Younger Dryas and Allerød summer temperatures at Gerzensee (Switzerland) inferred from fossil pollen and cladoceran assemblages

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Abstract

Linear- and unimodal-based inference models for mean summer temperatures (partial least squares, weighted averaging, and weighted averaging partial least squares models) were applied to a high-resolution pollen and cladoceran stratigraphy from Gerzensee, Switzerland. The time-window of investigation included the Allerød, the Younger Dryas, and the Preboreal. Characteristic major and minor oscillations in the oxygen-isotope stratigraphy, such as the Gerzensee oscillation, the onset and end of the Younger Dryas stadial, and the Preboreal oscillation, were identified by isotope analysis of bulk-sediment carbonates of the same core and were used as independent indicators for hemispheric or global scale climatic change. In general, the pollen-inferred mean summer temperature reconstruction using all three inference models follows the oxygen-isotope curve more closely than the cladoceran curve. The cladoceran-inferred reconstruction suggests generally warmer summers than the pollen-based reconstructions, which may be an effect of terrestrial vegetation not being in equilibrium with climate due to migrational lags during the Late Glacial and early Holocene. Allerød summer temperatures range between 11 and 12°C based on pollen, whereas the cladoceran-inferred temperatures lie between 11 and 13°C. Pollen and cladocera-inferred reconstructions both suggest a drop to 9–10°C at the beginning of the Younger Dryas. Although the Allerød–Younger Dryas transition lasted 150–160 years in the oxygen-isotope stratigraphy, the pollen-inferred cooling took 180–190 years and the cladoceran-inferred cooling lasted 250–260 years. The pollen-inferred summer temperature rise to 11.5–12°C at the transition from the Younger Dryas to the Preboreal preceded the oxygen-isotope signal by several decades, whereas the cladoceran-inferred warming lagged. Major discrepancies between the pollen- and cladoceran-inference models are observed for the Preboreal, where the cladoceran-inference model suggests mean summer temperatures of up to 14–15°C. Both pollen- and cladoceran-inferred reconstructions suggest a cooling that may be related to the Gerzensee oscillation, but there is no evidence for a cooling synchronous with the Preboreal oscillation as recorded in the oxygen-isotope record. For the Gerzensee oscillation the inferred cooling was ca. 1 and 0.5°C based on pollen and cladocera, respectively, which lies well within the inherent prediction errors of the inference models. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Allerød; cladocera; Gerzensee oscillation; oxygen isotopes; palaeoclimate; pollen; Preboreal oscillation; summer temperatures; transfer functions; Younger Dryas

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1. Introduction

Reconstructions of Late Glacial climate in the Alps have traditionally been based on glaciological features such as snow-line depressions (e.g. Maisch, 1995) and on biostratigraphical methods such as pollen or coleopteran (e.g. Atkinson et al., 1986). While snow-line depressions and fossil coleopteran assemblages can be expressed in terms of temperature changes, pollen-analytical results are commonly interpreted in a more qualitative and descriptive way. Recently, several different numerical inference models have been developed that allow quantitative climate reconstructions from fossil assemblages (e.g. Guiot, 1991; Walker et al., 1991; Pienitz et al., 1995; Lotter et al., 1997). Apart from pollen- and chironomid-based temperature reconstructions (e.g. Guiot et al., 1992; Lotter et al., 1999; Birks et al., 2000; Brooks and Birks, 2000), such transfer-function models have, however, rarely been applied to other biostratigraphical data (e.g. Duigan and Birks, 2000). Terrestrial vegetation, as represented by the fossil pollen record, may be expected to show a lagged response to a climatic change (Wright, 1984). Therefore, the use of a multi-proxy approach, including both terrestrial and aquatic organisms, is commonly considered a useful means to estimate the response lags of different organisms to climatic change.

The onset of climate change and the duration of transition phases between one climate state and another cannot often be unequivocally deduced from fossil biological assemblages because of the possibility of lagged response of these organisms. Oxygen isotopes may be used as independent indicators for climatic change, as they are considered to reflect climate change without delay (Wright, 1984; Ammann, 1989). Oxygen isotopes have also been used to reconstruct Late Glacial climate change. Many oxygen-isotope stratigraphies derived from lake deposits on the Swiss Plateau and in the Alps have revealed a characteristic pattern consisting of three major shifts on the order of 2–3‰ in $\delta^{18}O$ (e.g. Eicher and Siegenthaler, 1976; Eicher, 1987). Generally, shifts towards more negative values have been interpreted as reflecting decreases in mean annual temperatures and vice versa. Different isotope-fraction-ation processes, as well as the presence of detrital carbonates, do, however, hamper any straightforward interpretation of bulk carbonate $\delta^{18}O$ values in terms of temperature (Siegenthaler and Eicher, 1986; Lister, 1988).

The available biological and stable-isotope multi-proxy data from Gerzensee (Ammann et al., 2000) and the recent availability of different organism-specific climate transfer functions for the Alps (e.g. Lotter et al., 1997) provide the basis for a quantitative climatic reconstruction at this classical site for Swiss Late Glacial climate history (Eicher and Siegenthaler, 1976). The aim of the present study, therefore, is to reconstruct summer temperatures using different quantitative inference models and to estimate the magnitude of temperature change at the onset and end of the Younger Dryas stadial, as well as during the known minor Late Glacial climatic oscillations. The comparison of an oxygen-isotope stratigraphy, as an independent indicator for climate change, with such temperature reconstructions then allows estimates of the lags in the response of different organisms.

