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Ecological responses of aquatic invertebrates to climate change over the past ~400 years in a climatically ultra-sensitive lake in the Niedere Tauern Alps (Austria)

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With 6 figures

Abstract: A sediment core covering the past ~400 years from Lake Moaralmsee (central Austrian Alps), which has previously been judged to be ultra-sensitive to climate change due to its unusually cold water, was examined for its fossil invertebrates. The aim of this study was to investigate whether the faunal assemblages had experienced changes in their composition during periods of the Little Ice Age and recent climate warming. Although there was some general lag between the community changes of these animal groups, the faunal dynamics showed significant correlation between the principal component axes. A mutual break point in the assemblages occurred in the beginning of the 20th century corresponding to increased global and Alpine air temperatures. A gradual decrease in diversity was detected for chironomids, but the only major change in the diversity of Cladocera occurred between ~1900 and 1950AD when it was markedly lower. The results indicate that Lake Moaralmsee has gone through clear changes in its invertebrate fauna during the past centuries that were most likely related to climate warming, with the most dramatic changes occurring almost a century ago.

Key words: biodiversity, climate change, invertebrates, lakes, palaeolimnology, zooplankton.

Introduction

Freshwater ecosystems and their biodiversity are endangered by increased human interference and present climate change (Heino et al. 2009, Raunio et al. 2011). Cladocera (Crustacea: Anomopoda) and larvae of Chironomidae (Insecta: Diptera) are key components of the plankton and benthic fauna in lakes (Tolonen et al. 2005, Jeppesen et al. 2011), and can act as sentinels of climate change (Adrian 2009). The survival and success of these animals depends on factors related to temperature, habitat, food availability, predation, and water quality (Goulden 1971, Oliver 1971). The fossil remains of Cladocera and chironomids are well preserved in lake sediments and thus, the palaeolimnological techniques and use of sedimentary fossil assemblages provides a unique opportunity to hindcast past community and environmental dynamics in lakes during the past centuries or millennia that is not possible with any other monitoring data (Smol 2008). Unfortunately, despite their potential in biodiversity conservation and in assessments of ecological responses to climate change, relatively little work has been done on palaeoecological records from lake sedi-

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ments (Willis & Birks 2006 but see Sayer et al. 1999, Smol et al. 2005, Helama et al. 2007, Smol & Douglas 2007). Since palaeolimnology and aquatic ecology has thus far been largely disconnected (Sayer et al. 2010), it is extremely important to combine both perspectives to fully understand aquatic ecosystem dynamics (Smol 1990, Smol 1992, Saros 2009, Nevalainen 2010, Luoto & Raunio 2011). In addition to the long-term perspective, the benefits of palaeolimnological samples include integration of material from several habitats, but have the disadvantage of lower taxonomic resolution. However, there has been great improvement in fossil taxonomy during the recent years (Brooks et al. 2007, Szeroczyńska & Sarmaja-Korjonen 2007).

Alpine lake ecosystems are very susceptible to the influence of human activities and climate change (Psenner & Schmidt 1992, Skjelkvale & Wright 1998, Hausmann et al. 2002, Nevalainen et al. 2011). The European Alps have been subject to human influence in the past millennia and increasingly so in recent centuries when the climate has also changed radically (Koinig et al. 2002). As a direct consequence of global warming, an increase in water temperatures and decrease ice-covered period are related to ambient air temperatures (Livingstone 1997) and, indirectly, the Alpine lakes are influenced by the climate change through reduced snow cover and increased weathering and erosion (Sommaruga-Wögrath et al. 1997). Furthermore, anthropogenic influences, such as air-borne pollution and land-use (Alpine pastures), can be superimposed on climatic change (Heiri & Lotter 2003). The temperature increase in the Alps during the past century (up to 2 °C) has been much higher than the global average (0.7 °C) (Beniston 2006) making them particularly sensitive indicators of climate change (Adrian et al. 2009). Some of the effects of climate warming on aquatic ecosystems could include population and life-history changes, extinctions, shifts in geographical range, changes in species composition of communities, and changes in the structure and functioning of ecosystems (McCarty 2001, Walther et al. 2002).

The DETECTIVE (DEcadal deTECTion of biodIVErsity in alpine lakes) project of the Austrian Academy of Sciences focuses on the past, present, and future scenarios of global warming threatening the biodiversity of (ultra)sensitive aquatic ecosystems in the Niedere Tauern Alps in Austria. In this study, we describe historical shifts in invertebrate species composition of Lake Moaralmsee, located in the northern slope of the Niedere Tauern. Lake Moaralmsee is unusual in its thermal character when compared to other Niedere Tauern lakes; its summertime water temperatures (July epilimnetic water temperature ~10 °C) have been documented to be generally 6–7 °C cooler (Thompson et al. 2005). Contrary to other lakes, water temperature decreases in Lake Moaralmsee when air temperature increases and this is attributed to increased snow melt under higher temperature. According to the assessment by Thompson et al. (2005), of all the lakes in the central Austrian Alps, Lake Moaralmsee is most at risk to future climate change. Lake Moaralmsee will likely be subjected to marked reductions in the springtime snow-cover of its catchment, to pronounced increase in the open-water season, and to less frequent summer snow-cover. Following the increased air temperatures and disappearance of the snow patches, the water temperature of Lake Moaralmsee is projected to rise by 12 °C and also water discharge and ice-cover duration are expected to far exceed the variations experienced during the Holocene (Thompson et al. 2005). In general, Austrian lakes at the altitude of Lake Moaralmsee are likely to show maximum response to climate change because a one degree temperature change causes a 30 day change in ice-cover duration.

In this study, we aim to reveal the long-term dynamics of the Cladocera and chironomid fauna for the past ~400 years and examine possible connections to climate change. We hypothesize that the aquatic community changes are climate-driven and the biodiversity of this lake is especially vulnerable to increased air temperatures. There is a great need for knowledge on how climate changes have affected the Alpine region in the past and on how the ecosystems are responding to changing environmental conditions (Koinig et al. 2002, Bigler et al. 2006). Our study lake can be considered ecologically highly significant due to its location close to a treeline ecotone, which makes it extremely vulnerable to changing treeline in response to climate warming (Heegaard et al. 2006) and due to its physical sensitivity (snowmelt patterns) to climate change (Thompson et al. 2005).

Material and methods

Study site and sediment sampling

Lake Moaralmsee (47° 37′ N, 13° 80′ E) is located in the Niedere (Schladminger) Tauern Alps in Austria (Fig. 1). The Niedere Tauern forms a compact but imposing massif of crystalline and limestone bedrock. Moaralmsee is separated from the cirque back-wall to the south by an upper basin and a moraine field, making the basin mostly groundwater fed. The catchment is characterized by rocky cliffs and Alpine pastures and only a few short growing trees are present at its altitude of

Fig. 1. Locations of the study lake Moaralmsee in the Niedere Tauern Alps, Austria, and the downcore site.

1825m a.s.l. A hiking trail passes through the catchment but otherwise the lake is remote from human impact and settlement. A small outlet is located in the north. The maximum length of the oligotrophic and transparent lake is 232 m, maximum width 127 m, and maximum depth 6.1 m. Only a few small aquatic macrophyte stands are present in the basin and a low number of fish occupy the lake. The autumnal (August 2010) pH of the lake is 8.1 and the dissolved hypolimnetic oxygen is 11.3 mg l^{-1}. The water temperature in Lake Moaralmsee is unusually cold compared to other lakes at similar altitude in the region due to slower snowmelt caused by topographic features that reduce sunlight and influence wind impact. The summertime epilimnetic water temperature hardly exceeds 10 °C (Nevalainen 2012) and may cause the lake to be less stratified than similar lakes with warmer summertime surface waters.

A sediment core (Fig. 1) consisting of homogeneous gyttja was taken from Lake Moaralmsee using a small boat and an Uwitec gravity corer in 17 August, 2010. The short core (25 cm) from a water depth of 5.5 m was subsampled at 1-cm intervals. The samples were stored in plastic bags in a cold room at +4 °C.

