cladoceran fauna from Gerzensee is represented by 12 taxa and dominated by Chydoridae that had a relative abundance of 42–100% (average 83%) throughout the sequence (Fig. 2). The most frequently occurring taxa are *Chydorus sphaericus*, *Acroperus harpae*, *Alona affinis*, *Alonella excisa*, and *Alonella nana*, all of which have relative abundances of 10–55% throughout the record (Fig. 2). *Alona quadrangularis*, *Alonopsis elongata*, *Alona guttata*, and *Pleuroxus uncinatus* occur with relative abundances <10% and were not found continuously. The most important planktonic taxon is the *Eubosmina*-group (relative abundance 17–58%), whereas ephippia of *Daphnia longispina*-group were found sporadically. Cladocera concentrations range between 219 and 2428 (average 688) specimens cm^{-3} wet sediment throughout the record. Highest concentrations are found at 304–311 cm depth (13,582–13,653 yr BP). Six statistically significantly different zones were identified on the basis of changes in the Cladocera assemblages (Fig. 2):

Zone GRZcl-1 (414–389.5 cm, 15,676–15,066 yr BP)

The Cladocera assemblage from the Oldest Dryas consists of only few species, including *Acroperus harpae*, *Chydorus sphaericus*, *Alonella excisa*, *Alonella nana*, and the *Eubosmina*-group, all occurring with similar relative abundances.

Zone GRZcl-2 (389.5–373.5 cm, 15,066–14,672 yr BP)

Alonella nana increased to 55% during this period, whereas *Alona affinis*, *Alonella excisa*, and *Acroperus harpae* decreased to below 8%. The number of taxa in the assemblage increased in this period, with the sparse appearance of *Alona quadrangularis*, *Alona guttata*, and *Alonopsis elongata*.

Zone GRZcl-3 (373.5–355 cm, 14,672–14,279 yr BP)

A rapid increase in $\delta^{18}\text{O}$ at 374–370 cm is indicated at the beginning of the Late-Glacial Interstadial (Bølling–Allerød or GI-1e). In this zone, the largest lake-level changes were observed (Magny, 2013–this issue). *Alonella nana* decrease to similar abundances as in zone GRZcl-1, whereas *Chydorus sphaericus* and *Eubosmina* are most abundant. *Alonella excisa* and *Alona affinis* become more abundant again from 364 cm onwards. *Alona quadrangularis*, *Alona guttata*, and *Alonopsis elongata* continue to be part of the assemblage at low relative abundances.

Zone GRZcl-4 (355–327 cm, 14,279–13,763 yr BP)

This zone is characterized by the beginning of a shift towards higher abundances of *Alona affinis* and *Alonella excisa*, and the establishment of *Alona guttata*. At the same time *Chydorus sphaericus* and *Acroperus harpae* decreased. The assemblage also became more diverse with the appearance of *Alona guttata* var. *tuberculata* and *Pleuroxus uncinatus*.

Zone GRZcl-5 (327–290 cm, 13,763–13,380 yr BP)

The most prominent features in this zone are low abundances (<10%) of the *Eubosmina*-group and high abundances (23–56%) of *Alonella excisa*. We also observed the nearly continuous presence of *Alona guttata* var. *tuberculata*, *Pleuroxus uncinatus*, and *Alonopsis elongata*, which only occurred sporadically in other parts of the record. At 330–305 cm we found the highest Cladocera influx (40–230 remains $\text{cm}^{-2} \text{y}^{-1}$). The influx of *Eubosmina* was highest between 330–324 cm and then decreased rapidly, followed by high influx of Chydoridae at 320–305 cm. The high influx coincided with the highest Cladocera concentrations (up to 2400

