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RESEARCH ARTICLE

Climate change impacts on zooplankton and benthic communities in Lake Unterer Giglachsee (Niedere Tauern Alps, Austria)

Tomi P. Luoto[1,2] *and Liisa Nevalainen*[1,3]

[1] Research Institute for Limnology, University of Innsbruck, Mondsee, Austria
[2] Department of Geosciences and Geography, University of Helsinki, FI-00014 University of Helsinki, Finland
[3] Department of Environmental Sciences, University of Helsinki, Lahti, Finland

We examined a sediment core from a climatically sensitive High Alpine lake Unterer Giglachsee in the Niedere Tauern Alps in Austria. Our aim was to investigate long-term climate change impacts on aquatic invertebrates (Chironomidae, Cladocera) with a special focus on the ending of the Little Ice Age and the present climate warming. Although the changes in faunal assemblages were relatively subtle through the sedimentary record, a mutual faunal breakpoint at ~1900 AD was distinguished. In addition, the faunal dynamics correlated closely with instrumental Alpine temperature records and with reconstructed Northern Hemisphere climate development over the examined time period. In particular, significant relationships between relative taxa abundance and temperature were found with chironomids *Sergentia*, *Paracladius*, *Paratanytarsus austriacus*-type, *Cricotopus* (I.) *intersectus*-type, and *Cricotopus cylindraceus*-type and with cladocerans *Daphnia* and *Alonella excisa*. Our results also suggested that the most recent assemblages represent unique community compositions. We conclude that our study lake is sensitive to climate warming and the composition of the aquatic ecosystem in Unterer Giglachsee has changed due to the impact of increasing temperatures. We predict that the further increasing temperatures will have direct but also cascading effects on the sensitive lake, potentially causing an ecosystem turnover where the key taxon *Paracladius* may play an important role.

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1 Introduction

Today, freshwater ecosystems are severely endangered by the climate change and therefore, lakes, which can be considered to act as sentinels of climate change [1], are true hotspots of ecosystem change. At the long-term timescale and perspective, paleoecological archives provide the means to reveal how natural systems have responded to climatic changes through time. This information cannot be resolved from any monitoring data, which usually consist of only short period of observation compared to paleoecological deposits [2, 3]. In addition, sedimentary records provide a unique perspective on how today's ecosystems are likely to respond to future changes [4].

Zooplankton and zoobenthos, including Cladocera (Crustacea: Anomopoda) and larvae of Chironomidae (Insecta: Diptera), are key components of aquatic ecosystems [5, 6]. The survival and success of Cladocera and Chironomidae depends on several factors related to temperature, habitat, food availability, predation, and water quality [7, 8], but at a broad scale, the most important factor determining their distribution and abundance has often been found to be summer air temperature [9, 10]. The fossil

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Correspondence: Dr. Tomi P. Luoto, Department of Geosciences and Geography, University of Helsinki, P.O. Box 64, FI-00014 University of Helsinki, Finland
E-mail: tomi.luoto@helsinki.fi
Fax: +358-9-191-50826

remains of Cladocera and Chironomidae are well-preserved in lake sediments and can be identified from genus to species level [11, 12]. Thus, the palaeolimnological techniques and use of fossil invertebrate assemblages provides the unique opportunity to track past community dynamics in lakes.

Alpine lake ecosystems are very susceptible to environmental change [13]. Increase in water temperatures and decrease in ice-covered period are related to ambient air temperatures as direct consequences of the global warming [14]. In the Alps, the temperature increase during the past decades has been much higher than the global linear warming [15] that makes Alpine lakes particularly sensitive to climate change [1]. 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 [16, 17]. Already today, climate-driven changes can be observed at the global scale as population and life-history changes, extinctions, shifts in geographical range, and changes in community composition and in the structure and functioning of ecosystems [18].