To provide a chronology, a total of 15 samples from the sediment core were analyzed for ^{210}Pb activity (Fig. 2). The analyses were done in Laboratory of Quaternary Geochronology, Institute of Geological Sciences, Polish Academy of Sciences in Warsaw, Poland. ^{210}Pb activity of the sediments was determined indirectly via alpha-spectrometry measuring the ^{210}Po ($\alpha = 5.31$ MeV, $T1/2 = 138$ d) activity (Flynn 1968). The ^{210}Po is generated by the decay of ^{210}Pb and then ^{210}Bi and is assumed to be in equilibrium with the parent isotopes. As an internal yield tracer, the known amount of ^{208}Po was added to the weighted sample. Po was separated from the sample using strong hydrochloric and nitric acid and was deposited on silver disks (Flynn 1968). Activity of ^{210}Po and ^{208}Po was measured using OCTETE PC alpha spectrometer produced by ORTEC. Constant rate of unsupported ^{210}Pb supply model (CRS) was used to calculate sediment age (Appleby 2001). This model assumes a variable sedimentation rate, sediment compaction and mixing. Activity of unsupported (allochthonous) ^{210}Pb was calculated by subtraction of supported (autigenic) ^{210}Pb activity. Supported ^{210}Pb was determined by measurements of old sediments, which contain no allochthonous ^{210}Pb and assumed constant activity of authigenic ^{210}Pb along sediment column. Age-depth function was calculated using a randomization method and the curve was fitted using the LOESS procedure (Cleveland & Devlin 1988). In the lower part of the sediment core, dates were obtained through extrapolation of the sedimentation rates in the upper part of the core (cf. von Gunten et al. 2008). Because no plant macrofossils were found from the lower part of the core and there was not enough chitinous material available, we were not able to use radiocarbon dating to validate the chronology in the lower part of the core. Furthermore, as the lake is situated on calcareous bedrock, bulk sediment samples would be unsuitable and unreliable for radiocarbon dating in this site. Hence, extreme caution should be taken in the age interpretations of the lower part of the core. In addition, due to the aims in this study, we concentrate on the more recent changes in the lake communities.

Fossil analyses

The volumetric sediment samples of 1 cm^3 for fossil chironomid analysis were prepared applying standard methods described in Brooks et al. (2007), but without the pretreatment in KOH, because it was unnecessary due to low portion of organic matter. The sediments were sieved through a 100-µm mesh and the residue was examined using a Bogorov counting chamber (Gannon 1971) under a binocular microscope for extraction of the remains with fine forceps. The fossil remains were permanently mounted in Euparal® on microscope slides and identified under a light microscope at 400-times magnification. The identification of chironomids was based on the identification guides of Wiederholm (1983) and Brooks et al. (2007). A minimum of 50 head capsules was set as the target counting sum (Quinlan & Smol 2001).

The sediment samples for fossil Cladocera were prepared following the methods described in Szeroczyńska & Sarmaja-Korjonen (2007). In the laboratory, the samples were heated in 10 % KOH for approximately 15–20 min and washed and sieved through a 51-µm mesh under running tap water. The residues were then centrifuged for approximately 10 minutes to concentrate the fossil cladoceran remains and dyed with a few drops of glycerol-safranine. The prepared samples were mounted on microscope slides and analyzed for cladoceran remains under a light microscope with magnifications between

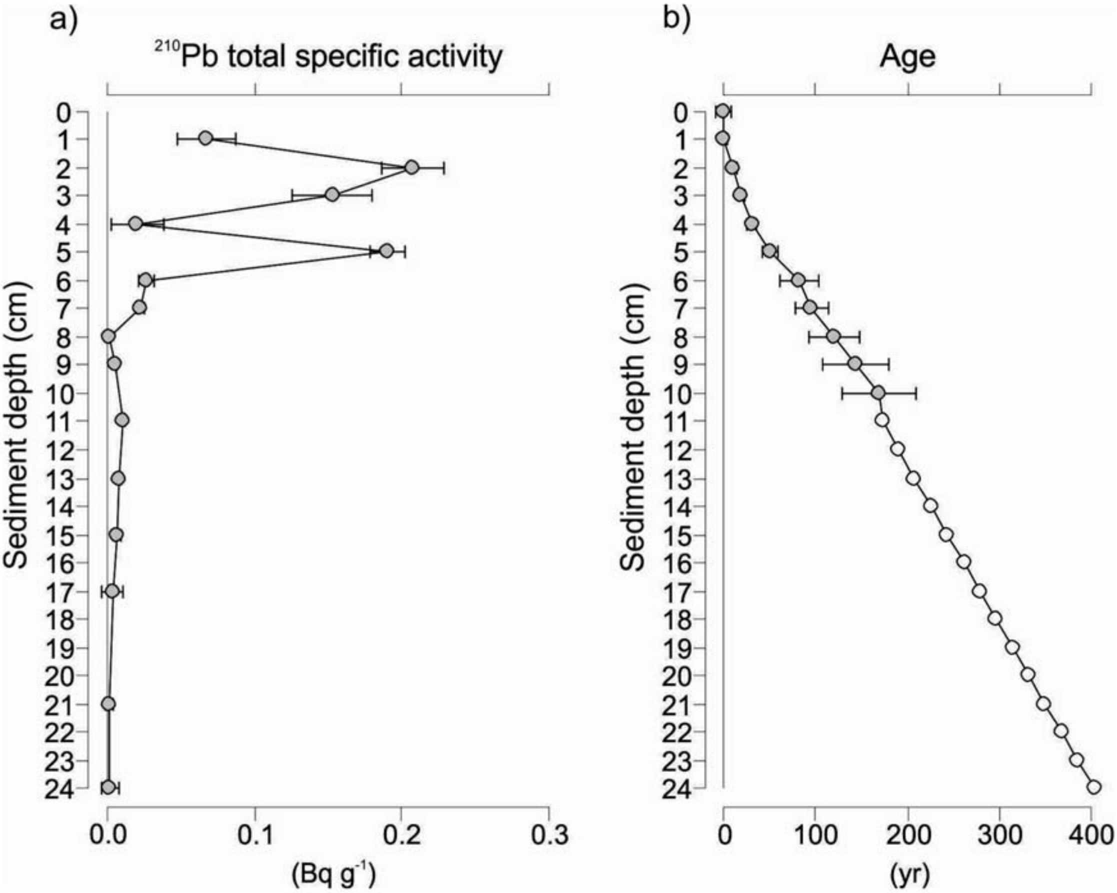

Fig. 2. Total specific activity of ^{210}Pb **(a)** and the associated time-depth model **(b)** for the sediment profile from Lake Moaralmsee in the Niedere Tauern Alps, Austria. Samples in the age-depth model from 11 cm downwards (white circles) are extrapolated from the ^{210}Pb chronology between 0 and 10 cm (gray circles).

100- and 400-times. Cladocera were enumerated as the number of most abundant body part (carapaces, headshields, postabdomens, ephippia) and identified following the identification key by Szeroczyńska & Sarmaja-Korjonen (2007). The minimum counting sum was set to 70 individuals because the cladoceran remains were very scarce. A minimum counting sum of 70–100 cladoceran individuals has proven to be satisfactory to characterize most assemblages, particularly in low-richness lakes (Kurek et al. 2010, Nevalainen 2010).

Numerical analyses

To choose between linear and unimodal methods, detrended correspondence analysis (DCA) was used to assess the length of compositional gradients. Consequently, due to the linear nature of the data, principal component analysis (PCA) was selected to investigate patterns in chironomid and Cladocera assemblages in the downcore data. The DCAs and PCAs were performed on square-rooted relative taxa abundances using downweighting of rare species and were run with the program CANOCO, version 4.52 (ter Braak & Šmilauer 2002). Species diversity was assessed using the Shannon index (Shannon 1948), $H' = \Sigma(P_i \ln P_i)$. The null model software EcoSim (Gotelli & Entsminger 2011) was used to apply the individual-based rarefaction approach on the incidence data for diversity calculations. The rarefaction approach was used to stabilize the variance in sample size. In the rarefaction, the number of individuals was set to ~50 in chironomids and 70 in cladocerans, corresponding to the counting sums.

To relate invertebrate assemblage changes to climate variability over the ~400-year time span covered by the sediment core, we used the general annual Northern Hemisphere reconstructed (tree-ring based) and instrumentally observed temperature data by D'Arrigo et al. (2006). For Alpine temperature variability we used the data by Auer et al. (2007). The temperature data were obtained through the World Data Center for Paleoclimatology and NOAA's National Climatic Data Center, Paleoclimatology Branch website (http://www.ncdc.noaa.gov/paleo/paleo.html) and through the HISTALP (Historical instrumental climatological surface time series of the greater Alpine region) website (http://www.zamg.ac.at/histalp/). Although fossil chironomids are often used to quantitatively reconstruct palaeotemperatures in the Alps (Heiri & Lotter 2005), we do not attempt it in this paper due to the unique nature of the thermal properties in Lake Moaralmsee (unusually low summertime water temperatures).