2. Site

Gerzensee (7°33′E, 46°50′N) is located on the Swiss Plateau close to the border of the Alps at an elevation of 603 m asl. The lake lies in a glacier-formed landscape characterised by moraines and drumlins and was formed at the end of the last glaciation (Eicher, 1979). Today it has a maximum water depth of 10 m, a volume of 0.164 km³, and a surface area of 0.27 km². Its catchment is 2.6 km², of which 80% is used as agricultural land, 5% is wooded, and 15% are urban areas.

The present-day climate in the Gerzensee catchment has a mean January temperature of −0.8°C, a mean July temperature of 17.6°C, a mean summer temperature (June, July, August) of 16.6°C, and a mean annual temperature of 8.3°C. Annual total precipitation is about 1050 mm.

3. Methods

The biostratigraphical data from Gerzensee used in this study include 118 pollen samples containing

a total of 124 taxa (Wick, 2000), whereas the cladocera data include 107 fossil samples and 14 taxa (Hofmann, 2000). The taxonomic consistency, especially for the fossil and modern pollen data sets where two different analysts were involved, has been verified (Birks, 1994, 1995). The oxygen-isotope data include 117 samples between the sediment depths of 169 and 300 cm.

For the temperature reconstruction using the quantitative inference models, pollen and spores of aquatic plants were excluded, whereas spores of terrestrial pteridophytes were included in the pollen sum. In the cladoceran fauna only the non-planktonic chydorids were used in the inference models. Pollen and chydorid percentages were transformed to their square root values in an attempt to stabilise their variance. The modern pollen data used for the inference models include 126 samples with a total of 272 taxa (Birks et al., in preparation) spanning a summer temperature (average of the months June, July, August) gradient between 4.5 and 20.6°C, whereas the modern cladoceran training set includes 61 samples and 30 taxa extending over a temperature gradient of 6.6 to 21.8°C (Lotter et al., 1997). The inference models used included linear-based partial least squares regression and calibration (PLS; Martens and Naes, 1989), and two unimodally based models (Birks, 1995): a weighted-averaging model with deshrinking by inverse regression (WA; ter Braak and van Dam, 1989; Birks et al., 1990), and a weighted averaging partial least squares model (WA-PLS; ter Braak and Juggins, 1993). All models were implemented using the program CALIBRATE (version 0.82, S. Juggins and C.J.F. ter Braak, unpublished software). The inspection for modern analogues, using squared chord distance as the dissimilarity coefficient, was carried out with the computer program MAT (S. Juggins, unpublished software) based on the *k*-nearest neighbour technique (ter Braak, 1995).

4. Results and discussion

4.1. Chronological setting

The Gerzensee oxygen-isotope stratigraphy measured on bulk-sediment samples (Schwander

et al., 2000) displays the two well-known major shifts at the onset and the end of the Younger Dryas, as well as the minor shifts termed the Gerzensee oscillation (Eicher and Siegenthaler, 1976) and the Preboreal oscillation. Both minor oscillations have been correlated with similar events in the isotope records from Greenland ice cores (Siegenthaler et al., 1984; Lotter et al., 1992b; Schwander et al., 2000). The Gerzensee oscillation is believed to be equivalent to the Killarney or amphi-Atlantic oscillation, sensu Levesque et al. (1993a,b). Because $\delta^{18}O$ shifts reflect climate change without a time lag, and because they are recorded in different archives (ice cores, marine and lacustrine sediments), they are considered to represent synchronous events at a hemispheric or even a global scale (Oeschger et al., 1984; Wright, 1989; Lotter et al., 1992b). Based on a numerical comparison of the fine-resolution Gerzensee curve with the GRIP oxygen-isotope record, Schwander et al. (2000) were able to date the Gerzensee record using the absolute ice-core chronology. On the basis of this correlation, each sample at Gerzensee comprises generally a time-span of between 10 and 20 years. Despite the lack of radiocarbon dates, estimates of sediment accumulation rates at Gerzensee are thus possible. Furthermore, the well-known problems in relation to the plateau of constant radiocarbon age at the Younger Dryas–Preboreal transition are overcome (Ammann and Lotter, 1989; Lotter et al., 1992a).

In the following, we use the terminology for the different Late Glacial sections established by Schwander et al. (2000). The terms Gerzensee oscillation (GE-O), Allerød–Younger Dryas transition (AL–YD), Younger Dryas (YD), Younger Dryas–Preboreal transition (YD–PB), and Preboreal oscillation (PB-O) have been defined by these authors solely on the basis of the oxygen-isotope stratigraphy. These terms, as they are used in this contribution, do not refer to chronozones or pollen assemblage zones that happen to have the same names (Ammann et al., 1994).