The multidisciplinary DETECTIVE (DEcadal deTECTion of biodIVErsity in alpine lakes) project of the Austrian Academy of Sciences studies the past, present, and future scenarios of global warming threatening the biodiversity of (ultra)sensitive aquatic ecosystems in the Niedere Tauern Alps in Austria. As a part of this project's long-term perspective, we here describe the invertebrate stratigraphy of Lake Unterer Giglachsee, which is located at a treeline ecotone making it ecologically extremely vulnerable [19]. Our key study organisms represent the benthic and planktonic components of this High Alpine aquatic ecosystem, which has been described as ultrasensitive to climate change [20]. In our study on dynamics of Cladocera and Chironomidae during the past centuries, we aim to reveal connections between the community shifts and documented climate change and seek if there has been a mutual climate-related threshold that has been crossed. We also project on how the natural system is likely to respond to future changes in the climate system.

2 Materials and methods

2.1 Study site, sediment sampling, and chronology

Lake Unterer Giglachsee (13°39′3″E, 47°17′0″N) 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. The catchment of the study lake is characterized by rocky cliffs and the basin is located at an altitude of 1922 m a.s.l. The site is remotely located and away from immediate human influence due to its elevation and catchment characteristics. An inlet located in the southwest connects Unterer Giglachsee to a smaller lake, Oberer Giglachsee. Unterer Giglachsee (16.8 ha) is oligotrophic and transparent lake with a maximum depth of 18 m. The late-summer (mid-August 2011) epilimnetic pH of the lake is ~8.0 and chlorophyll a is 2.4 μg L^{-1}. Thompson et al. [20] described the site as being ultrasensitive to climate change.

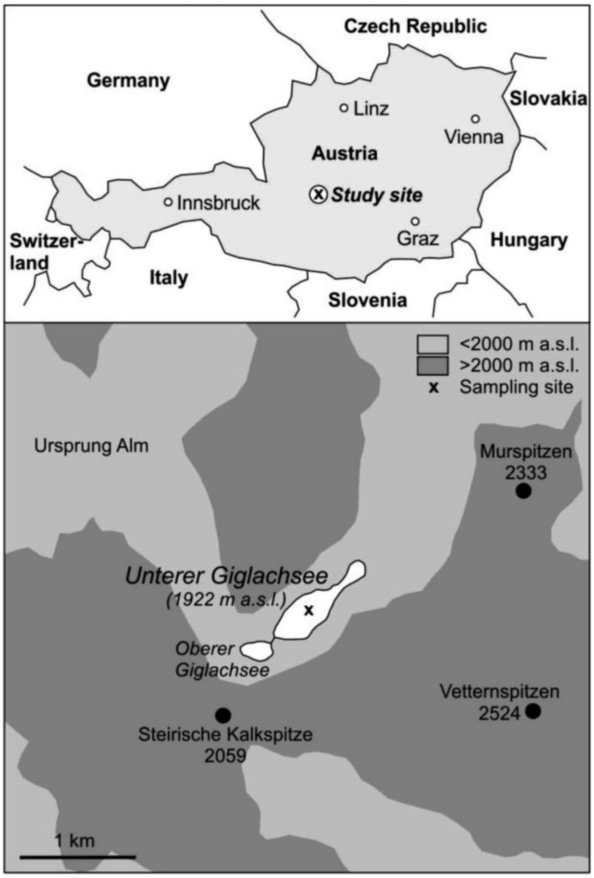

Figure 1. Location of Lake Unterer Giglachsee in the Niedere Tauern Alps in Austria.

A sediment core (Fig. 1) was derived from Lake Unterer Giglachsee using a small boat and a Kajak gravity corer in July 17, 2010. The short core (19 cm) from a water depth of 14.5 m was subsampled at 1-cm intervals. The topmost 12 cm were slightly darker in color compared to the lower part of the core. The samples were stored in plastic bags in a coldroom at +4°C.

