Holocene temperature changes in northern Fennoscandia reconstructed from chironomids using Bayesian modelling

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Abstract

The recently developed Bayesian multinomial calibration model, Bummer, was applied to the fossil chironomid assemblages of a lake situated at the present tree-line in northern Fennoscandia to reconstruct patterns in Holocene climates. The results are compared with inferences derived using non-Bayesian weighted averaging partial least-squares regression. The reconstruction exhibits both long-term trends as well as a series of shorter-term oscillations. Abrupt climatic excursions were particularly characteristic for the early Holocene period, with cooling episodes around 9200, 8600 and 8200 cal yr BP. The interval from ca 8000 to 5800 cal yr BP appeared to be warm and stable, but was followed by a pronounced climatic cooling around 5800 cal yr BP leading to a relatively long-lasting mid-Holocene temperature minimum between ca 5800 and 4000 cal yr BP. The reconstruction during the latter part of the Holocene is relatively featureless, which may partly be due to gradual shallowing of the lake by sedimentation that may have affected chironomid compositions, thereby masking the climate signal. The major climatic patterns in our reconstruction agree well with inferences from Greenland ice and marine sediments and are also in line with the previous reconstructions based on diatoms and pollen from the same core, although the finer-scale variations reflected by the three proxies do not always match. The overall results provide evidence for climatic complexity during the Holocene epoch and demonstrate that Bayesian modelling is highly suitable for reconstruction purposes. © 2002 Elsevier Science Ltd. All rights reserved.

1. Introduction

To predict the likely future direction, rate and magnitude of climate change, it is essential to know by how much, at what rate, and how often, climate has changed in the past, and to separate natural component from human-induced initiators of climate change. Because instrumental meteorological records are usually too short to cover the full variation in climate, the history of climate for earlier periods has to be reconstructed from other, indirect 'proxy' indicators. Lake sediments and the various organisms preserved in them have been commonly recognised as a major source of such proxy-climate data. This applies in particular to lakes situated at ecotonal boundaries, as such ecosystems have been shown to be highly responsive to even minor changes in climatic and environmental conditions (Rouse et al., 1997; Blom et al., 1998; Sorvari et al., 2002).

Early attempts to reconstruct climate from biological sedimentary remains were based on the application of single indicator species or assemblages of taxa and the results were often interpreted in a qualitative and descriptive manner. New numerical techniques and approaches are now available that allow quantitative reconstructions from floral and faunal remains usually with a high precision (Birks, 1995). These approaches involve a regional training, or calibration, data-set consisting of modern species assemblages and associated environmental data collected from a number of lakes spanning as full a range as possible of the environmental gradient(s) of interest (Charles and Smol, 1994; Birks, 1995). These data are used to establish a mathematical response function, or transfer function, that relates taxon distribution and abundance to the environmental parameter to be reconstructed.

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In this paper we apply a newly developed Bayesian multinomial Gaussian response model (Vasko et al., 2000) to fossil chironomid assemblages in a tree-line lake in Finnish Lapland to reconstruct Holocene palaeotemperatures. Chironomids (Insecta: Diptera: Chironomidae) are versatile non-biting midges, whose aquatic larvae are abundant and taxon-rich in most lakes. The heavily chitinised larval head capsules usually preserve well in lake sediments and can be readily identified, at least to the generic level. The value of chironomids as proxy indicators of climate change have been manifested by a number of studies reviewed by Walker (1995), Brooks (1996), and Battarbee (2000). Subsequently, several regional chironomid-temperature calibration functions have been generated during recent years in North America (Walker et al., 1991, 1997; Wilson et al., 1993) and Europe (Lotter et al., 1997; Olander et al., 1997, 1999).

The existing chironomid-temperature transfer functions have been used to quantify climates during Lateglacial times in Atlantic Canada and Europe with promising results (Levesque et al., 1993, 1994, 1997; Brooks and Birks, 2000a, b). However, up till now, only a few chironomid-inferred temperature reconstructions have been attempted for the full Holocene (Pellat et al., 2000; Rosén et al., 2001). One difficulty encountered when trying to reconstruct Holocene temperature fluctuations is that they were probably far less pronounced than during Lateglacial times (Korhola et al., 2000b; Broecker, 2001). Here we attempt, for the first time, to use our improved Bayesian chironomid-air temperature prediction model to infer temperature changes within the Holocene. As our up-dated chironomid-temperature calibration function has a high prediction accuracy of $\pm 0.8^\circ$C and a clearly lower systematic bias than any of the existing models we know, it should be—at least theoretically—sufficiently precise for tracking Holocene temperature changes, given the assumed sensitivity of the proxy source.

2. Materials and methods

2.1. Study area, site and sediment core

A 291-cm-long sediment core was sampled with a modified Livingstone piston corer and a Russian sampler from Lake Tsuolbmajavri (68°41′N, 22°05′E) for biostratigraphical analyses (for details, see Seppä and Weckström (1999)). The coring was carried out in the central part of the lake from the frozen lake surface. The lake is small (surface area = 13.9 ha), shallow ($Z_{max} = 5.35$ m), clear and oligotrophic, with a summer lakewater pH of about 7.4, conductivity of about $28\,\mu\mathrm{S}\,\mathrm{l}^{-1}$, and total phosphorus (TP) concentration below the analytical detection limit ($=5\,\mu\mathrm{g}\,\mathrm{l}^{-1}$). The measured mid-summer water temperature of the lake is
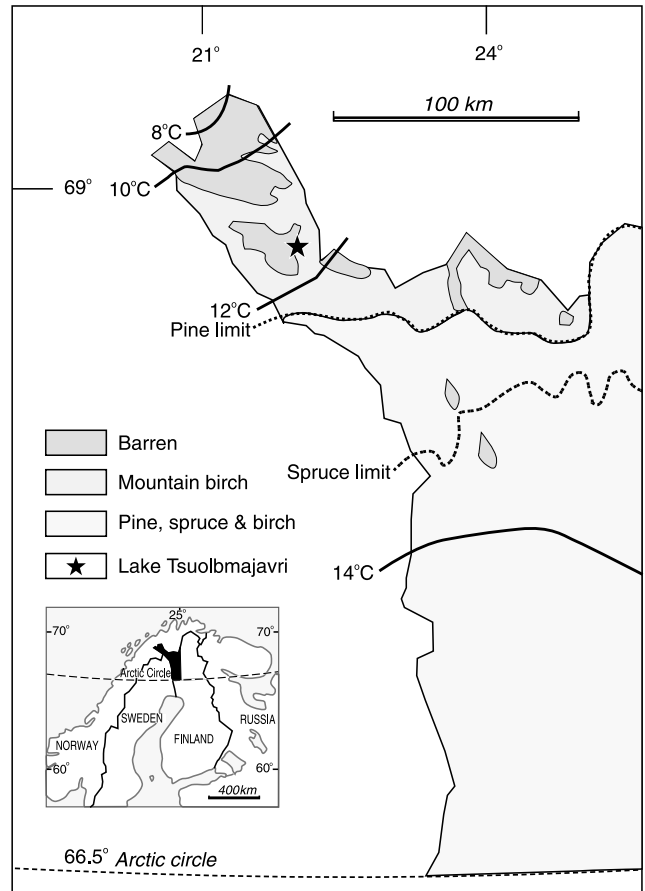

Fig. 1. The location of Tsuolbmajavri in relation to the main vegetation zones in Finnish Lapland. The isotherms of the mean July air temperatures (1961–1990) are indicated by solid lines and the northern limits of continuous occurrence of spruce (*Picea abies*) and pine (*Pinus sylvestris*) in the study area are indicated by broken lines (modified from Korhola et al (2001b)).

10.9°C and a site-specific altitude-corrected mean July air temperature is 11.0°C (this value is extrapolated from 11 nearby climate stations using an adiabatic lapse rate of $0.57^\circ\mathrm{C}\,100\,\mathrm{m}^{-1}$; see Olander et al. (1999)). The mean annual air temperature in the study area reaches about 2°C; annual precipitation is about 350 mm of which about 50% falls between June and September (Atlas of Finland, 1987).

Lake Tsuolbmajavri is located at an elevation of 526 m above sea level (a.s.l.) at the ecotone between boreal forest and the (oro)arctic tundra (Fig. 1). The site lies within the mountain birch (*Betula pubescens* ssp. *tortuosa*) woodland zone, though the tree line of mountain birch is located only ca 20 m above the altitude of the lake. In addition to mountain birch, the surrounding vegetation is characterised by a variety of shrubs and dwarf shrubs (e.g. *Empetrum nigrum*, *Vaccinium myrtillus* and *Betula nana*). The northern margin of the lake is covered by a small sub-alpine

peatland with *Salix lapponum*, *Carex* spp., *Rubus chamaemorus*, and various Sphagna as dominant species. The northern limit of continuous pine (*Pinus sylvestris*) is ≈ 30 km to the south of the lake.

The bedrock in the region consists of acidic and weathering-resistant Svecokarelidic orogenic plutonic rocks with granodiorites and quartz diorites as the dominant rock types. Basal till is the most common substrate type. Sporadic permafrost in the area is restricted to poorly drained plains covered by peatlands forming palsas (Seppälä, 1987). The lake, as in the whole of Fennoscandia, was covered by ice during the Late Weichselian glaciation. Deglaciation in the area took place ≈ 9400 ^{14}C yr BP (ca 10 300 cal yr BP) with the ice retreating from north to south (Lundqvist, 1991). More environmental data about the lake and its surroundings are given by Seppä and Weckström (1999), Seppä and Birks (2001), and Korhola et al. (in press).

The detailed pollen and diatom stratigraphies of the Tsuolbmajavri core have been published by Seppä and Weckström (1999) and the quantitative temperature reconstructions based on diatoms by Korhola et al. (2000b) and pollen by Seppä and Birks (2001). We compare our results here with these other records.

2.2. Chronology

The chronology of the core is based on 14 accelerator mass spectrometry (AMS) radiocarbon datings, carried out in collaboration with the dating laboratories of the University of Helsinki and the University of Uppsala (Ångström Laboratory). Age-depth models were created using calibrated radiocarbon dates. The ^{14}C dates were converted to calendar years (Before Present) (where 'present' is AD 1950) with the program CALIB 3.03c using the bidecadal tree-ring data-set A and method A (Stuiver and Reimer, 1993).