4.2. Inference models

The use of linear- or unimodal-based models for environmental reconstruction depends on the

relationship between organisms and the environmental variable of interest (ter Braak, 1987, 1995; Birks, 1995). Therefore, all taxa occurring in more than 20% of the modern samples were first tested statistically for their response models in relation to summer temperature by means of a hierarchical series of response models fitted by generalised linear modelling. In the modern pollen data 35.6% of the taxa showed statistically significant unimodal responses (skewed or symmetric) to summer temperature, 45.6% had sigmoidal response models, and 18.9% showed no statistically significant response to summer temperature (Birks et al., in preparation). In the modern cladoceran dataset, 42.1% showed a (symmetric) unimodal and 42.1% had a sigmoidal response model, whereas 15.8% of the taxa showed no significant relationship to summer temperature (Lotter et al., 1997). These results suggest that the use of either a linear or a unimodal inference model only might poorly model a large part of the taxon responses in the data. We therefore decided to apply both linear and unimodal models for the reconstruction of Late Glacial summer temperatures at Gerzensee, namely one linear (PLS) and two unimodal models (WA and WA-PLS). The PLS and WA-PLS models were selected to give a low root mean

squared error of prediction (RMSEP) in leave-one-out cross-validation and to contain the smallest number of 'useful' components (see Birks, 1998). The models are thus 'minimal adequate models' (sensu Birks, 1998). The statistical performances of the different summer temperature inference models are given in Table 1. The strength of the relationship between observed and predicted values (based on leave-one-out cross-validation), as expressed by the coefficient of determination (r^2), of all models is high, explaining 85–89% of the variance in all the pollen models, whereas the cladoceran models explain between 67 and 82% of the variance. The prediction errors (RMSEP) are measures of the predictive abilities of the modern training set. The RMSEP for the pollen-based models range between 1.3 and 1.4°C, whereas the RMSEP for the cladoceran models are slightly larger, between 1.5 and 1.8°C. The general features of the pollen and the cladoceran temperature reconstructions are comparable (Figs. 1 and 2). In the pollen-based models WA-PLS inferred the lowest summer temperatures and PLS suggested intermediate values. For the cladoceran-based models PLS inferred the lowest summer temperatures and WA-PLS gave intermediate values. WA models inferred the highest summer temperatures

Table 1

Statistics for the modern training sets in relation to summer temperature inference models (according to Birks et al., in preparation; Lotter et al., 1997). The range of sample-specific prediction errors for the individual fossil samples is also given for each inference model

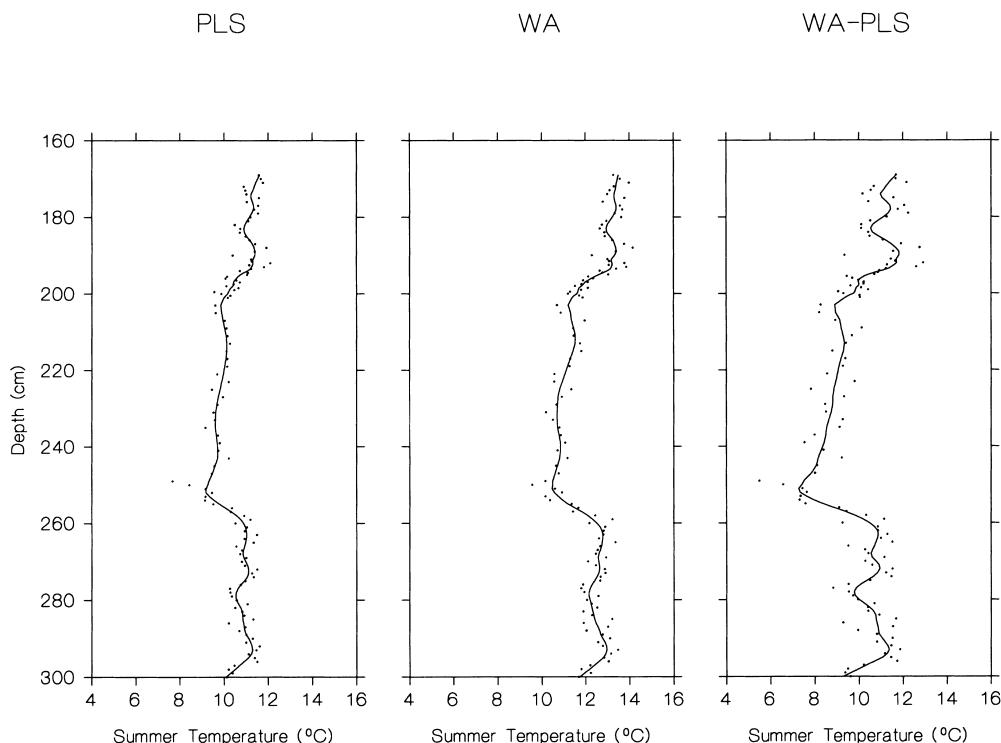| Model		Pollen	Cladocera
PLS	number of components	3	2
	$r^2_{(apparent)}$	0.971	0.868
	$r^2_{(jack-knifed)}$	0.872	0.760
	RMSEP$_{(jack-knifed)}$ (°C)	1.417	1.863
	Sample-specific prediction error range (°C)	1.72–3.29	1.84–2.97
WA	(simple WA, inverse deshrinking)		
	$r^2_{(apparent)}$	0.868	0.848
	$r^2_{(jack-knifed)}$	0.846	0.670
	RMSEP$_{(jack-knifed)}$ (°C)	1.436	1.465
	Sample-specific prediction error range (°C)	1.60–1.66	2.03–2.28
WA-PLS	number of components	3	2
	$r^2_{(apparent)}$	0.967	0.900
	$r^2_{(jack-knifed)}$	0.889	0.821
	RMSEP$_{(jack-knifed)}$ (°C)	1.317	1.597
	Sample-specific prediction error range (°C)	1.56–2.56	1.82–2.49