To provide a chronology, a total of 14 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-

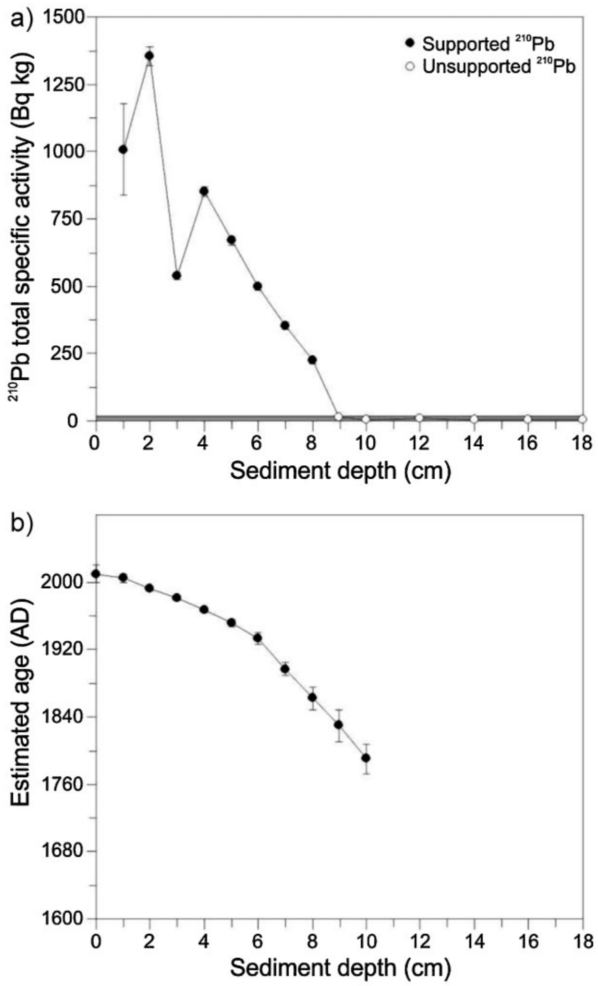

Figure 2. Total specific activity of ^{210}Pb (a) and the associated time-depth model (b) for the sediment profile from Lake Unterer Giglachsee in the Niedere Tauern Alps, Austria. Activity of supported ^{210}Pb is 9 ± 8 Bq kg^{-1}.

spectrometry measuring the ^{210}Po ($\alpha = 5.31$ MeV, $T_{1/2} = 138$ days) activity [21]. 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 [21]. 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 [22]. 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 profile. Age-depth function was calculated using randomization method [23]. Because no plant macrofossils were found 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.

2.2 Fossil invertebrate analyses

Volumetric sediment samples of 1 cm^3 for fossil Chironomidae analysis were prepared applying standard methods described in Brooks et al. [11], but without the pretreatment in KOH, because it was unnecessary due to the nature of the sediment. The sediments were sieved through a 100-µm mesh and the residue was examined using a Bogorov counting chamber 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 was based on the guides of Wiederholm [24] and Brooks et al. [11]. A minimum of 50 head capsules was set as the target counting sum [25].

The sediment samples for fossil Cladocera were prepared following the methods described in Szeroczyńska and Sarmaja-Korjonen [12]. 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 min to concentrate the fossil remains and dyed with a few drops of glycerol-safranine. The prepared samples were mounted on microscopic slides and analyzed for Cladocera remains under a light microscope with magnifications between 100- and 400-times. Cladocera were enumerated as the number of most abundant body part (carapaces, headshields, postabdomens, ephippia) and identified following the identification guide by Szeroczyńska and Sarmaja-Korjonen [12]. The minimum counting sum was set to 100 individuals. A minimum counting sum of 70–100 cladoceran individuals has proven to be satisfactory to characterize most assemblages [26].

2.3 Numerical methods

Principal component analysis (PCA) was used to investigate patterns in chironomid and Cladocera assemblages in the downcore data. The PCAs were performed with all taxa included and on square-rooted relative taxa abundances using the program C2 [27]. To find community thresholds, constrained cluster analysis (unweighted pair-group average, UPGMA), using chord distance measure (cut-off 1.0), was applied to the Cladocera and Chironomidae data. The cluster analysis was performed using the software PAST 2.08 [28].

