

## **Do Diatom, Chironomid, and Pollen Records Consistently Infer Holocene July Air Temperature? A Comparison Using Sediment Cores from Four Alpine Lakes in Northern Sweden**

Authors: Rosén, Peter, Segerström, Ulf, Eriksson, Lars, and Renberg, Ingemar

Source: Arctic, Antarctic, and Alpine Research, 35(3) : 279-290

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: [https://doi.org/10.1657/1523-0430\(2003\)035\[0279:DDCAPR\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035[0279:DDCAPR]2.0.CO;2)

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Do Diatom, Chironomid, and Pollen Records Consistently Infer Holocene July Air Temperature? A Comparison Using Sediment Cores from Four Alpine Lakes in Northern Sweden

Peter Rosén,\*†

Ulf Segerström,‡

Lars Eriksson,§ and

Ingemar Renberg\*

\*Department of Ecology and Environmental Science, Umeå University, SE-901 87 Umeå, Sweden.

Peter.Rosen@eg.umu.se;

Ingemar.Renberg@eg.umu.se

†Climate Impacts Research Centre, Abisko Scientific Research Station, Box 62, SE-981 07 Abisko, Sweden.

‡Department of Forest Vegetation Ecology, Swedish University of Agricultural Sciences, SE-901 83 Umeå, Sweden.

Ulf.Segerstrom@svek.slu.se

§Department of Environmental Assessment, Swedish University of Agricultural Sciences, Box 7050, SE-750 07 Uppsala, Sweden.

Lars.Eriksson@ma.slu.se

## Abstract

The aim of this study is to assess the performance of diatom, chironomid, and pollen transfer functions for inferences of July air temperature during the Holocene using sediments from four alpine lakes in an area with low human impact in northern Sweden. The study demonstrates that diatom, chironomid, and pollen assemblages in the sediment cores contain climate information so that present-day temperature at each lake can be inferred with reasonable confidence for most proxies. Most proxy records from the sites consistently infer a long-term decreasing trend in July air temperature from ca. 6000 cal yr BP until the present. However, there are also large variations in the temporal patterns of the inferred temperatures during some periods, especially before 7000 cal yr BP, when there are also nonsynchronous changes in loss-on-ignition in the four lakes. This variability indicates that local conditions (influence of snowfields, soil-forming processes) had a large impact on the organism assemblages in the early Holocene.

Long-distance transport of pollen into high alpine lakes makes temperature inferences from pollen transfer functions unreliable. Due to the uncertainties of the methods, predictive errors of the transfer functions, and variability caused by local catchment/lake characteristics, only long-term trends in climate can be inferred. High-resolution studies using diatoms, chironomids, and pollen for climate reconstruction are probably not meaningful during periods with small changes in climate (<1°C). Future research should concentrate on low-resolution, multiproxy, and multilake studies to further understand the relationship between the proxies and climate.

## Introduction

Impacts of climate change are a major concern today and have highlighted the need for long-term climate data. Lake sediments provide a useful archive for studies of past climate (Battarbee, 2000). During the last decade, a series of transfer functions aimed at temperature reconstruction using lake sediment records have been developed using diatoms (Pienitz et al., 1995; Vyverman and Sabbe, 1995; Wunsam et al., 1995; Lotter et al., 1997; Weckström et al., 1997; Rosén et al., 2000; Bigler and Hall, 2002), chironomids (Walker et al., 1991a; Lotter et al., 1997; Olander et al., 1999), and pollen (Anderson et al., 1991; Lotter et al., 2000; Rosén et al., 2001).