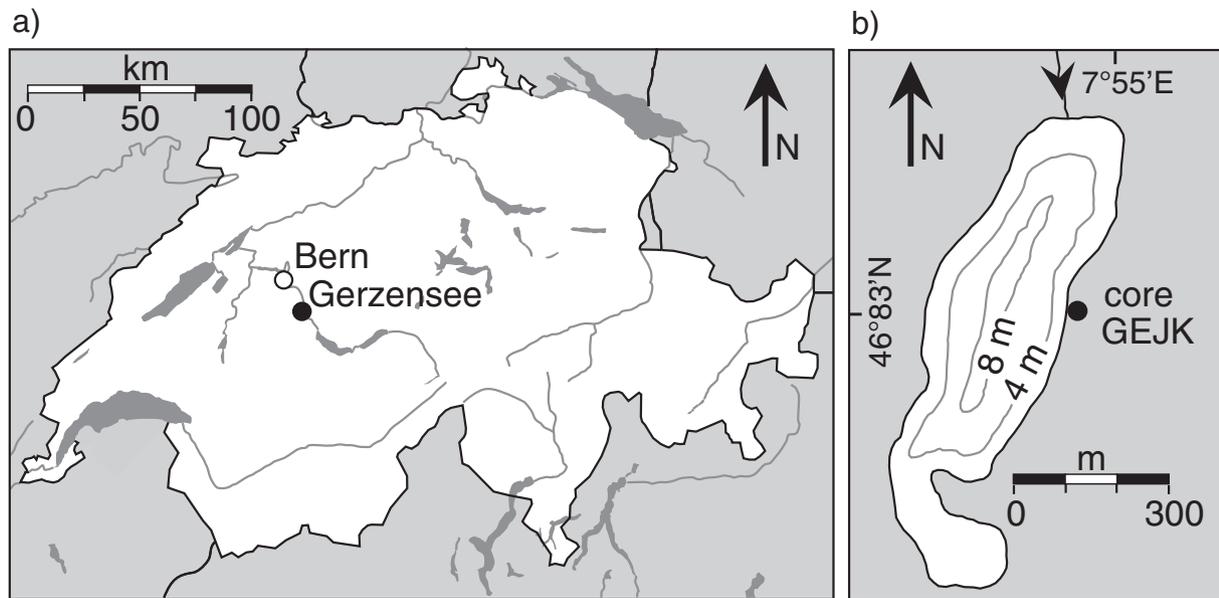


Fig. 1. Location of Lake Gerzensee (a), and location of core GEJK in the former littoral of the lake (b) after van Raden et al. (2013-this issue).

remains per ml wet sediment) and highest sediment accumulation rates ($0.1\text{--}0.15\text{ cm yr}^{-1}$) in this study. Usually, high sedimentation rates lead to a dilution of fossil remains, but this is not the case during this interval. The high Cladocera concentrations in this section make it unlikely that this is an artefact of the age model.

Zone GRZcl-6 (290–273 cm, 13,380–13,048 yr BP)

The *Eubosmina*-group was found again at high relative abundances (20–58%), and *Alona guttata* var. *tuberculata* increased to its highest abundance in the record. Simultaneously, we found a decrease of *Chydorus sphaericus*, *Acroperus harpae*, *Pleuroxus uncinatus*, and to a lesser extent *Alonella nana*.

4. Discussion

4.1. Response to climatic change

The dominant chydorid species, *Chydorus sphaericus*, *Acroperus harpae*, *Alonella nana*, *Alonella excisa*, and *Alona affinis* are described as cold-tolerant species living in oligotrophic, clear water lakes (Harmsworth, 1968; Whiteside, 1970), and they occur today most abundantly in Alpine lakes above 1500 m a.s.l. (Flössner, 1972; Lotter et al., 1997). *C. sphaericus* has been found in sediment records from full glacial conditions in northern Germany (Frey, 1958) and was dominant in Lac du Bouchet (Massif Central) during the Pleniglacial (Hofmann, 1991). After the rapid warming at the beginning of the Bølling (GI-1e) ca. 14,650 yr BP we observed gradual shifts in relative abundance of species rather than abrupt changes. For example, the abundance of *C. sphaericus* does not decrease immediately but only after 14,350 yr BP. It is possible that the decrease of *C. sphaericus* is the result of stronger competition with less cold-adapted taxa like *A. excisa*, *A. affinis*, and *Alona guttata*, which increase in abundance after 14,520, 14,480, and 14,340 yr BP, respectively.