Results

Chironomid assemblages

In the sediment core data, 26 chironomid taxa were identified. The assemblages were dominated by *Tanytarsus lugens*-type, which was present in all 25 sediment intervals having maximum abundance of 73.6 % (at 2 cm), and mean abundance of 54.7 % (Fig. 3). The dominance of *T. lugens*-type was rather consistent, although its abundance decreased between 8 and 7 cm when it reached the minimum of 28 %. In the bottom of the core (24 cm), other common chironomid taxa included *Psectrocladius sordidellus*-type, *Micropsectra contracta*-type, *Procladius*, and *Paratanytarsus austriacus*-type. *M. contracta*-type disappeared after 23 cm, but *P. sordidellus*-type remained relatively abundant until 18 cm, *Procladius* until 19 cm, and *P. austriacus*-type until 12 cm. *Paracladius* increased at 20 cm and had an abundance of ~30–40 % between 17 and 7 cm. *Heterotrissocladius marcidus*-type gradually increased from 14 cm until 7 cm. *P. austriacus*-type again increased from 9 cm and *Procladius* from 4 cm onwards and remained relatively abundant until the present.

Cladocera assemblages

Only 6 Cladocera taxa were identified from the core, of which 5 belonged to the family Chydoridae and 1 to the family Daphniidae. The most abundant taxon was *Chydorus sphaericus*-type, which occurred in all

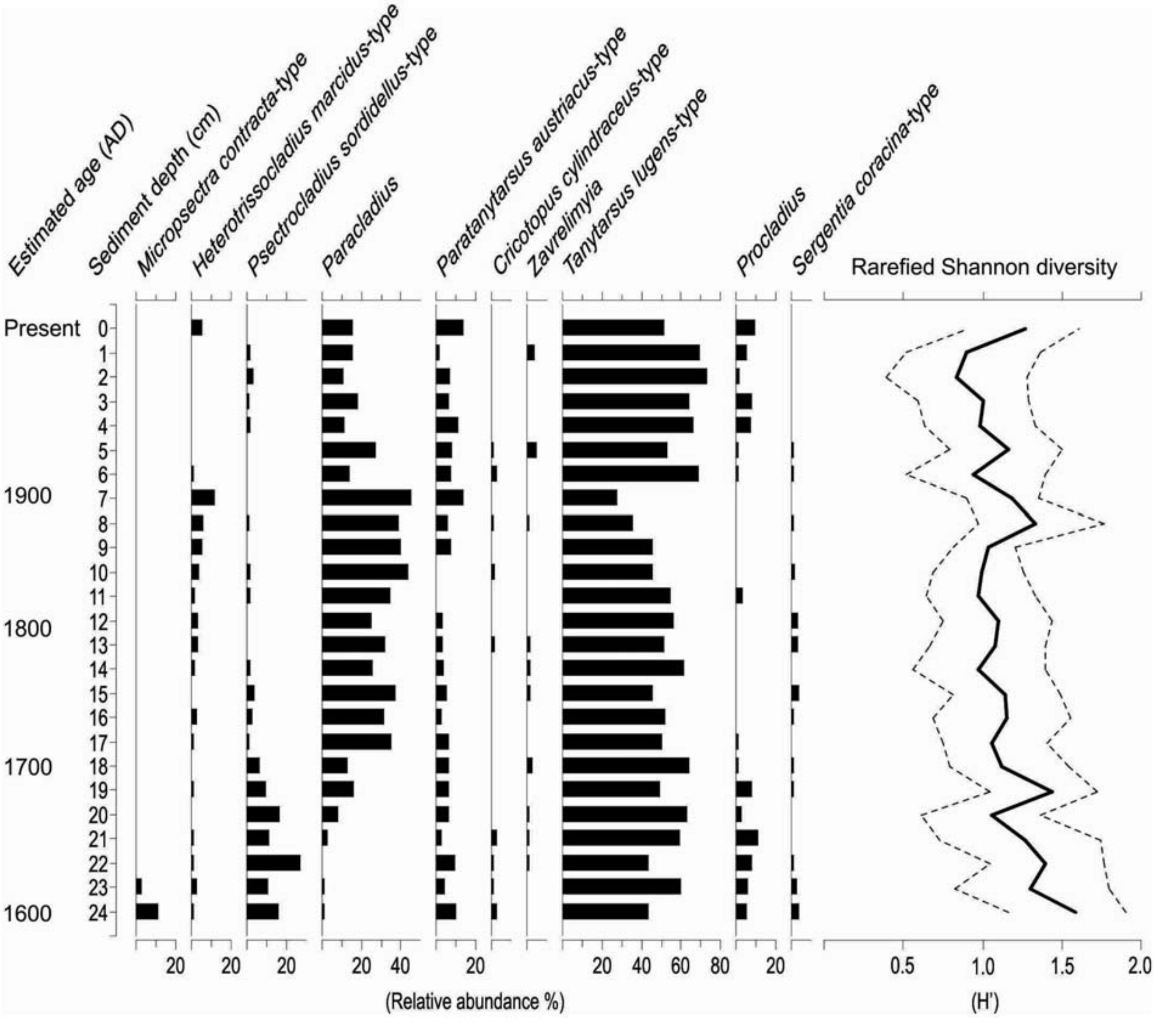

Fig. 3. Relative abundances of the most common chironomid taxa and rarefied Shannon index in the sediment core from Lake Moaralmsee in the Niedere Tauern Alps, Austria.

of the sediment intervals with maximum abundance of 86.8 %, and mean abundance of 38 % (Fig. 4). At the beginning of the stratigraphy (24–21 cm), *C. sphaericus*-type was at its lowest abundance of ~10 % and the Cladocera assemblages were dominated by *Alona affinis*. *Alona quadrangularis* was abundant (~20–40 %) from 24 until 7 cm and *Acroperus harpae* gradually increased from the bottom of the core until 15 cm, after which it slightly decreased. The dominance of *C. sphaericus*-type began at 18 cm and continued until 4 cm, when *A. harpae* became the dominating species (~40 %) until the present and also *A. affinis* increased.

Ordinations and diversity

The DCA of chironomid assemblages showed gradient lengths of 1.274 and 0.954 SD for axes 1 and 2, respectively, whereas for the Cladocera the gradient lengths were 0.843 and 0.505 SD suggesting the use of linear methods in further analyses, such as PCA. The chironomid PCA axis 1 showed correlation to the Cladocera PCA axis 1 ($r = 0.61$, $r^2 = 0.37$, $p = 0.001$) and a similar correlation was observed also between the PCA axes 2 ($r = 0.54$, $r^2 = 0.30$, $p = 0.005$). PCA axis 1 and 2 scores for chironomids and Cladocera are illustrated in Fig. 5.

The rarefied Shannon index showed a generally decreasing trend for the chironomids (Fig. 3). For the Cladocera, the diversity remained relatively stable, with the exception of the period between ~1900 and 1950AD when it was markedly lower (Fig. 4). A common faunal break point with decreasing diversity was detected at ~1930s (between 6 and 7 cm) coinciding with the onset of the present climate warming (Fig. 6).