After deletion of the basal date of 10,940 ^{14}C yr BP on the basis of its apparently too old age (the date is older than the approximate deglaciation date of the area suggesting the mobilisation of sediments accumulated in glacial times), the remaining dates suggest a fairly linear sediment accumulation rate. Age-depth models were developed by non-parametric weighted regression within the framework of generalised additive modelling (GAM) (Heegaard and Birks, unpublished). These models provide calibrated age estimates with their 95% confidence intervals for each studied sediment layer (Fig. 2). Note that this new age-depth curve deviates slightly from the linear regression age model used by Seppä and Weckström (1999) and by Korhola et al. (2000b). We use this new age model because it is statistically more robust than the old one, as assessed by a lower deviance with only one less
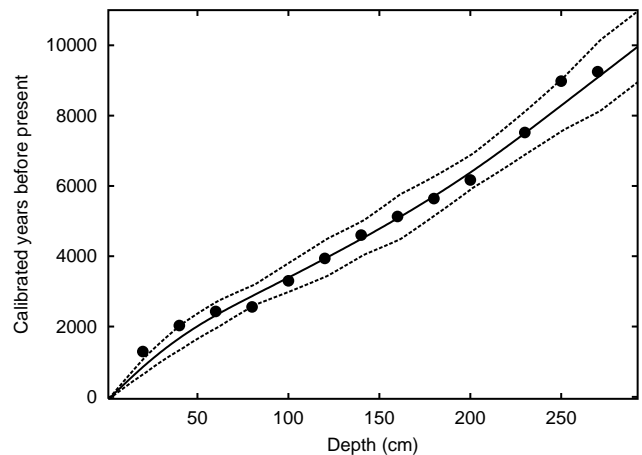

Fig. 2. The fitted age-depth model for Tsuolbmajavri based on 13 calibrated AMS radiocarbon dates (figure adapted from Seppä and Birks, 2001). The solid line represents the model fitted by a spline smoother and the dotted lines are the 95% confidence limits for the fitted model. More details of the radiocarbon assays are given in Seppä and Weckström (1999) and Korhola et al. (2000b).

degree of freedom. For more details of the revised chronology of the Lake Tsuolbmajavri, see Seppä and Birks (2001).

2.3. Chironomid analysis

The core was sampled for subfossil chironomids at intervals of 2 cm, equivalent to a temporal resolution of 50–70 yr. Subsequently, a few samples were taken at a higher resolution (1 cm contiguous samples) from sequences with rapid changes in chironomid composition, i.e., levels 183–185 and 273–275 cm. Sub-samples of 0.5–28.5 g wet weight were first treated with 10% KOH. Samples were then passed through a 105 μm sieve and transferred to a Bogorov counting tray. All head capsules were picked with fine forceps under a binocular microscope and mounted ventral side upwards on slides in Euparal. A minimum of 100 head capsules was counted per sample, which clearly exceeds the minimum abundance criterion of 40–50 head capsules per sample recently suggested by several authors on the basis of statistical tests (Heiri and Lotter, 2001; Larocque, 2001; Quinlan and Smol, 2001). The simulation experiments by Heiri and Lotter (2001) further demonstrated that by increasing the minimum count sum to about 100, a significant increase in the reliability of the results should be obtained in chironomid-based quantitative inferences. Identification was based mainly on Hofmann (1971), Sæther (1975), and Wiederholm (1983); also agreements made in the taxonomic harmonisation workshops within the international MOLAR and NORD-CHILL projects were followed. For a more detailed description of the taxonomy and methods used, see Olander et al. (1997, 1999).

2.4. Modern calibration set

The modern chironomid training data set used for the calibration models include, after data screening, 62 samples with a total of 52 chironomid taxa. The July mean air temperature (average from 1961 to 1990) ranges between 7.9°C and 13.8°C. The lakes sampled were small (median area = 9.6 ha) and shallow (median maximum depth = 5.3 m) basins with neutral waters (median pH = 7.1). Because of the shallow depth, most of the lakes are polymictic/isothermal (no significant temperature difference from top to bottom) (Korhola et al., 2002); consequently, the benthic communities in these lakes should also be in close harmony with the regional climate conditions. For more details and a map of the lakes used for the training set, see Olander et al. (1999), and Vasko et al. (2000).

2.5. Numerical methods

Only the main elements of the Bayesian Bummer model are described here. For fuller details, see Vasko et al. (2000).

We denote by y_{ik} the abundance of taxon k at site i, by y_i the vector of abundances of the taxa at site i, and by Y the matrix of abundances of the taxa at all of the sites. We denote by x_i the temperature at site i and by X the vector of temperatures at the sites. Finally, let y_0 be a fossil assemblage and x_0 a random variable that corresponds to the air temperature at the time the fossil assemblage was formed, which is unknown.

Given a statistical model for the relationship between temperature and taxon abundances, a reconstruction of the unobserved temperature x_0 can be obtained from the distribution

$$f(x_0|X, Y, y_0) \qquad (1)$$

conditional on the observed variables. Denote by θ the vector of parameters of the statistical model, and we get

$$f(x_0|X, Y, y_0) = \int f(x_0, \theta|X, Y, y_0)\, d\theta$$
$$\underset{\theta}{\propto} \int f(x_0, \theta) f(Y, y_0|X, x_0, \theta)\, d\theta, \qquad (2)$$

i.e., the distribution of x_0 is obtained by marginalising over the random variable vector θ. The terms of the marginal are the response functions $f(Y, y_0|X, x_0, \theta)$, specifying (i) the way in which species assemblages depend statistically upon environmental variables; (ii) the background assumptions concerning the sampling arrangement; and (iii) the conditional independence assumptions related to taxon and site interactions. In Bayesian terms, the distribution $f(x_0, \theta)$ is called the *prior distribution*. The prior distribution embodies our background knowledge related to the model parameters θ and missing values x_0.

In the Bummer model, we assume that the taxon abundances y_i at site i are multinomially distributed. In other words, the probability that a random individual from site i is of taxon k is some p_{ik}, where the p_{ik}'s of any site i sum to one. This taxon- and site-specific probability depends on the response of each taxon to the particular environmental conditions at the site.

Let λ_{ik} be the response of taxon k to some environment condition at site i (on some linear scale). We use the regression model

$$E(p_{ik}|x_i, \theta) = \frac{\lambda_{ik}}{\sum_j \lambda_{ij}}, \qquad (3)$$

for the proportions p_{ik}. Proportions p_{ik} for site i are Dirichlet distributed stochastic variables. The motivation for this is to leave room for the influence of latent variables such as unmeasured environmental variables and changing sedimentation rate.

The response curves are bell-shaped Gaussian curves controlled by parameters α_k (scaling factor), β_k (optimum) and γ_k (tolerance) (Fig. 3):

$$\lambda_{ik} = \alpha_k \exp\left[-\left(\frac{\beta_k - x_i}{\gamma_k}\right)^2\right]. \qquad (4)$$

Gaussian response curves can also represent practically linear and sigmoidal responses within the observed gradient, but with a more plausible extrapolation.

Bummer and its simpler variant Bum have been described in detail by Vasko et al. (2000) and Toivonen et al. (2001), respectively. Bayesian approaches to ecological modelling have been discussed by, e.g. Ellison (1996) and Robertson et al. (1999).

For the current data set and Bummer reconstruction, the joint prior distribution $f(x_0, \theta)$ (Eq. (2)) of temperatures and parameters was set in the following manner. First of all, each temperature x_0 to be reconstructed as
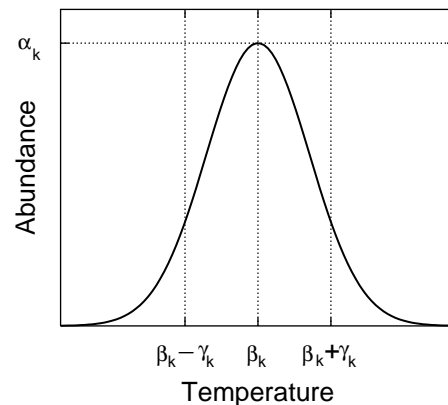

Fig. 3. Gaussian response curve for a taxon k, determined by α_k (scaling factor), β_k (optimum temperature), and γ_k (tolerance to temperature).

well as all species-specific parameters α_k, β_k, and γ_k are assumed mutually independent in the prior. The joint prior distribution is thus determined by the individual marginal priors.

The prior distribution for temperature has potentially the most direct influence on the reconstructions. Each temperature x_0 to be reconstructed is a priori normally distributed with an expected value of 11°C (the current temperature at the study site) and a variance of 1°C. This prior can be considered conservative: it is uniform over the whole history, it imposes no trends, and the fairly small variance restrains extreme values. Further on, since temperature is affected by multiple factors, the central limit theorem gives support to the shape of the distribution.

The prior distributions of species-specific parameters have an undirect effect on the reconstructions. The species optimum temperature β_k is a priori normally distributed with an expected value of 11 and a variance of 3. The rational for this choice is the assumption that species optima are on average the same as the (prior) mean temperature, but that quite extreme optima can also be plausible. The prior distribution of the tolerance parameter γ_k is the gamma distribution with hyperparameters 9 and 3, i.e., with an expected value of 3 and a variance of 1. The prior distribution of γ_k is defined to prefer relatively large tolerances in order to avoid overfitting response curves to random peaks in the data. The scaling factor α_k has a uniform prior distribution in [0.1, 50]. The absolute values of the scaling parameter have no direct interpretation since scaling of each species is considered only in relation to other species. They do have an effect on the variance of proportion p_{ik} (Eq. 3); our choice for the prior distribution allows large differences between samples due to latent variables. Our experiments (data not shown) and earlier results with Bum (Toivonen et al., 2001) have shown that reconstructions with the current data set and models are not sensitive to small changes in the parameter values of priors. The choice of prior distributions is rather a question of their form and magnitude than the exact parameter values.