The five cold-tolerant chydorid species that are dominant in the Oldest Dryas period of our record have also been found in Younger Dryas sediments at several locations across Europe (e.g., Frey, 1958; Hofmann, 2000; Szeroczynska, 2006), including Gerzensee itself. Hofmann (2000) describes the Cladocera assemblage changes in a littoral core <20 m from core GEJK, starting where this study ends at the level of the Laachersee tephra (ca. 13,035 yr BP) and continuing

through the Younger Dryas into the early Holocene. Hofmann (2000) found that the abundances of *Acroperus harpae* were lower during the Allerød and early Holocene and higher during the Younger Dryas, whereas the opposite pattern was observed for *Alona guttata* and *Alonella excisa*. Therefore, *A. harpae* was considered the most cold tolerant, followed by *A. excisa*, and *A. guttata*, indicating more temperate conditions. This agrees with our findings of highest abundance of *Acroperus harpae* in the oldest part of the record (before 15,450 yr BP), followed by an increase in *A. excisa* after 14,520 yr BP and the establishment of *A. guttata* after ca. 14,340 yr BP.

The gradual shift in species composition that we observed for Cladocera was also seen for chironomids, another group of aquatic organisms that was investigated in core GEJK (Lotter et al., 2012; Brooks and Heiri, 2013-this issue). The activity of chironomid larvae mainly depends on absolute temperatures or the length of the growing season, which is strongly correlated with summer temperature in north-temperate regions (Eggermont and Heiri, 2012), and it is likely that this also applies to Cladocera. Lotter et al. (2012) indicated that chironomid-inferred July temperatures increased gradually during GS-2a and GI-1 and suggested that this reflects the change in July insolation and summer temperatures. In contrast, carbonate $\delta^{18}\text{O}$ and terrestrial plant pollen changed more rapidly (Lotter et al., 2012), possibly because carbonate $\delta^{18}\text{O}$ reflects mean annual temperature in Gerzensee (Eicher and Siegenthaler, 1976), and vegetation is also affected by increased seasonality in this period. The gradual increase in summer temperatures in Gerzensee inferred from chironomid assemblages is consistent with the relatively slow changes observed in Cladocera assemblages.

Because of the high-frequency variability in the Cladocera record it is difficult to distinguish short-lived low-amplitude climatic changes in the Cladocera record. For example, we did not observe the Aegelsee and Gerzensee Oscillations that were present in the carbonate $\delta^{18}\text{O}$ (van Raden et al., 2013-this issue; von Grafenstein et al., 2013-this issue) or the pollen record (Ammann et al., 2013a-this issue). Aquatic organisms have a short life cycle, often shorter than one year, so they are more sensitive to high-frequency environmental change than, for example, terrestrial vegetation.

Overall, the number of taxa is greater in the Bølling–Allerød (GI-1) than the Oldest Dryas (GS-2), but it is not until ca. 13,900 yr BP that *Alona guttata* var. *tuberculata* and *Pleuroxus uncinatus* occurred, taxa that are often associated with warmer conditions (Harmsworth,