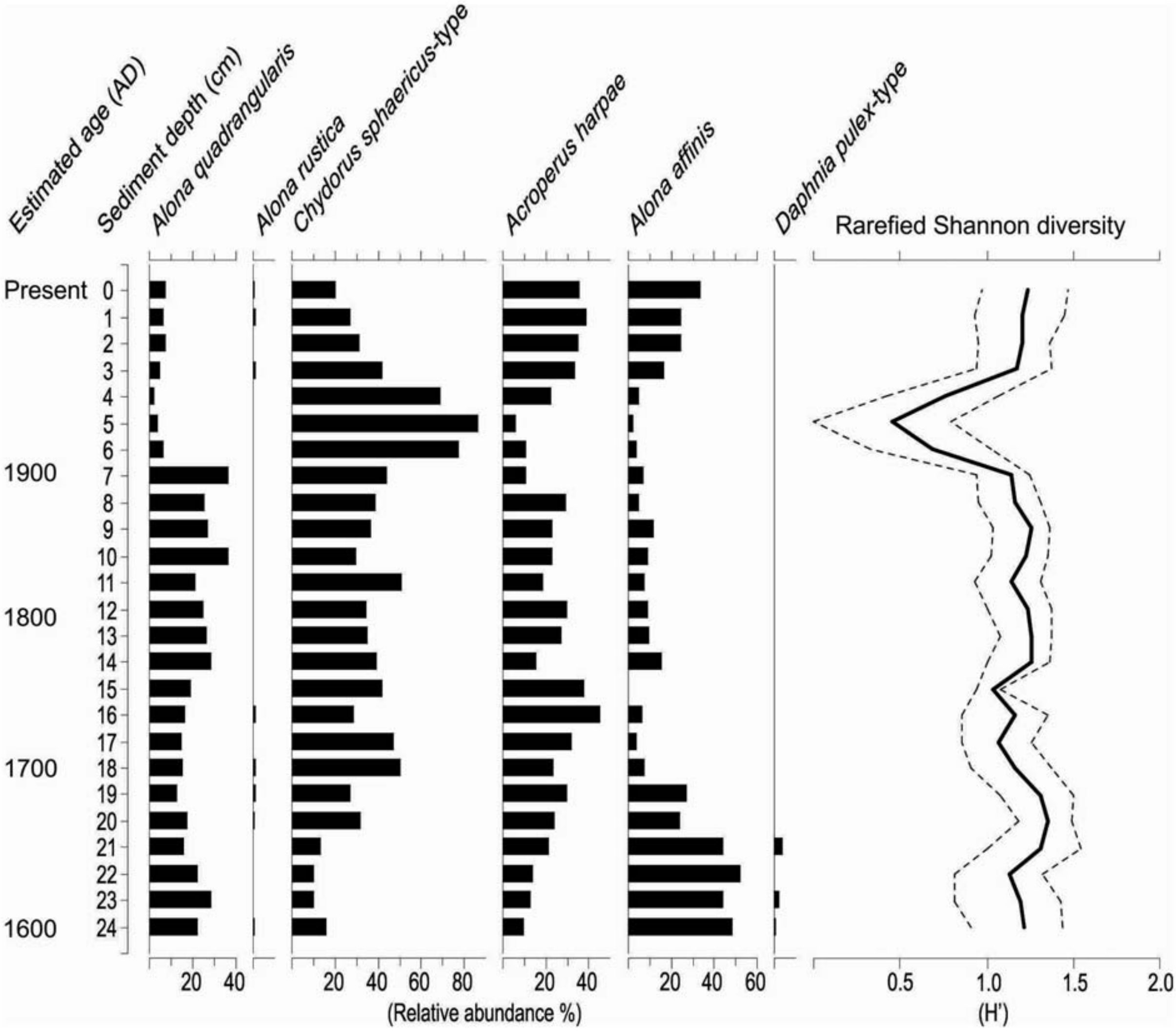

Fig. 4. Relative abundances of Cladocera taxa and rarefied Shannon index in the sediment core from Lake Moaralmsee in the Niedere Tauern Alps, Austria.

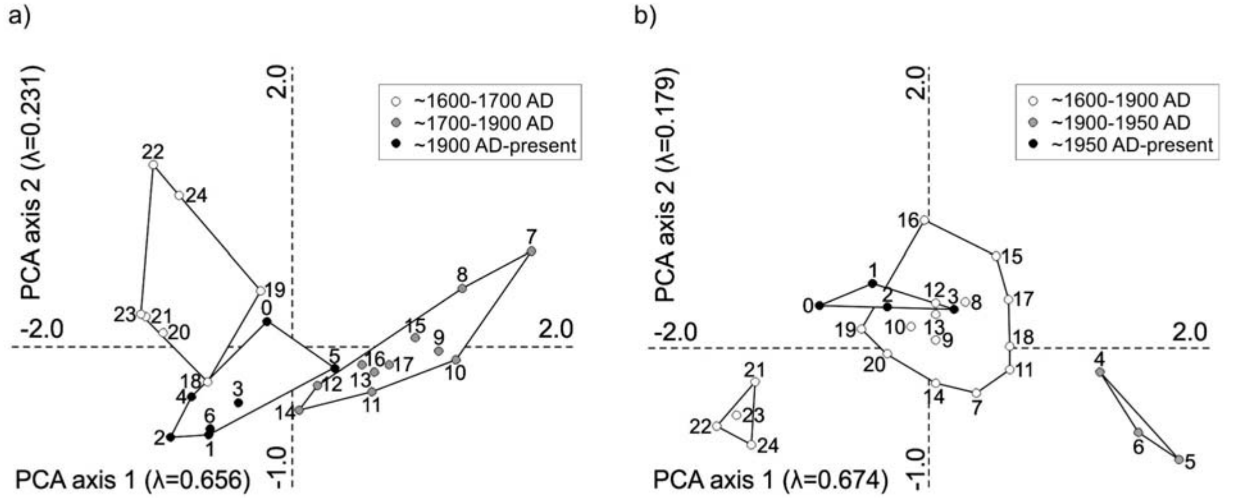

Fig. 5. PCA biplots of species and samples for the chironomid **(a)** and Cladocera **(b)** assemblages in Lake Moaralmsee in the Niedere Tauern Alps, Austria.

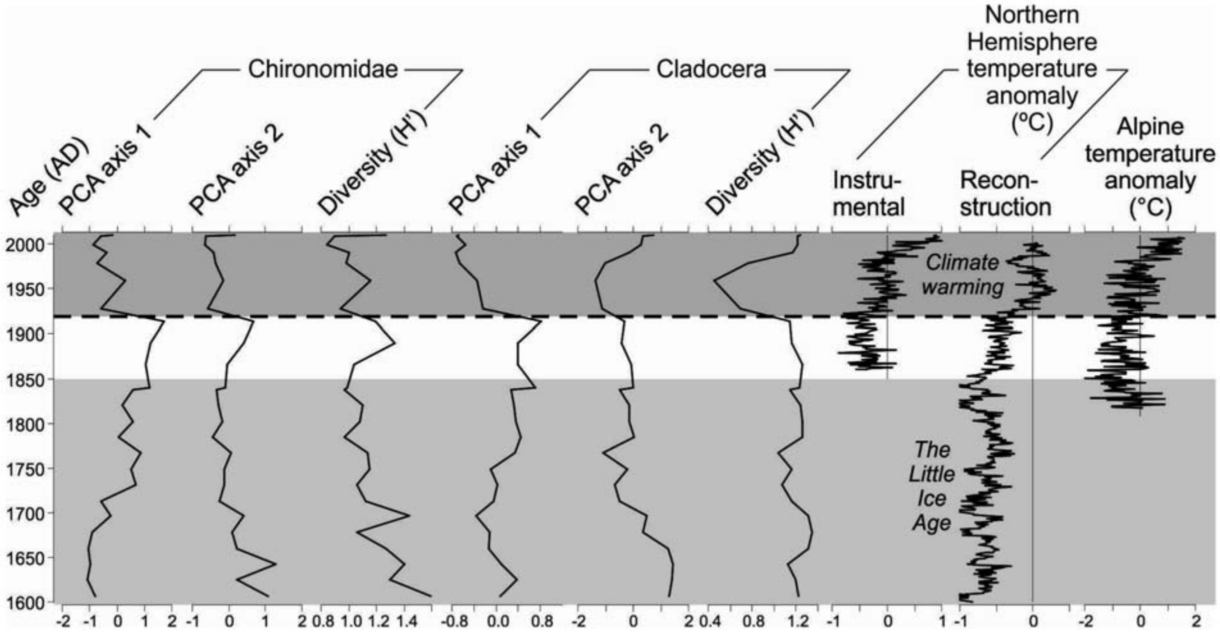

Fig. 6. PCA scores and diversity of Chironomidae and Cladocera in Lake Moaralmsee in the Niedere Tauern Alps in relation to annual temperature dynamics. The annual temperature reconstruction for Northern Hemisphere based on tree-ring data and Regional Curve Standardization (RCS) methodology (D'Arrigo et al. 2006), the Northern Hemisphere land-only instrumental temperature data (D'Arrigo et al. 2006) and the Alpine temperature data (Auer et al. 2007) are plotted as anomalies from 1961–1990AD mean. The gray bands indicate the periods of the Little Ice Age (prior 1850AD) and the recent climate warming. The dashed horizontal line corresponds to the mutual brake point in Chironomidae and Cladocera assemblages.

