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Late-glacial chironomid-based temperature reconstructions for Lago Piccolo di Avigliana in the southwestern Alps (Italy)

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Abstract

Chironomid headcapsules were used to reconstruct late glacial and early-Holocene summer temperatures at Lago Piccolo di Avigliana (LPA). Two training sets (northern Sweden, North America) were used to infer temperatures. The reconstructed patterns of temperature change agreed well with the GRIP and NGRIP $\delta^{18}O$ records. Inferred temperatures were high during the Bølling (ca 19 °C), slowly decreased to ca 17.5 °C during the Allerød, reached lowest temperatures (ca 16 °C) during the Younger Dryas, and increased to ca. 18.5 °C during the Preboreal. The amplitudes of change at climate transitions (i.e. Oldest Dryas/Bølling: 3 °C, Allerød/Younger Dryas: 1.5 °C, and Younger Dryas/Preboreal: 2.5 °C) were smaller than in the northern Alps but similar to those recorded at another site in northeastern Italy. Our results suggest that (1) Allerød temperatures were higher in the southern Alps and (2) higher during the Preboreal (1 °C) than during the Allerød. These differences might provide an explanation for the different responses of terrestrial-vegetation to late glacial and early-Holocene climatic changes in the two regions. Other sites on both sides of the Alps should be studied to confirm these two hypotheses.

Keywords: Late Glacial; Temperature; Chironomids; Vegetation dynamics; Italy

1. Introduction

Chironomids (non-biting midges) are insects having three major life stages: a terrestrial winged-insect stage, four aquatic larval stages, and a pupae stage. The larval headcapsule is made of chitin ($C_6H_{12}O_5N$) which is preserved in lake sediments for thousands of years. The headcapsules recovered from lake-sediment can be grouped into 'taxa', at genus-level in taxonomical classification and in certain cases even to species level, making it possible to characterize changes in past assemblages through time. Different taxa have specific ecological preferences and tolerances with respect to environmental variables, including temperature (Walker, 1990), contributing to their usefulness as proxy indicators. Chironomids are influenced by temperature for pupation, emergence, growth, feeding, and hatching (Walker and Mathewes, 1989; Lindegaard, 1997). As a

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consequence, both air and water temperatures have strong influence on the distribution of chironomids. Air and water temperatures are strongly correlated, and water-temperature data are less abundant than air-temperature data (e.g. Livingstone and Lotter, 1998), so altitude-corrected air-temperature data can be used to develop inference models.

Inference models have been developed in many regions (e.g. Walker et al., 1997; Lotter et al., 1997; Olander et al., 1999; Brooks and Birks, 2000b; Larocque et al., 2001; Porinchu et al., 2002; Heiri et al., 2003a; Larocque et al., 2006) and successfully applied to reconstruct millennial-scale climatic oscillations during the late glacial (summary in Brooks, 2006) and patterns of temperature changes (e.g. Palmer et al., 2002; Heiri et al., 2004; Larocque and Hall, 2004) that agreed well with reconstructions obtained from other proxies and archives (e.g. Bradley, 2000). In addition to validating chironomid-inferred temperature changes with proxy records, a comparison with meteorological data over the past 100 years suggest that chironomid-based reconstructions adequately inferred temperatures (Larocque and Hall, 2003). On the other hand, as suggested for a Holocene record by Velle et al. (2005), local changes in pH, water chemistry, and productivity may also influence chironomid assemblages and override the regional temperature signal. Brooks (2006) suggests that complex interactions among various factors affecting the chironomids during the Holocene might alter the temperature signal.

In the northern and western parts of the Alps various climatic reconstructions of the late-glacial climate are based on pollen and chironomid assemblages (e.g. Lotter et al., 2000; Hofmann, 2001; Heiri et al., 2003b). In the southern Alps, however, the lack of quantitative climate reconstructions (e.g. Heiri et al., in press) limits our comprehension of climatic patterns and of the biotic response of vegetation to climatic changes on both sides of a large mountain belt such as the Alps.

In this study we focus on two main features in the sequence of vegetation changes discussed by Finsinger et al. (2006): (1) deciduous oak (*Quercus*) expanded during the Allerød (~13,200 cal yr BP) in the southwestern Alps, i.e. ca. two millennia before its expansion in the northern Alps and Central Europe, and (2) hazel (*Corylus avellana* L.) expanded around 11,000 cal. yr BP, more or less at the same time as its expansion in northwestern and central Europe. From these results, Finsinger et al. (2006) suggested that (1) during the Allerød summer temperatures were higher in the southwestern Alps than in the northern Alps allowing the earlier establishment and expansion of *Quercus* populations in the southern Alps and (2) that during the early-Holocene summer temperatures in the southern Alps were higher than during the Allerød, explaining the establishment and expansion of *Corylus* populations only at that time and not during the Allerød. To verify these two hypotheses, we attempted a temperature reconstruction using chironomids at Lago Piccolo di Avigliana (LPA), concentrating our efforts on the Late Glacial/Holocene transition.

2. Methods

2.1. Study site

Lago Piccolo di Avigliana (LPA; 45°03′N; 07°23′E, 365 m a.s.l), is located in northwestern Italy (Fig. 1) at the boundary between the Po plain and the western Alps. The landscape was shaped by the Dora Riparia glacier during a series of advances. The lake is surrounded by moraines deposited during the Last Glacial Maximum (LGM), and the area has been ice-free since then (Petrucci et al., 1970). During the Younger Dryas glaciers were limited to small mountain tops outside the lake's catchment (Carraro et al., 2002).

The lake is 12 m deep and has an area of 0.58 km^2, with a catchment area of 8.1 km^2. The lake is part of a system of four distinct sediment basins separated by moraines. LPA receives its water from two seasonal inlets and from a drained basin where peat was excavated during the 19th century (Volta, 1955). The outlet is connected with Lago Grande di Avigliana. The exposed areas were intensively cultivated until the first half of the 20th century. Metamorphic rocks (calc–shists, serpentine, and peridotite) dominate the catchment (Petrucci et al., 1970).

The overlying vegetation in flat and humid areas is dominated by *Alnus glutinosa*, *Ulmus minor, Fraxinus excelsior*, *Quercus robur*, and *Salix alba*. *Castanea sativa*, *Quercus petraea*, *Corylus avellana*, *F. excelsior*, and *Quercus pubescens* dominate the hills, where drought-adapted species (*Q. pubescens*, *Opuntia vulgaris*, and *Celtis australis*) are abundant on south-exposed slopes. *Fagus sylvatica* and *Abies alba* are present at higher altitudes in the montane belt (Tosco, 1975).

The climate in the region is temperate, with annual precipitation of ca 880 mm (between 1797 and 1987 AD) and the mean annual temperature of 13 °C. January is the coldest month, with an average temperature of 2.2 °C, while July is the warmest month with an average of 23.9 °C (Biancotti et al., 1998). Temperatures in August are on average 20 °C (www.underground.com/NORMS).