Analysis: Kateřina Nováková

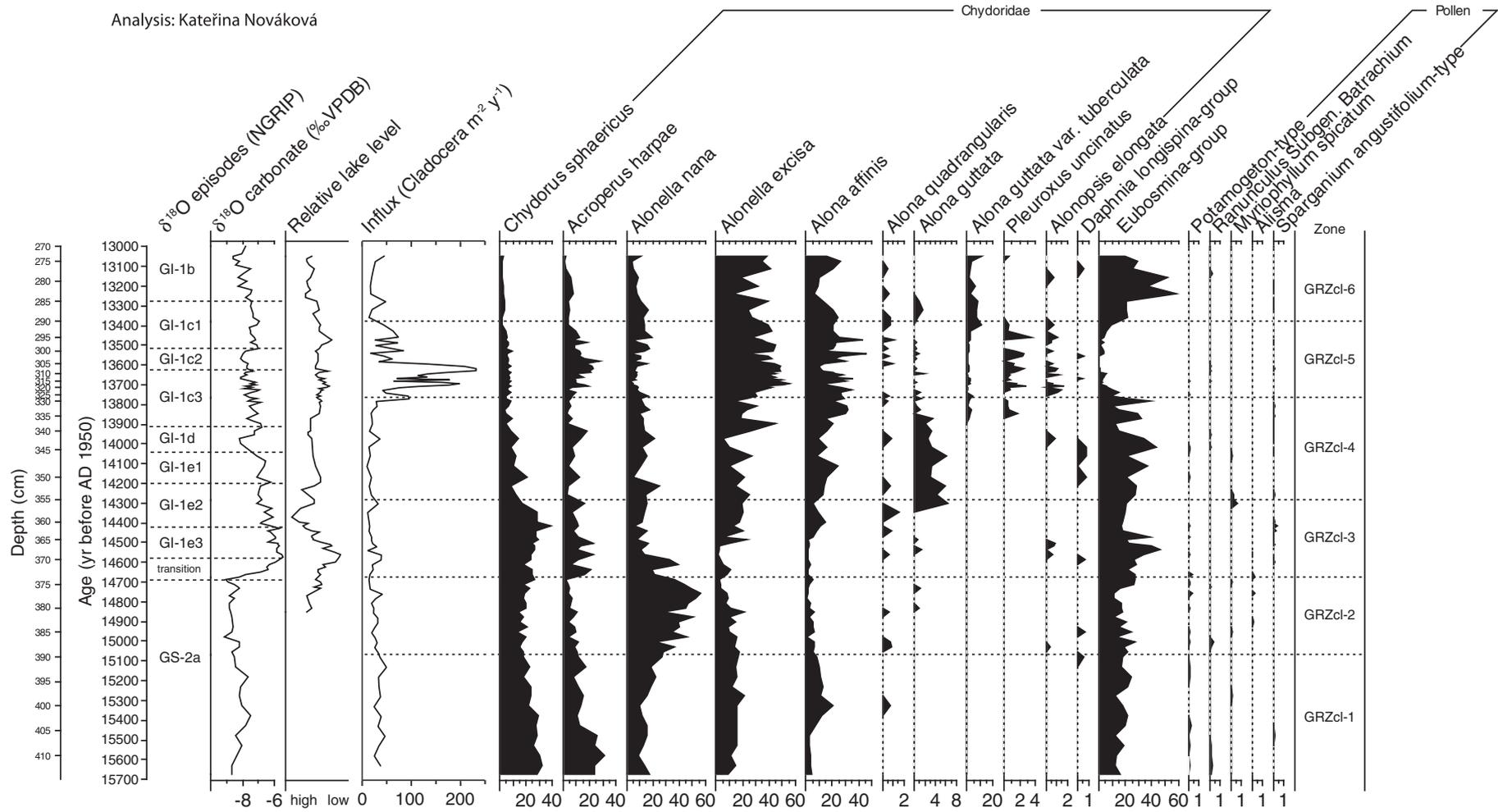


Fig. 2. Overview in sediment core GEJK of $\delta^{18}\text{O}$ values (van Raden et al., 2013-this issue), relative lake level (Magny, 2013-this issue), sediment accumulation rate, influx (sum of Cladocera remains), relative abundances of Cladocera taxa, and relative abundances of aquatic plant pollen (Ammann et al., 2013b-this issue).

1968; Lotter et al., 1997). This corresponds well with von Grafenstein et al. (2013-this issue) who argue that the decreasing trend in $\delta^{18}\text{O}$ values after the early Bølling reflects increasing summer temperatures at the sediment–water interface. Factors such as the occurrence of aquatic plants, nutrients, pH, alkalinity, and water depth also influence the abundance of Cladocera (Whiteside, 1970; Brodersen et al., 1998; Korhola and Rautio, 2001; de Eyto et al., 2003). However, it is difficult to disentangle the relative importance of various ecologic and climatologic factors on cladoceran assemblages because the littoral of lakes can have highly diverse and dynamic habitats. Several studies have investigated quantitative relationships between Cladocera assemblages in modern surface sediments and environmental parameters such as temperature, total phosphorus concentrations, and pH (e.g. Lotter et al., 1997, 1998; Brodersen et al., 1998; Kattel et al., 2008). Such studies can provide insight into the relative importance of environmental parameters. These so called ‘training sets’ have been designed to interpret the assemblages in profundal sediments, because they are most commonly used in palaeoenvironmental reconstructions. In our study, however, we use a littoral-sediment core, which limits the applicability of training sets to reconstruct past environmental change, since it can be expected that differences exist between cladoceran remains accumulating in littoral and profundal sediments (Kattel et al., 2007; Luoto et al., 2011).

