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ORIGINAL PAPER

Faunal (Chironomidae, Cladocera) responses to post-Little Ice Age climate warming in the high Austrian Alps

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Abstract Present climate warming strongly affects limnological and ecological properties of lakes and may cause regime shifts that alter structure and function in the water bodies. Such effects are especially pronounced in climatologically extreme areas, e.g. at high altitudes. We examined a sediment core from Lake Oberer Landschitzsee, Austrian Alps, which spans the period from the Little Ice Age (LIA) to present. We investigated whether post-LIA climate warming altered aquatic invertebrate communities and limnological status in this sensitive high Alpine lake. Fossil Cladocera (Crustacea) and Chironomidae (Diptera) and organic matter in the core were analyzed. Chironomids were used to assess the lake's benthic quality (i.e. oxygen availability). An instrumental Alpine temperature record was used to assess whether changes in the biotic assemblages correspond to post-LIA temperature trends. The planktonic and macro- and microbenthic invertebrate communities exhibit almost complete and simultaneous species turnover after the LIA, from about AD 1850 onward, when *Sergentia coracina*-type replaced oxyphilous *Micropsectra contracta*-type as the dominant macrobenthic taxon, and phytophilous *Acroperus harpae* outcompeted *Alona affinis* and *Alona quadrangularis* in the microbenthos. These directional community shifts corresponded with a period of reduced benthic quality, higher sediment organic content, and progressive climate warming, superimposed on Alpine land-use changes, until the early twentieth century. Detected changes suggest increased productivity and lower benthic oxygen availability. Faunal shifts were even more pronounced during the late twentieth century, simultaneous with enhanced warming. A new planktonic Cladocera species, *Bosmina longirostris*, typically absent from high Alpine lakes, colonized the lake and gradually became dominant toward the core top. Results show that post-LIA climate warming, coupled with increasing benthic and planktonic production, substantially altered the limnological and ecological status of this remote Alpine lake. Observed faunal turnovers provide evidence that temperature-driven ecological thresholds, whether associated directly or indirectly with greater human activity, have been crossed. Species abundances and distributions have changed in response to post-LIA and late twentieth century climate warming.

Keywords Alps · Aquatic invertebrates · Benthic quality · Climate change · Land use

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Introduction

Current climate warming is hypothesized to affect lake ecosystems in a manner comparable to that of eutrophication (Schindler 2001). In particular, climate warming is known to enhance biogeochemical processes, alter limnological ranges and habitats, and consequently restructure aquatic communities (Adrian et al. 2009; Schindler 2009). Both anthropogenic phenomena, current climate warming and nutrient enrichment, can be considered recent on a Quaternary timescale (Brönmark and Hansson 2002). Because long-term documentation of natural phenomena is limited, paleolimnological sediment archives (physical, chemical, and biological variables) can be used to detect linkages between climate and limnological and ecological processes. Current climate warming is known to be increasing nutrient input to lakes, forcing limnological and ecological perturbations that can result in ecosystem regime shifts (Jeppesen et al. 2009), but the long-term relationship between climate and productivity is complicated and often lake-specific. Some paleolimnological studies have demonstrated that a positive relationship exists between temperature and nutrients (Heiri and Lotter 2005; Schmidt et al. 2008), but others have found a negative correlation (Kirilova et al. 2009; Luoto et al. 2009). Reported overall effects of climate warming on sensitive lake ecosystems include, for example, increased nutrient availability and productivity, and intensified thermal stratification, which is primarily a consequence of changes in extent of ice and snow cover (Smol and Douglas 2007). Linkages between temperature and limnological variables, however, are complex and generally dependent on factors such as geographic and climatological context (Eggermont and Heiri 2012).

Lakes in the European Alps display a broad environmental gradient in climate and limnological conditions (Lotter et al. 1997, 1998) and are inhabited by unique aquatic invertebrate communities across these gradients (Lotter et al. 1997, 1998; Kamenik et al. 2007; Nevalainen et al. 2011). Warm lowland lakes often have high nutrient status and cold, high-altitude lakes are generally more oligotrophic (Heiri and Lotter 2005). Because long-term observational records on lake properties do not extend far back in time, sediment archives have been used to track long-term limnological and climatological trends in Alpine lakes. Paleolimnological investigations from high-altitude lakes in the Alps have suggested that late Holocene periods of climate amelioration, for example the Medieval Climate Anomaly (MCA), resulted in increased productivity (Schmidt et al. 2002, 2007, 2008), although opposite development has been described in some parts of the Alps (Hausmann et al. 2002). Coupling between climate and in-lake production is closely related to Alpine land-use, which has intensified during favorable climate periods and declined during periods of climate cooling, such as the Little Ice Age (LIA). Post-LIA sediment records, driven partly by climate warming and superimposed accelerated anthropogenic activities, show that some Alpine lakes experienced dramatic limnological and ecological changes during the post-LIA period (Millet et al. 2009; Nevalainen et al. 2011).

In common with sensitive Arctic lakes and ponds (Smol et al. 2005; Smol and Douglas 2007), high Alpine lakes are also susceptible to cascading effects of climate warming. In central Europe, climate warming can be anticipated to influence most Alpine ecosystems situated on ecological boundaries (Holt and Keitt 2005; Parker et al. 2008), for instance small high-altitude lakes near the tree line. This study focuses on the recent ecosystem history (~300 years) of a sensitive, high Alpine lake located in an ecotonal zone, slightly above the present tree line. We set out to address whether post-LIA climate warming altered the limnological and ecological status of this sensitive lake. We inferred past faunal responses to post-LIA climate warming using subfossil Cladocera and Chironomidae communities from a sediment core taken in Lake Oberer Landschitzsee, Austrian Alps.

