

Cladocera response to Late Glacial to Early Holocene climate change in a South Carpathian mountain lake

János Korponai · Enikő Katalin Magyari · Krisztina Buczkó · Sanda Iepure ·
Tadeusz Namiotko · Dániel Czakó · Csilla Kövér · Mihály Braun

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Abstract This study explores changes in cladoceran composition in a high mountain lake of the Retezat (Lake Brazi), the South Carpathian Mountains of Romania, during the Late Glacial–Early Holocene (14,500–11,600 cal. yr. BP) transition using a paleolimnological approach. The lake had a species poor cladoceran community throughout this period. *Daphnia longispina*, *Chydorus sphaericus* and *Alona affinis* were the most common, showing marked fluctuations

in their relative abundances through time. Distinct faunal response to warming at the Younger Dryas (YD)/Preboreal transition was recorded by increasing fossil densities and distinct community composition change: *Alona affinis* became dominant while numbers of *Chydorus sphaericus* dramatically decreased. In the Early Holocene, the productivity of Lake Brazi seem to have increased as reflected by higher numbers of Cladocera due to appearance of new species (*Alona rectangula*, *A. quadrangularis* and *A. guttata*) which are common in productive waters. Significant negative correlation was found between average dorsal length

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J. Korponai (✉)
West-Transdanubian District Water Authority,
Csik F. str. 4, Keszthely 8360, Hungary
e-mail: korponai.janos@nyuduvizig.hu

J. Korponai · C. Kövér
Department of Chemistry and Environmental Sciences,
University of West Hungary, Károly Gáspár tér 4,
Szombathely 9700, Hungary

E. K. Magyari
HAS-NHMUS Research Group for Paleontology,
P. O. Box 222, Budapest 1476, Hungary

K. Buczkó
Department of Botany, Hungarian Natural History
Museum, P.O. Box 222, Budapest 1476, Hungary

S. Iepure
Department of Mineralogy, Babes-Bolyai University,
Kogalniceanu 1, 3400 Cluj, Romania
e-mail: siepure@hasdeu.ubbcluj.ro

S. Iepure
Speleological Institute “Emil Racovitza”, Department
of Cluj (Biospeleology), Clinicilor 5, 400006 Cluj
Napoca, Romania

T. Namiotko
Department of Genetics, Laboratory of Limnology,
University of Gdansk, Kladki 24, 80-822 Gdansk,
Poland

D. Czakó
School of Earth Sciences and Geography, Kingston
University, Penrhyn Road, Kingston-upon-Thames,
Surrey KT1 2EE, UK

M. Braun
Department of Inorganic and Analytical Chemistry,
University of Debrecen, P.O. Box 21, Debrecen 4010,
Hungary

of daphnid ephippia and the NGRIP $\delta^{18}\text{O}$ isotope values. Given the absence of fish predation, changes in *Daphnia* ephippia size were taken to indicate climatic change: larger ephippium size inferred cold conditions during the Late Glacial, while smaller size reflected climate warming during the Early Holocene. We conclude that Cladocera fossils are good indicators of climatic change that happened during the transition from the Late Glacial to the Holocene. We found that climatic conditions can be tracked either by size distribution of *Daphnia* ephippia (larger ephippium size under colder climate) and/or by community change of cladocerans.

Keywords Cladocera remains · Chydorids · Climate change · Mountain lake · Romania

Introduction

Biological remains have been widely used as proxies to study the history of aquatic ecosystems (Buczkó et al., 2009a). Chitinous parts of cladocerans (headshields, carapaces, postabdomens and ephippia) are often well preserved in lake sediments (Frey, 1962, 1986, 1988), and considered a key proxy of past water depth (Hofmann, 1998; Sarmaja-Korjonen & Alhonen, 1999; Korhola et al., 2005), water temperature (Lotter et al., 1997; Duigan & Birks, 2000), eutrophication (Brodersen et al., 1998; Korhola & Rautio, 2001; Galbarczyk-Gąsiorowska et al., 2009) and paleoclimatic changes (Hofmann, 2001, 2003; Lotter et al., 2002).

In fossil assemblages, chydorid and bosminid remains dominate over others, especially over daphnids, due to their strongly chitinized body parts (Sarmaja-Korjonen & Alhonen, 1999). The ratio of planktonic (e.g. bosminids) to littoral (e.g. chydorids) Cladocera species is a widely used proxy for the reconstruction of water-depth changes (Sarmaja-Korjonen & Alhonen, 1999; Korhola et al., 2005). When water level decreases, the remains of littoral chydorids increase relative to the planktonic bosminids. The latter group, in turn, dominates when water depth increases (Sarmaja-Korjonen, 2001). This is due to the compositional and abundance changes of the aquatic vegetation: with increasing water depth, telmatophytes often become more abundant in the littoral zone allowing phytophilous Cladocera to colonize the lake margin (Whiteside et al., 1978).