4.2. Aquatic vegetation

The presence and diversity of aquatic vegetation have a great influence on the diversity of Cladocera, especially Chydoridae, which use aquatic vegetation as a substrate to live on and to shelter from planktivorous fish (Quade, 1969; Whiteside et al., 1978). It is likely that the increase of *Alonella nana* between ca 15,060–14,680 yr BP and the more diverse Cladocera assemblages after ca. 13,800 yr BP could be ascribed to a more diverse community of aquatic macrophytes rather than temperature change, because the increase of Cladocera abundance in these periods does not coincide with a change in climate. Indeed the occurrence of pollen of aquatic macrophytes in core GEJK suggests that different plants grew in the littoral zone of Gerzensee during these periods. These macrophytes included *Batrachium*, *Potamogeton*, *Sparganium angustifolium*, *Myriophyllum spicatum*, and *Alisma*. Pollen grains of these taxa occurred erratically throughout the core (Fig. 2; Ammann et al., 2013b-this issue), but it was not possible to infer changes in the abundance of aquatic plants from the pollen data.

4.3. Water level

The littoral location of the core GEJK is clearly reflected by the dominance of Chydoridae that live in the muddy sediment and between aquatic plants of the shallow part of lakes (Whiteside, 1970; Duigan, 1992). Planktonic taxa are less abundant, but *Eubosmina* is present in most of the record at relative abundances of approximately 20%. A notable exception to this is the period between ca. 13,760–13,420 yr BP, when we found strongly decreased numbers of *Eubosmina*. Possibly the location of core GEJK, a large carbonate platform, became too shallow for *Eubosmina*, forcing the planktonic Cladocera to live in deeper water away from the carbonate platform. Reduced water depth could have resulted in a more extensive littoral zone, which corresponds with the notably high concentrations and influxes of Chydoridae in this period compared with the periods before and after. Magny (2013-this issue) reconstructed lake-level changes based on the examination of macroscopic carbonate components of core GEJK. His results indicate low to intermediate lake levels in the same period of low *Eubosmina* abundance.

During an earlier period for which Magny (2013-this issue) reconstructed low lake levels (ca. 14,560–14,500 yr BP), however, we observed the opposite effect: an increase in *Eubosmina* abundance (both relative and absolute). It is difficult to explain the different reaction of the

Eubosmina-group to lake-level change in the two periods; possibly it is related to infilling of the basin, which contained at least 55 cm more sediment in the later period. Another explanation for this discrepancy is the succession of species within the *Eubosmina*-group. We did not distinguish between pioneer species *E. longispina* and other bosminids such as *E. coregoni* that appear later in the succession of post-glacial lakes (Nauwerck, 1991). In this light, we could explain the increase of the *Eubosmina*-group ca. 14,560–14,500 yr BP by an increase of species, leading to higher total numbers of *Eubosmina*, rather than by a change in lake-level.

5. Conclusions

The rapid warming at the beginning of the Bølling (GI-1e) ca. 14,650 yr BP was indicated by an abrupt 2‰ shift in carbonate $\delta^{18}\text{O}$ and a clear change in pollen assemblages. In contrast, we observed more gradual shifts in Cladocera assemblages, which is consistent with the gradual shift in assemblage composition of chironomids, another aquatic indicator group (Brooks and Heiri, 2013-this issue). Cladocera assemblages did not change immediately with the onset of the Bølling/Allerød, but after ca. 150–200 years and then a more diverse community developed after 350–800 years. The late response of the Cladocera assemblage compared with $\delta^{18}\text{O}$ could reflect the gradual increase in summer insolation and summer temperature and the time that is required to develop a more diverse aquatic vegetation.