Fig. 1. Pollen-inferred summer temperature reconstructions using a linear-based partial least squares model (PLS), and unimodal-based weighted averaging (WA) and weighted averaging partial least squares (WA-PLS) models. The dots mark the sample-specific pollen-inferred summer temperatures, whereas the solid line represents a LOWESS smoothed (span=0.1) summer temperature reconstruction.

for both the pollen and cladocera temperature reconstructions (Figs. 1 and 2).

Results of quantitative inference models can only be critically evaluated by independent data (Birks, 1995, 1998). Such independent data as represented by long time-series of, e.g., instrumental records, are very rarely available. Therefore, the plausibility of such models has often been tested by inspecting the fossil records for modern analogues. Birks et al. (1990) proposed to use the second percentile as close and the fifth percentile as good modern analogues. Applying this rule to the Gerzensee data, neither the fossil pollen nor the cladoceran assemblages have good or close modern analogues. This technique, however, looks only for the lowest dissimilarity between fossil and modern assemblages. It does not involve any underlying model of taxon–environment relationship (ter Braak, 1995). Because taxonomically

different assemblages may occur under the same environmental conditions, a lack of modern analogues does not a priori signify that an inference result is wrong. It rather signifies that either there is no present-day analogue for a specific past assemblage because of differences in the environment other than in the variable of interest (e.g. habitat, nutrients, competition, extinction, etc.), or that comparable assemblages have not been sampled in the modern training-set. Furthermore, inference models such as PLS, WA, and WA-PLS use a multivariate indicator-species approach to reconstruct past environments on the basis of specific taxon–environment relationships. Under the assumption that the ecological response to the environmental variable of interest (i.e. optima and tolerances) has not changed over the time of investigation (principle of uniformitarianism), the present-day pattern of taxon abundances in rela-

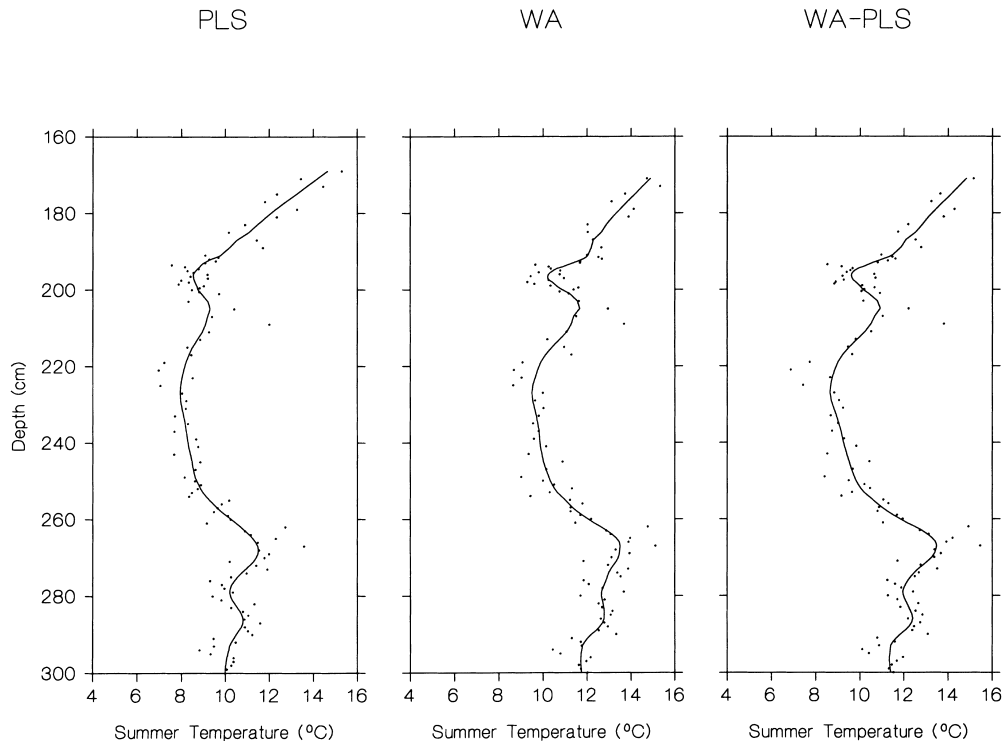PLS   WA   WA-PLS

Fig. 2. Chydorid-inferred summer temperature reconstructions using a linear-based partial least squares model (PLS), and unimodal-based weighted averaging (WA) and weighted averaging partial least squares (WA-PLS) models. The dots mark the sample-specific chydorid-inferred summer temperatures, whereas the solid line represents a LOWESS smoothed (span = 0.1) summer temperature reconstruction.

tion to its environment may be used to infer past environmental conditions (Birks, 1995). Experiments with simulated data of reconstruction performance under 'no analogue' situations (ter Braak, 1995; Birks, 1998) show that WA and WA-PLS (and to a lesser extent PLS) perform remarkably well under 'no analogue' conditions, as long as there are reliable estimates of the optima (WA) or regression coefficients (PLS, WA-PLS) in the inference model for some of the taxa of high numerical importance (high effective numbers of occurrences or N2 values; Hill, 1973) in the fossil data.