Discussion

Invertebrate communities between ~1600 and 1900AD

Interpretations of the stratigraphy of Lake Moaralmsee are hampered by the fact that the core is reliably dated only down to 10 cm, representing a timing of ~1850AD, while the chronology of the lower part of the core is established through extrapolation from the chronology of the upper part of the core. Therefore any dates estimated prior ~1850AD should be interpreted with extreme caution. However, for the purposes of our study, we are most interested in faunal changes post-1850, for which we have a relatively reliable chronology. There is also variability in the ^{210}Pb activity in the upper section of the core that deviates from the exponential decay curve, focused particularly on the sample at 4 cm (Fig. 2a) that may indicate disturbance in the sedimentation.

The early part of the sediment profile in Lake Moaralmsee between ~1600 and 1700AD was dominated by the chironomid *Tanytarsus lugens*-type and also the typical Alpine taxa *Psectrocladius sordidellus*-type, *Paratanytarsus austriacus*-type, and *Procladius* (Lotter et al. 1997) were common (Fig. 3). At ~1600AD, the cold and oligotrophic taxon *Micropsectra contracta*-type (Lotter et al. 1997, 1998) was one of the most abundant taxa, but disappeared quickly from the stratigraphy. In contrast, *Paracladius*, which has similar ecological preferences (Walker et al. 1991), began to increase its abundance towards ~1700AD. The chironomid diversity was at its highest between ~1600 and 1700AD (Fig. 3) indicating suitable habitat availability for these taxa, including vegetated and soft sediment environments (Brooks et al. 2007). For Cladocera, the early assemblages were dominated by the oligotrophic chydorid *Alona affinis* (Lotter et al. 1998) and also *A. quadrangularis, Chydorus sphaericus*-type, and *Acroperus harpae* were common (Fig. 4). These taxa are typical fauna in Alpine lakes situated at an altitude of ~2000 m a.s.l. (Bigler et al. 2006). The only planktonic Cladocera taxon found from Lake Moaralmsee was *Daphnia pulex*-type, which occurred only in the bottom of the sediment profile with low abundance, and it was extirpated before ~1700AD. Based on the ordination analyses, the Cladocera in particular had unique assemblages in the lowermost part of the core (Fig. 5), most likely coinciding with the lowest human impact on the aquatic ecosystem and the timing of the cold Little Ice Age (Grove 2004). The diversity of Cladocera was low throughout the core, as only six species were found, of which two were very rare. The low number of Cladocera taxa is typical for high altitude and latitude sites (Brancelj et al. 2009). Nevalainen (2012) found only the same six taxa from the surface sediment dataset of 20 samples representing the present fauna of Lake Moaralmsee.

At the mid-part of the sediment profile, between ~1700 and 1900AD, *Paracladius* greatly increased its abundance and became the most abundant chironomid taxon at the end of the 19th century replacing *T. lugens*-type. Both of these taxa are associated with cold and oligotrophic lakes in the Alps (Lotter et al. 1997, Lotter et al. 1998), but in the modern samples of Lake Moaralmsee *Paracladopelma* prefers shallow and intermediate water depths whereas *T. lugens* is restricted to the profundal area (Luoto 2012). This implies that a habitat change occurred in the lake at that time that could have been related to a decrease in lake level. However, in Yukon, Canada, *Paracladius* have been found to prefer the profundal zone (Engels & Cwynar 2011) making the lake level interpretation uncertain. In addition to *Paracladius*, *Heterotrissocladius marcidus*-type increased its abundance towards 1900AD, while *P. sordidellus*-type and *Procladius* became rare. *H. marcidus*-type is an oligo-mesotrophic taxon (Saether 1979, Raunio et al. 2010), whereas *P. sordidellus*-type is associated with aquatic vegetation (Tolonen et al. 2001, Luoto 2010) and *Procladius* with increased nutrient conditions (Brooks et al. 2001, Luoto 2011). These facts suggest that there was no increase in the influence of alpine land-use ('Almwirtschaft') at the time and submerged vegetation probably remained reduced.

For chironomids, the diversity between ~1700 and 1900AD generally decreased from the level found in the early part of the core. The Cladocera assemblages between ~1700 and 1900AD were characterized by increases in the abundances of *C. sphaericus*-type and *A. harpae* and a decrease in *A. affinis*, which lost its position as the dominant taxon. In contrast to the chironomid-based evidence, these changes may reflect increased nutrient conditions, because the total phosphorus optimum for *C. sphaericus* in the Alps has been shown to be higher than for the other taxa (Lotter et al. 1998). Also elsewhere in Europe, *C. sphaericus* has been found to be associated with nutrient-rich environments, although it is also present in oligotrophic waters (Brodersen et al. 1998, Chen et al. 2010, Nevalainen & Luoto 2010). However, due to its ubiquitous nature and plurality (Frey 1980) the indicator value of *C. sphaericus* remains ambiguous and its ability to colonize open water (de Eyto & Irvine 2001) may suggest that it was only exploiting an available niche.

Invertebrate communities from ~1900AD until the present

A common boundary was found for the chironomid and Cladocera communities at ~1900AD (between the samples at 6 and 7 cm) (Fig. 6). It is apparent that an ecological threshold was crossed at this time that was reflected in the chironomids as there was a decrease in *Paracladius* and *H. marcidus*-type and an increase in *Procladius* and *T. lugens*-type, which returned as the dominating taxon. The success of *T. lugens*-type and *Procladius* may be related to an elevated lake level because these taxa are known to live in the profundal (Tátosová & Stuchlík 2006, Brooks et al. 2007) and they also have elevated modern water depth optima in Lake Moaralmsee (Luoto 2012). In fact, Koinig et al. (2002) showed raised precipitation for the Tyrolian Alps since ~1900AD. Another explanation is that the changes during the last ~100 years were related to increased temperatures because *Procladius* is a warm indicator (Brooks & Birks 2001, Ilyashuk et al. 2011). *T. lugens*-type conversely has a broader distribution along the temperature gradient in the Alps (Lotter et al. 1997, Bigler et al. 2006) making its climate relations in the present core more difficult to interpret. In addition to increased lake level and climate warming, *Procladius* is known to thrive in lakes with elevated trophic status (Luoto 2011). This would also explain the negative correlation between the relative abundances of *Procladius* and *Paracladius,* since *Paracladius* has been found to have a strong association with very low DOC levels in the Alps (Bigler et al. 2006). Therefore, it is possible that the Alpine pasturing spread to the catchment of the lake at this time as the climate became more favourable. However, the fertilizing effect of possible pastures must have been low because the size of the catchment suitable for pasturing is very small. Schmidt et al. (2002) showed that expansions in alpine land-use have been closely related to warming climate in the Niedere Tauern Alps from the late Bronze Age onwards (~3500 years ago). In lakes with catchments more suitable for pasturing than in Moaralmsee, this would mean that under the present climate warming the decoupled effects of increasing temperatures and nutrient input would lead to cascading effects on the ecosystems.

The effects of warming climate can be interpreted also from the extirpation of cold water *Sergentia coracina*-type (Brodin 1986) during the early 20th century and by the fact that warm-preferring *Zavrelimyia* (Ilyashuk et al. 2011) had its maximum abundances in the 21th century. According to regional temperature variability detected from homogenized instrumental time series since the mid-18th century (Böhm et al. 2001), the mean July air temperatures began to critically increase from ~1930AD onwards and since then temperatures have risen ~1.5 °C with the fastest increase occurring from the 1980s onwards (Fig. 6). Simultaneously with the increased temperatures, atmospheric pollution has increased in the Austrian Alps (Koinig et al. 2002, Schmidt et al. 2008) and this makes it more difficult to pinpoint the ultimate factor that has determined the species assemblages in Lake Moaralmsee. For example, *Procladius* is known to tolerate metal contamination and thrive in polluted lakes after decline of other species (Ilyashuk et al. 2003), hence, it remains to be ultimately shown whether the species responses were related to climatological or limnological factors. However, considering that Lake Moaralmsee is a relatively unspoilt lake (Thompson et al. 2005), we suggest that the changes in chironomid communities have been driven by climatic factors.