Acknowledgements

We would like to thank Brigitta Ammann for initiating this project and for her useful comments on the manuscript. We acknowledge Florence Oberli for her kind help with slide-preparation and Jacqueline van Leeuwen for providing the pollen data for aquatic plants. This research was supported by the Grant Agency of Czech Republic: grant no. GAČR 206/09/1564.

References

- Ammann, B., Lotter, A.F., 1989. Late-Glacial radiocarbon- and palynostratigraphy on the Swiss Plateau. *Boreas* 18, 109–126.
- Ammann, B., van Leeuwen, J.F.N., van der Knaap, W.O., Lischke, H., Heiri, O., Tinner, W., 2013a. Vegetation responses to rapid warming and to minor climatic fluctuations during the Late-Glacial Interstadial (GI-1) at Gerzensee (Switzerland). *Palaeogeography, Palaeoclimatology, Palaeoecology* 391, 40–59 (this issue).
- Ammann, B., van Raden, U., Schwander, J., Eicher, U., Gilli, A., Bernasconi, S.M., van Leeuwen, J.F.N., Lischke, H., Brooks, S.J., Heiri, O., Nováková, K., van Hardenbroek, M., von Grafenstein, U., Belmecheri, S., van der Knaap, W.O., Magny, M., Eugster, W., Colombaroli, D., Nielsen, E., Tinner, W., Wright, H.E., 2013b. Responses to rapid warming at Termination 1a at Gerzensee (Central Europe): Primary succession, albedo, soils, lake development, and ecological interactions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 391, 111–131 (this issue).
- Bennett, K.D., 1996. Determination of the number of zones in a biostratigraphical sequence. *The New Phytologist* 132, 155–170.
- Björck, S., Walker, M.J.C., Cwynar, L.C., Johnsen, S., Knudsen, K.-L., Lowe, J.J., Wohlfarth, B., INTIMATE members, 1998. An event stratigraphy for the Last Termination in the North Atlantic region based on the Greenland ice-core record: a proposal by the INTIMATE group. *Journal of Quaternary Science* 13, 283–292.
- Brodersen, K.P., Whiteside, M.C., Lindegaard, C., 1998. Reconstruction of trophic state in Danish lakes using subfossil chydorid (Cladocera) assemblages. *Canadian Journal of Fisheries and Aquatic Sciences* 55, 1093–1103.
- Brooks, S.J., Heiri, O., 2013. Response of chironomid assemblages to environmental change during the early Late-glacial at Gerzensee, Switzerland. *Palaeogeography, Palaeoclimatology, Palaeoecology* 2013, 90–98 (this issue).
- Davidson, T., Sayer, C., Perrow, M., Bramm, M., Jeppesen, E., 2007. Are the controls of species composition similar for contemporary and sub-fossil cladoceran assemblages? A study of 39 shallow lakes of contrasting trophic status. *Journal of Paleolimnology* 38, 117–134.
- De Eyto, E., Irvine, K., García-Criado, F., Gyllström, M., Jeppesen, E., Kornijow, R., Miracle, M., Rosa Nykänen, M., Bareiss, C., Cerbin, S., Salujõe, J., Franken, R., Stephens, D., 2003. The distribution of chydorids (Branchiopoda, Anomopoda) in European shallow lakes and its application to ecological quality monitoring. *Archiv für Hydrobiologie* 156, 181–202.
- Duigan, C.A., 1992. The ecology and distribution of the littoral freshwater Chydoridae (Branchiopoda, Anomopoda) of Ireland, with taxonomic comments on some species. *Hydrobiologia* 241, 1–70.