An alternative approach to evaluate the reliability of reconstructions is to examine the taxonomic composition and abundance in each fossil sample in relation to the modern training set (Birks, 1995, 1998). The fossil pollen data-set includes 124 taxa, of which 111 are present in the modern training-

set. Most of the missing taxa do not have a strong influence on the outcome of the inference model, as they all have low (between 1 and 3) N2 values (Hill, 1973). Moreover, these taxa have abundances below 0.5% and thus do not influence the temperature reconstruction significantly. There are, however, some taxa with higher N2 values, for example *Ephedra distachya* type, that are absent from the modern training-set. The fossil cladoceran data-set includes 14 taxa, all of which are present in the modern training-set. *Acroperus elongatus* is present in the modern training-set with an N2 of only 1, whereas it has an N2 value of 31.04 and a maximum abundance of 4% in the fossil assemblages. This taxon occurs essentially during the colder phases of the Late Glacial, i.e. during the Gerzensee oscillation and the Younger Dryas stadial (Hofmann, 2000). Based on such low modern occurrences, the cladoceran-environment model

for that taxon may be rather weak. Sample-specific errors of prediction for each reconstructed value for the three different inference models have been estimated by leave-one-out jack-knifing and Monte Carlo simulation (Birks, 1998). The range of these errors is given in Table 1.

4.3. Inferred past climate change

Because it was not possible to decide which of the available inference models was the most appropriate for the fossil Gerzensee data, we used the results of all three models in a combined reconstruction (Birks, 1998, see Fig. 3). We fitted a LOWESS smoother (Cleveland, 1993; Trexler and Travis, 1993) using a span of 0.1 through the data points to permit ease of comparison of the different reconstructions and to produce a consensus reconstruction (Birks, 1998).

The Gerzensee pollen stratigraphy does not show much sign of any major climatic changes, being mainly dominated by *Pinus* and *Betula* pollen throughout the whole sequence (Wick, 2000). The Younger Dryas is very weakly marked in the pollen diagram through a slight increase of herb pollen, especially Gramineae and some heliophilous taxa such as *Artemisia*. It was therefore surprising that the pollen–summer temperature inference models produced such distinct results (Figs. 1–3). The pollen-inferred reconstruction suggests Allerød summer temperatures between 11 and 12°C. For the Younger Dryas (i.e. the phase with low $\delta^{18}O$ values) the pollen-inferred summer temperatures drop to 9–10°C. The lowest pollen-inferred summer temperatures (about 9°C) occur at the onset of the Younger Dryas, whereas the summer temperatures rise constantly by about 1°C throughout the Younger Dryas. For the Preboreal
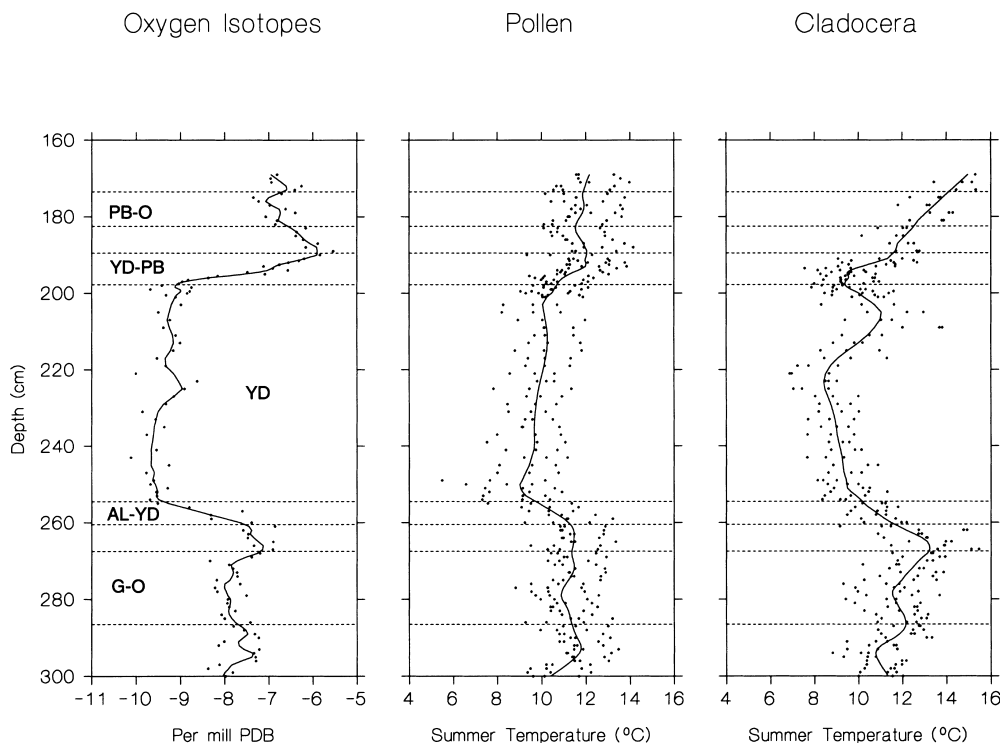