Chironomid (Walker et al., 1991b; Levesque et al., 1993; Smith et al., 1998; Lotter et al., 1999a; Brooks and Birks, 2000; Brooks and Birks, 2001) and pollen (Lotter et al., 2000) transfer functions seem to perform well in the late glacial period, when temperature underwent large changes. The transfer functions have so far been applied only in a limited number of investigations of Holocene climate (Korhola et al., 2000; Pellatt et al., 2000; Rosén et al., 2001; Brooks and Birks, 2001), and these studies have usually used only one proxy or one site. Most Holocene temperature reconstructions indicate temperature changes that are close to the prediction errors of the models. Therefore, the efficacy of reconstruction of past climate using transfer functions has not yet been fully demonstrated.

The objective of this study was to test the performance of the transfer function approach for the reconstruction of July air temperatures during the Holocene using diatoms, chironomids, and pollen. There is no standard describing how Holocene climate has varied over time against which the reconstructions for each proxy can be com-

pared, so we used a multiproxy and multisite approach. We compared reconstructions from four lakes situated from the treeline up to the high alpine area in the Scandes mountains, northern Sweden. The area was suitable for this test because low human impact made it easier to extract the climate signal from the data.

## Materials and Methods

The study area is situated within the UNESCO World Heritage site, Lapponia, in northern Sweden (Fig. 1). The altitude ranges from 300 to 2100 m with mountain birch (*Betula pubescens* ssp. *tortuosa*) as tree-limit species at about 700 m a.s.l. All lakes are small, head-water lakes with oligotrophic clear water (Fig. 1, Table 1). Jeknajaure, Sjuodjjaure, and Seukokjaure are situated in U-shaped valleys with gentle slopes up to the lakes that allow vegetation to migrate a relatively long distance with a small change in climate. The drainage area of Jeknajaure includes relatively steep mountains that reach 2000 m a.s.l.; Sjuodjjaure and Seukokjaure are surrounded by more gentle slopes. Niak is situated in a cirque surrounded by steep mountains up to 1900 m a.s.l. The ice cover extends from October to June/July. Mean July air temperature at each lake was extrapolated and corrected for altitude from a nearby climate station using a lapse rate of 0.57°C per 100 m elevation (Laaksonen, 1976).

Sediment cores were taken from the deepest part of each lake using a gravity corer (HTH-Teknik, Vårvägen 37, SE-951 49 Luleå); for deeper sediments a Russian or a modified Livingstone piston corer was used. Samples were taken approximately every 5 cm for comparison of reconstructed climate trends between lakes. Sjuodjjaure was