- Eggermont, H., Heiri, O., 2012. The chironomid–temperature relationship: expression in nature and palaeoenvironmental implications. *Biological Reviews* 87, 430–456.
- Eicher, U., 1979. Die $^{18}\text{O}/^{16}\text{O}$ - und $^{13}\text{C}/^{12}\text{C}$ -Isotopenverhältnisse in spätglazialen Stüsswasserkarbonaten und ihr Zusammenhang mit den Ergebnissen der Pollenanalyse. PhD Thesis, University of Bern.
- Eicher, U., Siegenthaler, U., 1976. Palynological and oxygen isotope investigations on Late Glacial sediment cores from Swiss lakes. *Boreas* 5, 109–117.
- Flössner, D., 1972. Kiemer- und Blattfüsser, Branchiopoda, Fischerchläuse, Branchiura, 60. Tierwelt Deutschlands, pp. 1–499.
- Frey, D.G., 1955. Längsee: a history of meromixis. *Memorie Ist. Italiana Idrobiologia. Memorie dell Istituto Italiano di Idrobiologia (Suppl. 8)*, 141–164.
- Frey, D.G., 1958. The Late Glacial cladoceran fauna of small lake. *Archiv für Hydrobiologie* 54, 209–275.
- Frey, D.G., 1959. The taxonomic and phylogenetic significance of the head pores of the Chydoridae (Cladocera). *Internationale Revue der Gesamten Hydrobiologie* 44, 27–50.
- Frey, D.G., 1986. Cladoceran analysis. In: Berglund, B.E. (Ed.), *Handbook of Holocene Palaeoecology and Paleoecology*. Wiley, Chichester, pp. 667–692.
- Frey, D.G., 1988. Littoral and offshore communities of diatoms, cladocerans and dipterous larvae, and their interpretation in paleolimnology. *Journal of Paleolimnology* 1, 179–191.
- Grimm, E.C., 1991–2011. Tilia. Illinois State Museum, Springfield, IL.
- Harmsworth, R.V., 1968. The developmental history of Blelham Tarn (England) as shown by animal microfossils, with special reference to the Cladocera. *Ecological Monographs* 38, 223–241.
- Hofmann, W., 1991. Stratigraphy of Chironomidae (Insecta: Diptera) and Cladocera (Crustacea) in Holocene and Würm sediments from Lac du Bouchet (Haute Loire, France). *Documents du C.E.R.L.A.T. Mémoires* 2, 363–386.
- Hofmann, W., 2000. Response of chydorid faunas to rapid climatic changes in four alpine lakes at different altitudes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 159, 281–292.
- Jeppesen, E., Agerbo Madsen, E., Jensen, J.P., Anderson, N.J., 1996. Reconstructing the past density of planktivorous fish and trophic structure from sedimentary zooplankton fossils. a surface sediment calibration data set from shallow lakes. *Freshwater Biology* 36, 115–127.
- Jeziorski, A., Yan, N.D., Paterson, A.M., DeSellas, A.M., Turner, M.A., Jeffries, D.S., Keller, B., Weeber, R.C., McNicol, D.K., Palmer, M.E., Melver, K., Arseneau, K., Ginn, B.K., Cumming, B.F., Smol, J.P., 2008. The wide-spread threat of calcium decline in freshwater lakes. *Science* 322, 1374–1377.
- Kattel, G.R., Battarbee, R.W., Mackay, A.W., Birks, H.J.B., 2007. Are cladoceran fossils in lake sediment samples a biased reflection of the communities from which they are derived? *Journal of Paleolimnology* 38, 157–181.
- Kattel, G.R., Battarbee, R.W., Mackay, A.W., Birks, H.J.B., 2008. Recent ecological change in a remote Scottish mountain loch: an evaluation of a Cladocera-based temperature transfer-function. *Palaeogeography, Palaeoclimatology, Palaeoecology* 259, 51–76.
- Korhola, A., 1992. The Early Holocene hydrosere in a small acid hill-top basin studied using crustacean sedimentary remains. *Journal of Paleolimnology* 7, 1–22.
- Korhola, A., Rautio, M., 2001. Cladocera and other branchiopod crustaceans. In: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), *Tracking Environmental Change Using lake Sediments: Zoological indicators, volume 4*. Kluwer Academic Publishers, Dordrecht, pp. 5–41.
- Korhola, A., Tikkanen, M., Weckström, J., 2005. Quantification of Holocene lake-level changes in Finnish Lapland using a cladocera – lake depth transfer model. *Journal of Paleolimnology* 34, 175–190.