Mountain lake ecosystems are sensitive to pollution and climate change (Battarbee et al., 2009; Battarbee, 2010), and hence considered ideal objects for reconstruction of past environmental changes. Climate change in mountain areas is a major concern especially as temperature at high altitude is increasing more rapidly than in the lowlands (Battarbee, 2010). Warming can have a direct effect on mountain lake biodiversity by—for example—causing a reduction in habitats available for cold stenothermic taxa (Čiamporová-Zaťovičová et al., 2010; Eggermont et al., 2010). Climate warming can also affect lake biota indirectly by modifying the behaviour of pollutants (Battarbee, 2010). In the last few decades, several international projects have focused on mountain lakes (e.g. Battarbee, 2002; Marchetto & Rogora, 2004; Catalan et al., 2009). Sediment records of high mountain lakes provide insights into both the history of lakes and mountain environments (Battarbee, 2002). Within the EMERGE project, Kernan et al. (2009) distinguished three limno-regions on the basis of their biota. The Carpathian Region is grouped together with the Pyrenees and Alps in the Alpine limno-region. It can be split further on the basis of the present Cladocera species into the Carpathians characterised by benthic/planktonic forms, and the rest of Europe (Alps, Pyrenees) characterised by benthic and plant-associated forms of Cladocera (Brancelj et al., 2009). The Carpathian region has been well investigated in these projects, especially the Tatra Mountains in the north, but less effort was made in the Retezat Mountains. Indeed, 49 lakes were studied in the Tatra Mountains, whereas only six lakes were studied in the Retezat Mountains (Camarero et al., 2009). Differences in Cladocera communities among mountain lakes can be largely explained by their geological history, isolation and size. Colonization of freshly formed lakes after glacier retreat has been fast in high latitude but not in high altitude districts (Williamson et al., 2001). The Retezat Mountains include a small lake district, exhibiting low Cladocera diversity (Brancelj et al., 2009).

In this study, we examine Cladocera community responses to rapid climate changes during the Late Glacial/Early Holocene transition (14,500–11,600 cal. yr. BP). According to several paleoclimate records, this terminal period of the last glaciation abounded in rapid warming and cooling episodes that were superimposed on orbital-forced gradual warming (Björck et al., 1998; Shakun & Carlson, 2010). Our aim is to examine the

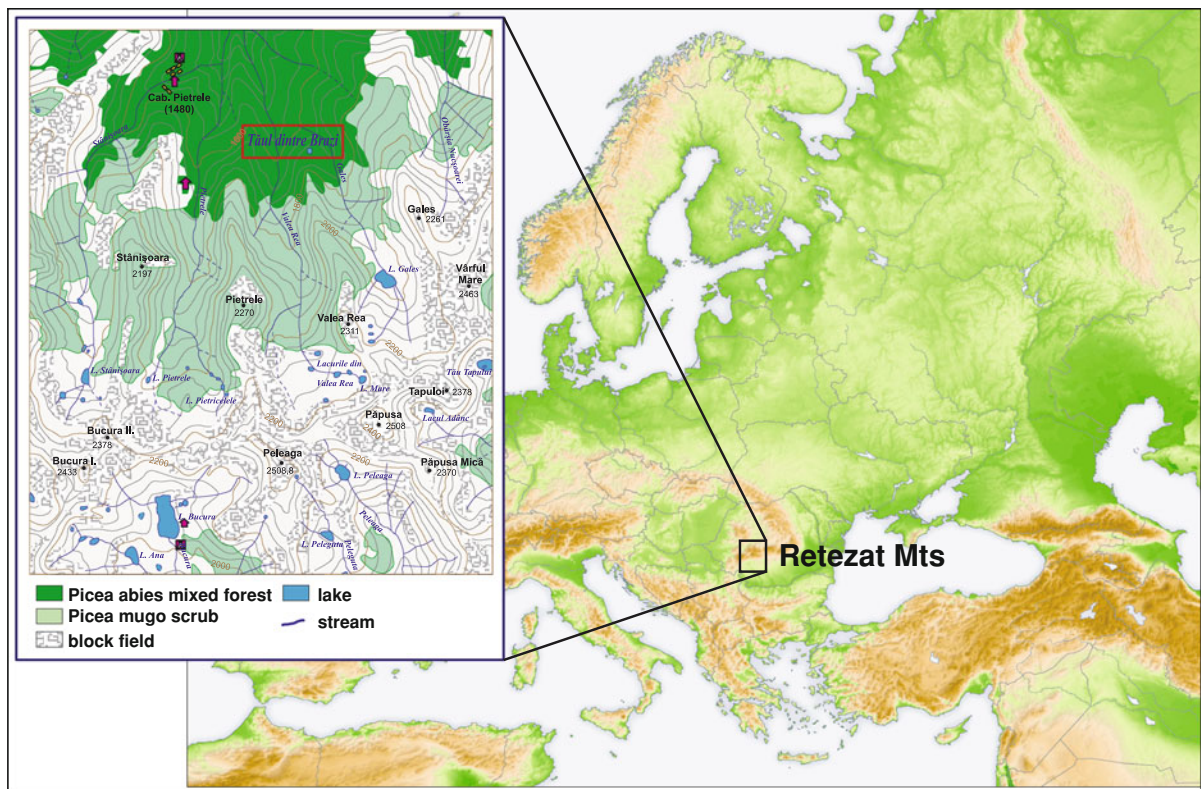


Fig. 1 Location of Lake Brazi in the Retezat Mts

impact of these rapid climatic changes on the aquatic ecosystems in the South Carpathian Mountains (Fig. 1). This study was conducted in the framework of the PROLONG project, focusing on environmental change during the Late Glacial (Magyari et al., 2009). Multi-proxy studies on several lake sediment sequences have been in progress since 2008, and results of the pollen, plant macrofossil, diatom, chironomid and chemical analyses have been published or are in press (Magyari et al., 2009, 2011; Buczkó et al., 2009b, in press; Tóth et al., 2011). This Cladocera record is expected to contribute to the reconstruction of limnological changes (trophic level, water depth and food web) in relation to climate change.