For climate variability, we used the general annual Northern Hemisphere reconstructed (tree-ring based) and instrumentally observed temperature data by D'Arrigo et al. [29]. For Northeastern Alpine temperature variability we used the data by Auer et al. [30]. 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/). To fit the temperatures with our record, they were inserted as ~20-year means. For linear relationships between faunal trends (PCA scores and relative taxa abundances) and temperature, Pearson product-moment correlation coefficient was used. Relationships having $p \leq 0.05$ were considered significant.

3 Results

In all, 32 Chironomidae and 9 Cladocera taxa were encountered from the sediment core from Lake Unterer Giglachsee. The most frequent and abundant Chironomidae were *Sergentia*, *Tanytarsus lugens*-type, and *Paracladius* that occurred in all of the samples (Fig. 3). In addition, *Thienemannimyia*-type was absent only from one sample (15 cm). *Sergentia* was the most abundant taxon at 18, 16, 14, and 1 cm, *T. lugens*-type at 13–11 cm, and *Paracladius* at 17–15, 10–2, and 0 cm. Chironomid taxa such as *Paratanytarsus austriacus*-type and *Heterotrissocladius grimshawi*-type decreased towards the upper part of the core, while increases were observed in the abundances of *Procladius* and *Cricotopus cylindraceus*-type. *Cricotopus* (I.) *intersectus*-type showed a peak in its abundance at 5 cm. Of the Cladocera, *Bosmina longispina* dominated through the sediment profile with abundance between 64 and 81%. In addition, *Acroperus harpae* and *Alona affinis* were common through the stratigraphy and they also occurred in every sample. A slight increase in the abundance of *Daphnia* and *Alona excisa* was observed in the upper part of the core (Fig. 4).

In both chironomid and Cladocera stratigraphies, the constrained cluster analysis, using a cut-off chord distance of 1.0, divided the sediment profile into two parts between the samples at sediment depths of 6 and 7 cm. Thus, a mutual faunal threshold was identified representing the timing of ~1900 AD. The PCA for chironomids resulted in eigenvalues of 0.190 and 0.148 for PCA axes 1 and 2, respectively. In cladocerans, PCA eigenvalues for axis 1 was 0.283 and for axis 2 0.228. The PCA ordination showed that the most recent samples (positive scores) were separated from the older samples (negative scores) along the PCA axis 1 (Fig. 5). The faunal zone between 6