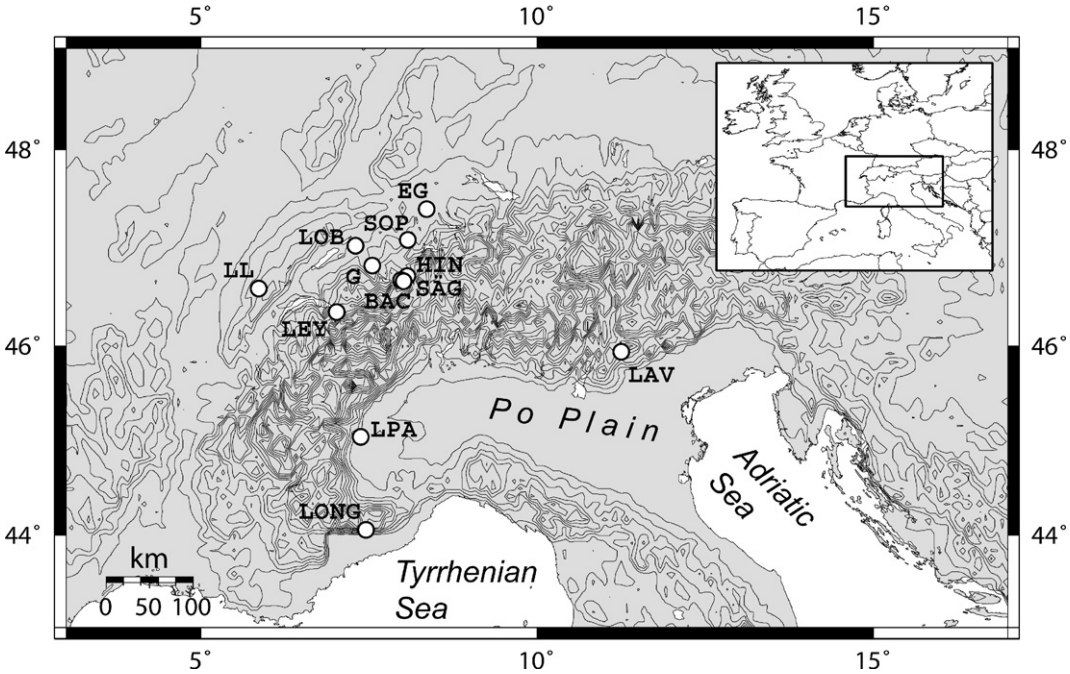

Fig. 1. Location map of Lago Piccolo di Avigliana (LPA) in northern Italy. Sites for comparisons are (EG) Egelsee (Larocque et al., submitted for publication), (HIN) Hinterburgsee (Heiri et al., 2003b) (LEY) Leysin (Brooks, 2000), (G) Gerzensee (Brooks, 2000), (SOP) Soppensee (Hofmann, 2001), (LOB) Lobsigensee (Hofmann, 2001), (SÄG) Sägistalsee (Heiri et al., 2003a), (BAC) Bachalpsee (Lotter et al., 2006), (LL) Lac Lautrey (Heiri and Millet, 2005), (LONG) Lac Long Inférieur (Gandouin and Franquet, 2002), and (LAV) Lago di Lavarone (Heiri et al., in press).

2.2. Sampling

Two sediment cores were extracted with an 8 cm-diameter piston corer (Merkt and Streif, 1970) from a floating platform. Core AVP1 (1492 cm in length below the sediment surface) was used for pollen, plant macrofossils, and loss-on-ignition (Finsinger, 2004; Finsinger et al., 2006; Finsinger and Tinner, 2006) and for chironomid analysis, and AVP2 was used to verify the core stratigraphy. The cores were brought to the laboratory and kept at 4 °C before sampling.

2.3. Loss-on-ignition

1 cm^3 samples were used for measuring the organic-matter content by loss-on-ignition at 550 °C for 4 h and for measuring carbonate content at 950 °C for 2 h (Heiri et al., 2001).

2.4. Chironomid analysis

Chironomid headcapsules were picked under a stereomicroscope from samples previously sieved in 200 µm and 100 µm meshes and dried for preservation. The head capsules were mounted on slides in a Hydro–Matrix solution. At least 50 head capsules per sample were identified. This number should provide accurate temperature estimates (Heiri and Lotter, 2001; Larocque, 2001). Identification of the headcapsules was made at 400× and 1000× and mainly followed Wiederholm (1983) and Oliver and Roussel (1983). *Glyptotendipes* type 2 referred to Fig. 10.30 in Wiederholm (1983). *Polypedilum* IIIC was similar to Fig. 10.61c in Wiederholm (1983).

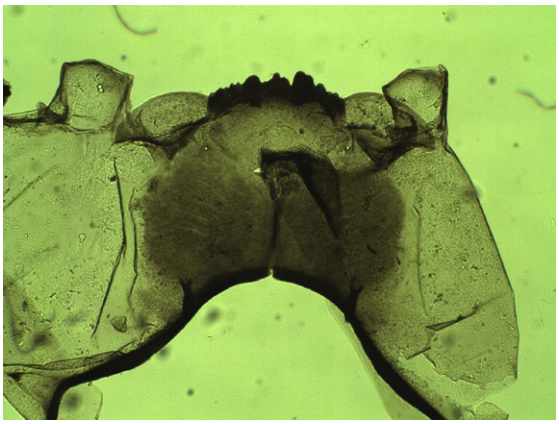

Fig. 2. Picture of a headcapsule with deteriorated mentum. The shape of the ventromental plates suggest that this headcapsule is that of *Chironomus*.

Table 1
Radiocarbon dating used to establish the depth-age relationship of the Lago Piccolo di Avigliana sediment core

Laboratory code	Depth (cm)	Reported age (^{14}C BP±1σ)	Mean calendar age (cal BP±2σ)
Erl-4558	175	1565±43	1445±95
Erl-4804	192	1741±38	1640±100
Erl-4805	335	3175±51	3410±150
Erl-4803	422	4460±51	5090±210
Erl-4802	481	5230±51	6040±140
Erl-4801	634	8723±63	9725±225
Poz-3930	678	9290±50	10,465±185
Poz-3918	695	9320±60	10,495±205
Erl-4800	714	10,248±64	12,050±305
Poz-3931	732	10,320±50	12,175±225
LST	768	11,066±12	12,975±55
Erl-4799	775	11,525±80	13,400±180
Erl-4798	806	12,395±102	14,500±450
Erl-4797	888	14,614±111	17,550±500
Poz-6497	909	14,930±80	18,275±325

Specialized keys were used to identify the Tanytarsini tribe (Brooks et al., 1997; Brooks et al., 2007). Here "*Tanytarsus* without spur" refers to Tanytarsini headcapsules without spur on their antennal pedestal. "*Tanytarsus* with spur" refers to Tanytarsini headcapsules with spur on their antennal pedestal.

Tanypodinae were separated following Rieradevall and Brooks (2001). If the headcapsules were too dirty to show the setae pores, they were classified as *Procladius* (square head, mandibles with dark ends) or Pentaneurini.

Some headcapsules had very deteriorated mentum (Fig. 2). Based on the shape of the ventromental plates, most of these deteriorated headcapsules were identified as belonging to the *Chironomus*-group. However, if the second last lateral tooth on the mentum was smaller than the other lateral tooth, headcapsules were classified as *C. anthracinus*-group, while headcapsules with lateral teeth of equal length were assigned to the *C. plumosus*-group.

2.5. Dating

The chronology was based on 13 ^{14}C AMS dates on identified terrestrial plant macrofossils (Finsinger and Tinner, 2006; Finsinger et al., 2006), one additional ^{14}C date on wood, and a microscopic distal ash layer stratigraphically and chemically identified as the Laacher See Tephra (LST) by Blockley et al. (2005) (Table 1). The weighted mean age of the middle cluster (i.e. 11,066±12 ^{14}C BP, Baales et al., 2002; 13,070–12,910 cal yr BP) was used for the LST. All ^{14}C ages were calibrated with the OxCal 3.1 program (Bronk Ramsey, 1995; Bronk Ramsey, 2001) and the IntCal04 data set (Reimer et al., 2004). The depth-age relationship (Fig. 3) was estimated by means of a generalized mixed-effect regression (Heegaard et al., 2005). In order to force the depth-age model to estimate the LST age, a higher weight (weight=1) was assigned to the tephra-inferred age.