Fig. 3. Oxygen-isotope stratigraphy from Gerzensee and the combined summer temperature reconstructions using the pollen- and chydorid-inferred results of the PLS, WA, and WA-PLS models. The dots mark the sample-specific summer temperatures, whereas the solid lines represent LOWESS smoothed (span=0.1) summer temperature reconstructions. PB-O: Preboreal oscillation; PB: Preboreal; YD: Younger Dryas cold phase; AL: Allerød; G-O: Gerzensee oscillation.

Table 2
Inferred summer temperatures (°C) for Gerzensee, averaged for different periods (see Fig. 3)

Period	Pollen	Cladocera
Preboreal, including the PB oscillation	11.9	12.4
PB oscillation	11.8	13.6
Preboreal, before the PB oscillation	12.0	11.0
YD–PB transitional phase	11.2	9.6
Younger Dryas, including the transitional phases	10.2	9.7
Younger Dryas, cold phase	9.9	9.5
AL–YD transitional phase	10.3	10.6
Allerød, after the Gerzensee oscillation	11.4	13.0
Gerzensee oscillation	11.2	12.0
Allerød, before the Gerzensee oscillation	11.3	11.2
Allerød, including Gerzensee oscillation	11.3	11.9

the pollen-based inference model suggests mean summer temperatures of 11.5–12°C.

The Late Glacial cladoceran assemblages are characterised by changes in the dominance of taxa such as *Acroperus harpae*, *Alonella excisa*, and *Alona affinis* (Hofmann, 2000). The cladoceran-inferred temperature curve suggests generally warmer Late Glacial summers (see Table 2) except during the Younger Dryas cold phase. The inferred Allerød temperatures range between 11 and 13°C (Fig. 3). The coldest part of the Younger Dryas (about 8.7°C), according the cladoceran model, is located in the middle part of the Younger Dryas. Towards the end of the Younger Dryas the clado-ceran-inferred summer temperatures rise from 9–10°C to 10–11°C and then fall again to between 9 and 10°C. The increased inferred temperatures are mainly due to a short-term change in the dominant *Acroperus harpae* and *Alona affinis* that have about the same thermal affinities in the modern training-set. At the same time, taxa with higher temperature optima, such as *Alonella nana*, *Alona guttata*, *Chydorus piger*, and especially *Alonella excisa*, increase in abundance and thus drive the model towards higher inferred temperatures. As neither the oxygen isotopes nor the pollen or other biostratigraphies suggest such a short-term warming towards the end of the Younger Dryas, it is likely that this feature of the cladoceran-inferred summer temperature is not real. We suggest that mechanisms such as changes in habitat availability or

competition may have led to these changes in cladoceran composition (e.g. Hann and Warner, 1987). At the end of the Younger Dryas the cladoceran-inferred summer temperatures rise from around 9.5°C to between 11 and 12°C at the beginning of the Preboreal. During the Preboreal the cladoceran-inferred summer temperatures rise constantly and reach between 14 and 15°C at the end of the investigated stratigraphical section.

Comparison with modern chydorid assemblages in surface sediments of lakes at different altitudes in the Alps (Lotter et al., 1997) shows that the Late Glacial assemblages from Gerzensee have the closest analogues in certain lakes above 1800 m asl, i.e above present-day treeline, whereas today's chydorid assemblages in Gerzensee are distinctly different. Moreover, the chydorid assemblages in lakes above 1800 m asl are very heterogeneous, suggesting that the complex environmental factor of elevation (including temperature) may not be strong enough to produce uniform assemblages and that there are other local environmental factors influencing the composition of the chydorid fauna. For the Gerzensee record this implies that the chydorid succession does not necessarily have to be associated with changes in temperature only.