Study site

Lake Oberer Landschitzsee (47°14′52″N, 13°51′40″E) is located at an altitude of 2,076 m a.s.l. on the southern slope of the Niedere Tauern, Lungau, in the Eastern Austrian Alps (Fig. 1). It is the topmost basin of a chain of three lakes and its outflow drains through Mittlerer Landschitzsee to Unterer Landschitzsee. The basins are on crystalline bedrock with mica-shists and metamorphic carbonates, and topmost Lake Oberer Landschitzsee is located at an ecotone, slightly above the present tree line formed by *Pinus cembra*, but below the potential tree line. Maximum depth of the basin is 13.6 m and the lake area is 8.8 ha. The catchment topography is steep (Fig. 1) and consists mostly of rocky slopes and alpine meadows with grasses and scattered dwarf pines (*Pinus mugo*). Bottom deposits of the littoral zone are characterized by gravels, and there are no emergent aquatic macrophytes. Submerged watermilfoil (*Myriophyllum* sp.), however, was observed in the water. The lake is inhabited by two morphs of Arctic charr (*Salvelinus alpinus*); small-bodied "blackriders" are very numerous, whereas larger "wild-caught charrs" are less frequent. These fish originated from medieval, fifteenth and sixteenth century stocking, but since then no stocking has occurred. Currently, there are no active pastures in the catchment, but cattle were observed grazing at the highest point in the catchment of Lake Unterer Landschitzsee in summer 2010. Limnological variables were measured with a multiparameter sonde 6600V2 (YSI Inc., Yellow Springs, OH, USA). Measurements indicated that the lake is currently oligotrophic, well oxygenated, and does not exhibit strong summer stratification (Table 1). The lack of summer stratification implies that the lake has no hypolimnion in the strict sense.

The lake was chosen for study because it is a remote, head-water mountain basin, which is currently located around the tree line, and is therefore closely coupled with atmospheric forcing factors. A further motivation for selecting this particular study lake was that previous paleolimnological investigation (Schmidt et al. 2008) suggested there had been long-term interactions between regional climate and lake trophic status. The late Holocene record of climate and land-use impacts on the lake suggested that during warm climate periods, such as the MCA, productivity increased, along with prolonged stratification and deteriorated hypolimnetic oxygen conditions. The previous paleolimnological record provided evidence that the lake may respond sensitively to periods of climate warming.

Materials and methods

Sediment sampling and analyses

A short sediment core, without visible lithological changes, was collected with a Kajak gravity corer from a small boat in July 2010. The water depth at the sampling point was 10.5 m and the retrieved core was 16 cm long. The core was sliced in 1-cm-thick intervals in the field and sub-samples were stored in plastic bags at +4 °C in a cold room prior to analysis.

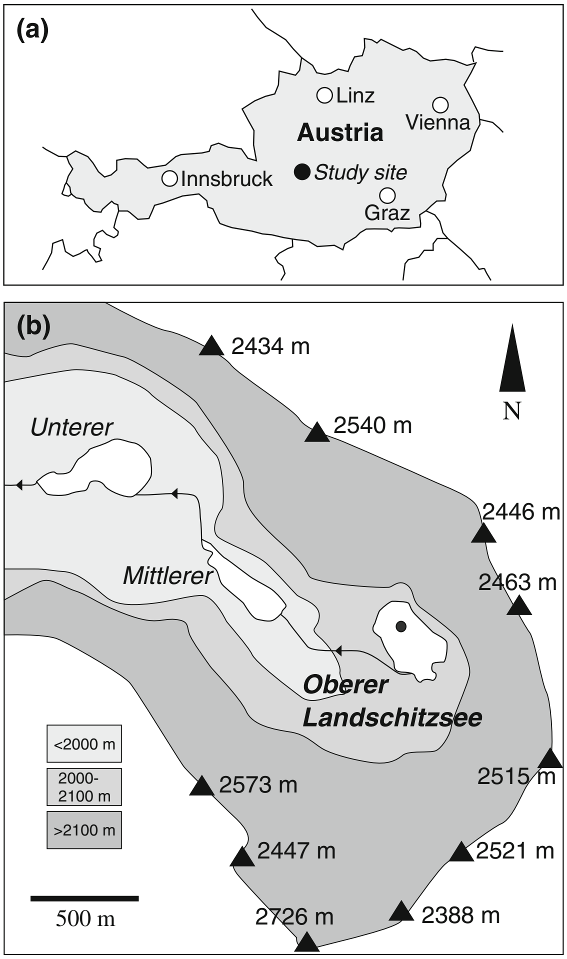


Fig. 1 Location of the study site in Austria (**a**) and adjacent topography of Lake Oberer Landschitzsee (**b**), where the sampling site is indicated with a *black circle* and mountain tops with *black triangles*

The sediment core was dated using the ^{210}Pb radiometric dating method in the Laboratory of Quaternary Geochronology, Institute of Geological Sciences, Polish Academy of Sciences in Warsaw, Poland. ^{210}Pb activity in the sediments was determined indirectly via alpha spectrometry, measuring the ^{210}Po ($\alpha = 5.31$ MeV, $T_{1/2} = 138$ d) activity (Flynn 1968). A known amount of ^{208}Po was added to the weighed sample as an internal yield tracer. Po was separated from the sample using strong hydrochloric and nitric acid and was deposited on silver disks (Flynn 1968). Activities of ^{210}Po and ^{208}Po were measured using an

Table 1 Limnological variables (August 2009): mean conductivity, total dissolved solids (TDS), pH, dissolved oxygen (DO), chlorophyll-*a* (Chl), and temperature for the entire water column and values in the hypolimnion (~12.5 m) and epilimnion (~1 m)

	Water column	Hypolimnion	Epilimnion
Conductivity (μS cm^{-1})	12.8	13.0	12.5
TDS (g L^{-1})	0.008	0.009	0.008
pH	7.4	6.8	8.1
DO (mg L^{-1})	8.5	9.1	7.8
Chl (μg L^{-1})	1.5	3.1	0.9
T (°C)	13.4	11.4	15.4

OCTETE PC alpha spectrometer produced by ORTEC. To estimate the age of sediment subsamples, the constant rate of unsupported ^{210}Pb supply (CRS) model was used (Appleby 2001). Activity of unsupported (excess) ^{210}Pb was calculated by subtracting supported (in situ) ^{210}Pb activity from total ^{210}Pb activity. Supported ^{210}Pb was determined from activity measurements in old sediments that contain no excess ^{210}Pb and it was assumed that supported ^{210}Pb activity remained constant throughout the sediment column. An age-depth function was calculated using the randomization method and the curve was fitted using the LOESS procedure (Cleveland and Devlin 1988). Age estimates in the lower parts of the sediment core were obtained through extrapolation of the linear sedimentation rates in the upper part of the core (von Gunten et al. 2008).