Materials and methods

Study site

The Retezat is the wettest massif in the Romanian Carpathians (precipitation: 1,400 mm year⁻¹ at 1,500–

1,600 m a.s.l.) due to Mediterranean and oceanic influences (Fig. 1). As a result, the effects of the last glaciation have been more significant here than elsewhere in the South Carpathians (Reuther et al., 2007). Numerous glacial lakes appear in the subalpine and alpine belts, and were formed following the retreat of the ice, mainly during the Late Glacial. So far, only a single radiocarbon dated pollen sequence provided information on the Late Glacial and Holocene vegetation history of the subalpine belt of the southern slopes (Farcas et al., 1999). In addition, diatoms and green algae were studied by Péterfi (1974) in Taul Zanogutii.

For the present research, a lake was selected on the northern slope in the subalpine belt (Fig. 1): Tăul dintre Brazi (TDB, core TDB-1; 45°23'47"N, 22°54'06"E; 0.5 ha; 1,740 m a.s.l.; 1 m water depth). The lake is fishless, and located below the timberline, in a mixed *Picea abies*–*Pinus cembra* forest. On the lakeshore *Sphagnum* ssp., *Juncus filiformis*, *Eriophorum vaginatum*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and *Rhododendron myrtifolium* form a floating carpet, together with *Pinus mugo*.

The climate of the area is temperate continental (Fărcaș & Sorocovschi, 1992). Annual temperature is 6°C at 800 m a.s.l. and −2°C at the mountain top (2,500 m). The 10°C July isotherm runs parallel with the upper tree limit, at an altitude of 1,900 m on the southern flank and around 1,800 m on the northern flank. Annual precipitation is between 900 and 1,800 mm. Snow duration is 100 days at low altitudes and over 200 days at 2,000 m; ice cover period is about 200 days (Cogălniceanu et al., 2004). Snow persists in the glacial basins even in the summer.

Field and laboratory analyses

Overlapping sediment cores were obtained in the summer of 2007 using a Livingstone piston corer operated from a platform. A chronological framework for the Late Glacial part of the composite core (TDB-1) was established using six AMS ^{14}C age determinations on terrestrial plant macrofossils. ^{14}C ages were calibrated into calendar years using BCal (Buck et al., 1999; <http://bcal.sheffield.ac.uk>) and the intcal09 calibration curve (Reimer et al., 2009). For depth-age modelling in the Late Glacial part of TDB-1, weighted nonlinear regression was used. Further details of the age-depth modelling are provided in Magyari et al. (2009). Sedimentation rates were calculated by the age-depth model.

Sediment lithology was examined and described in the laboratory. Organic matter content of the sediments was estimated by measuring the loss-in-weight upon ignition at 550°C (LOI₅₅₀) for 3 h of 1 cm³ subsamples taken at 1-cm interval (Heiri et al., 2001).

Subsamples (1 cm³) for Cladocera analysis were treated with 250 ml 10% KOH solution and heated at 80°C for at least 1 h; they were subsequently treated with HF to remove the mineral fraction. Subsamples were gently stirred to deflocculate all organic material without damaging the remains and sieved through a 65 µm mesh. Quantitative slides were prepared by pipetting 200 µl of each subsample volume on a microscope slide; they were mounted with glycerol jelly stained with safranin. All slides were examined under a light microscope at 100× and 400× magnification, and 200–250 Cladocera remains were counted from each sample (Goulden, 1969; Korhola & Rautio, 2001). All Cladocera remains (carapaces, headshields, postabdomen, ephippia and post-abdominal claws) were recorded separately, but only the

most frequent body parts for each taxon were used for estimating species abundance. Poorly fragmented remains were counted if they contained a clear diagnostic feature as proposed by Goulden (1969) and Korhola & Rautio (2001). Total concentration per cm³ was calculated and taxonomic identification followed Frey (1950, 1962, 1988, 1991), Goulden & Frey (1963), Goulden (1969), Gulyás & Forró (1999), Korhola & Rautio (2001), Sebestyén (1965, 1969, 1970, 1971), Szeroczyńska & Sarmaja-Korjonen (2007) and Whiteside et al. (1978). We calculated the influx of Cladocera remains using the sedimentation accumulation rate at the given depth. Dorsal length of minimum 30 *Daphnia* ephippia was measured by using a stereomicroscope with 0.01 mm accuracy, and body size was calculated with the equation of Jeppesen et al. (2002): upper limit of length (mm) = $0.60 \pm 0.03 + 1.43 \pm 0.04$ ephippial size (mm). Mandibles of phantom midge (*Chaoborus* sp.) were also recorded. Plotting of the diagrams was done using Psimpoll 3.00 (Bennet, 2005); this software was also used to define local cladoceran assemblage zones by CONISS (Birks & Gordon, 1985). Clusters were tested using the broken stick model in R statistical environment (R Development Core Team, 2010) with rioja (Juggins, 2009) and vegan (Oksanen et al., 2010) packages.

For ostracods, 7–12 cm³ fresh sediment was processed using standard methods (Griffiths & Holmes, 2000). All ostracod remains were hand-picked without any preliminary preparation. Recovered valves and carapaces were counted and identified under a stereomicroscope at 20× magnification using the key of Meisch (2000). Results were expressed as the total number of valves (both adult and juvenile) in 10 cm³ fresh sediment.