In addition to Bummer, the more commonly used weighted averaging partial least squares (WA-PLS; ter Braak and Juggins, 1993) regression was applied to the chironomid data. Past temperatures were inferred with the minimal adequate 2-component WA-PLS model (minimal adequate model is defined on the basis of the smallest number of orthogonal components that are needed to give a 5% or more reduction in RMSEP, see Birks (1998)). The WA-PLS model was implemented using the computer program WAPLS 1.0 (unpublished program by Juggins and ter Braak). The same program was also used to derive bootstrapped sample-specific error estimates (68.2% confidence intervals) for reconstructed values when using WA-PLS calibration.

In terms of prediction accuracy, as measured with leave-one-out cross-validation tests in the modern training set, the Bummer model outperforms the WA-PLS model (Vasko et al., 2000). First, the prediction error (RMSEP) of Bummer (0.80°C) is lower than that of WA-PLS (0.95°C). Second, Bummer has considerably lower systematic bias, as expressed by the linear least-squares error slope between model residuals and observed temperatures (Bummer: −0.12; WA-PLS: −0.37), and by the maximum bias (Bummer: 0.98°C; WA-PLS: 2.21°C).

The biostratigraphical data from Tsuolbmajavri used in this study include 148 chironomid samples containing a total of 50 taxa. Constrained optimal sum of squares partitioning with untransformed species percentage data was used for the zonation of the chironomid biostratigraphy (Birks and Gordon, 1985). The analysis was implemented using the programme ZONE (Lotter and Juggins, 1991). In an attempt to identify the number of statistically significant partitions, the broken-stick (b-stick) model and the associated approach described in Bennett (1996) was used.

3. Results

3.1. Chironomid stratigraphy and its ecological interpretation

In all, 50 chironomid taxa were recorded within the 148 core samples, of which 45 are present in the modern training data set. The missing taxa do not have a strong influence on the outcome of the reconstruction, as they all are present in low quantities ($<3\%$) and have low (between 1 and 4) N_2 values (the N_2 index determines the effective occurrence of species in a sample, see Hill (1973)).

The major changes in the chironomid fauna of Lake Tsuolbmajavri are summarised in the stratigraphic plot in Fig. 4. The most conspicuous features in the startigraphy are the distinct and repeated ups and downs in the frequencies of many of the 'cold water' taxa, in particular *Corynocera oliveri* and *Heterotrisso-cladius maeari* (the categorisation of chironomids to 'cold', 'warm', and 'intermediate' taxa are based on Olander et al. (1999) throughout the paper if not otherwise mentioned). The most common chironomid taxa in the profile, with Hill's N_2 values >100, include *Psectrocladius sordidellus*, Tanytarsini spp., *Sergentia coracina*, *Corynocera ambigua*, and Tanypodinae spp.; the two first mentioned are the only taxa present throughout the profile. The above-listed taxa predominate in waters and sediment cores of Finnish Lapland (Hirvenoja, 1998) and they were also among the most dominant taxa in the modern training data set of this study (Olander et al., 1999; Vasko et al., 2000). With the
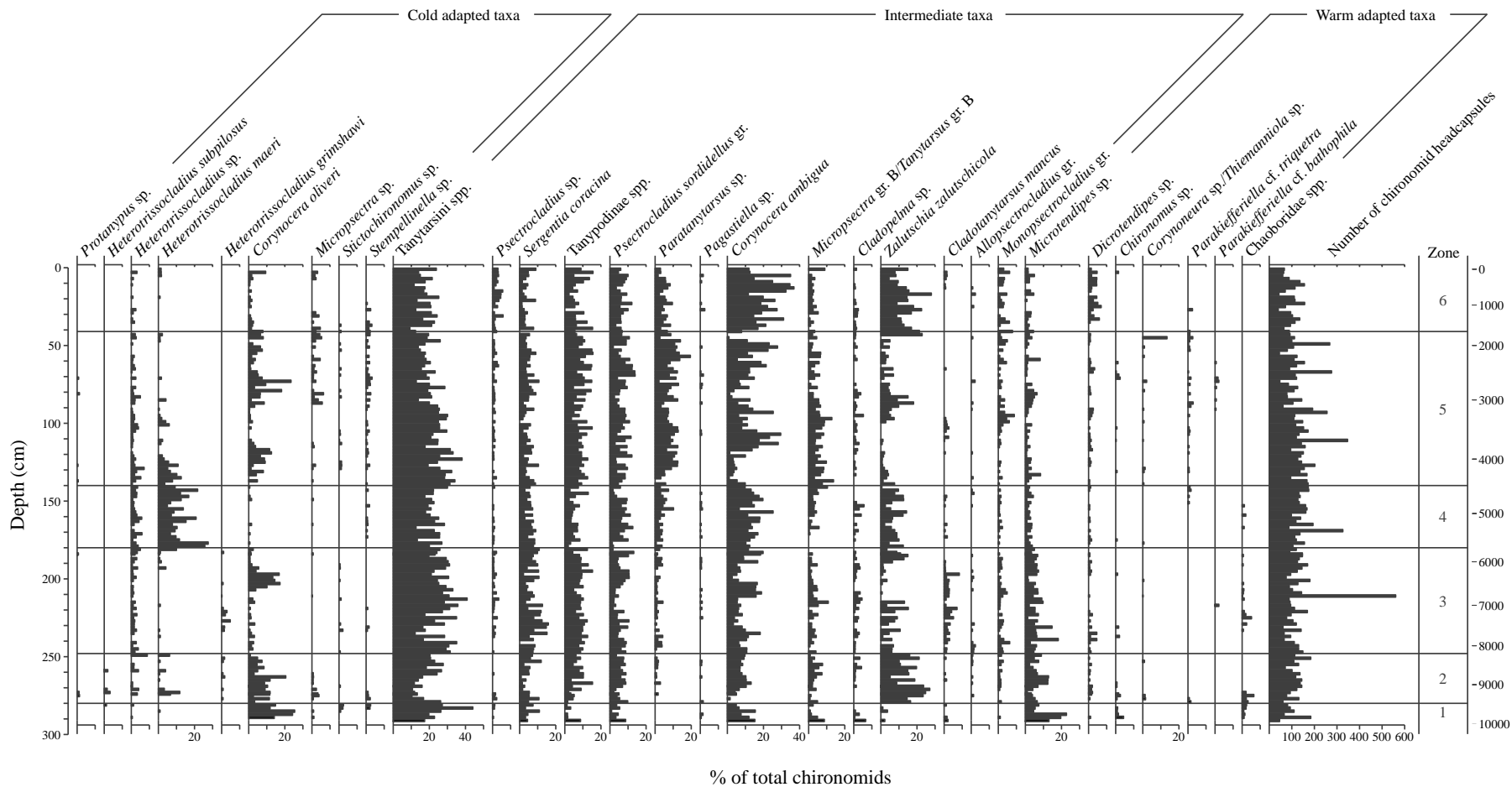
Fig. 4. Tsuolbmajarvi chironomid stratigraphy. Only selected taxa are displayed. The taxa are grouped according to their modelled temperature requirements.

exception of *S. coracina*, which seems to be typical of waters with low pH, calcium and alkalinity, these taxa were found in all types of water bodies in the modern data set, with no clear preference for any of the measured environmental gradients (Olander et al., 1999).

Optimal partitioning divided the profile into six statistically significant chironomid assemblage zones that are briefly described below. Following deglaciation (*Zone 1*, ca 10,000–9500 cal yr BP), the lake was rapidly colonised by a diverse chironomid fauna including both 'warm-water' taxa (*Microtendipes, Cladopelma*) and some common cold-stenotherms, such as *Corynocera oliveri* and *Stictochironomus*. Intermediate taxa (in terms of their temperature preference) such as *Corynocera ambigua* and Tanytarsini spp. were also common, with the latter taxon peaking up to 45% in this zone. This mixed chironomid composition suggests unstable limnological and environmental conditions during the early stage of the lake ontogeny.

Zone 2 (ca 9500–8200 cal yr BP) is characterised by distinct increases in many cold-stenothermal taxa such as *Heterotrissocladius maeari*, *Heterotrissocladius* sp. and *H. grimshawi* and reciprocal decreases in some 'warm-adapted' taxa, such as Chaoboridae. Various *Heterotrissocladius* taxa exhibit a trimodal distribution for this interval, the first peak being accompanied by *Protanypus* and *Micropsectra*. All these taxa were found to be associated with the coldest habitats in the modern training set (Olander et al., 1999; Vasko et al., 2000) and are known from the literature (Walker et al., 1991; Lotter et al., 1997, 1999; Brooks and Birks, 2000a, b) to prefer cold and oligotrophic profundal conditions.

Zone 3 (ca 8200–5700 cal yr BP) is dominated by Tanytarsini, Tanypodinae, *Sergentia coracina*, and *Microtendipes*. The last-mentioned taxon has its highest relative abundance in this zone after the initial disturbance phase; it is a thermophilic taxon typically inhabiting littoral and sublittoral sediments of temperate lakes (Wiederholm, 1983; Moller-Pillot and Buskens, 1990; Walker et al., 1991). *Sergentia coracina* is often described as 'cool-adaptive' (Wiederholm, 1983; Walker, 1990). However, in our modern data set we found this taxon to be typical of humic, slightly acidic sites (Olander et al., 1999), while in Norwegian lakes, *S. coracina* has been shown to be represented both in acid clearwater lakes (Raddum and Sæther, 1981) and in humic acid lakes which suggests the species is euryoxybiont. Its increased abundances in Zone 3 at Tsuolbmajavri might thus be related to increased humus content and associated pH decline of lakewater, which according to Seppä and Weckström (1999) took place in Tsuolbmajavri during this time period. On the other hand, *Psectrocladius sordidellus*-type and *Zalutschia zalutschicola* did not show any trend in this zone,

although these taxa too are considered as sensitive to acidification (Brodin and Gransberg, 1993). Thus, it seems that pH has had actually little influence on the dynamics of the chironomid assemblage. The distinct peak of *Corynocera oliveri* in the upper part of the zone suggests falling temperatures. This species thrives on mud bottoms of cold Palearctic lakes and ponds (Brundin, 1949).