Organic matter in the sediment, measured by loss-on-ignition (LOI) (Dean 1974), was determined from wet sediment sub-samples of 10–12 g. Wet samples were first dried at 105 °C for 12 h to determine water content, and then ignited in an oven at 550 °C for 2 h to determine the organic content of the dry matter.

Sediment samples for fossil chironomid analysis were prepared using standard methods described in Brooks et al. (2007), but without KOH pretreatment, which was unnecessary given the low organic content of the sediment. Volumetric sub-samples of 1 cm^3 were sieved through a 100-μm mesh and the residue was examined using a Bogorov counting chamber under a binocular microscope. Remains were extracted with fine forceps. All fossil chironomid remains were mounted in Euparal® on microscope slides and identified to the highest taxonomic resolution possible under a light microscope at 400× magnification to determine community composition. Identification of chironomids used the guides of Wiederholm (1983) and Brooks et al. (2007), and nomenclature follows that of Brooks et al. (2007). Indicator species of chironomids were used to infer the quality of benthic conditions with the benthic quality index (BQI), following Wiederholm (1980). The BQI employs a number of indicator taxa, which range from a score of one (eutrophic lakes with low benthic quality) to a score of five (oligotrophic lakes with high benthic quality). The indicator value of chironomids for benthic quality is determined mostly by oxygen availability (Brodersen and Quinlan 2006; Luoto and Salonen 2010).

Preparation of sediment samples for fossil Cladocera analysis followed standard methods (Szeroczyńska and Sarmaja-Korjonen 2007), but without the KOH treatment. Sediment sub-samples were weighed, washed, and sieved carefully through a 51-μm mesh under running tap water and dyed with a few drops of glycerol-safranine. Samples were mounted on microscopic slides and analyzed under a light microscope with magnifications between 100× and 400×. For community analysis, a minimum of 100 cladoceran individuals (Kurek et al. 2010) were enumerated as the number of the most abundant body part (carapaces, headshields, postabdomens, ephippia), and identified following the key of Szeroczyńska and Sarmaja-Korjonen (2007).

To depict high-resolution climate (i.e. temperature) variability during the time covered by the sediment core, from the LIA until present, we utilized the regional Alpine mean air temperature data from 1818 to 2007 AD (Fig. 2), provided by the HISTALP project data base (http://www.zamg.ac.at/histalp/). The coarse resolution subregion series used in the current study was that of high-altitude Alpine sites and the values (annual, October–March, and April–September) are depicted as arithmetic means of single station anomaly series (Auer et al. 2007).

Constrained un-weighted pair-group average (UPGMA) cluster analysis was used to group samples into local faunal zones to indicate temporal changes in fossil assemblages. The Bray-Curtis similarity index was used as a measure and a cut off value of <0.6 was set. Similarity percentage (SIMPER) analysis, with Bray-Curtis similarity index as a measure, was used to indicate taxa responsible for faunal changes between sample groups identified from the cluster analysis.

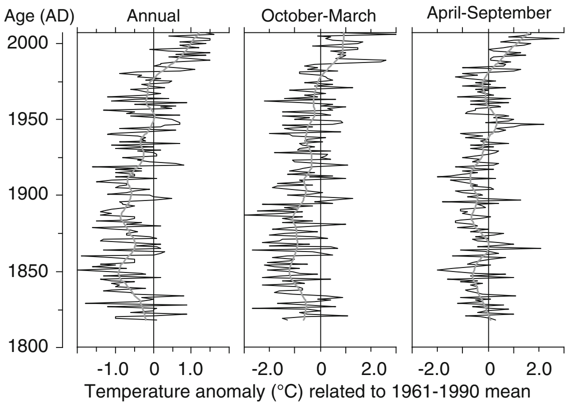


Fig. 2 The regional Alpine temperature development (AD 1818–2007) for high-altitude sites in the Greater Alpine Region (Auer et al. 2007) is based on coarse-resolution subregional means (CRSM) and produced by the HISTALP project (www.zamg.ac.at/histalp). The annual, winter period (October–March), and summer period (April–September) mean temperature variations are shown with *black lines* and the general trends (lowess smoothing, span 0.15) with *gray lines*

Thus, pairwise comparison between faunal zones was performed. Furthermore, detrended correspondence analysis (DCA) sample scores along the first DCA axis were used to illustrate directional shifts in fossil invertebrate communities. DCAs were run separately for both invertebrate groups and relative proportions (square-root transformed, down-weighted rare taxa) were used in the analyses. DCAs were run with CANOCO 4.52 software (ter Braak and Šmilauer 2002). Spearman's rank correlation coefficient (r_S) and the level of statistical significance (p) were used to assess the relationships between sediment properties and community-based indices (DCA axis 1 scores). These analyses were performed using the relative taxon abundances and conducted with Paleontological Statistics (PAST) software (Hammer et al. 2001).

Results

Sediment at 8 cm depth corresponded to about AD 1850 and dates of AD 1900 and 1950 corresponded to sediment depths of 5 and 2 cm, respectively (Fig. 3). As the oldest reliable time horizon was at 9 cm (AD ~1830), samples below this depth are considered to represent the LIA, which ended about AD 1850 in the Alps. Linear extrapolation of the sediment ages from the upper core (0–9 cm) provided an age estimate of about AD 1700 for the bottom of the core (16 cm).