Diatom and pollen analyses were performed on the same sediment core (TDB-1). 1 cm³ samples taken at 1-cm interval were processed using routine laboratory preparation methods. Further details are provided in Magyari et al. (2009, 2011) and Buczkó et al. (2009b). Green algae were counted on the pollen slides. In this study, we present a cumulative relative frequency curve for green algae that include *Pediastrum alternans*, *P. boryanum*, *P. integrum*, *Pediastrum kawrayski*, *Botryococcus* sp., *Scenedesmus* sp., Zygnemataceae and *Spyogyra* sp. Total green algae percentages are proportional to the main terrestrial pollen sum. Bog diatoms include the following taxa: *Frustulia* spp.,

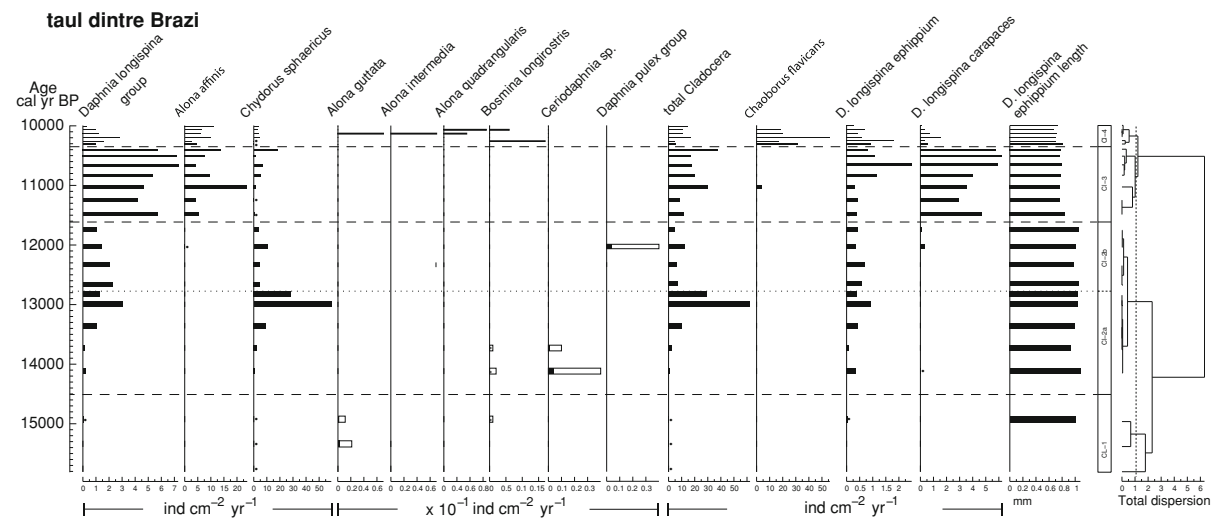


Fig. 2 Stratigraphy of cladoceran species in the Lake Brazí sediment core

Stenopterobia delicatissima and *Eunotia* taxa (mainly *E. exigua*). Their cumulative abundances are proportional to the total number of diatoms counted.

Greenland NGRIP $\delta^{18}\text{O}$ isotope data was used to detect warming/cooling events along the Late Glacial–Holocene transition (Rasmussen et al., 2006).

Results

A total of 17,190 Cladocera remains were counted in the sediments. These belong to nine cladoceran taxa. Remains of *Daphnia longispina* O. F. Müller group, *Alona affinis* (Leydig) and *Chydorus sphaericus* (O. F. Müller) were the most abundant (Fig. 2). Compositional changes in the cladoceran communities resulted in five statistically significant cladoceran assemblage zones (Fig. 3), however, we merged the two lowermost zones because of low fossil densities and diversity.

The studied core sediment sequence, corresponding to the period of 15,200–10,000 kyr. cal. yr. BP, yielded a total of 12,273 ostracod valves but ostracod abundances of individual sediment samples varied between 0 (two samples at the base of the sequence) and 97 valves per 10 cm³ of fresh sediment (average of 342). Although ostracod abundances were generally high, the recovered valves were decalcified, while still retaining a strong chitinous cuticle and often also the chitinous exoskeleton of the limbs.

The ostracod fossil assemblage (thanatocoensis sensu Boomer et al., 2003) proved to be monospecific, consisting of *Cypria ophtalmica* (Jurine) only (Fig. 3). Its concentration showed markedly high fluctuations throughout the Late Glacial and at the onset of the Holocene. It appears that *C. ophtalmica* colonized the lake around 14.3 cal. kyr. BP, i.e. after the period (15.7–14.5 cal. kyr. BP) when low organic content and a shallow and oligotrophic environment prevailed (indicated by a species poor assemblage of Cladocera).

Zone CI-1 (15,750–14,500 cal. yr. BP)

This zone is differentiated by the paucity of Cladocera. We found only a few remains of otherwise common species (*Daphnia longispina* and *Chydorus sphaericus*), some *Alona guttata* Sars headshields and carapaces and *Bosmina longirostris* (O. F. Müller) headshields (Fig. 2). The inferred daphnid size was large (2.1 mm) since dorsal length of daphnid ephippia was ca. 1 mm.

Cypria ophtalmica appeared around 14,800 cal. yr. BP, and abundances gradually increased towards the next zone, peaking at 14,400 cal. yr. BP.