2.6. Statistical analysis

The chironomid diagram was drawn with the C2 program (Juggins, 2003). Zonation methods followed the

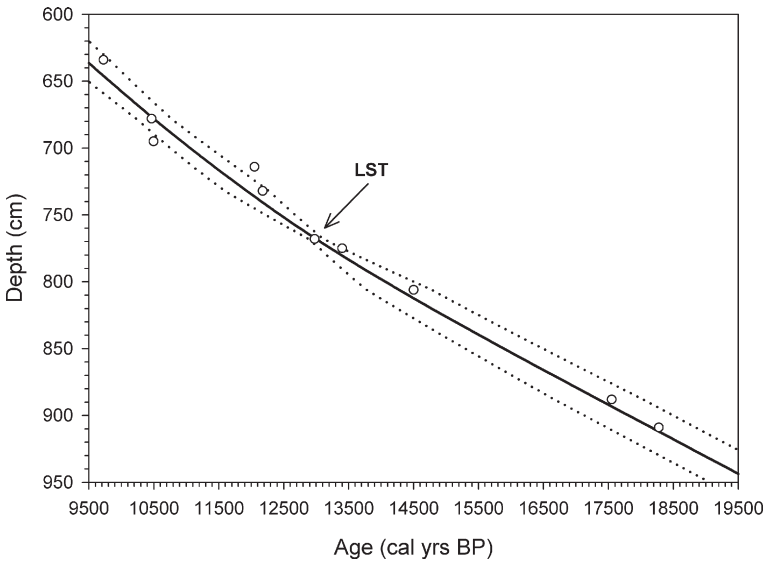

Fig. 3. Depth-age relationship (continuous line) between age (in calibrated years BP) and depth (in cm). Empty circles: calibrated ^{14}C dates. Dotted lines: upper and lower 2σ ranges for depth-age relationship.

recommendations of Birks and Gordon (1985) and Bennett (1996). Numerical zonation was carried out by optimal partitioning using sum of squares criteria (programs TRAN (Version 1.41) and ZONE (Version 1.2; Juggins, 1991)), and the number of statistically significant zone limits was determined with the broken-stick model (software BSTICK version 1.0, Bennett, 1996).

The major compositional changes of chironomid assemblages were assessed with ordination techniques, i.e. detrended correspondence analysis (DCA) (Hill and Gauch, 1980; Kovach, 1995). Percentage data were detrended by segments and square-root-transformed to stabilize their variances. Rare species were down weighted. If the longest gradient length was <2, linear response models (Principal Correspondence Analysis (PCA)) were used to assess the variance in the chironomid assemblages through time. The directional changes of assemblages through time were assessed by passively plotting the fossil samples into the transfer functions' canonical correspondence analysis (CCA) (e.g. Bigler et al., 2002). All ordinations were carried out with the program CANOCO version 4.5 (ter Braak and Smilauer, 2002).

2.7. Temperature reconstruction

To obtain chironomid-inferred temperatures, two models based on Larocque et al. (2006) and Larocque et al. (2001) were used. The model based on modern surface samples from 100 lakes in Sweden (Larocque et al., 2001) was used to infer temperatures from taxa that might have a similar biogeographical distribution similar to those found in the southern Alps. However, this transfer function lacked many taxa (e.g. *Glyptotendipes*, *Glyptotendipes* type 2, and *Endochironomus*) that have warmer optima (Larocque et al., 2006) and were well represented in the fossil samples. Also, the taxonomy was less well defined, for example the tribe Pentaneurini was not separated into different taxa in this model. In contrast, the transfer function from North America (a modification from Larocque et al., 2006; surface samples from 82 lakes) included all taxa present in the fossil samples, and taxonomy more refined than that of the Swedish transfer function. Other studies have reconstructed temperature for sites located outside the spatial range of the transfer functions' training-set sites, though from similar biogeographical areas (e.g. a Swiss transfer function to reconstruct temperature in a lake in France (Heiri and Millet, 2005), a Norwegian transfer function to reconstruct temperature in a lake in the UK (Langdon et al., 2004), a Swedish transfer function to reconstruct temperatures in various Russian lakes (e.g., Andreev et al., 2004; Ilyashuk et al., 2005). The North American transfer function used in this study was also used to reconstruct late-glacial temperature changes in a Swiss lake and provided accurate estimates of temperature-change amplitudes (Larocque et al., submitted for publication) when compared with the GRIP record (Dansgaard et al., 1993). In a previous attempt of merging a transfer function from North America and a transfer function from Europe, Lotter et al. (1999) found that a) the temperature optima of taxa estimated by these two transfer functions were similar and highly correlated and b) all inference-models based on these two training sets revealed similar patterns of Late-Glacial temperature change, also suggesting that amplitudes of temperature changes can be reconstructed at one site with a transfer function from another biogeographical region (i.e. a different continent).

Here the "applicability" of the two transfer functions will be estimated by three statistical methods: 1) the fit-to-temperature, 2) the presence of modern analogues, and 3) the percentage of taxa present in the fossil records and in the training sets. These statistical analyses follow recommendations by Birks (1998). The fossil samples were passively added to a CCA analysis of both training sets to determine if the fossil samples resembled the training-set samples and evaluate the applicability of the training sets. Lakes with characteristics (e.g. depth, elevation, pH) similar to those of LPA were found in both training sets, although all lakes in the Swedish training set were located at higher latitudes than LPA.

The North American transfer function comprised lakes in a study previously published (Larocque et al., 2006). Recently 10 other lakes were added to this training set, leading to a unimodal distribution of most chironomid taxa through the temperature gradient. The inference model developed with WA-PLS 2 components had an r^2 jack of 0.85 and a root-mean-square-error of prediction (RMSEP) of 1.12 °C. Details on this new transfer function are given below. The Swedish transfer function had an r^2 of 0.65, and the RMSEP was 1.12 °C (Larocque et al., 2001).

3. Results

3.1. Depth-age relationship

Estimated 2σ ranges are <200 years for ages <14,000 cal yr BP and increase to 300 years for ages >15,700 cal yr BP (Fig. 3). The difference between this depth-age relationship and the previously published relationship (Finsinger et al., 2006; Finsinger and Tinner, 2006) was at most as large as the 2σ ranges of the present model.