Generally, the pollen-inferred summer temperature curve follows the oxygen-isotope curve more closely than the cladoceran curve. The cladoceran-inferred temperature reconstructions suggest generally warmer summers than the pollen-inferred reconstructions. The observed discrepancies lie, however, well within the sample-specific prediction errors and the model-inherent prediction errors (see Table 1). There is a good agreement between the two inferred summer temperatures and the drop in the oxygen-isotope curve at the onset of the Younger Dryas (Figs. 3 and 4). At the end of the Younger Dryas, however, the pollen- and cladoceran-inferred curves react differently. The pollen data suggest a minor warming trend (that lies within the model-inherent error bars) before the major increase in $\delta^{18}O$, whereas the cladoceran-inferred warming was lagged. Aquatic organisms, such as cladocera, have a short generation time and thus could react faster to environmental change than terrestrial vegetation such as trees. In the temperate zone the occurrence and abundance
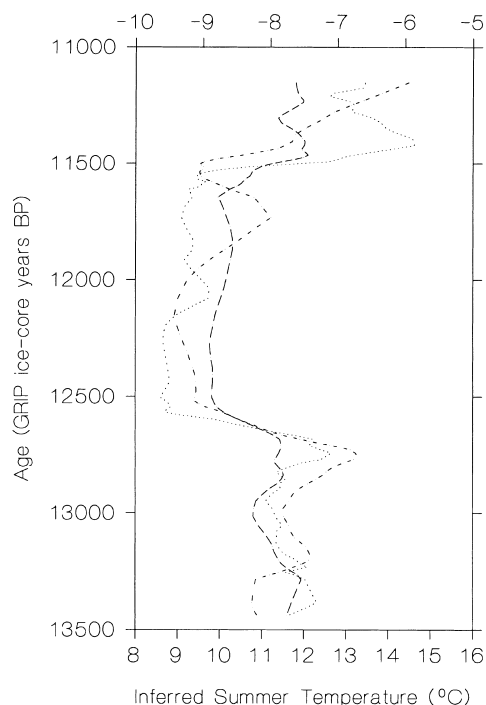
Fig. 4. Oxygen isotopes and inferred summer temperatures plotted versus GRIP ice-core ages B.P. (for details see Schwander et al., 2000). The top scale refers to the oxygen-isotope ratio (solid line) and is expressed in ‰ PDB. The inferred summer temperatures for pollen (dashed line) and chydorids (dotted line) are expressed as degrees Celsius (lower scale).

of aquatic organisms is, however, mainly influenced by the thermic climate and the length of the warm season, whereas for perennial terrestrial vegetation other climatic factors than summer temperatures may also be important: e.g. growing degree days, winter temperatures, late frost, humidity, and seasonality (Woodward, 1987). This may explain some of the discrepancies in the two inferred summer temperature curves. Furthermore, it may be assumed that the terrestrial vegetation was not in equilibrium with climate during the Late Glacial period (e.g. Ammann, 1989). It is therefore possible that the cladoceran-inferred Preboreal summer temperatures are more realistic, whereas the pollen-inferred temperatures may be too low due to a migrational lag of thermophilous plants.

4.4. Magnitude and rates of change

Schwander et al. (2000) correlate the Gerzensee oxygen-isotope record with the GRIP isotope curve and can thus transfer the absolute GRIP time scale to the Late Glacial Gerzensee stratigraphies (Fig. 4). This absolute time scale with small correlation errors, of the order of 10–20 years, allows estimates of the rates of inferred temperature change for the Late Glacial period.

Both the pollen- and cladoceran-inferred reconstructions suggest a cooling that may be related to the Gerzensee oscillation in the oxygen-isotope record. This isotope oscillation had a duration of 413 years (Schwander et al., 2000). The amount of cooling in summer temperatures before the oscillation is ca. 1°C in the pollen and ca. 0.5°C in the cladoceran-inferred summer temperatures. However, as the pollen-inferred summer temperatures already started to decrease before the onset of this isotope oscillation, the magnitude of temperature change might be overestimated.

The isotope curve suggests a duration for the transition Allerød–Younger Dryas of about 150–160 years. The pollen data suggest a decrease in summer temperatures of ca. 2.3°C that occurred over a time-span of about 180–190 years, whereas the change in the cladoceran-inferred summer temperature of ca. 3.1°C occurred within 250–260 years. The Younger Dryas–Preboreal transition in the isotope record lasted 48 years (Schwander et al., 2000). The pollen data suggest an increase of ca. 1.8°C within 160–170 years. Astonishingly, however, the pollen-inferred summer temperatures suggest the onset of climatic warming before the beginning of the major increase in the oxygen isotopes. The cladocera-inferred warming occurred shortly after the increase in $\delta^{18}O$ values. In a first step the cladoceran-inferred summer temperatures rose by 1.6°C within 100 years and then increased further. Neither the pollen nor the cladoceran-inferred summer temperatures give unequivocal evidence for a Preboreal oscillation that has a duration of between 263 (Schwander et al., 2000) and 150 years (Björck et al., 1996). In comparison with the isotope records in ice cores and in continental laminated lake sediments, where the transitional zones at the beginning and end of the

Younger Dryas are of the order of a few decades (e.g. Dansgaard, 1987; Goslar et al., 1993; Fischer, 1996), the biota-inferred cooling and warming at Gerzensee are substantially longer.

Using an indicator plant species approach, Isarin and Bohncke (1999) inferred a phase of maximum cold during the first part of the Younger Dryas in north and central Europe with a July temperature depression of between 4 and 5°C. Their minimum July temperatures, reduced for sea level elevation, for the first part of the Younger Dryas range between 15 and 16°C, whereas they lie between 15 and 17°C for the second part of the Younger Dryas. In a multi-proxy study focusing on the climatic oscillation of the Younger Dryas at a coastal lake site in western Norway, Birks et al. (2000) used different organisms to infer changes in July temperatures. Depending on the organisms used, the decrease in mean July temperature was between 2°C (pollen), 2.5–7.5°C (terrestrial vegetation analogues using plant macrofossils), <5°C (Trichoptera), 3–3.5°C (chironomids), and ca. 1°C (cladocera).