Zone CI-2 (14,500–11,600 cal. yr. BP)

Although not statistically significant, we divided this zone into two subzones (Clad-2a and Clad-2b) on the basis of visible changes in the Cladocera assemblages. *Daphnia longispina* and *Chydorus sphaericus* remains

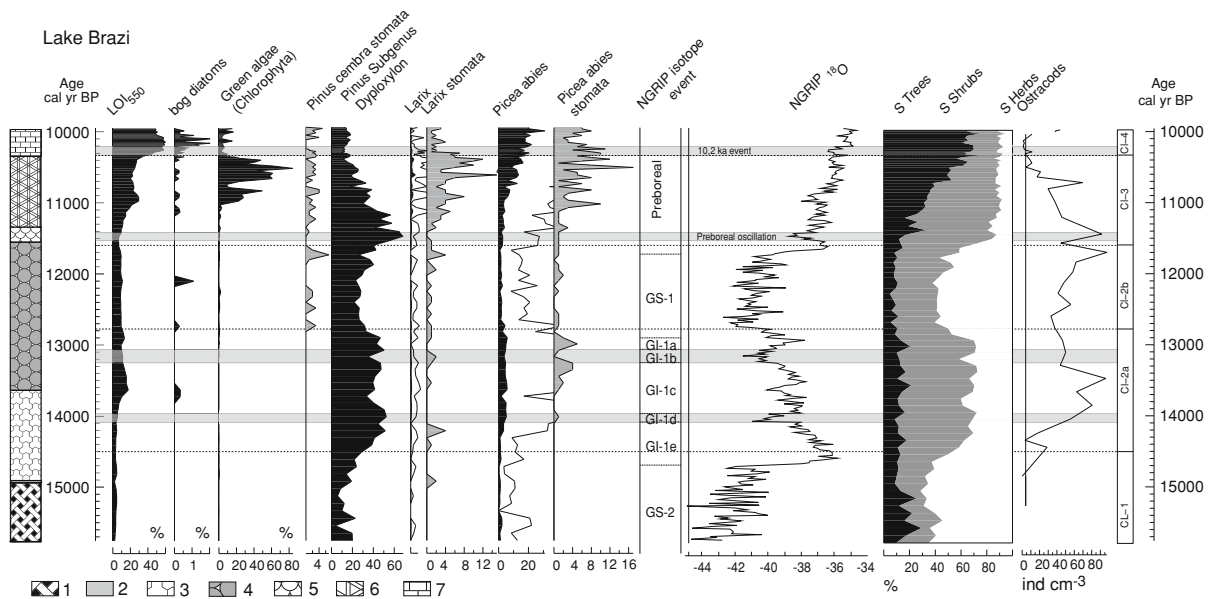


Fig. 3 Stratigraphy of LOI550, bog diatoms, green algae, plant macrofossils, NGRIP $\delta^{18}\text{O}$ record (Rasmussen et al., 2006), pollen percentages and ostracods. Grey brands correspond to cold events recorded in the NGRIP ice core; 1 = mid-grey-light brown silty clay; 2 = dark grey sand lens; 3 = mid-grey silty

clay with faint lamination; 4 = mid-grey-mid-brown clay gyttja with increased organic content; 5 = light grey-light brown silty clay; 6 = mid-grey-mid-brown silty gyttja; 7 = dark brown fine gyttja rich in plant macrofossils

were fairly abundant throughout both subzones. Besides these dominant species, Clad-2a zone was typified by some headshields, carapaces and ephippia belonging to *Bosmina longirostris* and *Ceriodaphnia* sp. From 13,350 cal. yr. BP, numbers of *Chydorus sphaericus* and *Daphnia longispina* started to increase, reaching a maximum at 13,000 cal. yr. BP (Fig. 2). In the Clad-2b subzone, which corresponds to the YD (12,800–11,600 cal. yr. BP), numbers of *Chydorus sphaericus* and *Daphnia longispina* again decreased and total cladoceran concentration also dropped significantly. At 12,000 cal. yr. BP, a few *Alona affinis* and *Daphnia pulex/pulicaria* Leydig group (probably European *D. pulicaria*) post-abdomens were found (Fig. 2). Ephippia size in Zone CI-2 was similar to that of the previous zone (*t* test: $t = -0.1863$, $df = 3.145$, P value = 0.8636; Fig. 4). Although dorsal length of daphnid ephippia in the Clad-2b was slightly larger, it did not differ significantly from that in Clad-2a (*t* test: $t = -0.6203$, $df = 286.784$, $P = 0.5355$). Average length of ephippia in Clad-2a and Clad-2b was 1.014 and 1.023 mm, respectively.

Within this zone, ostracod population size increased, in spite of a short decline at ca.

14,300 cal. yr. BP. Ostracod concentration showed a local maximum at 13,400 cal. yr. BP (961 individuals per 10 cm³ sediment).

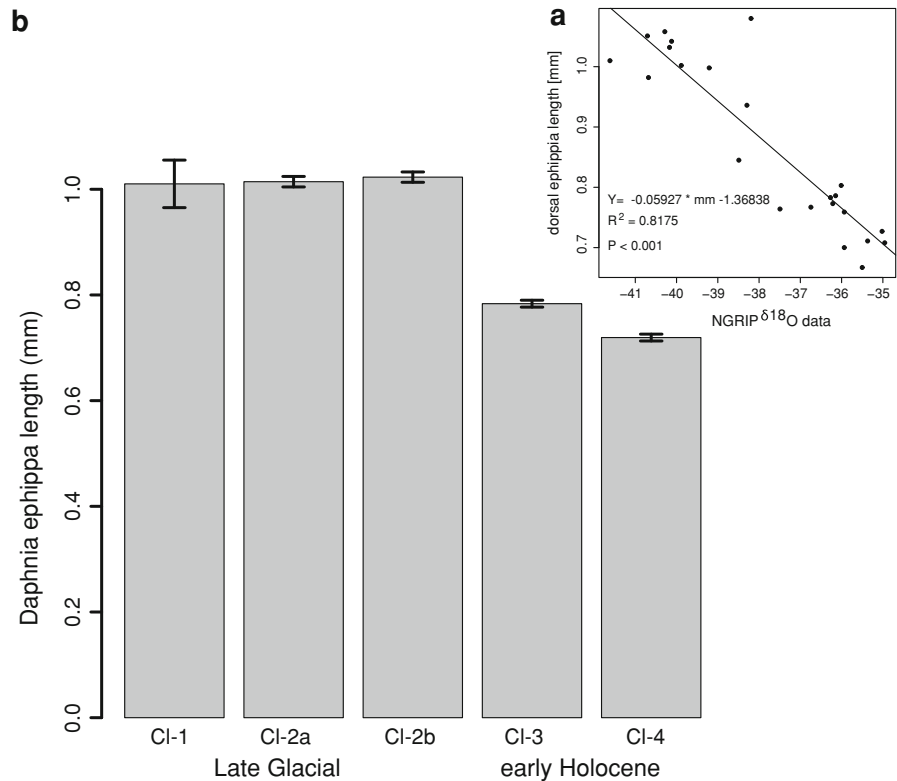
Zone CI-3 (11,600–10,350 cal. yr. BP)