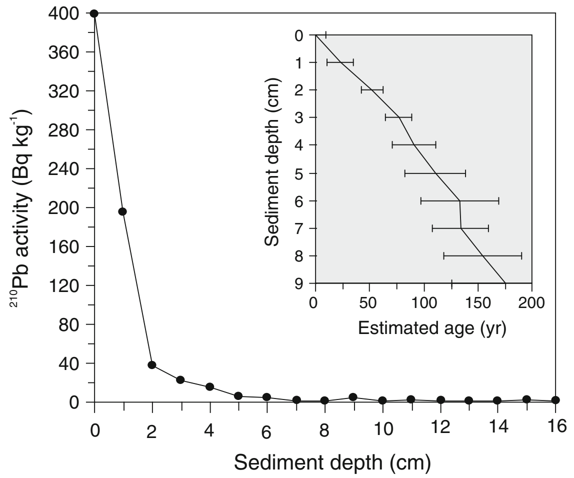


Fig. 3 Total specific ^{210}Pb activity and age-depth model (with error estimates) for the Oberer Landschitzsee core

A total of 24 chironomid taxa were identified from the 17 core samples. Chironomid assemblages (Fig. 4) prior to AD 1850 were dominated by *Micropsectra contracta*-type (30–40 %), *Procladius* (10–20 %), *Psectrocladius sordidellus*-type (5–20 %), and *Tanytarsus lugens*-type (<10 %). Between about AD 1850 and 1950 the dominant chironomid, *M. contracta*-type, decreased and other abundant taxa were progressively extirpated. At the same time, *Sergentia coracina*-type increased markedly (>50 %) and *Corynoneura arctica*-type and *Paratanytarsus austriacus*-type also started expanding. In the topmost samples (AD 1950-present), *Sergentia*, *C. arctica*-type, and *P. austriacus*-type decreased in abundance as *M. contracta*-type became more abundant. Cluster analysis (<0.6 Bray-Curtis similarity) indicated three major sample groups in the chironomid data (Fig. 4); zone CHI1 was formed of samples from 16 to 8 cm (until AD 1850), CHI2 of samples from 7 to 1 cm (until late twentieth century), and CHI3, the topmost sample (0 cm, the present). SIMPER identified, in descending order, *S. coracina*-type (increase), *M. contracta*-type (decrease), and *Procladius* (decrease) as taxa that contributed most to the faunal changes between CHI1 and CHI2, and *M. contracta*-type (increase), *S. coracina*-type (decrease), and *P. austriacus*-type (decrease) as those that contribute to the changes between zones CHI2 and CHI3.

Nine cladoceran taxa were encountered in the core samples, most of which were Chydoridae. Benthic *Alona affinis* (40–60 %) and *Alona quadrangularis* (20–40 %) and planktonic *Daphnia longispina*-type

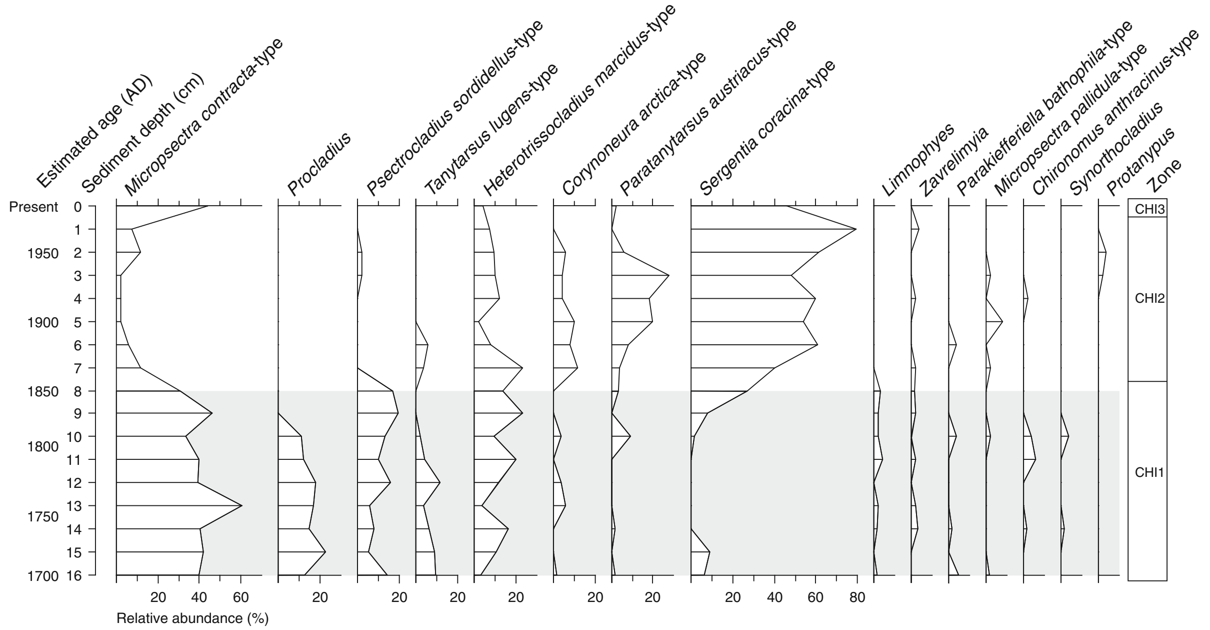


Fig. 4 Relative abundance of the most common Chironomidae (>2 % maximum abundance) in the sediment profile from Oberer Landschitzsee. The *gray band* indicates the Little Ice Age (prior to AD 1850)

(<10 %) dominated cladoceran assemblages in the LIA samples, prior to AD 1850 (Fig. 5). Around AD 1850-1900, *A. affinis* and *A. quadrangularis* decreased and *D. longispina*-type disappeared, and simultaneously, *Acroperus harpae*, *Chydorus sphaericus*-type, and *Alonella excisa* increased. A new planktonic species, *Bosmina longirostris* colonized the lake around AD 1950, increased markedly, and became the dominant species in the topmost samples, after AD 1950 AD. The cluster analysis divided Cladocera stratigraphy into three local faunal zones, which were stratigraphically the same as the chironomid zones; CLA1 between 16 and 8 cm, CLA2 between 7 and 1 cm, and CLA3 the topmost sample (Fig. 5). SIMPER detected in descending order that *A. harpae* (increase), *A. affinis* (decrease), and *A. quadrangularis* (decrease) contributed most to the changes between zones CLA1 and CLA2, whereas *B. longirostris* (increase), *A. harpae* (decrease), and *A. affinis* (decrease) were responsible for the faunal changes between zones CLA2 and CLA3.