Zone 4 (ca 5700–4500 cal yr BP) is delineated by declines in *Microtendipes* and Tanypodinae coupled with increased abundances of *Heterotrissocladius maeari* and *Heterotrissocladius* sp. suggesting a faunal response to falling temperature. *Corynocera ambigua* and *Zalutschia zalutschicola* also show relatively high frequencies in this zone. The former species is often regarded as a cold-stenotherm, yet the recent study by Brodersen and Lindegaard (1999) has shown that the species may occur in warm shallow lakes and that temperature may not be the limiting factor for its occurrence. We found no relationship between temperature and the distribution of *Corynocera ambigua* in our modern training data, yet the species showed some affinity with high-alkalinity and high-conductivity lakes (Olander et al., 1999). Hirvenoja (1998), however, considers the species to be polyoxyphilous and states that it benefits from cool and/or rainy conditions. *Zalutschia zalutschicola* showed no preference for any of the measured environmental gradients in our modern calibration set (Olander et al., 1999). However, several studies have demonstrated that the species may be useful as an indicator of both humic and acidic waters (Brundin, 1949; Mossberg and Nyberg, 1979; Walker et al., 1985). Seppä and Weckström (1999) show diatom-based total organic carbon (TOC) data for the site as well as *Sphagnum* spore accumulation rates. Both of these parameters show some correlation with the distributional pattern of *Zalutschia zalutschicola* in the core.

Zone 5 (ca 4500–1700 cal yr BP) is characterised by distinct declines in *Heterotrissocladius maeari* and *Heterotrissocladius* and contemporaneous rapid increases in *Corynocera oliveri*, *Micropsectra*, *Stempellinella*, *Corynocera ambigua*, and *Paratanytarsus* and more gradual increases in *Dicrotendipes*, *Psectrocladius* and *Monopsectrocladius*. The latter three taxa show clear affinity for shallower sites in the modern calibration set (Korhola et al., 2000a) and could therefore indicate progressive shallowing of the lake due to increased sedimentation.

Zone 6 (ca 1700–present) is dominated by *Zalutschia zalutschicola* and *Corynocera ambigua* accompanied by continuous increases in *Dicrotendipes*, *Psectrocladius* and *Monopsectrocladius*. *Corynocera oliveri* and *Paratanytarsus* show declining trends. These compositional changes most probably reflect further shallowing of the lake due to progressive sedimentation as well as

increased lakewater TOC content, which according to Seppä and Weckström (1999) was characteristic of the lake during the recent millennia. The increasing TOC concentrations were most probably due to inwash of organic substances from the expanding *Spahgnum*-dominated peatlands in the catchment. Walker et al. (1985) have demonstrated, using data from shallow, acid humic lakes and bog pools in Atlantic Canada, that *Zalutschia zalutschicola* and *Monopsectrocladius* in particular are characteristic taxa of bog lakes strongly affected by humic substances and encircling *Sphagnum* peatlands.

3.2. Climate reconstruction

The chironomid-inferred mean July air temperature for the Holocene ranges between about 9°C and 11°C with a slight overall cooling trend from the early Holocene to the present (Fig. 5). The reconstruction features both long-term climatic trends as well as a series of shorter-term temperature fluctuations. Fig. 5 illustrates the full quantification of uncertainty related to the Bummer reconstruction, that allows us to study the most probable areas in (time, temperature)-plane given the observed data and model assumptions. The shades indicate probability densities: The darker the shades, the higher the posterior probability. The marginal posterior probability surface of the environmental variable

represents the variability and probability density values for any given time period more illustratively than the traditional point estimates such as the expected value and variance. Further, Fig. 5 illustrates the Bayesian perspective explicitly: there is no certain true reconstruction in the presence of uncertainty. Instead, there are more or less probable reconstructions given the observed data and model assumptions.

Fig. 5 suggests that climate during the early Holocene was particularly unstable. However, little can be concluded about the nature of the conditions during the very first few hundreds of years of the Holocene on the basis of this record, since the prediction accuracy (credibility) of the reconstruction is quite low (indicated by widespread grey colour in Fig. 5). The uncertainty probably reflects late deglaciation of the area and the resulting heterogenous chironomid fauna during the onset of lake colonisation when the chironomids were not yet in equilibrium with their local environmental conditions. Such unstable limnological and biological conditions are thought to be characteristic of the first developmental phases of Finnish lakes at a time when the catchments were not yet stabilised and erosion rates were high (Korhola and Tikkanen, 1991; Korhola, 1992).

The record suggests fairly low but steadily rising summer temperatures during the early Holocene. This warming trend is interrupted by three successive cooling events with amplitudes of 1–1.5°C at around 9200, 8600
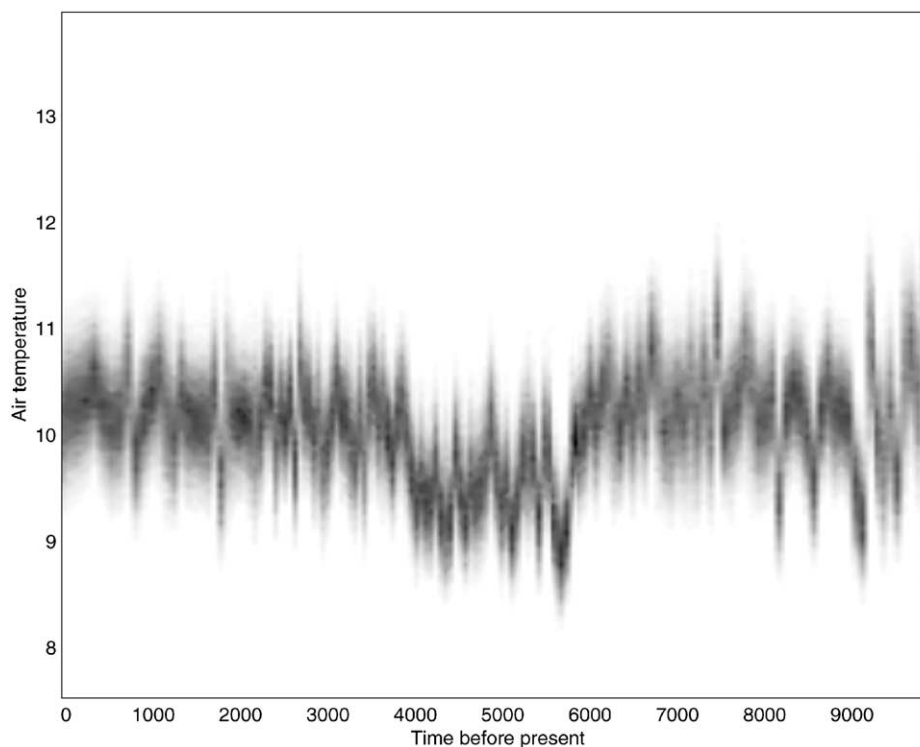

Fig. 5. Inferred July mean temperature at Tsuolbmajavri, presented as sample-specific posterior distributions using the Bayesian Bummer model for each sediment layer studied. Darker shades indicate higher posterior densities.
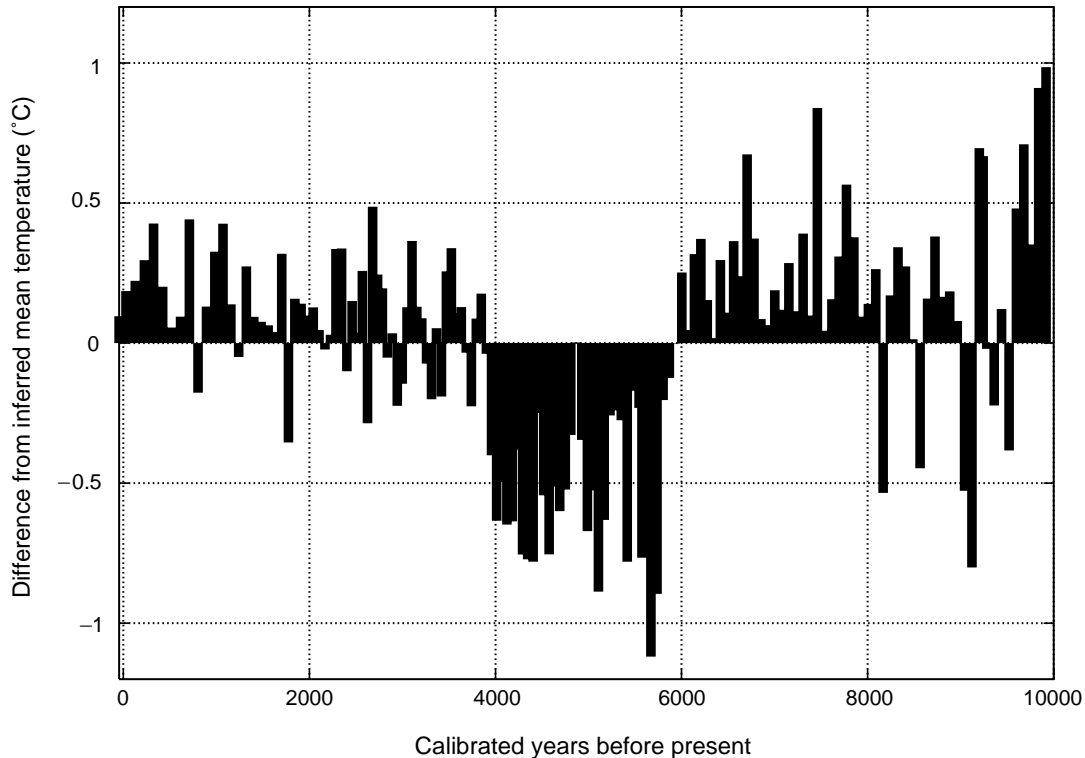
Fig. 6. Inferred July mean temperature at Tsuolbmajavri, presented as the pointwise difference from the average of all reconstructed temperatures. The inferred temperatures are pointwise posterior expectations from the Bayesian Bummer model; the average temperature (at '0' in the graph) is 10.05°C.

and 8200 cal yr BP. In contrast to the earlier temperature fluctuations in the record, these distinct cooling episodes are marked by high posterior probability densities (Fig. 5).

The interval between ca 8000 and 5800 cal yr BP appears to have been warm and stable. Temperatures during this 'climatic optimum' stayed constantly above the inferred mean of Holocene temperature (Fig. 6). The model suggests that summers in northern Fennoscandia were warmest around 7500–6500 cal yr BP when the mean July temperature at Tsuolbmajavri rose to slightly above 10.5°C. There is a sudden drop of an amplitude of ca 1°C in inferred mean July temperatures at around 5800 cal yr BP, heralding a relatively long-lasting mid-Holocene temperature minimum between ca 5800 and 4000 cal yr BP. This was clearly the coolest episode during the entire Holocene, with temperatures remaining constantly below the predicted Holocene mean (Fig. 6) and significantly lower than the rest of the period (Figs. 7 and 8). Within the cold interval, particularly cool summers appear to have prevailed at about 5800, 5000 and 4200 cal yr BP.