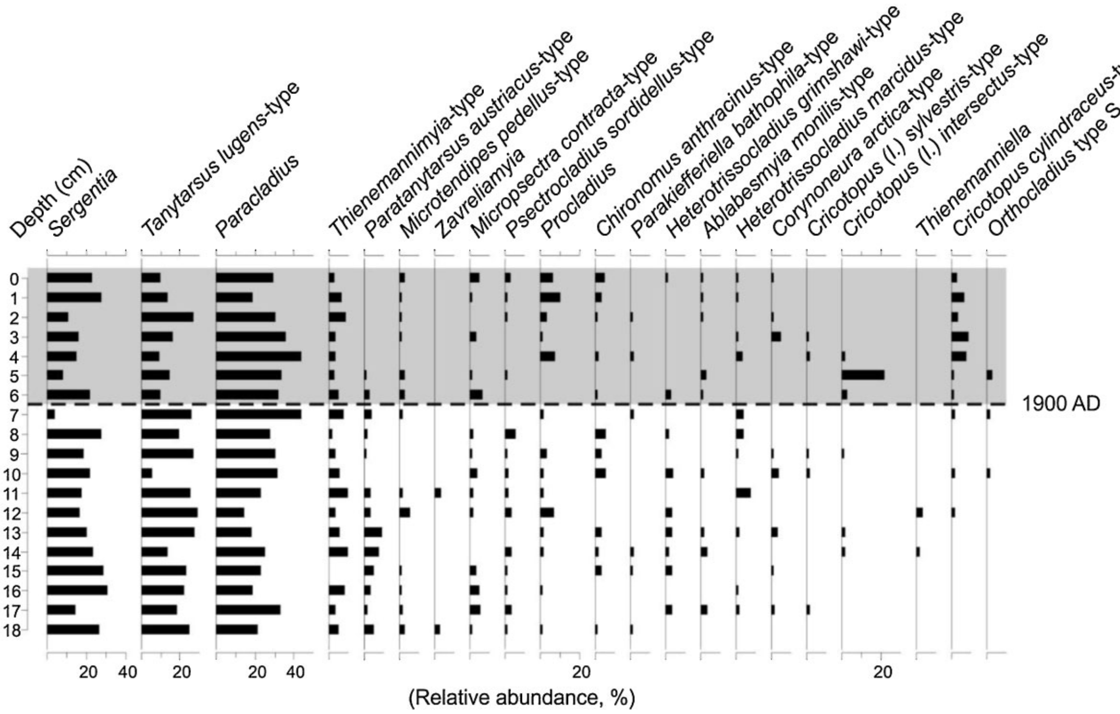

Figure 3. Chironomidae stratigraphy from Lake Unterer Giglachsee in the Niedere Tauern Alps, Austria. The faunal breakpoint (cluster analysis) at ~1900 AD is drawn as a dashed line.

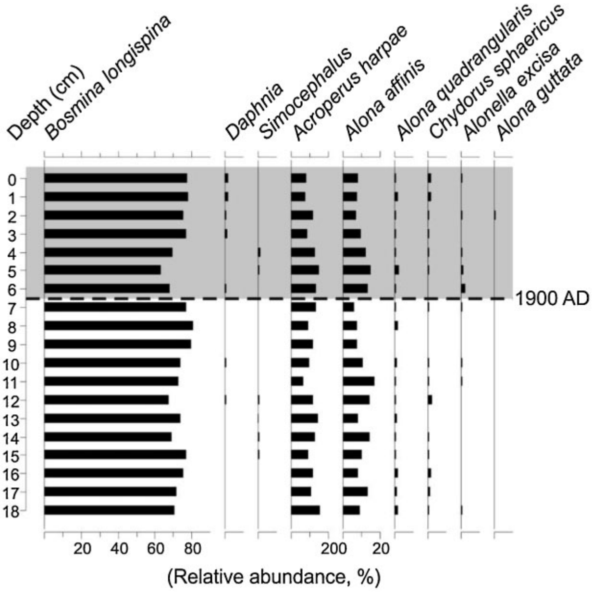

Figure 4. Cladocera stratigraphy from Lake Unterer Giglachsee in the Niedere Tauern Alps, Austria. The faunal breakpoint (cluster analysis) at ∼1900 AD is drawn as a dashed line.

and 7 cm was separated from the pre- and post-1900 AD samples mostly according to the PCA axes 2 (Fig. 5). When examining the chironomid PCA axis 1 scores, representing the main direction of variance in species data, the values showed correlation to the Northern Hemisphere temperature evolution (Fig. 6, Table 1). Of particular Chironomidae taxa, relative abundances of *Sergentia*, *Paracladius*, *P. austriacus*-type, *Cricotopus* (I.) *intersectus*-type, and *C. cylindraceus*-type had strong ($R > 0.5$) and significant ($p < 0.05$) relationship with Northern Hemisphere temperatures, whereas in Cladocera such correlation was found only with *Alonella excisa*. Although no correlation was found between Cladocera PCA axis 1 scores and Northern Hemisphere temperatures, the PCA scores correlated with the short-timespan instrumental Northeastern Alpine temperature record ($R = 0.59$, $p = 0.033$) and also *Daphnia* showed correlations with the instrumental Alpine temperatures ($R = 0.69$, $p = 0.010$).