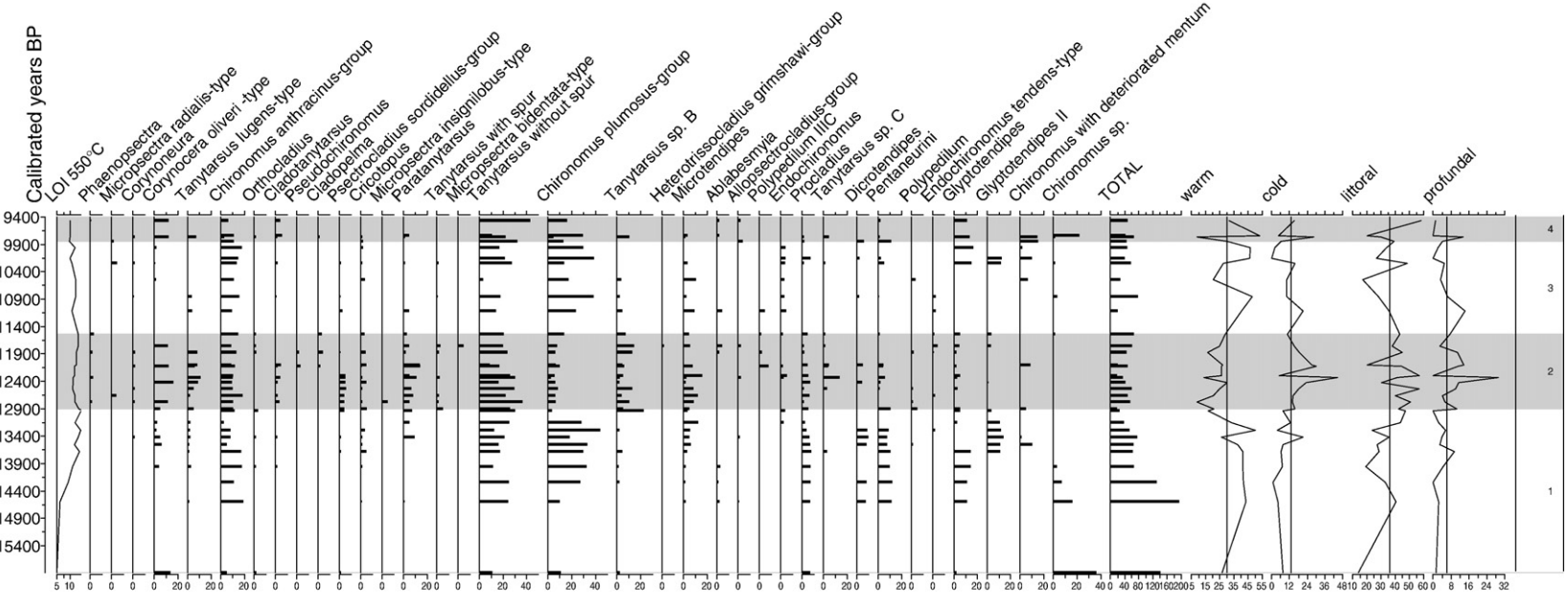

Fig. 4. Chironomid stratigraphy at LPA. Loss on ignition (LOI) is in % dry weight (%dw). The percentages for each taxon are represented. TOTAL is the number of headcapsules in a sample. Warm is the percentage of taxa considered as warm indicators, cold is the percentage of taxa considered as cold indicators, littoral is the percentage of taxa considered as littoral taxa, and profundal is the percentage of taxa considered as cold taxa.

3.2. Chironomid assemblages

Of the 43 taxa found in the fossil assemblages, 30 had percentages higher than 3% in at least two samples and were represented in Fig. 4. Five significant zones were calculated with the ZONE program (Juggins 1991), but zones 4 and 5 consisted of only three samples (2 in zone 4, one in zone 5), so these two zones were combined.

Zone 1 (ca 15,800–12,700 cal yr BP) was dominated by the *Chironomus plumosus*-group, *Chironomus anthracinus*-group, and *Tanytarsus* without spur. *Microtendipes* and *Glyptotendipes* had percentages reaching 20%, *Microtendipes* having higher values at the end of the zone while *Glyptotendipes* had higher percentages at the beginning. *Procladius*, *Tanytarsus lugens*-type, *Glyptotendipes* type 2, and *Corynocera oliveri* were present at about 5%. The number of headcapsules was high (200) at the beginning of the zone but decreased to about 50 at the end of the zone. Warm taxa had percentages above the average (between 45 and 55%) during that period. Littoral and profundal taxa were below the average, but littoral taxa dominated (around 25%) compared to profundal taxa (around 4%).

In zone 2 (ca 12,700–11,700 cal yr BP) both *Chironomus*-groups decreased. Cold taxa with optima lower than 10 °C (*Paratanytarsus*, *Phaenopsectra*, *Pseudochironomus*, *Tanytarsus lugens*-type, *Tanytarsus* sp. C, *Tanytarsus* with spur, *Cladopelma*, and *Corynocera oliveri*) increased. They made up to 40% of the assemblage. *Phaenopsectra* and *Pseudochironomus* were only recorded in this zone. Warm taxa (*Glyptotendipes, Pentaneurini*, *and Endochironomus*) were present, but their percentages were lower than the average. The number of headcapsules ranged between 40 and 80. Littoral and profundal taxa percentages were above the average in that zone, and littoral taxa still dominated (between 50–60%) over profundal taxa (16–32%).

In Zone 3 (ca 11,700–9,800 cal yr BP), both *Chironomus*-groups increased again to percentages similar to those in zone 1. Many of the cold taxa decreased or disappeared. Pentaneurini, *Procladius*, and *Corynocera oliveri* increased at the end of this zone.

In the last zone (ca 9,800–9,400 cal yr BP) both *Chironomus*-groups decreased, while *Corynoneura*, *Glyptotendipes*, and *Tanytarsus* sp. B increased.

3.3. PCA analysis

A DCA analysis (not shown here) indicated that the longest gradient length was 1.793, suggesting the use of linear response models for further analysis. PCA axis 1 explained 22.5% of the variance, whereas PCA Axis 2 explained 11.1% (Fig. 5). Samples belonging to zone 2 (12,700 and 11,700 cal yr BP) were mainly located on the right-hand side of the PCA diagram (axis 1 scores > 0), indicating their dissimilarity with respect to chironomid assemblages in samples of zones 1, 3, and 4 (Bølling, Allerød, and early Holocene) (axis 1 scores < 0).

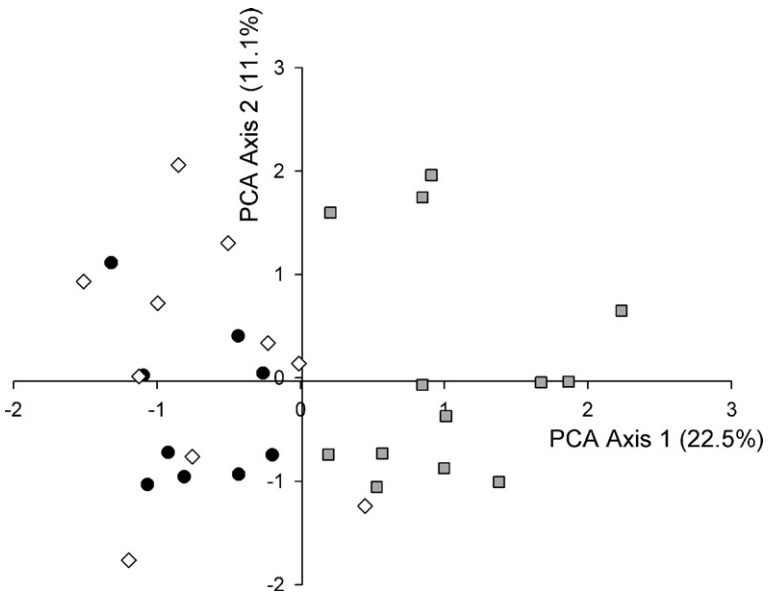

Fig. 5. PCA analysis of the fossil records. The black circles are samples from zone 1 (ca 15,800 to 12,700 cal yr BP), the gray squares are samples from zone 2 (ca 12,700 to 11,700 cal yr BP), and the white diamonds are samples from zones 3–4 (ca 11,700 to 9400 cal yr BP).