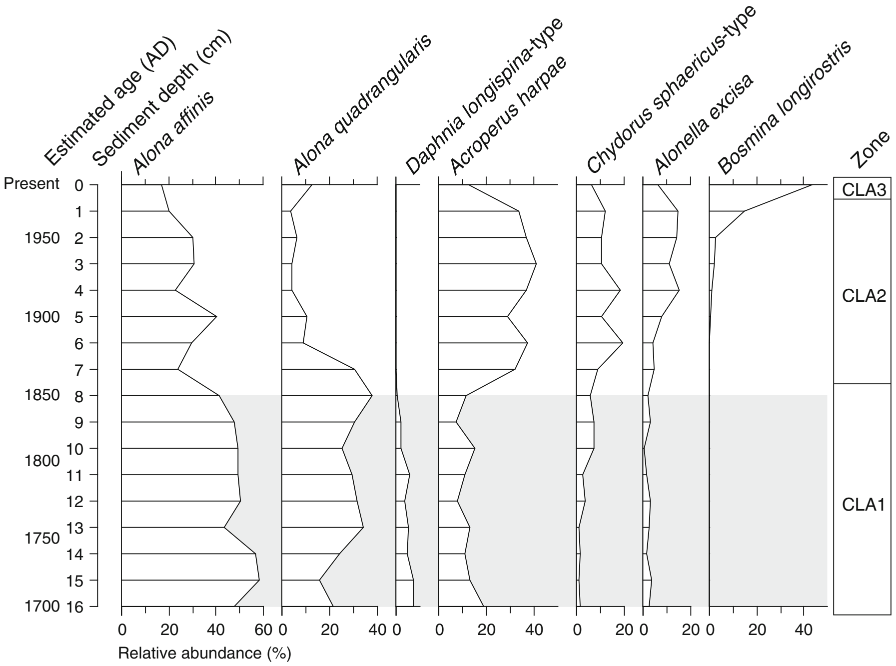
Organic content in the sediment profile (Fig. 6) showed a generally increasing trend from the bottom (~20 %) to top (~30 %) of the core. The chironomid-based BQI indicated high benthic quality in the LIA section of the core and reduced quality for the post-LIA period (Fig. 6). The DCAs provided gradient lengths of 1.922 (chironomids) and 1.280 (cladocerans) SD units for axis 1 and 1.246 and 0.496 for axis 2, respectively. Eigenvalues for DCA axis 1 and 2 were 0.364 and 0.084 for the chironomid data and 0.201 and 0.022 for Cladocera. The DCA sample scores for chironomid and Cladocera assemblages along DCA axis 1 decreased from high values (>1.0 SD) during the LIA to low values (<0.5 SD) until the present. The decline in values started during the LIA, at 11 cm, and zero values were reached for chironomids at about AD 1900 (5 cm) and for cladocerans in the topmost, modern sample. Chironomid sample scores increased slightly after AD 1950. Spearman's correlation matrix (Table 2) indicated that organic matter had a strong (negative) relationship with benthic quality and with DCA axis 1 scores, and that benthic quality correlated strongly (positively) with DCA axis 1 shifts, at a significance level of $p < 0.001$.

Discussion

The Little Ice Age (faunal zones CHI1 and CLA1)

The chironomid communities of Lake Oberer Landschitzsee during the LIA, prior to 1850 AD, were

Fig. 5 Relative abundance of the most common Cladocera (>2 % maximum abundance) in the sediment profile from Oberer Landschitzsee. The *gray band* indicates the Little Ice Age (prior to AD 1850)



dominated by *M. contracta*-type. *P. sordidellus*-type, *Procladius* and *T. lugens*-type were also common (Fig. 4). These taxa occur widely in European Alpine lakes (Lotter et al. 1997; Bigler et al. 2006). *Procladius* is characterized as a eurytopic taxon, whereas *M. contracta*-type, *T. lugens*-type, and *P. sordidellus*-type are generally associated with cold and/or oxygenated waters (Lotter et al. 1997; Quinlan and Smol 2001; Luoto 2009; Millet et al. 2010). As chironomids have been demonstrated to be sensitive indicators of temperature conditions (Brooks 2006), the stability of the cold-associated chironomid communities in the lower part of the core until about AD 1850 suggests that this entire period is indeed representative of the LIA (Figs. 4, 6), with even the deepest samples not extending back in time to the MCA. The temporal range of the LIA, based on glacial maximum extent in the Alps, is generally agreed to have lasted until AD 1850 (Ivy-Ochs et al. 2009), although this is not clearly represented in the Alpine temperature record (Fig. 2, Auer et al. 2007) because the series does not include data for previous centuries.

Cladoceran assemblages during the LIA were dominated by *A. affinis* and *A. quadrangularis* (Fig. 5). These benthic chydorid species are recorded as major components of Alpine cladoceran communities in the Niedere Tauern region in Austria (Kamenik et al. 2007) and also in Alpine lakes in Italy and Switzerland (Lotter et al. 1997; Bigler et al. 2006; Nevalainen et al. 2011). Furthermore, these species usually dominate during cold late-glacial and post-glacial conditions, occur in cold northern lakes (Korhola 1999; Hofmann 2000), and can thus be characterized as cold-tolerant. Although chydorids are usually typified as littoral, they are not restricted to the littoral zone and may utilize all benthic, deep-water habitats (Nevalainen 2011, 2012), even the profundal zone (Flössner 2000), where they are exposed to limnological variability, such as oxygen availability. Despite numerous occurrences of the two *Alona* species in cold lakes/climates, their distribution is not well known and mostly governed by their ability to survive on sediment, in the absence of aquatic macrophytes.