The inferred late-Holocene climate is surprisingly featureless, fluctuating only between 10°C and 10.5°C during the past 4000 years. A brief cold oscillation can, however, be distinguished with some confidence at about 1800 cal BP. No warming trend can be shown for the past few centuries on the basis of our
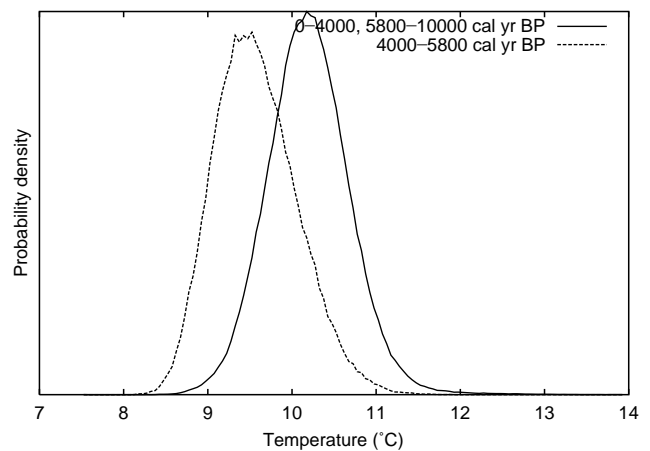

Fig. 7. Comparison of inferred temperature distributions for 4000–5800 cal yr BP and for the reminder of the period. Graphs show the marginal Bummer posterior densities integrated over the respective time intervals.

reconstruction, in contrast to earlier interpretations based on data from the study area (Korhola et al., 2000b; Sorvari et al., 2002) and to the general view of climatic behaviour in the northern high latitude regions (Overpeck et al., 1997). The present-day chironomid-inferred mean July air temperature is about 10.2°C.
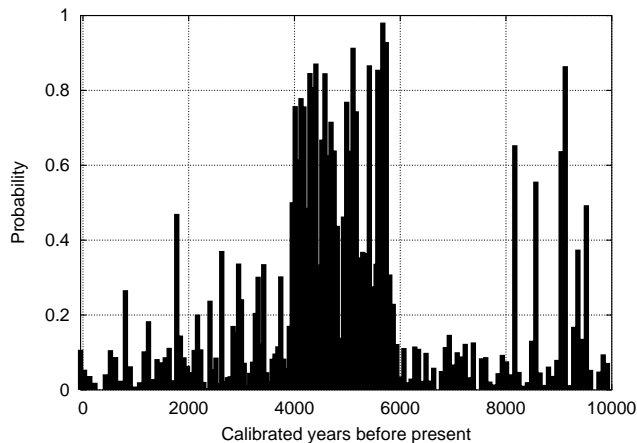
Fig. 8. Sample-specific probabilities that the temperature was below 9.66°C (one standard deviation below the mean of all reconstructed temperatures).

3.3. Comparison to WA-PLS model

The inferred mean July air temperatures based on the Bummer model and the two-component WA-PLS show a generally similar picture for the Holocene, with highly fluctuating early Holocene temperatures, warm mid-Holocene, minimum values around 4000–5000 cal yr BP, and slightly increased temperatures toward the present (Fig. 9). However, the Bummer reconstruction indicates cooling events at around 9200, 8600, and 8200 cal yr BP with much more confidence, and a more rapid decline in temperature during the mid- Holocene (5800 cal yr BP) (Figs. 9 and 10). The WA-PLS reconstruction suggests more gradual decrease in temperature starting much earlier, at about 7000 cal yr BP. Further-more, the Bummer model suggests the period between 4000 and 2000 cal yr BP to have been generally warmer than that suggested by the WA-PLS model (Fig. 10). Finally, the temperature predictions of the WA-PLS model are systematically about 1°C higher than the Bummer temperature predictions (Fig. 9). A closer time-series analysis, in which the correlation coefficient is calculated for each sediment layer and its p value estimated by Monte Carlo simulation (using a window width of ca 1500 years), indicates that, apart from the early Holocene, the two records behave generally similarly, with a particularly good fit for the time intervals 2700–4000 and 4500–6300 cal yr BP (Fig. 11).

In the absence of any objective, direct means to evaluate, which one of the two models gives a more reliable picture, the only course is to make an indirect assessment based on their general predictive abilities. From the perspective of the model performance, the Bummer results clearly have higher predictive power and lower inherent systematic and maximum bias than the WA-PLS model (Vasko et al., 2000), so that

the Bummer model allows extrapolations with a higher degree of confidence. We believe that the Bummer model yields a more realistic picture of Holocene climatic fluctuations, especially, since it has lower bias (see Birks (1998) and Vasko et al. (2000)), so that the extreme values should be represented more accurately than is the case with the WA-PLS reconstruction.

4. Discussion

4.1. Reconstruction using Bayesian vs. frequentist statistics

Reconstructing environmental variables from biological assemblages is a difficult multivariate calibration problem and a variety of numerical techniques have been suggested for this purpose. In general, there are two different statistical approaches for parameter estimation: the so-called frequentist and Bayesian approaches. The major difference between these two approaches lies in the fact that while traditional frequentist methods assume that parameters being estimated have fixed values and that data are random observations from some population, the Bayesian approach assumes that parameters are random variables and that the data are fixed ('all there is') (Box and Tiao, 1992). Bayesian methods use a probability rule (Bayes theorem) to calculate a posterior probability distribu-tion of parameters from the observed data and a prior distribution, which summarises the prior knowledge of the parameters, i.e. what is expected by the investigator before the experiment is conducted. Most of the calibration models used in climate reconstructions, such as weighted averaging (WA) regression and its extension WA-PLS regression, are based on the idea of inverse calibration, where the environment is thought of as being a function of biological assemblages—i.e., the proxy indicator of climate is regarded as the 'predictor variable' and regressed against the climate variable, the 'response variable' (see Birks (1995) and ter Braak (1995)). However, inverse calibration has several weak-nesses and it usually produces a systematic discrepancy, or bias, in the model estimates, as elegantly shown by Robertson et al. (1999). Our work on the application of Bayesian methodologies to the reconstruction task has demonstrated that many problems associated with the conventional approaches can be overcome or at least markedly reduced by using the full probability models based on Bayesian inference in the framework of the classical calibration (Mannila et al., 1998; Vasko et al., 2000; Toivonen et al., 2001).

The major advantages of Bayesian models over more traditional models are that ecological knowledge can be embedded in the models in an elegant, mathematically

A. Bummer reconstruction
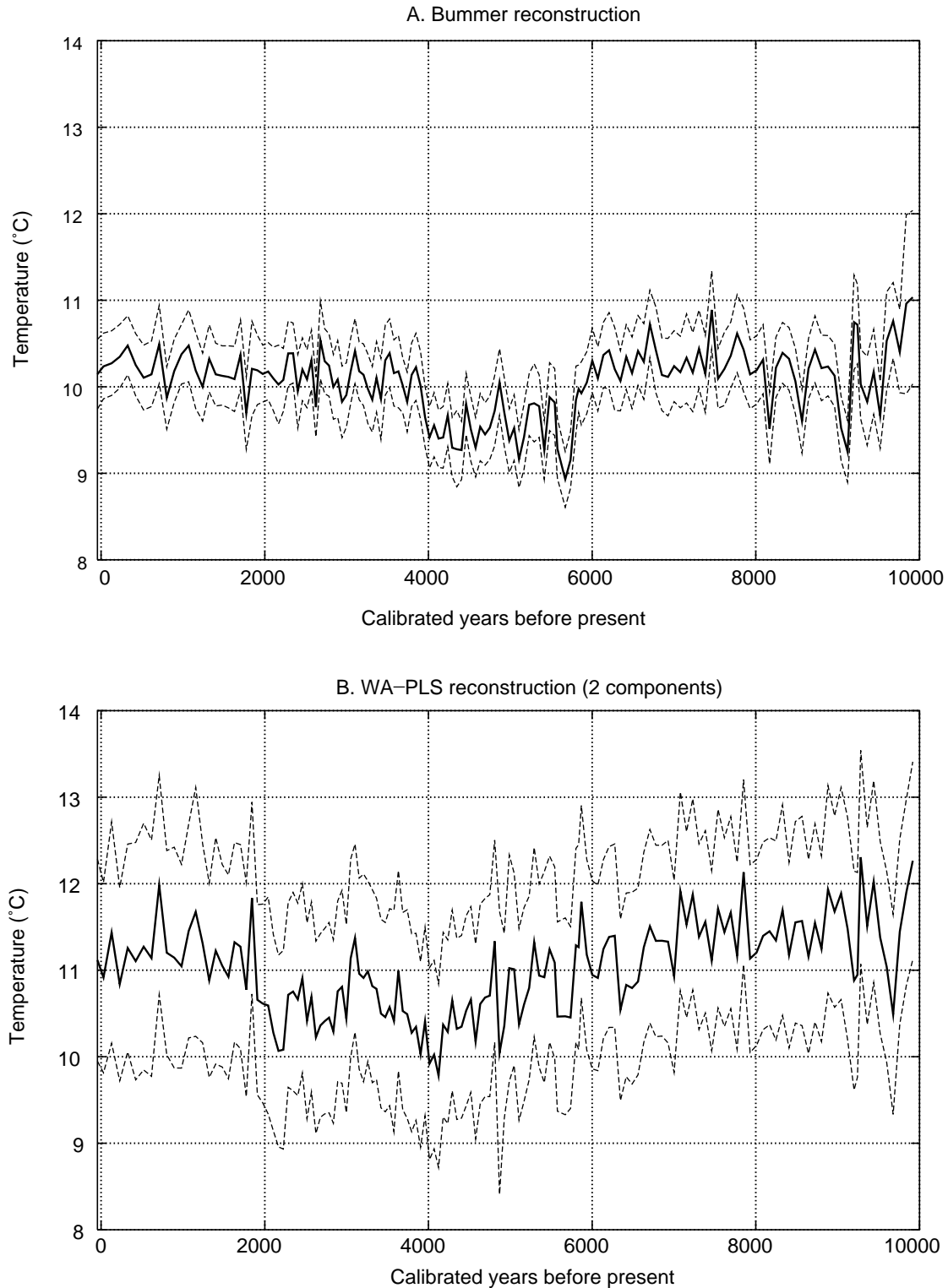
B. WA–PLS reconstruction (2 components)

Fig. 9. Inferred July mean temperature at Tsuolbmajavri: (A) Reconstruction with the Bayesian Bummer model. The solid line represents pointwise posterior expectations and the dashed lines indicate pointwise 68.2% (appr. one standard error) credible intervals; (B) reconstruction with WA-PLS (2 components). Dashed lines indicate pointwise standard errors (68.2%) of predictions, based on bootstrapping (1000 cycles).