3.4. CCA analysis

With the North American transfer function, all the fossil samples were located within the assemblages of the training set (Fig. 6a). CCA Axis 1 explained 45.3% of the variance, and CCA axis 2 13.5%. Most fossil samples moved along the temperature gradient, indicating that chironomid-assemblage changes were mainly driven by temperature. Water depth might have been also at play, but its influence was less important than temperature.

Most samples were located at the higher limit of the temperature gradient in the Swedish training set (Fig. 6b), suggesting that warmer climate would be less accurately inferred with this transfer function. CCA Axis 1 explained 35.6% of the variance and CCA axis 2 15.6%. The assemblages were clearly ordered along a line parallel to the temperature gradient, suggesting that this factor was the main driving force for compositional changes.

3.5. The North American transfer function

Ten more lakes were added to the training set previously published by Larocque et al. (2006). All were located north of the transect, up to Ellesmere Island. Fig. 7 illustrates the distribution of the taxa (only those present in the LPA fossil record) along the temperature gradient. Based on this graph and the calculated temperature optima, *Micropsectra radialis*-type,

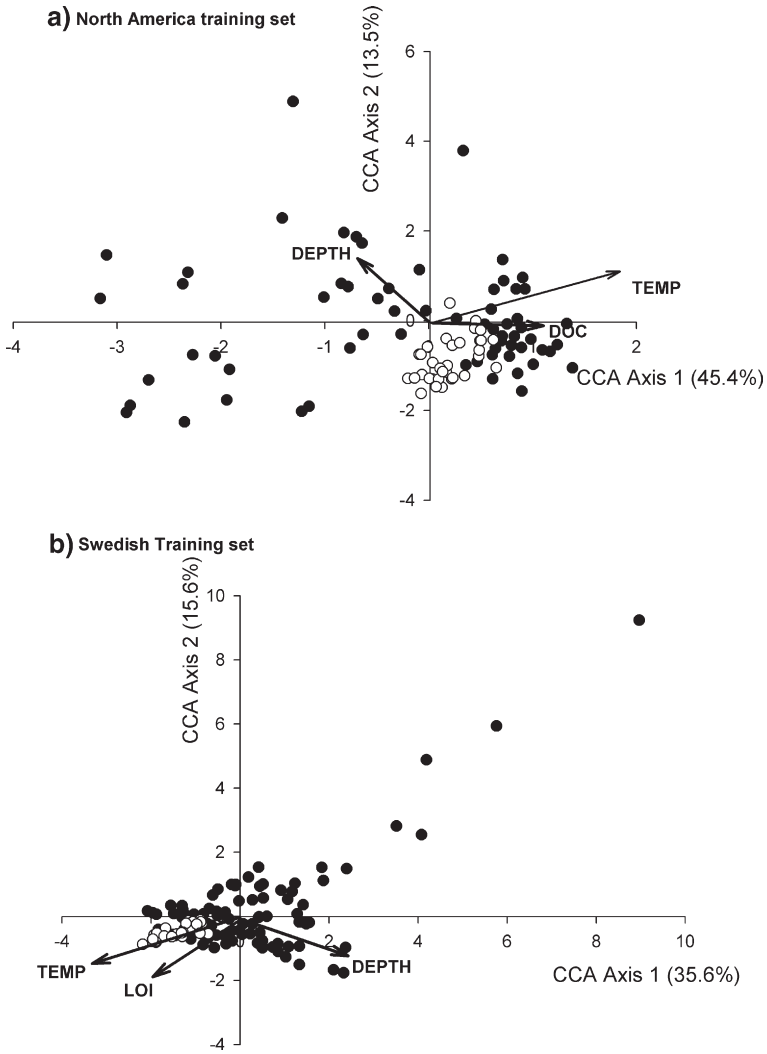

Fig. 6. CCA analysis of the training-set lakes (black circles) with the fossil samples (empty circles) added passively in the ordination for a) the North American training set and b) the Swedish training set.

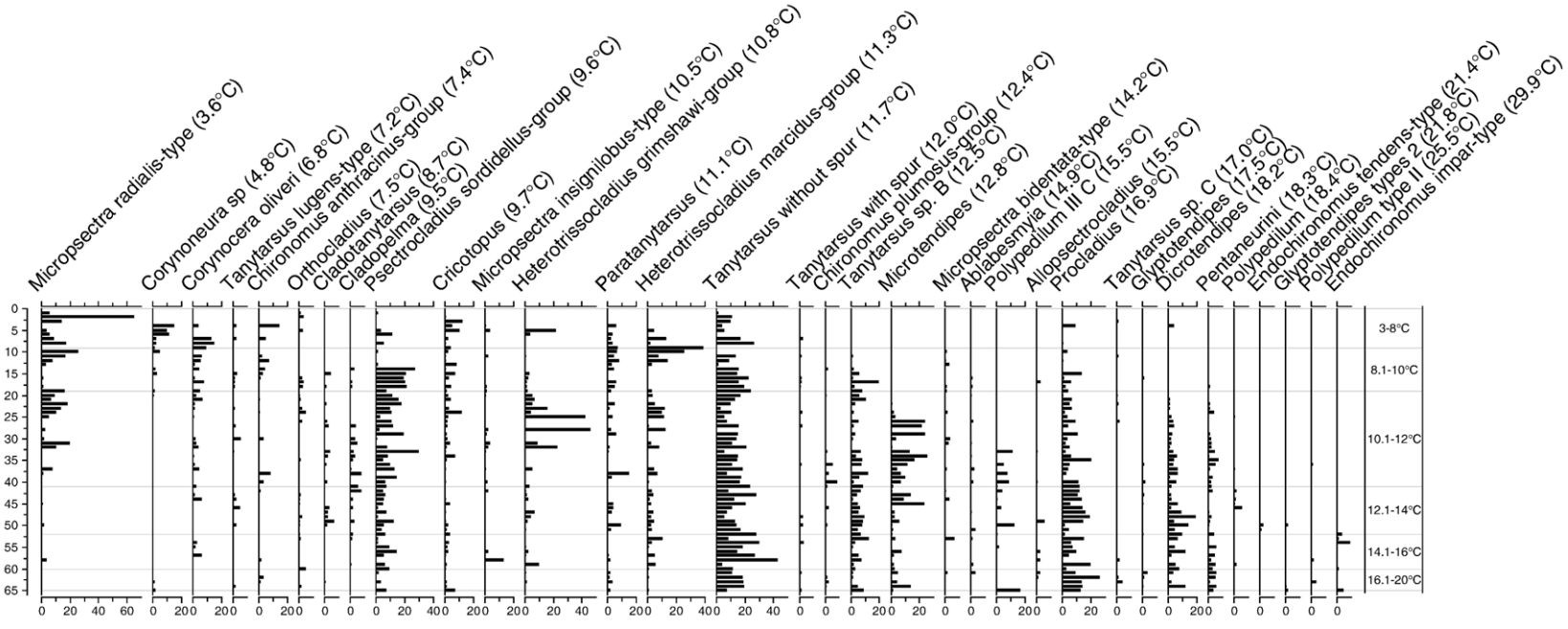

Fig. 7. Chironomid abundances (as percentages; only taxa present in the fossil record of LPA) in the extended North American training set (i.e. training set as in Larocque et al. (2006) plus 10 additional lakes). Samples ordered by increasing temperature (°C).