High benthic quality, measured as BQI, *sensu* Wiederholm (1980), suggested that near-bottom oxygen conditions were good in Lake Oberer Landschitzsee during the LIA (Fig. 6). It is also likely that the high abundance of the sediment-associated *Alona* species was related to favorable benthic conditions, including oxygen availability. These findings are in agreement with the low (~20–25 % LOI) organic content of the sediment (Fig. 6), which is attributed to low lake productivity (Willemse and Törnqvist 1999; Nesje and Dahl 2001; Shuman 2003). The relationship between benthic quality and organic

Fig. 6 Organic matter, benthic quality, and detrended correspondence analysis axis 1 scores of Chironomidae (DCA1 CHI) and Cladocera (DCA1 CLA) assemblages in the Oberer Landschitzsee sediment core

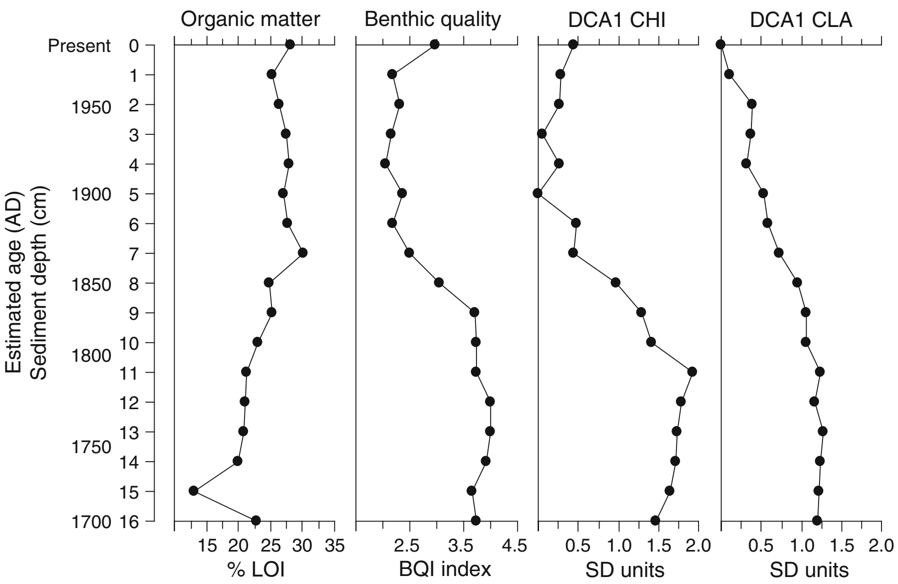


Table 2 Spearman's rank correlations (r_S) and levels of statistical significance (p) between organic matter (LOI), benthic quality (BQI), and detrended correspondence analysis axis 1 scores of Chironomidae (DCA1 CHI) and Cladocera (DCA1 CLA) assemblages

	Organic matter	Benthic quality	DCA1 CHI	DCA1 CLA
Organic matter		$p = < 0.001$	$p = < 0.001$	$p = < 0.001$
Benthic quality	$r_S = -0.76$		$p = < 0.001$	$p = < 0.001$
DCA1 CHI	$r_S = -0.78$	$r_S = 0.88$		$p = < 0.001$
DCA1 CLA	$r_S = -0.82$	$r_S = 0.86$	$r_S = 0.87$	

matter in the Oberer Landschitzsee core also supports this interpretation (Table 2), although the observed relationship may be spurious, given their mutual dependence in the sediment core. As stated above, the long-term relationship between climate and limnological variables is very complex and probably site-specific, as cold climate was previously shown to both increase and reduce near-bottom oxygen availability (Schmidt et al. 2008; Kirilova et al. 2009; Luoto and Salonen 2010). Results from Lake Oberer Landschitzsee suggest that the cold climate during the LIA was associated with good near-bottom oxygen conditions, and that this was most likely a consequence of low productivity and low decomposition of organic matter during the short ice-free period with cold water (Figs. 2, 6).

Post-LIA period (faunal zones CHI2 and CLA2)

A major simultaneous change occurred in the chironomid and cladoceran communities in the middle of the sediment core, when *S. coracina*-type increased dramatically and replaced *M. contracta*-type as the dominant chironomid taxon, and the two *Alona* species were outcompeted by *A. harpae* (Figs. 4, 5). Furthermore, the chironomid taxa *Procladius*, *P. sordidellus*-type and *T. lugens*-type and the planktonic cladoceran taxon *D. longispina*-type were extirpated. This complete faunal turnover coincided with the end of the LIA around AD 1850 and was also evident in the progressive shifts of the previously stable invertebrate assemblage scores along the DCA axis 1 toward clearly lower values (Fig. 6). Accordingly, the faunal turnover was reflected in the BQI, which declined toward the late nineteenth century and suggested reduced near-bottom oxygen availability. The dramatic change in the BQI was mostly driven by an increase in the newly dominant *S. coracina*-type (*Phaenopsectra coracina* in Wiederholm 1980) and simultaneous decrease in *M. contracta*-type (genus *Micropsectra* in Wiederholm 1980) (Figs. 4, 6). These taxa were also identified as drivers of the chironomid community change by SIMPER. *Sergentia* is an indicator of poor oxygen conditions (Quinlan and Smol 2001; Luoto and Salonen 2010). It is able to tolerate temporary anoxia, given its ability to accumulate glycogen and degrade it by anaerobic metabolism. The dominance of *Sergentia* and especially *S. coracina*-type in Lake Oberer Landschitzsee is interesting because it is presently extremely rare in the Swiss Alps (Lotter et al. 1997; Bigler et al. 2006; O. Heiri personal communication). Additionally, the dramatic decrease of *Micropsectra*, a genus very sensitive to reduced hypolimnetic oxygen (Quinlan and Smol 2001; Luoto and Salonen 2010), strongly suggests reduced oxygen availability. Furthermore, organic matter increased, with values of $\sim 5\ \%$ in the transition zone from the LIA to the post-LIA period, about AD 1850 (Fig. 6). This increase is of such magnitude that it was likely caused by substantial environmental change (Shuman 2003), and correlated strongly (negatively) with changes in the fauna and BQI (Table 2). Significant correlations should be interpreted cautiously, however, as they do not provide evidence for causality.