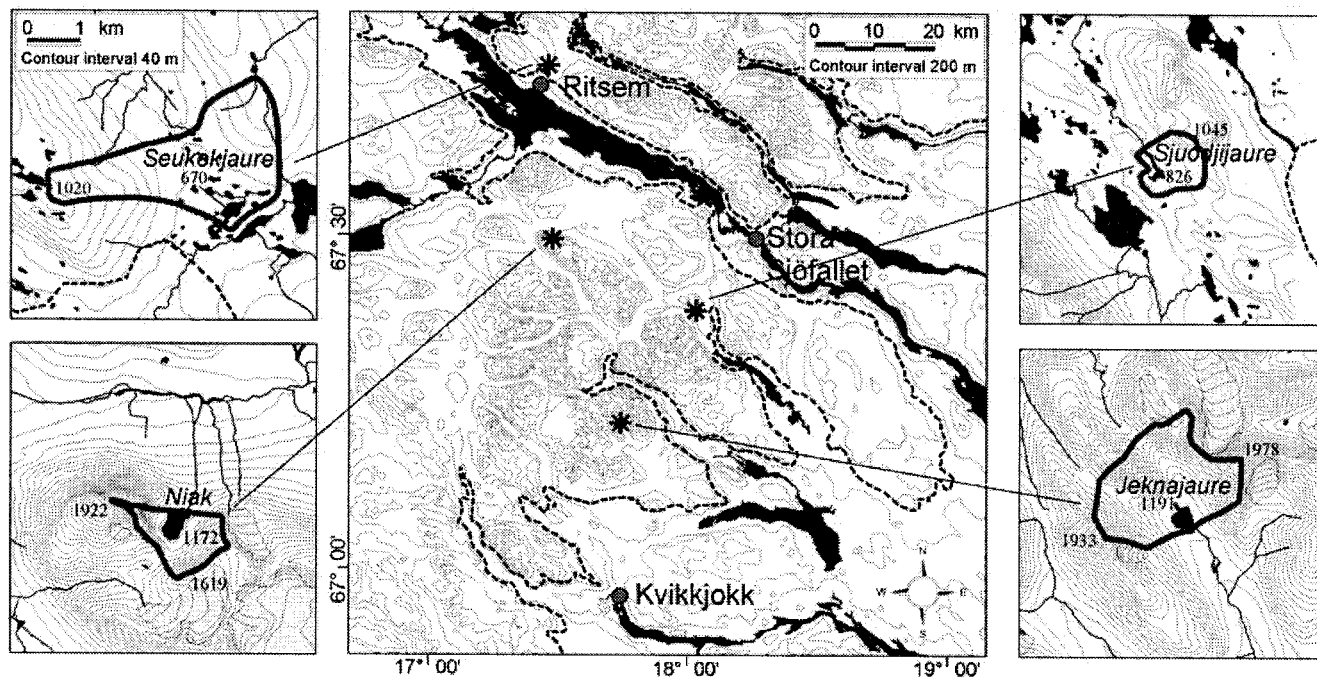


FIGURE 1. Map showing the study area and the four study lakes: Jeknajaure, Niak, Sjuodjijaure, and Seukokjaure. The line on the overview map indicates the birch forest limit. The lines on the small maps indicate the drainage areas for the lakes; shaded areas are glaciers.

analyzed at higher resolution, and those results were reported by Rosén et al. (2001).

Preparation and taxonomy of diatom, chironomid, and pollen analyses followed standard methods and were described by Rosén et al. (2001). Radiocarbon dating of terrestrial macrofossils and bulk sediment samples was performed using accelerator mass spectrometry (AMS) (Ångström Laboratory, Box 534, SE-751 21 Uppsala).  $^{14}\text{C}$  dates were calibrated to calendar years BP (i.e., 1950 A.D.) following Stuiver and Reimer (1993). Age-depth modeling for Sjuodjijaure was made using generalized additive models by Heegaard and Birks (pers. comm.).

Diagrams for diatoms, chironomids, and pollen were made using TILIA 2.0 and TILIAGRAPH 1.25 (Grimm, 1993). The computer program ZONE 1.2 (Juggins, 1991; Lotter and Juggins, 1991) was used to assess major changes in the fossil assemblages using optimal sum of squares partitioning (Birks and Gordon, 1985). The broken-stick model was used to test whether the proposed zonations were statistically significant (Jolliffe, 1986; Jackson, 1993; Bennett, 1996).

Analogue matching using squared chi-squared distance as the dissimilarity measure was used to assess whether the fossil diatom, chironomid, and pollen assemblages had good analogues in the modern training sets. Ninety-nine permutations were used to assess the approximate statistical significance of the dissimilarity coefficients. Fossil samples were considered good analogues if they lay within the 5% percentile. The program ANALOG 1.6 was used for analogue matching (Birks et al., 1990).

The transfer functions were developed from the same region as the study lakes (Rosén et al., 2000). For diatoms, a three-component weighted averaging partial-least squares regression (WA-PLS) model, using  $(\ln + 1)$  transformed diatom percentages data from 60 lakes, was selected as the minimal adequate model ( $R^2_{\text{jack}} = 0.74$  and root mean squared error (RMSEP) =  $0.88^\circ\text{C}$ ; 12% of the gradient). For better reconstruction of high alpine lakes, eight additional high alpine lakes (Bigler et al., 2002) from the Abisko area 100 km north of Lapponia were included in addition to those used in the diatom transfer function of Rosén et al. (2000). For chironomid-based temperature recon-