Corynoneura, *Corynocera oliveri*, *Cricotopus*, *Chironomus anthracinus*-group, *Psectrocladius sordidellus*-group, *Orthocladius*, *Cladopelma*, *Cladotanytarsus*, and *Tanytarsus lugens*-type are cold (optimum less than 10 °C) taxa, and *Polypedilum*, *Endochironomus impar*-type, *Glyptotendipes* type 2, *Glyptotendipes*, *Tanytarsus* sp.C, *Pentaneurini, Dicrotendipes*, and *Procladius* are warm taxa (with temperature optima >15 °C). When compared to optima in the Swedish and Swiss training sets (Larocque et al., 2001 and Lotter et al., 1999, respectively) three taxa had warmer temperature optima in those training sets, namely *Cladopelma*, *Cladotanytarsus*, and *Microtendipes*. On the basis of these differences, these taxa were not included in the sum of cold taxa (Fig. 4). *Chironomus plumosus*-group, which has a temperature optimum at 12.5 °C (Fig. 7), has optima higher than 15 °C in the Swedish and the Swiss training sets (unpublished data) and was thus considered as a warm taxon in the sum in Fig. 4. All other taxa had similar optima in all transfer functions considered.

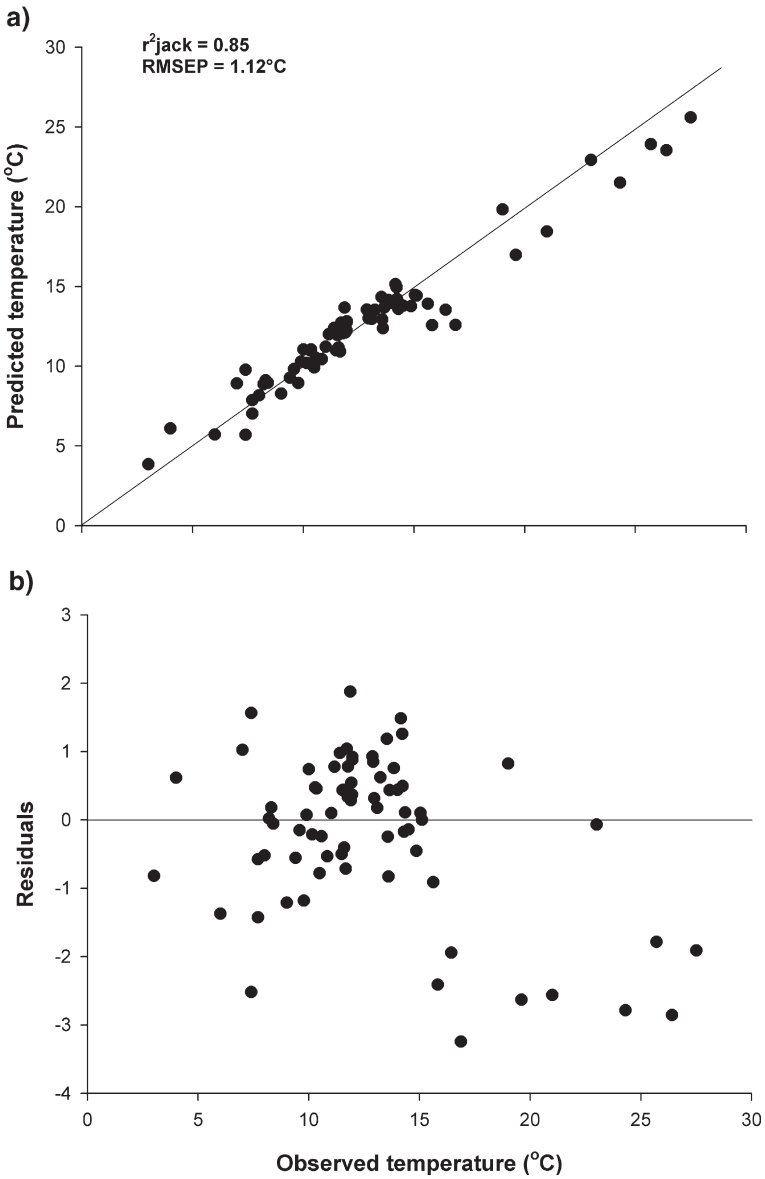

Fig. 8. a) Relationship between chironomid-inferred temperatures (predicted) and observed temperatures. The line indicates the 1:1 relationship. b) Relationship between residuals (i.e. predicted – observed temperatures) and observed temperature.

The relationship between observed and predicted temperatures is shown in Fig. 8a and the residuals in Fig. 8b. Those two graphs indicate that temperatures of lakes at the warmer edge of the gradient tend to be under-estimated.

3.6. Temperature reconstruction

The two inference models provided similar reconstructions (Fig. 9), although they were based on samples with low percentages of taxa present in the Swedish training set. Ten samples had less than 80% of taxa present in the Swedish training set, 2 had poor-fit to temperature and no-modern analogues, and one sample had poor-fit to temperature. With the North American training set, four samples had poor-fit-to-temperature, and one inference was based on an assemblage with less than 80% of taxa in the training set. However, with both transfer functions, a temperature maximum of 18.8 °C at ca. 14,700 cal yr BP was recorded. A peak in the δ^{18}O ratios was similarly recorded in Greenland ice cores (e.g. Dansgaard et al., 1993; Rasmussen et al., 2006) at the onset of the Bølling. In the reconstruction based on the North American transfer function, inferred temperature gradually decreased subsequently, and three small-amplitude temperature decreases were recorded at ca. 13,900, 13,400 and 12,900 cal yr BP that might correspond to climatic cooling events recorded in several Greenland ice cores and dated at ca. 14,000, 13,600, and 13,100 cal. yr BP in NGRIP. These three decreases were also inferred with the Swedish transfer function, but the decreasing trend between 14,700 and 12,800 cal yr BP followed a different pattern. With the latter transfer function the sample dated at ca 13,700 cal yr BP provided a higher inferred-temperature (18.7 °C) than with the North American training set. Thus the average inferred-temperature during the Bølling was 18.7 °C, while during the Allerød it was 17.5 °C. Between ca 12,600 and 11,700 cal. yr BP inferred-temperatures are low, as recorded with both transfer functions and in the NGRIP and GRIP records. The average temperature during that period, corresponding to the Younger Dryas, was 16.0 °C, indicating a change with amplitude of ca 1.5 °C. A sharp increase of temperature followed this colder period, when temperatures with both transfer functions oscillated around 18.5 °C. The amplitude of temperature change at the Younger Dryas/early Holocene transition was ~2.5 °C. Although the NGRIP and GRIP records indicate an increasing trend in temperature until ca. 9000 cal yr BP, the reconstruction based on the North American transfer function showed more or less stable temperatures around 18 °C, whereas the inferred-temperatures ranged between 17.5 and 18.5 °C with the Swedish transfer function.