It is likely that post-LIA climate warming, which is well documented in glacial records in the Alps (Ivy-Ochs et al. 2009) and also in instrumental Alpine climate records (Fig. 2, Auer et al. 2007), enhanced nutrient loading to Lake Oberer Landschitzsee and cumulatively caused the observed paleolimnological shifts in faunal assemblages, benthic quality, and organic matter from AD 1850 to the twentieth century (Figs. 4, 5, 6). These changes were most likely attributable to reduced hypolimnetic oxygen availability. There exists a direct link between temperature and productivity in lakes, as climate warming changes limnologial variables by altering physical (hydrology, temperature, stratification, ice phenology, catchment characters) and biological (primary production, microbial activity) factors (Parker et al. 2008; Adrian et al. 2009) that likely enhance lake productivity. Furthermore, it is even possible that the coupling effects of climate warming, and consequent increased productivity led to an onset of summer stratification due to larger temperature differences between hypolimnetic and epilimnetic waters (Smol and Douglas 2007), resulting in the prevalence of *S. coracina*-type and a decline of *M. contracta*-type (Fig. 4), a consequence of reduced oxygen availability in the hypolimnion.

The Alpine temperature series, however, shows only a slight increase in temperature during the period AD 1850–1900 (Fig. 2, Auer et al. 2007) and this magnitude of change does not necessarily lead to major changes in nutrient conditions. Additionally, high Alpine lakes are usually strongly oligotrophic and nutrient status of high Alpine lakes is more related to land use than direct temperature effects (Heiri and Lotter 2005). The current sediment record of aquatic invertebrates cannot separate direct from indirect climate effects. Changes in land use, such as expansion of active pastures to the catchment, may have served as a supplementary, or even principal forcing factor behind the observed faunal shifts and changes in BQI and LOI between AD 1850 and 1950 (Figs. 4, 5, 6). Previous studies showed that land use, especially pasturing, has had a major effect on high-altitude lakes in the Alps (Schmidt et al. 2002, 2008; Kamenik et al. 2002) and that land use practices have intensified strongly during the twentieth century, likely contributing to the early twentieth century limnological variability in Lake Oberer Landschitzee. Over a longer temporal scale, throughout the late Holocene, in-lake processes including increased productivity, onset of stratification, and deteriorated near-bottom oxygen condition, have dominated during warm climate periods in Lake Oberer Landschitzsee. These conditions have occurred mainly as a result of intensified Alpine land use (Schmidt et al. 2008), as pastures generally extended far higher into the mountains during climate amelioration. Accordingly, we presume that during the post-LIA climate warming, active alpine pastures extended into the lake catchment and provided additional input of nutrients, as a consequence of increased excretion by grazers and enhanced erosion, leading to even higher productivity and generation of organic matter, and further impact on benthic conditions in the lake. Apparently, at present (summer 2010), there are no active pastures around Lake Oberer Landschitzsee, as cows were observed only at lower altitude, in the catchment of Unterer Landschitzsee (Fig. 1).

According to SIMPER, *A. harpae*, *A. affinis,* and *A. quadrangularis*, in descending order, yet with similar contributions, were the species driving the community turnover in cladocerans (Figs. 5, 6). As discussed above, it is likely that chydorids, such as the two *Alona* spp. also prefer well-oxygenated benthic habitats. Thus, the reduced benthic quality (Fig. 6) of Lake Oberer Landschitzsee after the LIA may have set up new environmental regimes for microbenthic taxa. Although *A. harpae* is usually characterized as a phytophilous species, i.e. is common in aquatic vegetation (Fryer 1968; Whiteside et al. 1978), its increase in the post-LIA section of Lake Oberer Landschitzsee does not indicate appearance of extensive macrophyte stands, because the lake currently lacks a well-developed vegetation in the littoral zone and the shallow littoral is covered by gravels. Because the two *Alona* species have highly divergent ecological preferences relative to those of *A. harpae* (Kamenik et al. 2007; Nevalainen et al. 2011; Nevalainen 2011), it is possible that submerged vegetation beds, including those formed of *Myriophyllum* sp., expanded in Lake Oberer Landschitzsee after the LIA, providing more suitable habitats for the phytophilous *A. harpae* over the sediment-associated *Alona* species. In the Italian and Swiss Alpine lakes, *A. harpae* has been observed to be strongly associated with potassium (Nevalainen et al. 2011), which consequently is related to lake productivity and/or aquatic vegetation (Nicholls et al. 1996). Furthermore, *P. austriacus*-type and *C. arctica*-type are known to be associated with submerged macrophytes (Brooks et al. 2007; Luoto 2010). Thus, because *Myriophyllum* was observed around the depth of the sampling point during the coring of Lake Oberer Landschitzsee, it is likely that submerged *Myriophyllum*, indicative of increased benthic production, started to succeed in the lake during the post-LIA period, under ameliorating climate (Fig. 2).

The pre-AD 1850 section of the Oberer Landschitzsee core contained free-swimming *Procladius,* which was identified by SIMPER to significantly contribute to assemblage change from zone CHI1 to CHI2, and planktonic *Daphnia*, which were later extirpated from the lake, coinciding with the end of the LIA and with the decreasing trend in benthic oxygen (Figs. 4, 5, 6). Because size-selective predation by fish is a powerful top–down control on aquatic invertebrate communities (Brooks and Dodson 1965), and the presence of fish is known to influence the distribution of large-bodied *Daphnia* (Nevalainen et al. 2011) and the success of *Procladius* larvae (Heiri and Lotter 2003) in Alpine lakes, a classical explanation for the observed shifts would be the impact of foraging fish that were introduced to the lake at the time of faunal change. Although Arctic charr are currently numerous in Oberer Landschitzsee (Zink et al. 2007), they were introduced into the lake more than two centuries prior to the observed decline of *Procladius* and *Daphnia* and the change in faunal assemblages. Furthermore, the most pronounced changes in chironomid and Cladocera communities occurred among benthic, rather than planktonic species. These faunal shifts were most likely related to a change in near-bottom environmental conditions associated with climate amelioration of the post-LIA period. As stated above, it is possible that the post-LIA climate warming caused the onset of summer stratification, followed by oxygen stratification, and even oxygen deficit in the deep-water zone. It has recently been shown that the abundance and phenology of planktonic cladocerans may be regulated by climate-linked factors (i.e. water temperature, timing of thermal stratification, and hypolimnion depth) in their habitat (Manca and DeMott 2009). Thus, as many planktonic aquatic invertebrates use vertical migration and the hypolimnion as a refuge to avoid fish predation (Wright and Shapiro 1990), the development of a hypolimnion with low oxygen availability may have prevented their migration, resulting in their being consumed and ultimately extirpated by fish, as suggested by the sediment record (Figs. 4, 5). Nevertheless, we cannot rule out the possibility that a change in population structure or abundance of Arctic charr around AD 1850 in Lake Oberer Landschitzsee, possibly even related to the limnological changes, played a significant role in the decline of *Daphnia* and *Procladius*, as these taxa are easily consumed by Arctic charr (Jeppesen et al. 2001; Winfield et al. 2002).