structions, a weighted average model with inverse deshrinking (Birks et al., 1990) was used on a 40-lake training set ( $R^2_{\text{jack}} = 0.44$ , root mean square error of prediction based on leave-one-out jack-knifing (RMSEP) =  $1.02^\circ\text{C}$ ; 18.5% of gradient). Lakes with fewer than 50 head capsules in the samples were excluded from the transfer function. For pollen, a one-component WA-PLS regression model, using square-root transformed pollen percentages from 55 lakes, was selected as the minimum adequate model ( $R^2_{\text{jack}} = 0.33$ , RMSEP =  $1.20^\circ\text{C}$ ; 22.2% of gradient). Identical statistical procedures were used to develop the diatom, chironomid, and pollen transfer functions (Rosén et al., 2000) and made using CALIBRATE 0.81 (Juggins and ter Braak, 1993). The surface samples from the study lakes were not included in the training sets.

Species optima and tolerances to July air temperature were calculated according to Rosén et al. (2001). For details, see also ter Braak and Looman (1986), Huisman et al., (1993), and Birks (1995). Sample specific errors were estimated using the computer program WAPLS 1.0 (Juggins and ter Braak, 1995). To estimate how much of the error is caused by sample preparation and counting, 10 separate samples from 95-cm depth from Seukokjaure were prepared for diatom analyses and counted. See Birks (1995, 1998) for statistical details of the transfer functions, model evaluation by leave-one-out cross-validations, and sample-specific error.

Correspondence analysis was used to explore changes in the diatom assemblages through time. Sample scores from the reconstruction lakes were compared with sample scores from the 60-lake training set (Rosén et al., 2000) to assess how downcore diatom composition in the four lakes compared to diatom composition in surface sediments from lakes with different catchment vegetation. All ordinations were performed using the computer program CANOCO (ver. 3.12) (ter Braak, 1991).

## Results

### SEDIMENT DATING AND LOSS-ON-IGNITION

Radiocarbon dates are reported in Table 2. Bulk samples from Sjuodjijaure gave consistently older ages (170–1300 yr.) than dates

based on terrestrial macrofossils from the same levels (Rosén et al., 2001). The chronology for Sjuodjijaure was therefore based only on radiocarbon dating from five levels using terrestrial macrofossils. Macrofossils were absent in Jeknajaure and Niak, and only one level in Seukokjaure could be dated with a terrestrial macrofossil. We therefore based the chronologies for Seukokjaure and Jeknajaure on a comparison of pollen assemblages with Sjuodjijaure. The single sample from Seukokjaure supported this chronology. For Jeknajaure, this pollen-based chronology suggested younger dates than the four radiocarbon dates but fell within  $2\sigma$ . For Niak, the chronology was based on the mean value in the calibrated range since no pollen diagram was available. The two high alpine lakes (Jeknajaure and Niak) have loss-on-ignition values  $<10\%$ , while there are considerably higher values in the other lakes (Fig. 6).

#### DIATOM, CHIRONOMID, AND POLLEN STRATIGRAPHIES IN THE FOUR LAKES

A total of nine biotic stratigraphies was recorded. Dates where three or more of these change significantly in the four lakes were found at 8000–7500, 6000, 5500–5000, 4100–3700, and 1000 cal BP. These changes in the assemblages from the four lakes are identified as zones in Figures 2–4.

##### Jeknajaure

Most diatoms were benthic, and below 60 cm (ca. 6000 cal yr BP) *Fragilaria* spp. and *Navicula digitulus* dominated the sediment (Fig. 2). Around 60 cm there was a large change in the diatom community: all *Fragilaria* species decreased and different species of *Achnanthes* and *Aulacoseira* increased in frequency. At the transition between the two communities *Fragilaria contruens* var. *venter* had a major peak (67%). Due to the low concentration of head capsules, chironomids from Jeknajaure were not counted.