This zone can be described as an *Alona affinis* zone, since this species dominated basically all intervals with a peak concentration at 11,000 cal. yr. BP. Numbers of *Daphnia longispina* group almost doubled, while the concentration of *Chydorus sphaericus* decreased to one-sixth compared to the previous zone (Fig. 2). The lower boundary of this zone coincides with the beginning of the Holocene (11,600 cal. yr. BP). Adult females of daphnids had smaller ephippia (average size: 0.78 mm; *t* test: $t = 24.6193$, $d = 577.213$, $P < 0.001$) than in the Late Glacial.

CI-4 zone (10,350–10,000 cal. yr. BP)

In this zone, diversity of cladocerans increased. *Alona guttata* and *Bosmina longirostris* reappeared, and remains of other *Alona* spp. [*Alona intermedia* Sars and *Alona quadrangularis* (O. F. Müller)] also occurred. The number of *Daphnia* remains, then

Fig. 4 *Daphnia ephippia* length in the different cladoceran zones



again, fell dramatically in this zone. *Chaoborus flavicans* (Meigen) larval mandibles were found in noticeable numbers. Average ephippia size was significantly smaller compared to the previous zone (mean size: 0.72 mm; *t* test: $t = 6.9659$, $df = 47$ 9.232, $P < 0.001$; Fig. 2).

Discussion

Cladocera community structure

The Cladocera fauna in the surface sediments of Lake Brazi is species poor, consisting of four species only (*Alona affinis*, *A. quadrangularis*, *Daphnia longispina* and *Chydorus sphaericus*; Korponai unpublished data). These species inhabit almost every type of lake and pond, and are often doing well in stressed environments (Hořická et al., 2006; Sacherová et al., 2006; Brancelj et al., 2009). They are also common in remote lakes in Europe (Naidenow, 1975; Hofmann, 2000; Sacherová et al., 2006; Brancelj et al., 2009). High altitude lakes in Europe often contain a less speciose Cladocera fauna compared to similar lakes at

high latitude, and they are characterised by *Daphnia* dominance (Manca & Comoli, 1999; Lotter et al., 2002; Hořická et al., 2006; Brancelj et al., 2009). Similar to our findings, Lotter et al. (2002) found an extremely low Cladocera diversity in Hagelseewli at 2,339 m a.s.l., with the presence of *Chydorus sphaericus* and *Daphnia pulex/pulicaria* group only. Similar Cladocera communities were also found in all other studied lakes in the Retezat Mountains (Straškrábová et al., 2006; Brancelj et al., 2009; Catalan et al., 2009). Straškrábová et al. (2006) found that all these lakes had a low trophic status (oligotrophic–mesotrophic statuses); they described them as being pristine, not having undergone eutrophication by human impact.

Lake paleoenvironment and Cladocera remains

As mentioned, Lake Brazi is located in the coniferous forest belt (dominant species are *Picea abies* and *Pinus cembra*). According to the pollen data, plant macrofossil data and stomata records, afforestation started at the beginning of the Late Glacial interstadial, around 14,500 cal. yr. BP (Magyari et al., 2011). The initial phase was characterised by sparse mixed

coniferous tree cover (with *Pinus mugo*, *P. cembra*, *Larix decidua* and *Picea abies*). Tree and shrub cover decreased during the YD, but all major conifers seem to have survived. At the onset of the Holocene warming, closed mixed conifer forest developed. At first, it was dominated by *Larix decidua*, whereas *Picea abies* dominated after ca. 10,600 cal. yr. BP (Magyari et al., 2009, 2011).

During the Oldest Dryas (i.e. upper part of GS-2 stadial, at 14,700 cal. yr. BP), the Greenland oxygen isotope record indicates a cold climate (NGRIP $\delta^{18}\text{O}$, Fig. 3). Our Cladocera assemblage zone Cl-1 covers this period and is characterised by the paucity of Cladocera species. We found only a few Cladocera remains of *Chydorus sphaericus*, *Daphnia longispina* group, *Alona guttata* and *Bosmina longirostris*. These species are common in arctic/subarctic lakes, especially in relatively younger regions; they are ubiquitous species with wide tolerance (Samchyshyna et al., 2008). Low sediment organic content (LOI_{550}) and sporadic occurrence of diatoms also imply that Lake Brazi was a young oligotrophic lake during this Oldest Dryas period (Nowiński & Wiśniewska-Wojtasik, 2006; Buczkó et al., in press). Relatively high pollen frequencies of ruderal and heliophilous herbaceous plants in combination with the overall absence of terrestrial plant macrofossils suggested that directly after the retreat of the glacier from the Gales-valley, the lake-shores were mostly barren (Magyari et al., 2011). Tóth et al. (2011) found a few cold stenoterm chironomid taxa in the lake sediment, which also confirms the cold climate conditions during the Oldest Dryas. Furthermore, results of the diatom analyses suggested that the lake received intense summer inflow, since lotic diatoms were abundant (e.g. *Hannaea arcus*; Buczkó et al., 2009b, in press) and ostracod remains were missing between 15,200 and 14,700 cal. yr. BP (Fig. 3).