For the Cladocera, the beginning of the 21st century was characterized by a strong increase in *C. sphaericus*-type, which began to dominate, and decreases in all the other taxa. Based on the PCA, the chironomid samples of the 21st century were located between the samples estimated to be of age ~1600–1700AD and ~1700–1900AD and a similar pattern was also observed for the Cladocera samples between ~1950AD and present (Fig. 5). However, the Cladocera samples between ~1900 and 1950AD showed clearly dissimilar community composition based on the first PCA axis (Fig. 6) due to the dominance by *C. sphaericus*-type. After ~1950AD, the dominant *C. sphaericus* decreased, while species often associated with macrophytes, such as *A. harpae, A. affinis*, and *A. quadrangularis* (Whiteside et al. 1978), increased suggesting increased nutrient conditions. However, it is also possible that the longer growing season caused the increased macrophyte coverage. Koinig et al. (2002) observed that overall changes in relative Cladocera assemblages occurred independently of temperature dynamics in another Austrian alpine lake. Therefore, it is again possible that the Cladocera fauna in Lake Moaralmsee also responded to non-climatic factors, such as lake productivity, atmospheric pollution, or even food web changes (e.g. Goulden 1971, Manca & Armiraglio 2002, Nevalainen et al. 2011). However, Bigler et al. (2006) showed from a Swiss Alpine data set of 30 lakes that *C. sphaericus* has total dominance in cold lakes situated above an altitude of 2500 m a.s.l., whereas the other taxa found from Lake Moaralmsee had lower altitudinal distributions, with the exception of *D. pulex*-type. Therefore, it is very likely that the faunal changes in Lake Moaralmsee since the ~1950s onwards were driven by the present climate warming. Bigler et al. (2006) also showed a clear relationship between *C. sphaericus*-type and low DOC, whereas Lotter et al. (1998) showed that *C. sphaericus*-type had high trophic optimum in Swiss Alpine lakes compared to the other taxa found from Lake Moaralmsee emphasizing the problematic relationship between the effects of temperature and lake productivity in Alpine lakes. However, it is more than likely that both of these factors, although having a strong correlation, also have independent effects on the aquatic fauna.

The diversity of chironomids further decreased during the last century with the lowest average *H'* in the stratigraphy. Nyman et al. (2005) found that treeline ecotonal areas are sensitive for taxa richness. Therefore, it is possible that the number of chironomid taxa will increase in the future as the treeline approaches Lake Moaralmsee. In the present data, chironomid diversity clearly increased at the topmost sample representing modern times. The lowest diversity for the Cladocera was found between ~1900 and 1950AD where only four species were present, as both *D. pulex*-type and *A. rustica* were absent. However, the Cladoceran diversity again increased after ~1950AD following the reappearance of *A. rustica* in the community, although with a very low abundance. The increase in diversity following the warming climate is in agreement with the distribution results by Bigler et al. (2006) who showed that Cladocera diversity of cold lakes was very low and it increased towards mid-altitudes and warmer climate conditions.

Nevalainen (2012) showed from the surface sediment assemblages that the modern distribution of Cladocera within Lake Moaralmsee is heterogeneous and demonstrated clear niche separation of the taxa and ecological thresholds dependent on water depth. A similar depth-dependency was also observed with the modern chironomid fauna (Luoto 2012). The regional winter precipitation is relatively high (Koinig et al. 2002) corresponding with the observed high modern lake level in Moaralmsee that may be a result of the recent enhanced climate warming that is reflected as an increased snow patch melt from the catchment (cf. Beniston 1997) and consequently causing higher water table. During the time of sampling, there were still small snow patches in the lake's catchment and it is possible that prior to most recent decades, snow patches have covered a wider area of the catchment of the lake and thus constrained water inflow. Various factors are related to water depth, such as macrophyte distribution, substrate type, and inlake limnological and temperature gradients that influence the distribution and abundance of these invertebrate taxa (Whiteside & Harmsworth 1967, Rautio 1998, Brodersen et al. 2001, Tolonen et al. 2001, Tolonen et al. 2003, Nevalainen 2011). Furthermore, the effects of UV-radiation vary across the lake bottom, as less radiation enters the deepest parts of the basin (Rose et al. 2009). Transparent Alpine lakes, such as Moaralmsee, are particularly susceptible to UV-exposure (Sommaruga 2001), which has been increasing since the prolonged sunspot minimum (Maunder Minimum) between 1645 and 1715AD (Eddy 1976). Cladocera in particular are known to be sensitive to UV-radiation (Rautio & Korhola 2002), and it is likely that in addition to planktonic taxa, such as *Daphnia*, the benthic species living in the littoral areas, such as *A. quadrangularis* (Nevalainen 2012), are in greater danger from increased radiation than those preferring deeper waters, such as *A. affinis*.

Due to the ecological and limnological sensitivity of Lake Moaralmsee, anthropogenic warming and increasing land-use will further test its ecological resilience and potentially induce more dramatic shifts in community composition in the future. When thresholds are crossed, community composition turnover will become high and pronounced and regime shifts towards new ecological states will likely occur. Similar to arctic lakes (Smol et al. 2005, Luoto et al. 2011), the shifts in communities are characterized by taxonomically diverse and increasingly productive systems.

Conclusions

Our results showed that clear shifts in aquatic communities of Lake Moaralmsee have occurred with the most prominent change at ~1930s. This time period also marks the onset of the present climate warming and thus, we suggest that the aquatic ecosystem was most disturbed at the initial phase of the warming. However, it is likely that further ecological thresholds will be crossed in the future following the projected accelerated warming. The more recent effects of the present climate warming will probably cascade in the near future due to the disappearance of summertime snow patches, most likely leading to a new ecological state of the lake. This study shows that palaeoecological data from palaeolimnological archives can be used for long-term ecological assessments of aquatic systems in conservation, preservation, and biodiversity projects.

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References

Adrian, R., O'Reilly, C. M., Zagarese, H., Baines, S. B., Hessen, D. O., Keller, W., Livingstone, D. M., Sommaruga, R., Straile, D., Van Donk, E., Weyhenmeyer, G. A. & Winder, N., 2009: Lakes as sentinels of climate change. – Limnol. Oceanogr. **54**: 2283–2297.

Appleby, P. G., 2001: Chronostratigraphic techniques in recent sediments. – In: Last, W. M. & Smol: J. P. (eds): Tracking environmental changes using lake sediments. Volume 1: Basin analysis, coring, and chronological techniques. – Kluwer Academic Publishers, Dordrecht, pp 171–203.

Auer, I., Böhm, R., Jurkovic, A., Lipa, W., Orlik, A., Potzmann, R., Schöner, W., Ungersböck, M., Matulla, C., Briffa, K., Jones, P. D., Efthymiadis, D., Brunetti, M., Nanni, T., Maugeri, M., Mercalli, L., Mestre, O., Moisselin, J.-M., Begert, M., Müller-Westermeier, G., Kveton, V., Bochnicek, O., Stastny, P., Lapin, M., Szalai, S., Szentimrey, T., Cegnar, T., Dolinar, M., Gajic-Capka, M., Zaninovic, K., Majstorovic, Z. & Nieplova, E., 2007: HISTALP – Historical instrumental climatological surface time series of the greater Alpine region 1760–2003. – Int. J. Climatol. **27**: 17–46

Beniston, M., 1997: Variations of snow depth and duration in the Swiss Alps over the last 50 years: Links to changes in large-scale climatic forcings. – Clim. Change. **36**: 281–300.

Beniston, M., 2006: Mountain weather and climate: a general overview and a focus on climatic changes in the Alps. – Hydrobiologia **562**: 3–16.

Bigler, C., Heiri, O., Krskova, R., Lotter, A. F. & Sturm, M., 2006: Distribution of diatoms, chironomids and cladocera in surface sediments of thirty mountain lakes in south-eastern Switzerland. – Aquat. Sci. **68**: 154–171.

Böhm, R., Auer, I., Brunetti, M., Maugeri, M., Nanni, T. & Schöner, W., 2001: Regional temperature variability in the European Alps: 1760–1998 from homogenized instrumental time series. – Int. J. Climatol. **21**: 1779–1801.

Brancelj, A., Kernan, M., Jeppesen, E., Rautio, M., Manca, M., Šiško, M., Alonso, M. & Stuhlík, E., 2009: Cladocera remains from the sediments of remote cold lakes: a study of 294 lakes across Europe. – Adv. Limnol. **62**: 269–294.

Brodersen, K. P., Whiteside, M. C. & Lindegaard, C., 1998: Reconstruction of trophic state in Danish lakes using subfossil chydorid (Cladocera) assemblages. – Can. J. Fish. Aquat. Sci. **55**: 1093–1103.

Brodersen, K. P., Odgaard, B. V., Vestergaard, O. & Anderson, N. J., 2001: Chironomid stratigraphy in the shallow and eutrophic Lake Søbygaard, Denmark: chironomid-macrophyte co-occurrence. – Freshw. Biol. **46**: 253–267.