Pollen of *Hippophae rhamnoides*, *Salix* spp., Graminae spp., and a diverse assemblage of herb pollen and fern spores suggested more open vegetation and wet conditions below 95 cm (prior to ca. 9000 cal yr BP) (Fig. 2). Between 95 and 60 cm (ca. 9000–6000 cal yr BP) *Alnus*, *Betula*, and *Pinus* pollen dominated the sediment and *Juniperus* became more common. Above 60 cm (ca. 6000 cal yr BP to present)

TABLE 1

Location and environmental characteristics of the study lakes

| Variables               | Jeknajaure  | Niak                    | Sjuodjijaure        | Seukokjaure         |
|-------------------------|-------------|-------------------------|---------------------|---------------------|
| Latitude (°N)           | 67°13'      | 67°30'                  | 67°22'              | 67°46'              |
| Longitude (°E)          | 17°48'      | 17°31'                  | 18°04'              | 17°31'              |
| Altitude (m a.s.l.)     | 1191        | 1172                    | 826                 | 670                 |
| Lake area (ha)          | 15          | 19                      | 7                   | 11                  |
| Drainage area (ha)      | 438         | 153                     | 114                 | 617                 |
| Drainage area/lake area | 29          | 8                       | 16                  | 56                  |
| Catchment vegetation    | alpine      | alpine                  | alpine              | at treeline         |
| Bedrock                 | amphibolite | amphibolite/<br>granite | granite/<br>syenite | granite/<br>syenite |
| Max. depth (m)          | 9.1         | 13.2                    | 4.2                 | 6.1                 |
| July air temp. (°C)     | 7.8         | 7.9                     | 9.8                 | 10.6                |
| pH (units)              |             | 6.4                     | 6.3                 |                     |
| Sediment core           |             |                         |                     |                     |
| length (cm)             | 101         | 210                     | 255                 | 141                 |
| Sampling year           | 1998        | 2000                    | 1996                | 1996                |

*Alnus* and *Betula* decreased markedly and *Picea* was recorded continuously. Tree pollen were likely transported long distances.

##### Niak

Most diatoms were benthic, and in the sediment below 120 cm (ca. 5000 cal yr BP) *Fragilaria* spp. dominated the flora, with a decreasing trend throughout the Holocene, while the relative abundance of *Achnanthes* spp., *Aulacoseria* spp., and *Navicula schmassmanni* increased (Fig. 2).

Due to the low concentration of chironomid head capsules and problems with long-range transportation of pollen in open areas, chironomids and pollen from Niak were not counted.