consistent, and natural way, the conceptual structure of the probability model is easy to conceive, there are no requirements (e.g. continuity) on variable types, no

deshrinking is needed, and that by using probability distributions rather than point estimates, more information is achieved about the taxon responses, model
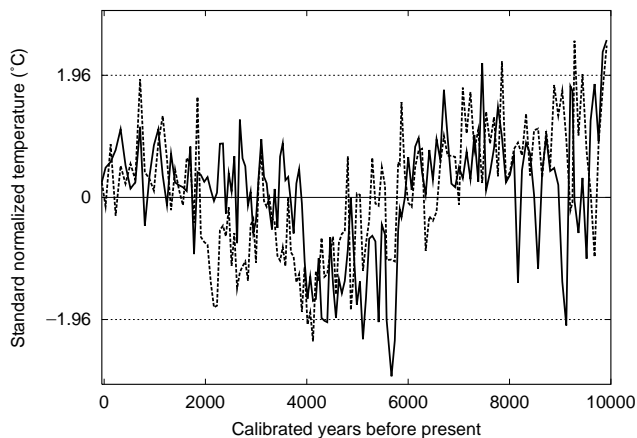
Fig. 10. Standard normalized reconstructions for the Bummer (solid line) and WA-PLS model (dashed line). The thin dashed lines indicate 95% ($\pm 1.96\sigma$) interval for the relative variability of the standard normalized reconstruction.
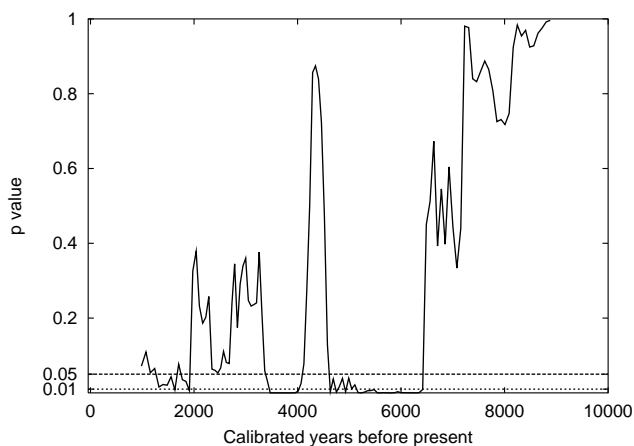

Fig. 11. p values for the local correlation between temperatures inferred using Bummer and WA-PLS. The p value is obtained by using a sliding window of 24 sediment layers and it indicates the probability at which the observed correlation occurs by chance supposing reconstructions were independent within the window; the end points of the curve are the midpoints of the first and the last window (p values were estimated by comparing the observed correlations to the correlations of 10,000 pairs of random permutations of the windows).

behaviour and statistical uncertainty related with the process (Vasko et al., 2000; Toivonen et al., 2001). Most conventional methods use point estimates of response functions as intermediate results, leading to possible 'rounding errors' in the reconstructions. Bayesian methods, on the other hand, lend themselves more naturally to a process where probability distributions are used instead of point estimates throughout the calibration process. In addition, various marginal distributions and credible intervals (with pure probability interpretation) of interest are accessible that are not attainable in the frequentist context, but which

would certainly be interesting in analysing palaeoenvironmental datasets. Figs. 5, 7, 8 and 9A illustrate this strength of full probability modelling. It should be pointed out that in Figs. 9A and B the Bayesian credible intervals derived by the Bummer model and the bootstrap error for WA-PLS both rely on estimates of the amount of uncertainty in the reconstructed temperatures. The Bayesian credible intervals indicate the total effect of uncertainties in the statistical model and in the modelled responses, expressed and handled in the form of probability distributions throughout the calibration process. The error estimations are not directly comparable, since bootstrapping only reflects the robustness of WA-PLS point predictions against some uncertainty in the available sample, whereas Bummer predicts probability distributions in the first place with a multitude of inherent uncertainties included. Bayesian credible intervals have a direct probability interpretation; 'The probability that θ lies in the interval is α', whereas frequentist confidence intervals have the interpretation; 'If we were able recompute confidence intervals for a large number of data-sets collected in the same way as ours, about $\alpha \times 100\%$ of them would contain the true value of θ'. The first interpretation provides us an actual probability statement based only on the observed data (not on the data that may have occurred but did not) and background knowledge in the form of independence assumptions, prior distributions and their hyperparameters. The latter interpretation is not too comforting, since we possess exactly one dataset.

Consequently, we believe that Bayesian models can be made ecologically more realistic than the traditionally used models and are expected to extrapolate better, which is important for reconstructions based on fossil data.

4.2. Limitations of the approach

There are many uncertainties and potential problems in our approach that should be recognised when interpreting the results. For example, the magnitude of the sample-specific credible intervals in the reconstruction is on average about $\pm 0.8°C$, and many of the finer-scale temperature variations lie within the error estimates of the model. However, the probability density surface (Fig. 5) also clearly shows distinct peaks and areas with confidently defined temperature changes. Chronological control may also be insecure; the uncertainties (one standard deviation) in the age-depth model alone range from about 150 yr at the upper part of the core to about 300–500 yr at the core bottom. Possible counting errors and changes in lake sedimentological and taphonomical processes may also have produced some extra 'noise' in our data. We are also aware that climate and other environmental factors may

sometimes produce quite similar signals to biological data that are difficult to differentiate.

Below we show that at least some of the above-mentioned concerns are unwarranted and that we are on secure ground when making interpretations of the large-scale patterns in our records. However, the many fine-scale changes inherent in our reconstruction still remain problematic; are they real or only noise? In attempting to answer this question, some logical arguments can be applied. For example, short-term events can be identi-fied with more confidence when they are 'produced' by taxa whose ecological indicator value is well-established in the modern data, when the taxa behind the changes are well represented both in modern and fossil data, when the ecological mechanisms and causations behind the changes can be elucidated, and when the events are replicated by several proxy indicators at the same time. The first three criteria are clearly fulfilled in the present study as shown in the subsequent discussion. However, with respect to the last criterion, one should recall that different organisms may respond to climatic forcing with different time lags and that different proxies reflect different components of the climate system, which simply shows its truly dynamic behaviour (Birks et al., 2000). Although most of the existing calibration functions have been generated with the aim of inferring mean July temperatures, we cannot be sure what is the complex but unknown variable or set of interacting variables that actually determine the critical thermal budget for presence and survival of various organisms (Korhola et al., 2001b). For example, July temperature is a variable that is known to be linearly related to several climatic and climate-related factors such as annual degree days, mean summer temperature, duration of ice cover, and length of growing season (Shuter et al., 1983; Livingstone, 1997; Lotter et al., 1997).

4.3. The chironomid response

The changes in the chironomid fauna in Tsuolbma-javri suggest a primary response to temperature although lake dystrophication/acidification and changes in lake depth may also have played a role. The temperature control on the chironomid fauna was particularly evident during the first half of the Holocene epoch. The inferred temperatures are largely affected by the abundance of various intermediate/thermophilic taxa such as Tanytarsini, Tanypodinae, *Sergentia coracina*, and *Microtendipes*, while the actual shape of the temperature curve is driven by *Heterotrissocladius* and other cold-stenothermic profundal taxa that reveal peak abundances in the profile. Protanypus, although present in low levels, always accompanies the peaks in *Heterotrissocladius* or *C. oliveri* (Fig. 4). In the modern reference data (Olander et al., 1999; Vasko et al., 2000)

these taxa exclusively inhabit the coldest sites. They also are a hallmark feature of the Younger Dryas event for many chironomid sites in Canada (Walker et al., 1991; Levesque et al., 1993; Cwynar and Levesque, 1995) and Europe (Brooks et al., 1997). Although a substantial deepening of the lake might produce similar chironomid changes, it is unlikely that the early Holocene water levels of Tsuolbmajavri differed appreciably from today's as the maximum water level is set by a bedrock sill, above which excess water drains. Moreover, during the period of maximum occurrence of the cold-adapted chironomids, about 6000–4500 cal yr BP, water levels in small lakes in Lapland should actually have been significantly lower than at present (Eronen et al., 1999). We therefore conclude that temperature fluctua-tion is the only factor that can explain the repeated and quite massive peaks of the well-known cold-water midges in Tsuolbmajavri. Without marked periods of cooling, there would have been little chance of refuge for cold-adapted species in such a shallow-water lake.

During the past 4000 yr, however, lake depth seems to have become a more important factor affecting the midge distributions. This can be seen in the form of steadily increasing abundances of some littoral, 'shal-low-water' Chironomidae, notably *Psectrocladius*, *Monopsectrocladius* and *Dicrotendipes*. The shallowing of the lake was in this case not due to drier climate or lower precipitation (the climate has actually become more humid during the past millennia, see Eronen et al. (1999), Seppä and Birks (2001) and Snowball et al. (submitted), but through progressive sedimentation. In our modern training set, temperature and lake depth are closely coupled so that the shallowest lakes are usually also the warmest. Fairly similar faunal changes might therefore be expected if one or the other of the parameters under consideration would abruptly change. It is therefore questionable whether the increases of some warm-water taxa during the late-Holocene reflect climate warming per se, or whether their increase is only mirroring the change in lake's thermal environment controlled by the gradually decreasing lake depth. The initial maximum depth of the lake was slightly above 8 m in the onset of the Holocene, whereas around 4000 cal yr BP, it was already about 2 m less. Such a decline in maximum depth would have meant an even greater decline in mean depth and in the overall volume of the lake.