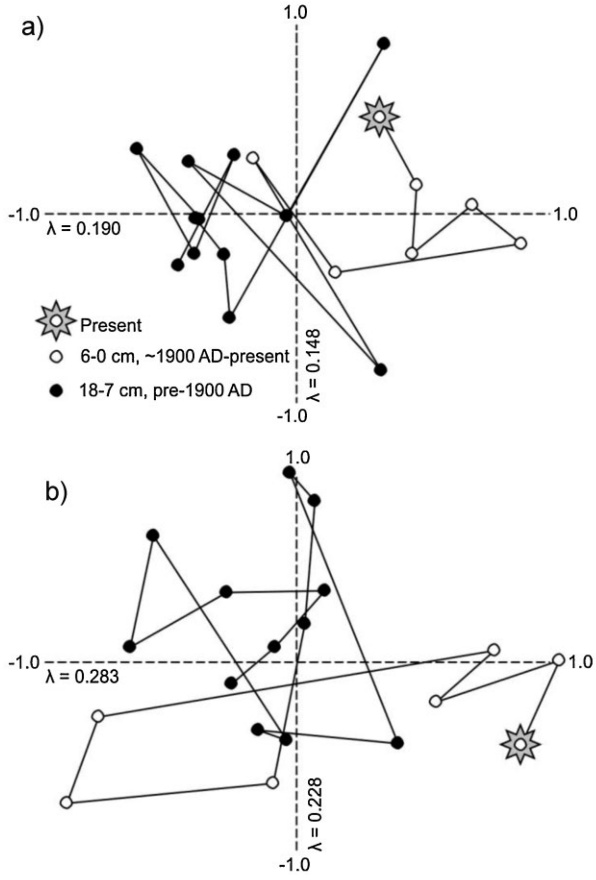

Figure 5. Principal component axes 1 (horizontal) and 2 (vertical) for Chironomidae (a) and Cladocera (b) based on the sedimentary records from Lake Unterer Giglachsee in the Niedere Tauern Alps, Austria.

4 Discussion

The sediment record from Lake Unterer Giglachsee in the Niedere Tauern Alps, contain two significant climatic episodes of the Holocene, the Little Ice (LIA, ∼1550–1850 AD), and the present climate warming (from ∼1900 AD onwards). However, due to the lack of chronological control in the lower part of the core, no reliable estimate can be given for the core base, which we, nevertheless, interpret to have accumulated during the LIA. Although previous studies have shown that in many European mountain lakes Chironomidae and Cladocera assemblages during the LIA were completely different compared to more recent assemblages (e.g., [31, 32]), the LIA faunal assemblages in Lake Unterer Giglachsee were dominated by the same taxa as during the past century and a half (Figs. 3 and 4). The most abundant Chironomidae were *Sergentia*, *T. lugens*-type, and *Paracladius*, while *B. longispina* dominated the Cladocera assemblages with *A. harpae* and *A. affinis*. These taxa are rather typical components of the invertebrate communities in the Niedere Tauern lakes [33, 34]. Among the dominating Cladocera, no distinct trends were recognized in their abundances that could have been related to climate development. However, the more infrequent *Daphnia* and *Alonella excisa* slightly increased in the upper part of the core (Fig. 4). This is in good agreement with the previous results from the Niedere Tauern lakes that showed that these taxa are absent from the modern samples of high