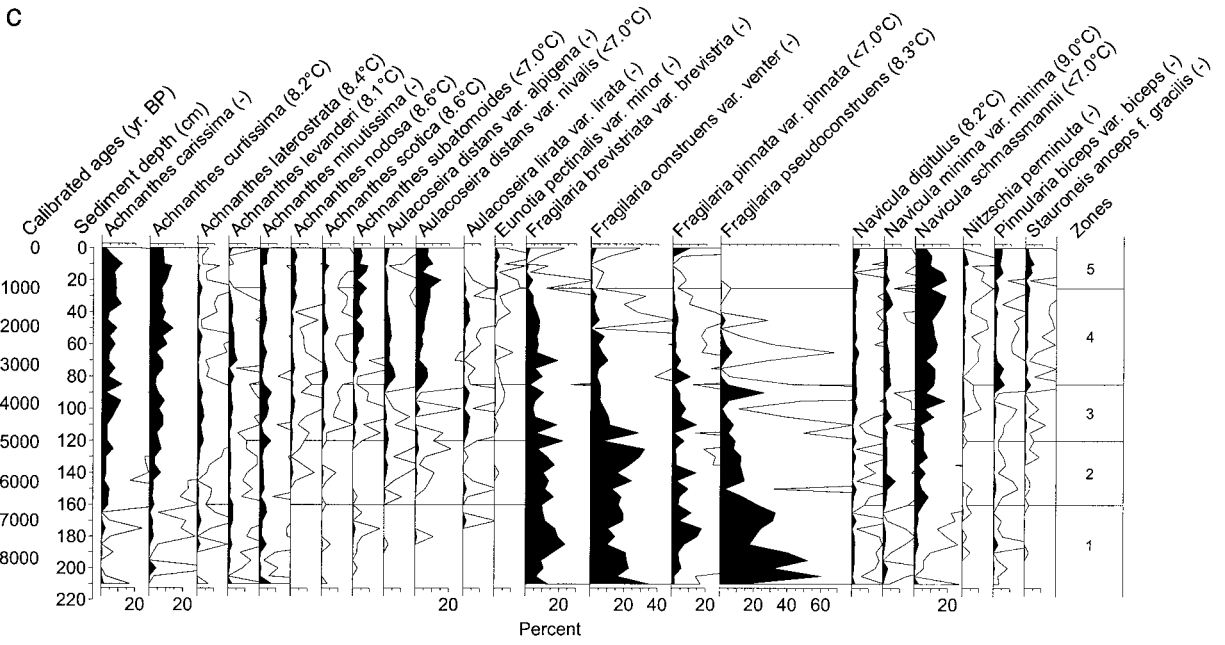
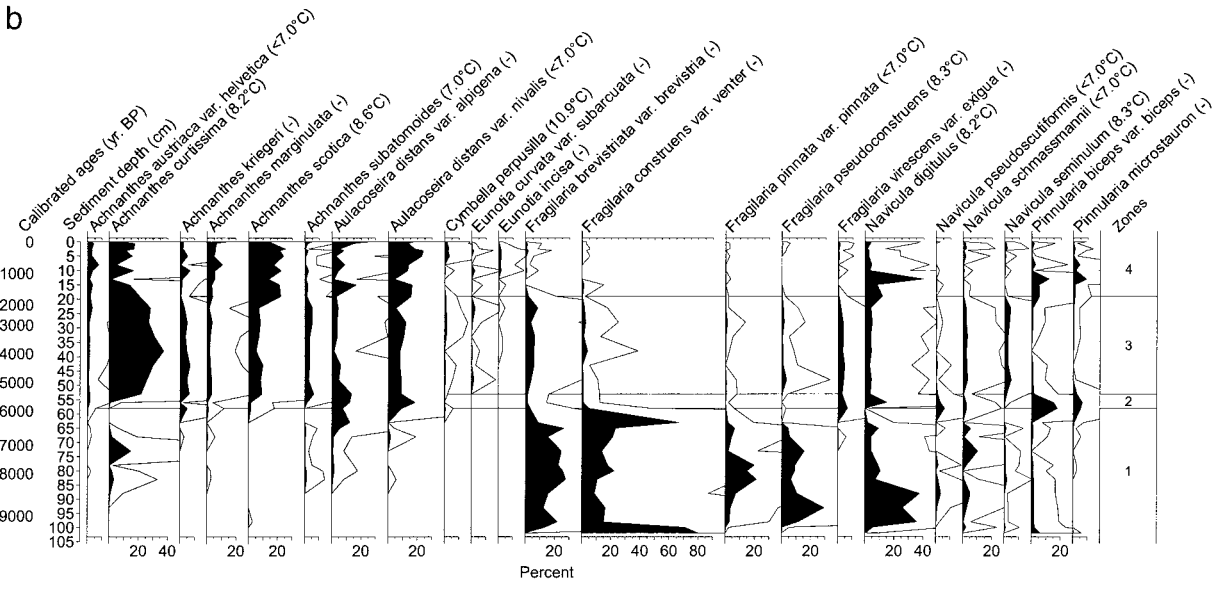
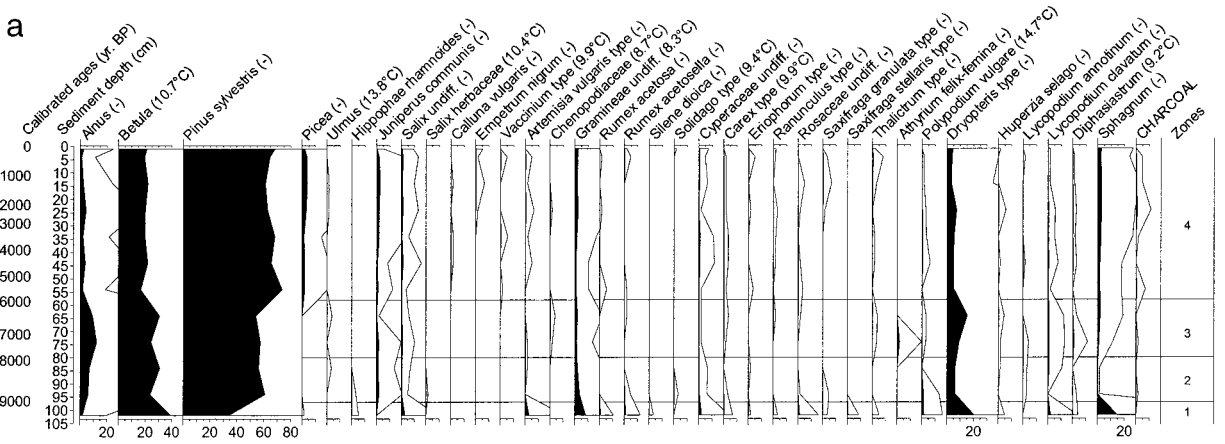
##### Sjuodjijaure