The catchment-driven slight natural acidification of Tsuolbmajavri may also have influenced the chironomid compositions, in particular during the time of the 'climatic optimum' (8000–6000 cal yr BP), when the frequencies of the acid-sensitive species *Sergentia coracina* exhibited a slight increase and when the lake experienced a gradual drop in pH (Seppä and Weckström, 1999). However, changes in limnological conditions (dystrophication, natural acidification) in

Tsuolbmajavri have been quite insignificant and have always proceeded gradually (Seppä and Weckström, 1999) for which reason they cannot explain the sudden shifts in the chironomid compositions.

To facilitate the discussion, we shall divide the Tsuolbmajavri temperature record into four parts and discuss the climate behaviour within these time horizons in some details.

4.4. Unstable early Holocene ca 10,000–8000 cal yr BP

Inferred July air temperatures during the early Holocene were about the same as today, but with several rapid excursions between warm and cold periods. The record indicates three successive cold 'spells' of an amplitude of 0.8–1.2°C at around 9200, 8600 and 8200 cal yr BP. These events are due to distinct peaks in *Heterotrissocladius* and some other cold-adapted chironomids suggesting a pronounced change in the lake's thermal environment. Our results are in general agreement with inferences based on diatoms and pollen from the same core; they all infer relatively low but rising temperatures during the early Holocene, while diatoms additionally suggest a distinct drop in temperatures at around 8200 cal yr BP (Korhola et al., 2000b; Seppä and Birks, 2001). The results shown here also correspond well with the chironomid-based temperature inferences from a near-by lake Sjuodjijaure, in northern Sweden (Rosén et al., 2001), that similarly show rather low early Holocene temperatures with several successive, abrupt changes. In Sjuodjijaure, both chironomids and diatoms infer cooling events at around 8500 and 8200 cal yr BP (Rosén et al., 2001).

Evidence for a distinct glacier expansion after about 8500 cal yr BP, which culminated around 8200 cal yr BP, occurs in glacier-fed lakes of Hardangerjøkulen and central Jotunheim, southern Norway (Dahl and Nesje, 1996; Matthews et al., 2000). The glaciochemical time series from the Summit, Greenland, ice core, provides additional evidence of the climatically labile early Holocene in the North Atlantic region. There is a distinct increase in concentrations of sea salts and terrestrial dusts in Summit snow during the period 8800 to 7800 cal yr BP suggesting an expansion of the north polar vortex or intensification of meridional air flow, and thus climatic cooling (O'Brien et al., 1995). In the Greenland ice records, a number of other proxy indicators, such as snow accumulation, $\delta^{18}O$ values, and calcium and CH_4 concentrations, also indicate a climate anomaly lasting from ca 9000 to 8000 cal yr BP (Alley et al., 1997). The direct temperature measurements from the borehole of the GRIP core along with the isotope record from the NorthGRIP ice core in Greenland further suggest that present-day-like temperature conditions prevailed in the region around 9000 cal yr BP, and that maximum Holocene tempera-

tures were not reached before 8000 cal yr BP (Dahl-Jensen et al., 1998; Johnsen et al., 2001).

The first (≈ 9200 cal yr BP) and the last (≈ 8200 cal yr BP) of the early Holocene events we infer correspond in timing roughly to the well-known 'Bond events' inferred from the lithic/petrologic proxies of the North Atlantic deep sea sediments (Bond et al., 1997). Furthermore, the most recent of these events might additionally be connected with the widely known '8200 cal yr BP event', the mechanism of which is a subject of growing controversy (Alley et al., 1997; de Vernal et al., 1997; Klitgaard-Kristensen et al., 1998; von Grafenstein et al., 1998; Barber et al., 1999). There is accumulating evidence that the '8200 cal yr BP event' affected terrestrial and aquatic systems in northern Fennoscandia (Dahl and Nesje, 1996; Snowball et al., 1999, submitted; Korhola et al., 2000b; Matthews et al., 2000; Nesje et al., 2000; Rosén et al., 2001).

The relatively low temperatures predicted by our model for the early Holocene contrast with investigations by Kullman (1995) who found tree megafossils at a high elevation site from the northern most Scandes mountains of Sweden from the same period, which would indicate much warmer summers. Thus, although there seems to be some grounds to match the above-described climatic excursions with the short-term events known from elsewhere in the North Atlantic region, their occurrence must be tested by additional high-resolution climate proxy series from climatically critical regions in northern Fennoscandia. On the other hand, because these supposed early Holocene oscillations were short-lived (≈ 60–100 yr) and are represented by just 2–4 cm of sediment on average, they may have gone undetected in northern Fennoscandia by conventional sampling at 5 or 10 cm intervals.

4.5. 'Thermal optimum' ca 8000–5800 cal yr BP

The summer temperatures at Tsuolbmajavri rose gradually and reached their Holocene maxima between ca 7800 and 6500 cal yr BP. Pollen-inferred temperatures from Tsuolbmajavri similarly suggest maximum temperatures between ca 7950 and 6750 cal yr BP (Seppä and Birks, 2001), while diatoms suggest that the summers were warmest slightly later, ≈ 7000–5500 cal yr BP (Korhola et al., 2000b). These results are in general agreement with several previous studies, which suggest high summer temperatures during the early/mid-Holocene in northern Fennoscandia. For example, there is evidence for general glacier retreat in Vuolep Allakasjaure between ca 7900 and 6900 cal yr BP (Karlén, 1998), while according to Nesje and Kvamme (1991) and Nesje et al. (1994), glaciers in western Norway were also withdrawing, or advanced only sporadically, from ca 8800 to 6800 cal yr BP. Recent investigations from the

Jotunheimen area, southern Norway, suggest that glaciers were completely absent from ca 7900 to at least 5300 cal yr BP (Matthews et al., 2000). The diatom, chironomid, pollen, and near-infrared spectroscopy records from the alpine lake of Sjuodjijaure, northern Sweden, indicate increased summer temperatures from ca 7300 cal yr BP (Rosén et al., 2001).

Numerous pollen studies suggest that Scots pine (*Pinus sylvestris* L.) spread to northern Fennoscandia ca 8000–7000 cal yr BP and reached its maximum distribution in the mid-Holocene (Hyvärinen, 1975; Berglund et al., 1996; Seppä, 1996). According to MacDonald et al. (2000), the density of trees north of the modern tree line on the Kola Peninsula, Russia, was highest between ca 7800 and 5800 cal yr BP. Pollen data from Tsuolbmajavri further suggest that pine was locally present in the surroundings of the lake at least from ca 6900 to 5700 cal yr BP (Seppä and Weckström, 1999). However, there is some discrepancy between our temperature inference and the available Fennoscandian pine megafossil data, which indicate a later beginning and a later ending for the 'thermal maximum'. Although the oldest pine trunks found from northern Fennoscandia date back to ca 7500 cal yr BP (Zetterberg et al., 1996), the maximal occurrence of pine megafossils in Finnish Lapland was only between ca 6000 and 4000 cal yr BP, when the pine tree line was located about 200 m higher than its present altitude (Eronen and Huttunen, 1993; Eronen et al., 1999). The obvious asynchrony between the maximum occurrence of pine megafossils and the chironomid-inferred warmest period at Tsuolbmajavri may be due to inaccuracies in dating or may be related to the fact that the northern and elevational extension of pine was controlled additionally by precipitation, as pine in northern Fennoscandia shows preference for dry sites characterised by thin snow beds. Seppä and Birks (2001) show some evidence of decreased precipitation from ca 7000 cal yr BP onwards in northern Fennoscandia. Also, a possible weaker preservation of megafossils under a more humic and oceanic early Holocene climatic regime may have introduced a bias in the subfossil record. According to Eronen et al. (1999), many pine trees found as megafossils grew in situ on the shores of the lakes during a low water level phase between about 6000 and 4000 cal yr BP, and were subsequently submerged and buried as the water level rose. Thus, the clustering of megafossil findings around 6000–4000 cal yr BP may be, at least in part, an artefact of preservation. In general, there seems to be a considerable age scatter in the records for maximum distribution of pine in northern Fennoscandia (Berglund et al., 1996; Dahl and Nesje, 1996; Seppä, 1996; Barnekow, 1999; Eronen et al., 1999), suggesting a highly diachronous pattern of coniferous tree-line changes in the region.

Supporting evidence for our reconstruction of a warmer than present early/mid-Holocene can also be sought from various Greenland ice and North Atlantic deep-sea records. For example, O'Brien et al. (1995), on the basis of measurements of soluble impurities in Greenland ice, inferred a warm climatic phase that lasted from about 7900 to 6300 cal yr BP, and which was associated either with the northward shift of polar vortex contraction or weaker meridional circulation. Interestingly, the interval from ca 8000 to 6000 cal yr BP (centered at ca 6600 cal yr BP) was also the longest uninterrupted Holocene warm period in the ice-rafting record reported by Bond et al. (1997). Based on direct temperature measurements from two boreholes on the Greenland ice sheet, Dahl-Jensen et al. (1998) suggest warmer than present climate between ca 8000 and 5000 cal yr BP.

4.6. Mid-Holocene cooling ca 5800–4000 cal yr BP

Considerable evidence exists for the mid-Holocene cooling at ca 5800 cal yr BP in northern Fennoscandia. This is supported by our new data. Pollen evidence indicates that the tree limit of pine started to retreat in northernmost Fennoscandia at about this time (Hyvärinen, 1975; Seppä, 1996), while glaciers in northern Sweden became more active again (Karlén, 1988). There are also indications of increased interannual variability in the Finnish tree-ring records from ca 5800 cal yr BP onwards, suggesting a shift towards increased climatic instability (Zetterberg et al., 1996; Eronen et al., 1999). A temperature drop at about this time is further supported by data of glacier variations and relative equilibrium line altitude (ELA) fluctuations of maritime glaciers in western Norway, which suggest a shift from mild/wet winters towards cold/dry winters around 6000 cal yr BP (Nesje et al., 2000). From the North Atlantic perspective, chemical indicators of windblown sea salt in the GISP2 ice core suggest that cooling started by ca 6100 cal yr BP and lasted till ca 5000 cal yr BP (O'Brien et al., 1995), while measurements from two deep boreholes on the Greenland Ice Sheet demonstrate a slightly more recent drop in ice temperatures, at about 5000 cal yr BP (Dahl-Jensen et al., 1998).