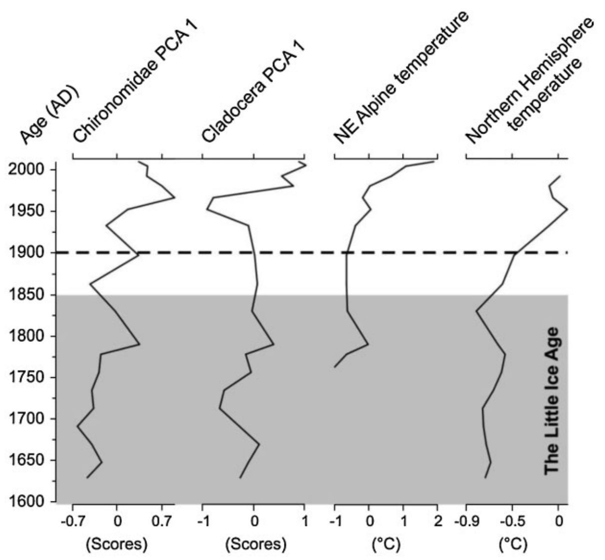

Figure 6. Principal component axis 1 scores for Chironomidae and Cladocera from Lake Unterer Giglachsee in the Niedere Tauern Alps, Austria, compared with instrumental Northeastern Alpine [30] and reconstructed Northern Hemisphere [29] temperatures. Note that the chronology is reliably dated only in the upper part of the sediment sequence (see Fig. 2), whereas the timing of the Little Ice Age is unsolved and the given dates are accurate only for the temperature data.

elevation lakes and prefer warmer/intermediate temperatures [33].

Of the dominating Chironomidae, *Sergentia* and *Paracladius* had significant relationships (negative and positive, respectively) with temperature (Table 1) and also *T. lugens*-type had generally lower abundance in the record from 1900 AD onwards, although its relationship with temperature through the core was neither linear nor significant statistically. *P. austriacus*-type and *H. grimshawi*-type decreased towards the upper part of the core, while increases were observed in the abundances of *Procladius* and *C. cylindraceus*-type. Of these taxa, the relationships between temperature trends were significant with *P. austriacus*-type and *C. cylindraceus*-type (Table 1). In addition, a significant relationship was found between temperature and *Cricotopus* (I.) *intersectus*-type, which peaked at ~1930–1950 AD, corresponding to the increased Northeastern Alpine and Northern Hemisphere temperatures [29, 30, 35]. *Cricotopus* (I.) *intersectus* is known to be associated with aquatic vegetation [36, 37], and thus, its abundance during this warm episode may have been related to expansion of aquatic vegetation.

Table 1. Correlation between reconstructed Northern Hemisphere temperature [29] and principal component analysis axis 1 scores for Chironomidae and for Cladocera as well as relative taxa abundances in the sediment core

	Northern Hemisphere temperature	
	r	*p*-Value
Chironomidae PCA 1	0.71	0.002
Cladocera PCA 1	0.04	0.879
Sergentia	0.57	0.017
Paracladius	0.55	0.021
Paratanytarsus austriacus-type	0.54	0.026
Cricotopus (I.) *intersectus*-type	0.49	0.046
Cricotopus cylindraceus-type	0.70	0.002
Daphnia	0.46	0.064
Alonella excisa	0.63	0.007

In the opposite, the decrease in the abundance of *Sergentia*, *P. austriacus*-type and *H. grimshawi*-type and increase in *Procladius* and *C. cylindraceus*-type may be more related to direct effects of temperature increase. It has been shown that *P. austriacus*-type and *H. grimshawi*-type are indicators of cold lakes and *Procladius* and *C. cylindraceus*-type are indicators of warm lakes [11, 38]. Although the cold-indicating *Paracladius* [39] had positive relationship with increasing temperatures, a major decrease in its abundance in Lake Unterer Giglachsee during the most recent decades, corresponding to the further increasing Alpine temperatures, was apparent (Fig. 3). In fact, a previous study from an adjacent Niedere Tauern lake (Moaralmsee) showed that *Paracladius* can still be very abundant at present at these altitudes (~1800–1900 m a.s.l.) [34]. However, modern samples from the Swiss Alps show that the occurrence of this Alpine key species at this altitude is very close to its climatic threshold [17].

The PCA results showed that the most recent samples (0–4 cm in chironomids and 0–3 cm in cladocerans) were separated from the older samples along the PCA axis 1, although the patterns were complex (Fig. 5). Importantly for the present study, the PCA axis 1 scores, representing the main direction of variance in species data, showed correlation to the Northern Hemisphere and Northeastern Alpine temperature evolution (Fig. 6, Table 1) providing at least some evidence for climate-driven ecosystem change in Lake Unterer Giglachsee. Furthermore, the cluster analysis identified a mutual faunal zone between 6 and 7 cm (Figs. 3 and 4), representing the timing of ~1900 AD, and this threshold was also evident in the faunal assemblage scores as a difference along the secondary PCA axis (Fig. 5). In climatic context, this timing coincides with the accelerated increase in Northern Hemisphere temperatures (Fig. 6).