- Kurek, J., Korosi, J., Jeziorski, A., Smol, J., 2010. Establishing reliable minimum count sizes for cladoceran microfossils sampled from lake sediments. *Journal of Paleolimnology* 44, 603–612.
- Lotter, A.F., Eicher, U., Birks, H.J.B., Siegenthaler, U., 1992. Late-glacial climatic oscillations as recorded in Swiss lake sediments. *Journal of Quaternary Science* 7, 187–204.
- Lotter, A.F., Birks, H.J.B., Hofmann, W., Marchetto, A., 1997. Modern diatom, Cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal of Paleolimnology* 18, 395–420.
- Lotter, A.F., Birks, H.J.B., Hofmann, W., Marchetto, A., 1998. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. *Journal of Paleolimnology* 19, 443–463.
- Lotter, A.F., Birks, H.J.B., Eicher, U., Hofmann, W., Schwander, J., Wick, L., 2000. Younger Dryas and Allerød summer temperatures at Gerzensee (Switzerland) inferred from fossil pollen and cladoceran assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology* 159, 349–361.
- Lotter, A.F., Heiri, O., Brooks, S., van Leeuwen, J.F.N., Eicher, U., Ammann, B., 2012. Rapid summer temperature changes during Termination 1a: high-resolution multi-proxy climate reconstructions from Gerzensee (Switzerland). *Quaternary Science Reviews* 36, 103–113.
- Luoto, T., Nevalainen, L., Kultti, S., Sarmaja-Korjonen, K., 2011. An evaluation of the influence of water depth and river inflow on quantitative Cladocera-based temperature and lake level inferences in a shallow boreal lake. *Hydrobiologia* 676, 143–154.
- MacArthur, R.H., 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences of the United States of America* 43, 293–295.
- Magny, M., 2013. Climatic and environmental changes reflected by lake-level fluctuations at Gerzensee from 14,850 to 13,050 yr BP. *Palaeogeography, Palaeoclimatology, Palaeoecology* 391, 33–39 (this issue).
- Merkt, J., Streif, H.J., 1970. Stechrohrbohrgeräte für limnische und marine Lockersedimente. *Geologisches Jahrbuch* 88, 137–148.
- Nauwerck, A., 1991. The history of the genus *Eubosmina* in Lake Mondsee (Upper Austria). *Hydrobiologia* 225, 87–103.
- Quade, H.W., 1969. Cladoceran faunas associated with aquatic macrophytes in some lakes in northwestern Minnesota. *Ecology* 50, 170–179.
- Sarmaja-Korjonen, K., Hyvärinen, H., 1999. Cladoceran and diatom stratigraphy of calcareous lake sediments from Kuusamo, NE Finland. Indications of Holocene lake-level changes. *Fennia* 177, 55–70.
- Stockmarr, J., 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores* 13, 615–621.
- Szeroczyńska, K., 2006. The significance of subfossil Cladocera in stratigraphy of Late Glacial and Holocene. *Studia Quaternaria* 23, 37–45.
- van Raden, U.J., Colombaroli, D., Gilli, A., Schwander, J., Bernasconi, S.M., van Leeuwen, J., Leuenberger, M., Eicher, U., 2013. High-resolution late-glacial chronology for the Gerzensee lake record (Switzerland): $\delta^{18}\text{O}$ correlation between a Gerzensee-stack and NGRIP. *Palaeogeography, Palaeoclimatology, Palaeoecology* 391, 13–24 (this issue).
- von Grafenstein, U., Belmecheri, S., Eicher, U., van Raden, U.J., Erlenkeuser, H., Andersen, N., Ammann, B., 2013. The oxygen and carbon isotopic signatures of biogenic carbonates in Gerzensee, Switzerland, during the rapid warming around 14,685 years BP and the following interstadial. *Palaeogeography, Palaeoclimatology, Palaeoecology* 391, 25–32 (this issue).
- Whiteside, M.C., 1970. Danish Cladocera: modern ecology and core studies. *Ecological Monographs* 40, 79–118.
- Whiteside, M.C., Williams, J.B., White, C.P., 1978. Seasonal abundance and pattern of chydorid Cladocera in mud and vegetative habitats. *Ecology* 59, 1177–1188.