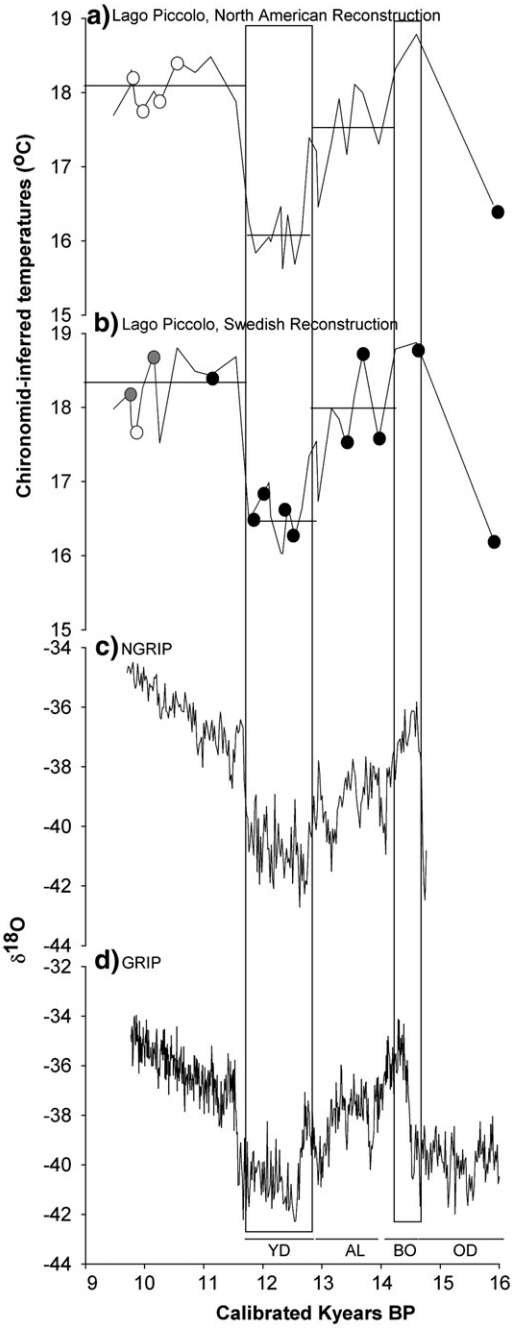

Fig. 9. Chironomid-inferred temperatures at LPA calculated with a) the North American and b) the Swedish transfer functions compared to c) the NGRIP (Rasmussen et al., 2006) and d) GRIP δ^{18}O records (Dansgaard et al., 1993 and Rasmussen et al., 2006). Black circles=less than 80% of taxa present in the set; grey circle=poor-fit to temperature and no-modern analogues; empty circle=poor-fit to temperature. OD=Oldest Dryas, BO=Bølling, AL=Allerød, YD=Younger Dryas.

4. Discussion

4.1. Ecosystem changes at LPA

The PCA analysis indicated that changes in chironomid assemblages occurred throughout the late glacial at LPA. The most distinct change (as indicated by the PCA analysis, Fig. 5) occurred contemporaneous with the Younger Dryas (Fig. 9), when cold taxa as well as littoral and profundal taxa had percentages higher than the average, suggesting that these changes were not created by a change in lake-water level. Depth was a factor explaining the distribution of chironomids in most training sets (e.g. Olander et al., 1999; Korhola et al., 2000; Brooks and Birks, 2000b; Larocque et al., 2001, 2006), and it was always hard to disentangle the effect of each factor on the chironomid assemblages. But the CCA analysis also indicated that temperature was mainly driving the chironomid assemblages at LPA, not depth.

The ecosystem changes in response to the Younger Dryas were less striking at LPA than in chironomid records from lakes located north of the Alps (Table 2). Common taxa found in most sites were *Tanytarsus lugens*-type (a cold-stenotherm), *Microtendipes* (an intermediate taxon) and *Tanytarsus* sp. C. The latter has a high temperature optimum in the Swedish and North American training sets (17.0 °C), but it was described as a cold taxon in Switzerland (Brooks and Birks, 2000b). At LPA, the assemblages throughout the record were dominated by intermediate and warm taxa, very likely because this site is located at lower elevation and had a warmer climate than the studied sites in the north. The changes were nevertheless still important enough to record a pattern of temperature changes similar to the pattern in the GRIP and NGRIP records.

4.2. Patterns of climatic change as inferred from chironomid records in Europe

The late-glacial temperature reconstruction at LPA showed a climatic-change pattern similar to those recorded by $\delta^{18}O$ in Greenland ice-core records (e.g. GRIP and NGRIP, Fig. 9). Temperatures increased with an amplitude of ca 3 °C from the Oldest Dryas to the Bølling. A similar amplitude was reconstructed with chironomid records at Lago di Lavarone, northeastern Italy (Heiri et al., in press), in Switzerland at Egelsee (Larocque et al., submitted for publication) and Gerzensee (Lotter et al., unpublished data), and at Lac Lautrey, France (Heiri and Millet, 2005), as well as from pollen assemblages at Gerzensee (Lotter et al., unpublished data). At LPA highest inferred temperatures were recorded at the onset of the Bølling, and they slowly decreased during the Allerød. A similar trend was reconstructed with chironomid assemblages at Whitrig Bog, southeastern Scotland (Brooks and Birks, 2000a), at Hawes Water, northern England (Bedford et al., 2004), and at Egelsee (Larocque et al., submitted for publication), as well as by $\delta^{18}O$ records north of the Alps (von Grafenstein et al., 1999, 2000; Frisia et al., 2005). At Lago di Lavarone, however, Allerød chironomid-inferred temperatures were slightly higher (by 1 °C) than during the Bølling, suggesting that a temperature change might explain the expansion of thermophilous tree-species at that time, as discussed by Finsinger (2004). Although the same increase of thermophilous tree-species was observed at LPA (Fig. 10), the reconstructed temperatures from chironomids were not higher during the Allerød than during the Bølling at our studied site.

Coldest air temperatures were inferred at LPA during the Younger Dryas, when chironomid taxa having cold/

Table 2
Chironomid assemblages at various sites during the late glacial in the Alpine region

Periods	LPA, I	Lac Lautrey, FR	Lac Long, FR	Soppensee, CH	Gerzensee, CH	Leysin, CH
Bolling/ Allerod	*C. plumosus-group*	*Chironomus*		*C. plumosus-group*	*C. plumosus-group*	
	Pentaneurini		*Tanytarsus sp.*	*Tanytarsus sp.*	*Tanytarsus sp.*	*Tanytarsus sp.*
	Glyptotendipes					*Tanytarsus sp. C*
		Tanytarsus sp				
	Dicrotendipes	*Dicrotendipes*			*Dicrotendipes*	
		P. sodidellus		*Sergentia*		
	Procladius	*C. ambigua*	*C. oliveri-type*			
Younger Dryas	*C.oliveri-type*	*Micropsectra*	*Micropsectra*		*Micropsectra*	*Micropsectra*
	Tanytarsus sp. B					
	T. lugens-type	*T. lugens-type*	*Tanytarsus sp.*	*T. lugens-type*	*Tanytarsus sp. C*	*Tanytarsus sp. C*
	Microtendipes	*Microtendipes*	*Microtendipes*			
	P. sordidellus-group		*Diamesa*		*Parakiefferiella*	*Parakiefferiella*
	Paratanytarsus		*Sergentia coracina*			