The Cladocera assemblage zone Clad-2a covers the Late Glacial Interstadial (GI-I) (Fig. 3). Fossil Cladocera communities consisted of *Chydorus sphaericus* and *Daphnia longispina* group. Both taxa reached maximum abundances at 13,000 cal. yr. BP, which is the final part of the GI-1a interstadial (Björck et al., 1998). This concentration peak likely indicates increasing nutrient availability and longer growing seasons. This finding seems to be supported by the chironomid-inferred peak in summer temperatures at 13,000 cal. yr. BP (8.6°C; see Tóth et al., 2011). In the

GI-1a interstadial, warm climate resulted in an environment with intensive chemical weathering of the granite bedrock together with soil development in the lake catchment. In Lake Brazi, enhanced nutrient input is indicated by the increasing biogenic silica values and dominance of benthic diatoms (Buczkó et al., 2009b, in press). Presence of epiphytic diatoms, such as Cymbelloids, point to the formation of lakeshore macrophyte vegetation (mosses). Similarly, the occurrence of *Ceriodaphnia ehippia* suggests macrophyte covered littoral habitats (Korhola & Rautio, 2001). Increasing sediment organic content after 14,000 cal. yr. BP suggests increased lake productivity. Since fish were likely absent in the lake during the Late Glacial, zooplankton abundance likely reflects other factors, such as food supply/availability. Since *C. sphaericus* is indicative of harsh conditions, high abundances of this species could point to increased trophic status or increased turbidity. High numbers of *Daphnia*, the again, could also point to increased lake productivity besides the presence of more extensive pelagic habitats (Korhola & Rautio, 2001). Since ostracods feed on organic detritus, higher numbers during the Late Glacial interstadial (Fig. 3) could also reflect increasing in-lake productivity.

The YD stadial (GS-1) (12,800–11,600 cal. yr. BP) does not appear as a separate assemblage zone in the Cladocera record despite a distinct decrease in the total concentration of Cladocera remains. This could be explained by the YD survival of several taxa present during the Late Glacial interstadial. The species that disappeared had already declined in the second part of the interstadial (see, e.g. *Ceriodaphnia* sp. and *Bosmina longirostris* in Fig. 3). The largest population decline was observed for *Chydorus sphaericus* and *Daphnia longispina* group (between 12,800 and 12,500 cal. yr. BP). This is most likely attributable to a pH decrease as inferred from changes in the diatom flora; such a pH decrease could arise from a sudden increase of the duration of ice cover at 12,800 cal. yr. BP (Buczkó et al., in press). In-lake algal productivity likely decreased because of the shorter growing season and low pH, and this likely affected the Cladocera fauna feeding on them (Manca & Armiraglio, 2002). Changes in the terrestrial vegetation were also detected; this suggested a strong regional vegetation response to the YD cooling that involved deforestation and spread of steppe-tundra and snowbed vegetation (with *Soldanella* and

Primula). Around Lake Brazi, however, all conifer trees (except for *Picea abies*) survived this cooling suggesting that the summer temperatures declined modestly. This finding was also corroborated by the chironomid-based summer temperature reconstruction (Fig. 3; Magyari et al., 2011; Tóth et al., 2011).

The Holocene transition at 11,600 cal. yr. BP is well marked in the Cladocera record and coincides with zone CI-3 (Fig. 3). The appearance of *Alona affinis* coincides with warmer climate, similarly to lakes in the Alps and Pirin Mountains (Hofmann, 2000; Stefanova et al., 2003). The number of daphnid carapaces also increased significantly but ephippia number did not (Fig. 2). It seems that these taxa outcompeted *C. sphaericus* which almost disappeared at this transition. The sudden rise in Cladocera fossil densities refers to a rapid increase in lake productivity. Increasing productivity is also suggested by higher organic content (Fig. 3). A further increase in primary production at 11,000 cal. yr. BP is reflected by high abundance of green algae (*Pediastrum boryanum*, *P. integrum* and *P. angulosum*) (Fig. 3). *Pediastrum* species appear to be good indicators of productivity in arctic and high mountain lakes (Sarmaja-Korjonen et al., 2006; Weckström et al., 2009). Apparently, terrestrial vegetation also responded to rapid warming as evidenced by the pollen and plant macrofossil records. Arboreal cover and conifer species abundance increased rapidly at 11,600 cal. yr. BP (Fig. 3; Magyari et al., 2011). *Larix* became the most abundant by ca. 11,400 cal. yr. BP, but some thousand years later (~10,300 cal. yr. BP) *Picea abies* took over and *Larix* gradually declined (Magyari et al., 2011). *Larix* remains decompose easier than *Pinus* or *Picea* needles; hence, they may have accelerated external nutrient loads and therefore lake productivity (Daubenmire & Prusso, 1963).