Brodin, Y. W., 1986: The postglacial history of Lake Flarken, southern Sweden, interpreted from fossil insect remains. – Int. Rev. ges. Hydrobiol. **71**: 371–432.

Brooks, S. J., Bennion, H. & Birks, H. J. B., 2001: Tracing lake trophic history with a chironomid-total phosphorus inference model. – Freshw. Biol. **46**: 513–533.

Brooks, S. J. & Birks, H. J. B., 2001: Chironomid-inferred air temperatures from Lateglacial and Holocene sites in north-west Europe: progress and problems. – Quat. Sci. Rev. **20**: 1723–1741.

Brooks, S. J., Langdon, P. G. & Heiri, O., 2007: The identification and use of Palaeoarctic Chironomidae larvae in palaeoecology. QRA Technical Guide No. 10. – Quaternary Research Association, London.

Chen, G., Dalton, C. & Taylor, D., 2010: Cladocera as indicators of trophic state in Irish lakes. – J. Paleolimnol. **44**: 465–481.

Cleveland, W. S. & Devlin, S. J., 1988: Locally-weighted regression: an approach to regression analysis by local fitting. – J. Am. Statist. Assoc. **83**: 596–610.

D'Arrigo, R., Wilson, R. & Jacoby, G., 2006: On the long-term context for late twentieth century warming. – J. Geophys. Res. **111**: D03103, DOI:10.1029/2005JD006352.

de Eyto, E. & Irvine, K., 2001: The response of three chydorid species to temperature, pH and food. – Hydrobiologia **459**: 165–172.

Eddy, J. A., 1976: The Maunder Minimum. – Science **192**: 1189–1202.

Engels, S. & Cwynar, L. C., 2011: Changes in fossil chironomid remains along a depth gradient: evidence for common faunal thresholds within lakes. – Hydrobiologia **665**: 15–38.

Flynn, W. W., 1968: The determination of low-levels of polonium-210 in environmental materials. – Analyt. Chim. Acta **43**: 221–227.

Frey, D. G., 1980: On the plurality of *Chydorus sphaericus* (O. F. Müller) (Cladocera, Chydoridae) and designation of a neotype from Sjaelsø, Denmark. – Hydrobiologia **69**: 83–123.

Gannon, J. E., 1971: Two counting cells for the enumeration of zooplankton micro-crustacea. – Transact. Am. Microscop. Soc. **90**: 486–490.

Gotelli, N. J. & Entsminger, G. L., 2011: EcoSim: Null models software for ecology. Version 7. – Acquired Intelligence Inc. & Kesey-Bear, Jericho, VT 05465

Goulden, C. E., 1971: Environmental control of the abundance and distribution of the chydorid Cladocera. – Limnol. Oceanogr. **16**: 320–331.

Grove, J. M., 2004: Little Ice Ages: Ancient and Modern. – Routledge, London.

Hausmann, S., Lotter, A. F., van Leeuwen, J. F. N., Ohlendorf, C., Lemcke, G., Grönlund, E. & Sturm, M., 2002: Interactions of climate and land use documented in the varved sediments of Seebergsee in the Swiss Alps. – Holocene **12**: 279–289.

Heegaard, E., Lotter, A. F. & Birks, H. J. B., 2006: Aquatic biota and the detection of climate change: are there consistent aquatic ecotones? – J. Paleolimnol. **35**: 507–518.

Heino, J., Virkkala, R. & Toivonen, H., 2009: Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. – Biol. Rev. **84**: 39–54.

Heiri, O. & Lotter, A. F., 2003: Alpine lake: long-term trends, sensitivity to disturbance, and resilience of fauna. – J. Paleolimnol. **30**: 273–289.

Heiri, O. & Lotter, A. F., 2005: Holocene and Lateglacial summer temperature reconstruction in the Swiss Alps based on fossil assemblages of aquatic organisms: a review. – Boreas **34**: 506–516.

Helama, S., Nielsen, J. K. & Valovirta, I., 2007: Conchology of endangered freshwater pearl mussel: conservation palaeobiology applied to museum shells originating from northern Finland. – Bollettino Malacologico **43**: 161–170.

Ilyashuk, B., Ilyashuk, E. & Dauvalter, V., 2003: Chironomid responses to long-term metal contamination: a paleolimnological study in two bays of Lake Imandra, Kola Peninsula, northern Russia. – J. Paleolimnol. **30**: 217–230.

Ilyashuk, E. A., Koinig, K. A., Heiri, O., Ilyashuk, B. P. & Psenner, R., 2011: Holocene temperature variations at a high-altitude site in the eastern Alps: a chironomid record from Schwarzsee ob Sölden, Austria. – Quat. Sci. Rev. **30**: 176–191.

Jeppesen, E., Noges, P., Davidson, T. A., Haberman, J., Noges, T., Blank, K., Lauridsen, T. L., Søndergaard, M., Sayer, C., Laugaste, R., Johansson, L. S., Bjerring, R. & Amsinck, S. L., 2011: Zooplankton as indicators in lakes: a scientific-based plea for including zooplankton in the ecological quality assessment of lakes according to the European Water Framework Directive (WFD). – Hydrobiologia **676**: 279–297.

Koinig, K. A., Kamenik, C., Schmidt, R., Augusti-Panareda, A., Appleby, P., Lami, A., Prazakova, M., Rose, N., Schnell, Ø. A., Tessadri, R., Thompson, R. & Psenner, R., 2002: Environmental changes in an alpine lake (Gossenköllesee, Austria) over the last two centuries – the influence of air temperature on biological parameters. – J. Paleolimnol. **28**: 147–160.

Kurek, J., Korosi, J. B., Jeziorski, A. & Smol, J. P., 2010: Establishing reliable minimum count sizes for cladoceran subfossils sampled from lake sediments. – J. Paleolimnol. **44**: 603–612.

Livingstone, D. M., 1997: Break-up dates of alpine lakes as proxy data for local and regional mean surface air temperatures. – Clim. Change **37**: 407–439.

Lotter, A. F., Birks, H. J. B., Hofmann, W. & Marchetto, A., 1997: Modern diatom, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. – J. Paleolimnol. **18**: 395–420.

Lotter, A. F., Birks, H. J. B., Hofmann, W. & Marchetto, A., 1998: Modern diatom, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. – J. Paleolimnol. **19**: 443–463.

Luoto, T. P., 2010: Hydrological change in lakes inferred from midge assemblages through use of an intralake calibration set. – Ecol. Monogr. **80**: 303–329.

Luoto, T. P., 2011: The relationship between water quality and chironomid distribution in Finland – a new assemblage-based tool for assessments of long-term nutrient dynamics. – Ecol. Indic. **11**: 255–262.

Luoto, T. P., 2012: Intra-lake patterns of aquatic insect and mite remains. – J. Paleolimnol. **47**: 141–157.

Luoto, T. P., Nevalainen, L., Kubischta, F., Kultti, S., Knudsen, K. L. & Salonen, V.-P., 2011: Late Quaternary ecological turnover in High Arctic Lake Einstaken, Nordaustlandet, Svalbard (80° N). – Geografiska Annaler A **93**: 337–354.

Luoto, T. P. & Raunio, J., 2011: A comparison of chironomid-based total phosphorus training sets developed from contemporary pupal exuviae and sedimentary larval head capsules to infer lake trophic history. – Fundam. Appl. Limnol. **179**: 93–102.

Manca, M. & Armiraglio, M., 2002: Zooplankton of 15 lakes in the Southern Central Alps: comparison of recent and past (pre-ca 1850AD) communities. – J. Limnol. **61**: 225–231.

McCarty, J. P., 2001: Ecological consequences of recent climate change. – Conserv. Biol. **15**: 320–331.

Nevalainen, L., 2010: Evaluation of microcrustacean (Cladocera, Chydoridae) biodiversity based on sweep net and surface sediment samples. – Écoscience **17**: 356–364.

Nevalainen, L., 2011: Intra-lake heterogeneity of sedimentary cladoceran (Crustacea) assemblages forced by local hydrology. – Hydrobiologia **676**: 9–22.

Nevalainen, L., 2012: Distribution of benthic microcrustaceans along a water depth gradient in an Austrian Alpine lake – Sedimentary evidence for niche separation. – Limnologica **42**: 65–71.