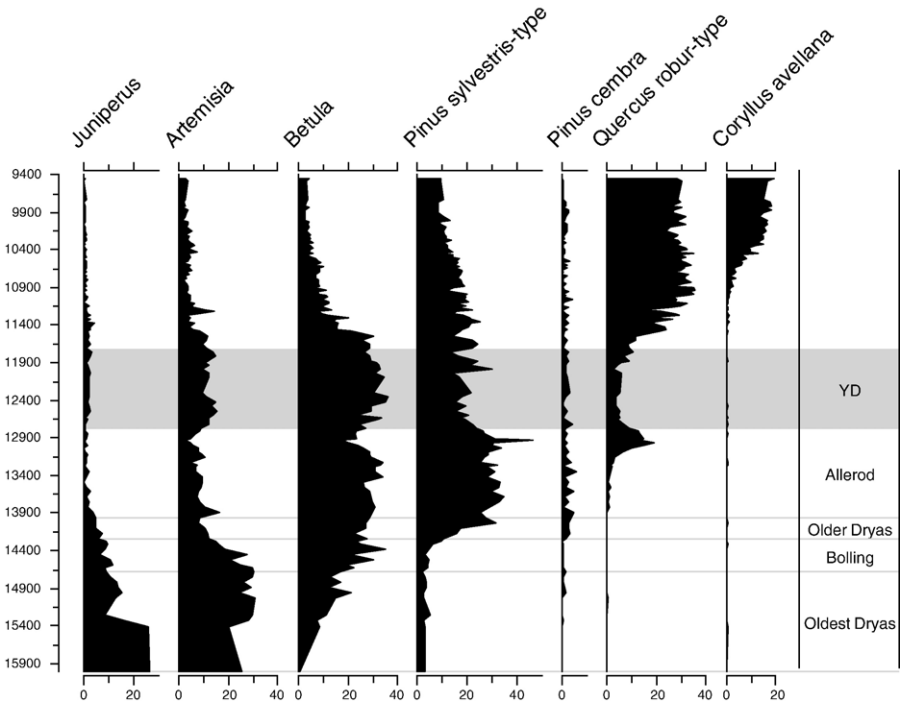

Fig. 10. Summary of the pollen stratigraphy. Only the major tree taxa are presented. A complete diagram can be found in Finsinger (2004) and Finsinger et al. (2006).

intermediate optima increased and warm indicator taxa decreased. The amplitude of change between the Bølling/Allerød period and the Younger Dryas was about 1.5 °C. This amplitude was smaller than recorded at Hawes Water (Bedford et al., 2004) and at Whitrig Bog (Brooks and Birks, 2000a) but in a range similar to that recorded in northeastern Italy (Heiri et al., in press) (Table 3).

Early-Holocene temperatures were generally high at the beginning of the Holocene in the northern Alps and northern Europe (Porinchu and Cwynar, 2000; Stefanova et al., 2003; Caseldine et al., 2003; Heiri et al., 2004, 2003; Larocque and Hall, 2004). Mean annual temperature in and around the Alps increased by ca 3–6 °C in the early Holocene (Eicher, 1994; Schwander et al., 2000). Instead, the amplitude of temperature increase at LPA was about 2.5 °C, which is slightly smaller than at higher latitudes but similar to the amplitude recorded at Lago di Lavarone (Heiri et al., in press).

Table 3
Comparison of temperature reconstructions in the northern and southern Alps

Site	Latitude	Proxy	Allerød
North Alps			
Switzerland			
Egelsee	770 m a.s.l.	Chironomids	15–16 °C
Gerzensee	603 m a.s.l.	Pollen/cladocera	12–14 °C
France			
Lac Lautrey	788 m a.s.l.	Chironomids	18.4–19.4 °C
South Alps			
Italy			
LPA	365 m a.s.l.	Chironomids	17.5–18.5 °C
Lago di Lavarone	1100 m a.s.l.	Chironomids	17–18 °C

The reported temperatures have been calculated at LPA's elevation.

4.3. Terrestrial vegetation responses to climatic changes

The temperature reconstruction at LPA attempted to test two hypotheses posed by the differences and similarities observed in the pollen records of northern and southern sites of the Alps. One major difference was that *Quercus* populations expanded 2000 years before in the southern sites, while *Corylus* appeared in the early Holocene, a timing similar to the one observed at the northern sites (Finsinger et al., 2006). Two hypotheses were suggested to explain these differences/similarities (Finsinger et al., 2006; Vescovi et al., 2007):

1) During the Allerød, summer temperatures might have been higher in the southern Alps than in the northern Alps, explaining the expansion of *Quercus* 2000 years prior to its expansion in the northern Alps.

2) During the early Holocene, summer temperatures in the southern Alps might have been higher than during the Allerød, explaining the expansion of *Corylus*.

The pollen diagram at LPA (Fig. 10) showed the same vegetation pattern as recorded at other sites in the southern side of the Alps: the establishment of *Quercus* before the Younger Dryas, while *Corylus* established in the Preboreal. To answer the first hypothesis, we compare temperature inferences during the Allerød between the northern sites and the southern sites. To do so, a correction factor of 0.6 °C per 100 m (Lotter et al., 1999) was used to correct for the different elevation of sites. Allerød temperatures were effectively higher in the southern Alps by 2–3 °C compared to the sites in Switzerland (Table 3). However, at Lac Lautrey (France), where *Quercus* did not expand before the Younger Dryas (Magny et al., 2006), higher summer temperatures were inferred as well. This might be due to the fact that *Corynocera ambigua*, considered as a cold-stenotherm taxon in many models (Olander et al., 1999; Brooks and Birks, 2000b; Larocque et al., 2001, 2006) was present at high percentages in the fossil assemblages of Lac Lautrey, but it was not present in the Swiss training set used for temperature reconstruction (Heiri and Millet, 2005). Possibly if *C. ambigua* had been included in the training set the temperature estimates would have been in the same range as those reconstructed at Egelsee (Larocque et al., submitted for publication), thus colder than reconstructed. These results suggest that the first hypothesis could be accepted, that climate was warmer during the Allerød in the southern Alps than in the northern sites.

In order to test the second hypothesis, Allerød and early-Holocene inferred temperatures at two sites in northern Italy (LPA: this study; and Lago di Lavarone: Heiri et al., in press) were compared. At LPA the average temperature during the early Holocene (18.5 °C) was 1 °C higher than the average temperature during the Allerød (17.5 °C). The difference is, however, within the error of estimate of the method (RMSEP = 1.12 °C) and was therefore not significant. On the other hand, comparisons between modern instrumental records of temperature and chironomid-inferred temperatures indicate that small variations of temperature of about 0.5 °C can be reconstructed by chironomid analysis (Larocque and Hall, 2003; Larocque et al., submitted for publication). In addition, the Swedish and the North American transfer functions have a tendency to under-estimate high temperatures, a common feature ('edge effects') of WA and WA-PLS based climate reconstructions (Birks, 1998). When the temperature estimates of LPA are compared with chironomid-inferred temperatures obtained at Lago di Lavarone, correcting for elevation by a lapse rate of 0.6 °C per 100 m (Lotter et al., 1999), the temperatures during the Bølling/Allerød and the Younger Dryas periods were similarly inferred at LPA and at Lago di Lavarone, but the temperatures in the early Holocene at LPA were ca 2 °C lower than at Lavarone. However, a difference of ca 1.5 °C between the Holocene and the Allerød inferences was also observed at Lago di Lavarone, possibly indicating that early-Holocene summer temperatures were higher than during the Allerød in the southern Alps.

5. Conclusion

The chironomid-inferred temperature changes at LPA seemed to be mostly synchronous with the δ^{18}O-inferred events from Greenland (e.g. GRIP and NGRIP records) and with temperature records in England, Scotland, Norway, and southern Germany. After a warming at the onset of the Bølling, summer temperatures decreased gradually until the end of the Allerød. The Younger Dryas cooling and the subsequent climate warming at the onset of the Holocene were also clearly visible in our chironomid record. However, the amplitude of temperature change at climatic transitions was smaller than observed at sites located in the northern Alps but agreed well with another record in the southern side of the Alps. The comparison between chironomid-inferred temperatures at sites south and north of the Alps indicate that 1) the summer temperatures during the Allerød were higher in the southern Alps, and 2) the early Holocene was slightly warmer than the Allerød, as hypothesized on the basis of a comparison of several pollen stratigraphies. Other pollen-independent temperature reconstructions should be obtained to validate further these hypotheses, which may be fundamental to extend our understanding of past biotic responses to climatic changes.

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