In contrast to data on zooplankton from Italian and Swiss Alpine lakes and a lake from the Niedere Tauern

Alps where *Daphnia* has generally declined since pre-industrial times [32, 40], the present results showed a slight increase in relative *Daphnia* abundance towards the present. The Alpine zooplankton turnover has most likely been initiated and driven by altered limnological ranges in water temperature, ice-cover period, stratification, and primary production. In the Niedere Tauern lakes, distribution of *Bosmina* is restricted by a climatic threshold at ~2000 m a.s.l., above which it is absent [33]. Our study lake is located below this threshold at 1922 m a.s.l. allowing *B. longispina* to dominate (Fig. 4). Therefore, because *B. longispina* has already been present and dominated in Unterer Giglachsee for centuries, *Daphnia* has not have had the chance to succeed in the lake, while its abundance in the present continues to be very low. With the current knowledge, it is still too early to predict whether *Daphnia* will further increase or decrease (cf. [32]) following the climate warming, but it is very likely that *Bosmina* will remain as the dominant taxon in this lake in the future as well based on its Alpine distribution patterns and preference for warmer lakes [17, 33]. It should also be noted that it was not possible to determine the influence of food web changes on the Cladocera community dynamics in this study. However, it has been shown that *Daphnia* is especially sensitive to fish predation [41] and Lake Unterer Giglachsee is currently inhabited by the Arctic char (*Salvelinus alpinus*). Because there is no knowledge on the size or presence of past fish populations in the lake, we cannot separate the predation influence on the invertebrate communities from the influence of climate change.

Although the Cladocera assemblages in Unterer Giglachsee have been rather homogenous during the past centuries (Fig. 4) with only subtle post 1900 AD changes, the Chironomidae assemblages showed a more heterogeneous nature (Fig. 3). For the future, presuming that the climate will continue warming, we project that the taxa having significant relationship with temperature (Table 1) will experience the most drastic changes. Such extrapolation into the future is possible due to the rather linear, although accelerated, increase in temperature through our record. However, this approach cannot resolve the serious questions related to the climatically indirect multiple stressors that may cascade in the future. Despite the missing knowledge on the influence of these stressors and the probable no-analog situation, it is likely that the cold indicating taxa, such as *Sergentia* and *P. austriacus*-type, will decrease in abundance, while warm-preferring taxa, such as *Cricotopus* species, will increase their success. These changes can be direct causes of surface water warming and lengthened open-water season or indirect causes through increased productivity, changes in mixing depth, and ecological interactions (e.g., [42]), for example. In Lake Unterer Giglachsee, *B. longispina* and *Paracladius* are close to their climatic thresholds [17, 33]. Because *B. longispina* is already dominant at the lake and will likely further benefit from the increasing temperatures, the most critical key species in Unterer Giglachsee is probably the cold-adapted *Paracladius*, which has a very sharp climate-driven distribution range in the Alps [17]. The boundary of this distribution range is extremely close to the current climate conditions at Lake Unterer Giglachsee. Therefore, if the climatic threshold for *Paracladius* is crossed in the future, the potential sudden disappearance of this Alpine key species can dramatically change the ecosystem composition and functioning of this climatically ultra-sensitive lake.

As a conclusion, the 20th century faunal changes in Lake Unterer Gighlachsee are in agreement with previous studies from the Niedere Tauern Alps [32, 43, 44] and other Alpine regions [16, 45, 46] emphasizing the role of climate-mediated limnological variables in structuring Alpine aquatic communities. Under this context, we predict that the altitudinal distribution and abundance of specific climate-sensitive invertebrate taxa will experience significant changes in the future along with increasing temperatures, resulting in substantial ecosystem reorganization in Alpine lakes.

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