On the basis of the decrease in $\delta^{18}O$ and under the assumption of no evaporative enrichment (see Siegenthaler and Eicher, 1986), changes in mean annual temperatures of 3–6°C have been suggested for the Younger Dryas (Eicher, 1991). Using an ostracod-inference model in Bavarian lakes, von Grafenstein et al. (1994) suggested a Younger Dryas mean annual air temperature decrease of 6–7°C, whereas Schwalb et al. (1994) implied an increased seasonality and thus a more continental climate during the Younger Dryas with a temperature drop of 3–4.5°C. Based on stable-isotope data from ostracods and molluscs analysed in a Gerzensee sediment core close to the one used in this study, von Grafenstein et al. (2000) estimate mean annual air temperature anomalies of −2°C for the Allerød, and between −4.5 and −5.3°C for the Younger Dryas. Using the coleopteran-based Mutual Climatic Range method, Lemdahl (2000) proposes a July temperature decrease at Gerzensee from 20°C during the Allerød to 10°C during the Younger Dryas. Based on geomorphological features in the Alps, such as moraines of Younger Dryas (Egesen) age, depressions of the mean annual temperature of 3–4°C (Haeberli,

1991) and of the mean summer temperature of 1.0–1.4°C (Maisch, 1995) have been deduced. The inferred Younger Dryas summer temperature decrease of between 2 and 3°C and of 0.5–1°C for the Gerzensee oscillation appear rather low compared with the above-mentioned results. However, annual temperatures may not give enough information about climatic seasonality when summer temperatures are only one relevant climatic aspect for the biota. Plant macrofossil analyses (Tobolski and Ammann, 2000) as well as the occurrence of pine stomata at Gerzensee (Wick, 2000) and at many other sites on the Swiss Plateau indicate that the Late Glacial pine–birch woodland opened but persisted during the Younger Dryas (Tobolski, 1985; Lotter, 1988), suggesting that Gerzensee was located below treeline. Treeline is primarily related to summer temperatures (Dahl, 1986, 1998), but a complex set of different climatic and site factors, as well as the specific adaptations of trees, actually defines the forest limit in a particular locality (e.g. Tranquillini, 1992). The present-day treeline ecotone usually coincides with the 10°C July isotherm and with a mean summer temperature of between 9 and 10°C (Dahl, 1986). Given the model-inherent errors of reconstruction, both the pollen and cladocera summer temperature reconstructions would suggest some forest growth at Gerzensee during the Younger Dryas, but would suggest that this site was probably close to the forest ecotone.

5. Conclusions

The multi-proxy study of the Late Glacial at Gerzensee offered a unique opportunity to apply for the first time the pollen and cladocera transfer functions established for the Alps (Lotter et al., 1997; Birks et al., 2000). Having the oxygen-isotope record as an independent and rapid signal for temperature change and using two independent biota, namely terrestrial vegetation represented by the pollen record and aquatic organisms represented by benthic cladocera to hindcast Late Glacial climate change, we can now evaluate the summer temperature inference models. Several points deserve special mention.

(1) Although the environmental gradients in

the modern training-sets, in our case summer temperature, are in most cases long, there are a number of taxa that have their ecological optima outside the lower or upper end of the gradient, with the effect that they show a linear or sigmoidal rather than a unimodal behaviour in relation to the environmental variable of interest. As a consequence, linear-based inference models tend to perform better with these taxa but do not perform well with taxa that have a unimodal relationship to their environment. This makes the choice of a specific inference model difficult, because either model would not perform optimally for some of the taxa present in the fossil record. We therefore use both linear- and unimodal-inference models for regression and calibration purposes, and use the combined results for reconstruction purposes.

(2) The inferred summer temperatures based on both biota are generally consistent and in good agreement. The discrepancies in the reconstructions are within the model-inherent errors of prediction. The inferred temperature changes generally follow the shifts in the oxygen-isotope curve. Inferred summer air temperature anomalies range between -3.5 and $-5.5°C$ for the Allerød, -6.5 and $-7.5°C$ for the Younger Dryas, and between -1.5 and $-5.5°C$ for the Preboreal.

(3) The amplitude of the pollen- and cladoceran-inferred summer temperature change for the Younger Dryas is considerably smaller than suggested by other biotic or abiotic reconstructions. From an ecological point of view a critical evaluation of the available data, however, suggests that at least at Gerzensee the Younger Dryas summer temperatures of 9–10°C make ecological sense. Lower summer temperatures would not allow the persistence of a pine–birch woodland as independently and unambiguously indicated by plant macrofossils and pine stomata.

(4) Pollen-inferred summer temperatures during warm phases such as the Allerød and Preboreal are generally lower than the corresponding cladoceran-inferred temperatures. This might be a result of the terrestrial vegetation not being in equilibrium with climate due to migrational lags of thermophilous taxa during these periods.

(5) The transitional zones in the oxygen isotopes, as observed in ice cores and continental laminated lake sediments, at the onset and end of the Younger Dryas are of the order of a few decades. The corresponding pollen- and cladoceran-inferred temperature decreases and increases, however, are of the order of several decades to centuries, suggesting that biological systems need some time to adapt to the new thermic environment.

(6) Further multi-proxy investigations with consistent and high taxonomical resolution using different terrestrial and aquatic organisms are needed to get a regional, synoptic picture of the magnitude and extent of Late Glacial climate change.

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