Late twentieth and early twenty-first century (zones CHI3 and CLA3)

Cluster analysis of both invertebrate assemblages classified the topmost sample, indicative of the late twentieth and early twenty-first century (Fig. 3), into separate clusters (Figs. 4, 5). After about AD 1950 and predominantly in the core-top sample, the chironomid community again became dominated by *M. contracta*-type, but the other taxa present in the early part of the core did not return, such as the cold-indicator, *T. lugens*-type (Fig. 4). Furthermore, *S. coracina*-type decreased, but remained an important component of the macrobenthic community. SIMPER suggested that the highest contribution to the faunal change was a consequence of the increase in *M. contracta*-type. Among the cladocerans, a new planktonic species, *B. longirostris*, which according to SIMPER was mostly responsible for the faunal changes in the group, colonized the lake around AD 1950 and began to dominate in the topmost sediment layer (Fig. 5). Because *B. longirostris* is typically absent or rare in high Alpine lakes (Lotter et al. 1997; Kamenik et al. 2007; Nevalainen et al. 2011) and associated with high nutrient levels (Chen et al. 2010) and/or warm lakes at low altitudes (Lotter et al. 1997; Kamenik et al. 2007), colonization of Lake Oberer Landschitzsee by *B. longirostris* from about AD 1950 onwards may indicate the onset of pronounced, late twentieth century climate warming (Fig. 2) and associated enhanced primary production. Indeed, there is unpublished evidence of a dramatic change in the diatom community composition in the lake during the last decade (R. Kurmayer and R. Schmidt personal communication). Apparently, *B. longirostris* very recently succeeded in migrating to and colonizing the high-altitude site (Fig. 5). If this was a consequence of climate warming, as hypothesized here, this finding can be regarded as a previously undescribed sign of a change in species distribution patterns in the Alps. Similar to the chironomid community, the cladoceran assemblages did not return to the LIA status (Figs. 4, 5), as also evident in the DCA axis 1 scores (Fig. 6). Rather, the community shift was permanent.

The BQI increased in the core-top sample (Fig. 6), suggesting enhanced hypolimnetic oxygen availability relative to the post-LIA period (*ca.* AD 1850–1950) in Lake Oberer Landschitzsee. This is in accordance with measured summer hypolimnetic oxygen, which was 9.1 mg L^{-1} in August (Table 1), indicating well oxygenated near-bottom waters during the summer and unstratified conditions. The lake is currently oligotrophic, with low chlorophyll-*a* concentrations (Table 1), but previous long-term paleolimnological data for the Landschitzsee lakes (Schmidt et al. 2002, 2007, 2008) indicate periods of increased production, associated with warm climate conditions. Thus, although not instrumentally monitored, it is likely that in recent decades in-lake production has increased as a consequence of climate warming, as growing seasons lengthen and nutrient fluxes from catchments increase (Michelutti et al. 2005; Smol et al. 2005). There was a slight increase in organic matter in the topmost sediment sample (Fig. 6), which is likely related to lake productivity (Willemse and Törnqvist 1999; Nesje and Dahl 2001; Shuman 2003). The improved benthic quality in the post-AD 1950 section of the core (Fig. 6) may appear surprising at first glance because during enhanced climate warming and increased production it might be presumed that benthic quality would deteriorate. It is possible, however, that during recent decades, deep-water oxygen conditions have improved relative to the post-LIA period, as a consequence of breakdown of thermal stratification and mixing of the entire water column during summer (Table 1). Land use in the catchment has also changed in recent decades and became less intense, as pasturing now occurs at lower elevations in the catchment of Lake Unterer Landschitzsee (Fig. 1). This trend is apparent in the entire northern and Central Alps (Niedrist et al. 2009). The data of Schmidt et al. (2008) also indicate that land use indicators have decreased continuously in the recent past, even in Lake Oberer Landschitzsee. This may point to recent decoupling of land use and climate warming. Additionally, increased late twentieth century anthropogenic atmospheric emissions, e.g. nitrogen, have caused nutrient enrichment of remote lakes (Wolfe et al. 2001; Elser et al. 2009), which may explain the most recent changes in Lake Oberer Landschitzsee.

Conclusions

Long-term, decadal and centennial linkages between climate and the ecological structure of lakes are complex. Nevertheless, proxy climate data from sediment cores collected in lakes often display clear trends with respect to the period of post-Little Ice Age (LIA) climate warming, a time that is also influenced by human activities. In high Alpine Lake Oberer Landschitzsee, limnological conditions and aquatic invertebrate communities evidently shifted from the condition and structure prevailing during the LIA, toward a completely new state. This change was driven by post-LIA climate warming and associated expansion of Alpine pasturing. The post-LIA period was characterized by increased productivity, success of submerged macrophyte beds, and reduced oxygen availability in the deep-water zone. These changes are reflected in the community structure of aquatic invertebrates, which show almost complete and simultaneous species turnover. The observed community turnover provides evidence that temperature-driven ecological thresholds, whether related to direct mechanisms or indirect factors controlled by human activity, have been crossed. Species abundances and distributions changed in response to post-LIA and pronounced late twentieth century climate warming.

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