From ca. 10,300 cal. yr. BP, mixed *Picea abies*–*Pinus cembra* woodland formed around the lake, but *Pinus mugo* remained abundant on the lakeshore (Magyari et al., 2011). Decomposition of *Picea* and *Pinus* needles and inflow from podzol soil likely caused a considerable pH decrease in the lake water leading to dystrophy (Korsman et al., 1994). This change is reflected by the occurrence of acidophilous diatoms (e.g. *Frustulia saxonica*, *Stenopterobia delicatissima* and *Eunotia exigua*; Buczkó et al., 2009b) and the establishment of *Sphagnum* species on the lakeshore (Magyari, unpublished data). Occurrence of

Chaoborus flavicans confirms shallow and dystrophic environments since this species typically lives in small lakes characterised by shallowness and dense aquatic vegetation; yet, it is absent from transparent, oligotrophic lakes holding fish (Luoto & Nevalainen, 2009). Cladocera assemblages apparently responded to this decrease in pH by a considerable population decrease of daphnids (Fig. 2). The population of *Cypria ophthalmica* decreased significantly at the beginning of the Holocene, likely as a response to rapid warming. Chironomid-inferred summer air temperature reached 13.2°C by 9,970 cal. yr. BP; this is higher than at the present day (Tóth et al., 2011).

At ca. 10,200 cal. yr. BP, a short cooling event is detected by the NGRIP $\delta^{18}\text{O}$ record (Fig. 3); this is also reflected by several biotic proxies from Lake Brazi (Fig. 3). Pollen accumulation rates of broad-leaved taxa (*Corylus*, *Ulmus*, *Fraxinus* and *Quercus*) decreased, while *Larix decidua* disappeared (Magyari et al., 2011). Cladocera numbers also fell significantly (Fig. 2) suggesting a response to cooling and maybe also decreasing nutrient availability. Yet, later on, they increased both in abundances and species number. This indicates that more extensive submerged vegetation favourable for *Alona*.

Chydorid distribution in the Late Glacial sediment of Lake Brazi was very similar to the Late Glacial and Early Holocene Cladocera assemblages of the Swiss alpine lakes, e.g. Lake Hérémence at 2,290 m (Hofmann, 2000) and to Lake Dalgoto in the Balkan Pirin Mountains at 2,310 m (Stefanova et al., 2003). During the YD, the chydorid fauna consisted of *Chydorus sphaericus* only, similar to other lakes at high altitude (Catalan et al., 2009). At lower altitude in the Alps, lakes currently have a more diverse Cladocera community and they had a more speciose Cladocera fauna during the Late Glacial as well (Hofmann, 2000; Korhola & Rautio, 2001).

Daphnia ephippia and temperature

Changes in *Daphnia* population size were estimated by ephippia counts. Jeppesen et al. (2002, 2003) revealed that numbers and size of ephippia reflect environmental changes in lake ecosystems. More specifically, they found a good correspondence between the abundance of *Daphnia* and *Bosmina* ephippia in the surface sediment and contemporary data along a temperature gradient. We found a

moderately increasing ephippium number during the YD relative to the Late Glacial interstadial in Lake Brazi. This contrast with the situation in a southern Balkan lake, where Stefanova et al. (2003) found extremely low concentration of ephippia in the early Holocene in Lake Dalgoto. It can likely be explained by climatic difference as Lake Brazi is situated at lower altitude. At lower altitude, environmental conditions likely became favourable earlier than at higher elevation.

In Lake Brazi, we found a negative correlation between average ephippium length and the NGRIP $\delta^{18}\text{O}$ isotope values ($y = -0.0593 * \text{mm} - 1.368$; $R^2 = 0.8175$; $P < 0.001$; Fig. 4). Mean dorsal length of daphnid ephippia thus decreased with increasing temperature and inferred *Daphnia* body size was larger (Fig. 4). *Daphnia* ephippia size did not differ significantly within the Late Glacial (Fig. 4), but it did differ between the Late Glacial and the Early Holocene.

Food availability (Boersma, 1997), presence of predators (Jeppesen et al., 2002) and temperature (Perrin, 1988) have a significant effect on the sizes of adult daphnids. Size at maturity is larger under high food conditions and in fishless environments. However, productivity of Lake Brazi was lower in the Late Glacial than in the Holocene that is supported by low sediment organic matter and low Cladocera abundance during the Late Glacial. Ephippia size was smaller in spite of higher food availability in the Holocene.

Invertebrate predators (e.g. *Chaoborus* larvae, copepods) increase body size of cladocerans, while vertebrate predators decrease it (Brooks & Dodson, 1965). Jeppesen et al. (2002) used ephippia size for the reconstruction of fish abundance changes in Danish lakes. Measuring the size distribution of fossil Cladocera remains can thus be used to infer past changes in food web. Since Lake Brazi is fishless, predation pressure most likely comes from invertebrates. Since invertebrates as *Chaoborus* and copepods principally feed on smaller sized Cladocera species (Black & Hairston, 1988), *Daphnia* ephippia are usually larger in the presence of invertebrate predators. *Chaoborus* remains (invertebrate predators) were only found in zone C1-4, when ephippia size was the smallest. Yet, since Lake Brazi lacks fish, other factors must have accounted for the decreasing daphnid body size during the Early Holocene.

Perrin (1988) found that adult *Simocephalus* size correlates negatively with temperature, moreover Atkinson's rule (Atkinson, 1994) states that ectotherms decrease in size with increasing temperature and species composition can also alter. Temperature was higher in the Holocene, thus it is very likely that temperature is one of the possible factor structuring size distribution of daphnids in the Lake Brazi, particularly at the onset of the Holocene. However, Hamrová et al. (2010) described a daphnid species shift in Štrbske Lake due to environmental changes. They found larger *Daphnia longispina* ephippia in the lower sediment, whereas smaller ephippia of *D. galeata* were found in the top sediments. They argued that both a rise in fish predation pressure and an increase in trophic level played a role.

In sum, we conclude that both species shift and climate change (larger ephippia under colder climate) played a role in the size distribution of daphnids in the Late Glacial and early Holocene lake ecosystem of Lake Brazi.

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