Inferred temperatures from diatoms and pollen in Tsuolbmajavri show parallel trends with our record and also document the mid-Holocene cooling (Korhola et al., 2000b; Seppä and Birks, 2001). Pollen suggest approximately concomitant cooling to our record at ca 5700 cal yr BP, while diatoms indicate a decreasing trend in temperatures from ca 6200 cal yr BP and a clear minimum around 4200 cal yr BP, which is somewhat later than that in our study. These slight temporal discrepancies may be due to different responses to changes in the

ecosystem or to differences in calibration methods and statistical uncertainties in the reconstruction. For example, WA-PLS suggests more gradual cooling than does Bummer for this period in our record (Fig. 9A and B).

The cooling phase in the present Bummer-model curve around 5800 cal yr BP has the most abrupt onset of any events of our Holocene record. A major ice-rafting episode is suggested by Bond et al. (1997) at this time. The next ice-rafting period occurred according to Bond et al. (1997) around 4200 cal yr BP, which also appears to coincide with a cool phase in our record. This concurrence between cool summers in northern Fennoscandia and periods of enhanced ice-rafting recorded in a marine core from the North Atlantic may reflect large-scale Holocene variability in the atmospheric circulation over northwest Europe.

4.7. Stable late-Holocene ca 4000–present

The chironomid-inferred mean July temperatures do not show any clear trends or shorter-term fluctuations during the past 4000 years. These results contrast with temperature inferences from pollen and diatoms from Tsuolbmajavri that either show a gradual decrease in reconstructed temperatures (pollen; Seppä and Birks (2001)) or demonstrate several small variations during the late-Holocene (diatoms; Korhola et al. (2000b)). A generally colder climate with some short-term transitions is indicated during the past four millennia by a lowering of the pine tree limit (Kullman, 1995; Barnekow, 1999), glacier advances (Nesje and Kvamme, 1991), and increased erosion (Snowball et al., 1999). Occurrence of a climatically very unfavourable period is marked in the Finnish dendrochronology around 2200 cal yr BP with very few subfossil pines (Eronen et al., 1999). This period is not shown in our temperature curve. Instead, there is a major peak (>20%) of the cold chironomid taxon *Corynocera oliveri* preceding this event at around 2700 cal yr BP.

A significant feature in our reconstruction is the lack of evidence for a multicentennial 'Medieval Climate Anomaly' and a persistently cold 'Little Ice Age', both of which are clearly recognisable, e.g. by glacier fluctuations (Matthews, 1991; Matthews et al., 2000) and are also present in the diatom-inferred temperatures from Tsuolbmajavri (Korhola et al., 2000b). As said before, we assume that the shallowing of the lake in the late-Holocene has influenced the chironomid record and thus confounded the climate signal.

4.8. Linkages to North Atlantic climate

Our results indicate that significant climatic oscillations took place in northern Fennoscandia during the Holocene, which were superimposed upon a long-term cooling trend most probably reflecting orbital forcing. Recent palaeoclimatic studies present strong evidence for abrupt, natural climatic changes within the Holocene epoch that are most likely of a global nature (O'Brien et al., 1995; Dahl and Nesje, 1996; Alley et al., 1997; Bond et al., 1997; Bianchi and McCave, 1999; Hu et al., 1999). For example, Bond et al. (1997) have demonstrated, using lithological proxies from North Atlantic deep-water sediments, that repeated cooling events have been characteristic for the past 100,000 years, including the Holocene, with an average period close to 1500 years. During each of these episodes, cool, ice-bearing waters from the north of Iceland were transported as far south as the latitude of Great Britain. Bond et al. (1997) indicate a close temporal agreement between their inferred shifts in ocean circulation in the North Atlantic and changes in the chemical composition of soluble impurities in the Greenland ice (O'Brien et al., 1995). They attribute this synchronicity to the strong link between the Greenland atmosphere and Atlantic surface-water dynamics.

The present North Atlantic ocean masses are characterised by heat and moisture loss to the atmosphere from the north-east trending North Atlantic Drift (continuation of the Gulf Stream), ensuring mild air masses across to the European continent (Hoerling et al., 2001). It is well established that this northwards transfer of heat, via the thermohaline circulation (THC) of the North Atlantic Ocean, has regulated climate in high-latitude Europe on a wide range of timescales, from decades to millennia (Keigwin et al., 1994; Rahmstorf et al., 1996; Snowball et al., 1999, submitted). In particular, THC, which influences the formation of North Atlantic Deep Water in the Nordic/Arctic seas, strongly affects the climate in the region and has been shown to play a major role in either triggering or amplifying rapid climate changes in northwest Europe (Broecker, 1997). The atmospheric response to these ocean changes include the spatial pattern and amplitude of the North Atlantic Oscillation (NAO), the effect of which on the long-term climatic features in Fennoscandia has recently been discussed in Nesje et al. (2000).

The overall climate trend in our record agrees reasonably well with the temperature reconstructions from the Greenland ice-sheet boreholes (Dahl-Jensen et al., 1998) and the new stable isotope data from the NorthGRIP core (Johnsen et al., 2001) in demonstrating that (i) maximum Holocene temperatures were not reached immediately after deglaciation but only between ca 8000 and 6000 cal yr BP, (ii) the mid-Holocene cooling was more abrupt and slightly earlier than previously thought, and (iii) that there existed several short-lived climate oscillations in particular in the early Holocene times. In addition, some of the early and mid-Holocene events we infer (e.g. ≈9200, ≈8200,

≈ 5900 cal yr BP) seem to correspond in timing roughly to the above-discussed 'Bond events' inferred from the lithic/petrologic proxies of the North Atlantic deep sea sediments (Bond et al., 1997) suggesting that the general climate trend inherent in our reconstruction might have followed the larger-scale patterns in the North Atlantic climate. However, the ultimate reasons for the relatively low early Holocene temperatures and successional cooling events in our record, if real, probably lie in more local causes, likely connected to the late deglaciation of the area. The early Holocene in northern Fennoscandia was a period of continued transition from glacial to interglacial, with the ice sheet still covering much of northern Sweden and NW Finland at around 10,000 cal yr BP. We argue that the final collapse of the Scandinavian ice sheet and influxes of meltwater from the diminishing ice frequently interrupted the gradual intensification of North Atlantic THC and affected the regional air flow and circulation patterns. The thermohaline conveyor is known to be highly unstable and hence sensitive to the freshwater/salt balance of the region (Broecker et al., 1985). Ocean circulation modelling studies suggest that a relatively small increase in freshwater flux to the Arctic sea could cause deep-water formation in the north Atlantic to cease (Mikolajewicz and Maier-Reimer, 1994; Rahmstorf, 1994; Rahmstorf et al., 1996). THC intensity then peaked for an extended period between ca 8000 and 5800 cal yr BP, which promoted a stable 'thermal maximum' in Fennoscandia and the rapid retreat and disappearance of many mountain glaciers.

Intrestingly, Hu et al. (1999) recently suggested that there were also abrupt changes in North American climate during early Holocene time. Using stable oxygen-isotope measurements from sedimentary carbonate and varve thickness data, they demonstrated a marked cooling from 8900 to 8300 cal yr BP, followed by an additional cooling about 8200 cal yr BP. The reason for the first of these coolings was probably regional, being related with the final collapse of the Laurentide ice near Hudson Bay and associated re-organisation of regional atmospheric circulation, while the 8200 cal yr BP event was apparently connected to the North Atlantic THC. While it is possible to invoke feedback mechanisms related to melting of remnant ice sheets for climate variability documented during the early Holocene, it is not possible to invoke these mechanisms for the variability seen in late-Holocene climate.

5. Conclusions

1. We have reconstructed long-term summer temperature changes quantitatively from subfossil midge remains preserved in lake sediments, using a Bayesian full-probability model with an accuracy of ca 0.8°C. Bayesian inference is particularly suitable for calibration purposes, because it gives a principled way to solve statistical inversion problems such as reconstructing causes (environmental conditions) from the effects (species abundances). Further, the use of full-probability distributions rather than point estimates conserves the inherent statistical uncertainty throughout the inference and helps to estimate its effect on the reconstructions.

2. Our chironomid-based summer temperature reconstruction is generally consistent with other independent proxy records from the same study site and elsewhere from northern Fennoscandia by showing an unstable early Holocene between ca 10,000 and 8000 cal yr BP, a 'thermal maximum' between ca 8000 and 5800 cal yr BP, and a distinct cooling around ca 5800 cal yr BP. The period of the 'thermal maximum' represented the longest uninterrupted warm period in our record, and we argue that this environmental stability allowed tree-line and thermophilous plants to move northwards and upwards.

3. The last 4000 yr in our record are rather featureless, which contrasts with evidence from tree lines, forest composition, glacier activity, stable isotopes and catchment erosion that all point to a general cooling of climate during the latter part of the Holocene. The reason for the uneventful late-Holocene may lie in gradual shallowing of the study lake by sedimentation that may have affected chironomid compositions and disturbed the climate signal.

4. The record implies that in addition to a long-term cooling trend reflecting orbital forcing and summer insolation, significant short-term climatic oscillations took place in northern Fennoscandia during the Holocene. Distinct cooling episodes of an amplitude of 0.8–1.2°C were inferred around 9200, 8600, 8300 and 5800 cal yr BP. The cooling phase around 5800 cal yr BP had the most abrupt onset of any events of our Holocene record.

5. The similarities in the reconstructed climatic patterns between our data and some of the marine and Greenland ice core data suggest climatic linkages between the North Atlantic and northern Fennoscandia and indicate regional controls of the observed climatic transitions. Our results indicate that the Fennoscandian mainland climate may have been influenced by the North Atlantic ocean–atmosphere circulation system.

6. Due to the errors associated with radiocarbon chronologies, it is difficult to unambiguously correlate palaeoclimatic records of high-frequency events. There is a need to synchronise palaeoclimate records using methods that are independent of regional response to climate forcing.

Acknowledgements

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