Nevalainen, L. & Luoto, T. P., 2010: Implications for the use of sedimentary invertebrate communities to infer past presence of fish. – Knowledge Manage. Aquat. Ecosyst. **396** (5): 1–13.

Nevalainen, L., Luoto, T. P., Levine, S. & Manca, M., 2011: Modern and pre-Industrial Age distributions of Cladocera in Italian and Swiss Alpine lakes. – Hydrobiologia **676**: 173–185.

Nyman, M., Korhola, A. & Brooks, S. J., 2005: The distribution and diversity of Chironomidae (Insecta: Diptera) in western Finnish Lapland, with special emphasis on shallow lakes. – Glob. Ecol. Biogeogr. **14**: 137–153.

Oliver, D. R., 1971: Life history of Chironomidae. – Annu. Rev. Entomol. **16**: 211–230.

Psenner, R. & Schmidt, R., 1992: Climate-driven pH control of remote alpine lakes and effects of acid deposition. – Nature **356**: 781–783.

Quinlan, R. & Smol, J. P., 2001: Setting minimum head capsule abundance and taxa deletion criteria in chironomid-based inference models. – J. Paleolimnol. **26**: 327–342.

Raunio, J., Paasivirta, L. & Hämäläinen, H., 2010: Assessing lake trophic status using spring-emerging chironomid pupal exuvia. – Fundam. Appl. Limnol. **176**: 61–73.

Raunio, J., Heino, J. & Paasivirta, L., 2011: Non-biting midges in biodiversity conservation and environmental assessment: Findings from boreal freshwater ecosystems. – Ecol. Indic. **11**: 1057–1064.

Rautio, M., 1998: Community structure of crustacean zooplankton in subarctic ponds – effects of altitude and physical heterogeneity. – Ecography **21**: 327–335.

Rautio, M. & Korhola, A., 2002: Effects of ultraviolet radiation and dissolved organic carbon on the survival of subarctic zooplankton. – Polar Biol. **5**: 460–468.

Rose, K. C., Williamson, C. E., Saros, J. E., Sommaruga, R. & Fischer, J., 2009: Differences in UV transparency and thermal structure between alpine and subalpine lakes: implications for organisms. – Photochem. Photobiol. Sci. **8**: 1244–1256.

Saether, O. A., 1979: Chironomid communities as water quality indicators. – Holarctic Ecology **2**: 65–74.

Saros, J. E., 2009: Integrating neo- and paleolimnological approaches to refine interpretations of environmental change. – J. Paleolimnol. **41**: 243–252.

Sayer, C. D., Roberts, N., Sadler, J., David, C. & Wade, P. M., 1999: Biodiversity changes in a shallow lake ecosystem: a multi-proxy palaeolimnological analysis. – J. Biogeogr. **26**: 97–114.

Sayer, C. D., Davidson, T. A., Jones, J. I. & Langdon, P. G., 2010: Combining contemporary ecology and paleolimnology to understand shallow lake ecosystem change. – Freshw. Biol. **55**: 487–499.

Schmidt, R., Koinig, K. A., Thompson, R. & Kamenik, C., 2002: A multiproxy core study of the last 7000 years of climate and alpine land-use impacts on an Austrian mountain lake (Unterer Landschitzsee, Niedere Tauern). – Palaeogeogr. Palaeoclimatol. Palaeoecol. **187**: 101–120.

Schmidt, R., Roth, M., Tessadri, R. & Weckström, K., 2008: Disentangling late-Holocene climate and land use impacts on an Austrian Alpine lake using seasonal temperature anomalies, ice-cover, sedimentology, and pollen tracers. – J. Paleolimnol. **40**: 453–469.

Shannon, C. E., 1948: A mathematical theory of communication. – Bell System Techn. J. **27**: 379–423, 623–656.

Skjelkvale, B. L. & Wright, R. F., 1998: Mountain lakes: Sensitivity to acid deposition and global change. – Ambio **27**: 280–286.

Smol, J. P., 1990: Are we building enough bridges between paleolimnology and aquatic ecology? – Hydrobiologia **214**: 201–206.

Smol, J. P., 1992: Paleolimnology: an important tool for effective ecosystem management. – J. Aquat. Ecosyst. Health **1**: 49–58.

Smol, J. P., 2008: Pollution of lakes and rivers: a paleoenvironmental perspective, 2nd ed. – Blackwell Pub, Malden, MA.

Smol, J. P. & Douglas, M. S. V., 2007: Crossing the final ecological threshold in high Arctic ponds. – Proc. Natl. Acad. Sci. U.S.A. **104**: 12395–12397.

Smol, J. P., Wolfe, A. P., Birks, H. J. B., Douglas, M. S. V., Jones, V. J., Korhola, A., Pienitz, R., Rühland, K., Sorvari, S., Antoniades, D., Brooks, S. J., Fallu, M.-A., Hughes, M., Bronwyn, E. K., Laing, T. E., Michelutti, N., Nazarova, N., Nyman, M., Paterson, A. M., Perren, P., Quinlan, R., Rautio, M., Saulnier-Talbot, E., Siitonen, S., Solovieva, N. & Weckström, J., 2005: Climate-driven regime shifts in the biological communities of arctic lakes. – Proc. Natl. Acad. Sci. U.S.A. **102**: 4397–4402.

Sommaruga, R., 2001: The role of solar UV radiation in the ecology of alpine lakes. – J. Photochem. Photobiol. B: Biol. **62**: 35–42.

Sommaruga-Wögrath, S., Koinig, K., Schmidt, R., Sommaruga, R., Tessadri, R. & Psenner, R., 1997: Temperature effects of the acidity of remote alpine lakes. – Nature **387**: 64–67.

Szeroczyńska, K. & Sarmaja-Korjonen, K., 2007: Atlas of Subfossil Cladocera from Central and Northern Europe. – Friends of the Lower Vistula Society, Świecie, Poland.

Tátosová, J. & Stuchlík, E., 2006: Seasonal dynamics of chironomids in the profundal zone of a mountain lake (Ľadové pleso, the Tatra Mountains, Slovakia). – Biologia, Bratislava **61**: 203–212.

Submitted: 18 April 2012; accepted: 20 August 2012.

ter Braak, C. J. F. & Šmilauer, P., 2002: CANOCO Reference Manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (Version 4.5). – Microcomputer Power, Ithica.

Thompson, R., Kamenik, C. & Schmidt, R., 2005: Ultrasensitive Alpine lakes and climate change. – J. Limnol. **64**: 139–152.

Tolonen, K. T., Hämäläinen, H., Holopainen, I. J. & Karjalainen, J., 2001: Influences of habitat type and environmental variables on littoral macroinvertebrate communities in a large lake system. – Arch. Hydrobiol. **152**: 39–67.

Tolonen, K. T., Hämäläinen, H., Holopainen, I. J., Mikkonen, K. & Karjalainen, J., 2003: Body size and substrate associations of littoral insects in relation to vegetation structure. – Hydrobiologia **499**: 179–190.

Tolonen, K. T., Holopainen, I. J., Hämäläinen, H., Rahkola-Sorsa, M., Ylöstalo, P., Mikkonen, K. & Karjalainen, J., 2005: Littoral species diversity and biomass: concordance among organismal groups and the effects of environmental variables. – Biodivers. Conserv. **14**: 961–980.

von Gunten, L., Heiri, O., Bigler, C., van Leeuwen, J., Casty, C., Lotter, A. F. & Sturm, M., 2008: Seasonal temperatures for the past ~400 years reconstructed from diatom and chironomid assemblages in a high-altitude lake (Lej da la Tscheppa, Switzerland). – J. Paleolimnol. **39**: 283–299.

Walker, I. R., Smol, J. P., Engström, D. R. & Birks, H. J. B., 1991: An assessment of Chironomidae as quantitative indicators of past climatic change. – Can. J. Fish. Aquat. Sci. **48**: 975–987.

Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O. & Bairlein, F., 2002: Ecological responses to recent climate change. – Nature **416**: 389–394.

Whiteside, M. C. & Harmsworth, R. V., 1967: Species diversity in chydorid (Cladocera) communities. – Ecology **48**: 664–667.

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.

Wiederholm, T. (ed.), 1983: Chironomidae of the Holarctic region: keys and diagnoses. Part 1. Larvae. – Entomol. Scand. Suppl. **19**. Borgströms Tryckeri AB, Motala, Sweden.

Willis, K. J. & Birks, H. J. B., 2006: What is natural? The need for a long term perspective in biodiversity conservation. – Science **314**: 1261–1265.