Most diatoms were benthic, and *Fragilaria* spp. and *Achnanthes* [*minutissima* agg.] dominated the sediment below 210 cm (ca. 7300 cal yr BP) (Fig. 3). Between 210 and 128 cm (ca. 7300–3900 cal yr BP), *Achnanthes* [*minutissima* agg.] declined in frequency and *Brachysira*

TABLE 2

Radiocarbon dates from Jeknajaure, Niak, Sjuodjijaure, and Seukokjaure. Calibrated ages are within  $2\sigma$

| Lake         | Material                | Sediment depth (cm) | Dates ( $^{14}\text{C}$ yr BP) | Calibrated age (yr BP) |
|--------------|-------------------------|---------------------|--------------------------------|------------------------|
| Jeknajaure   | Bulk sediment           | 26                  | 2565 ± 70                      | 2780–2360              |
| Jeknajaure   | Bulk sediment           | 63                  | 5840 ± 75                      | 6850–6460              |
| Jeknajaure   | Bulk sediment           | 89                  | 8170 ± 80                      | 9370–8770              |
| Jeknajaure   | Bulk sediment           | 102                 | 8800 ± 90                      | 9980–9520              |
| Niak         | Bulk sediment           | 210                 | 7810 ± 170                     | 9140–8200              |
| Sjuodjijaure | Terrestrial macrofossil | 39.5–40             | 1360 ± 160                     | 1550–940               |
| Sjuodjijaure | Bulk sediment           | 40–41               | 1535 ± 65                      | 1540–1300              |
| Sjuodjijaure | Terrestrial macrofossil | 70                  | 1700 ± 160                     | 1810–1400              |
| Sjuodjijaure | Bulk sediment           | 70–71               | 2150 ± 70                      | 2330–1940              |
| Sjuodjijaure | Bulk sediment           | 107–108             | 3265 ± 65                      | 3630–3360              |
| Sjuodjijaure | Terrestrial macrofossil | 143                 | 3835 ± 70                      | 4420–3990              |
| Sjuodjijaure | Bulk sediment           | 175–176             | 5300 ± 75                      | 6280–5910              |
| Sjuodjijaure | Bulk sediment           | 210–211             | 6800 ± 70                      | 7700–7480              |
| Sjuodjijaure | Bulk sediment           | 230–231             | 8620 ± 80                      | 9850–9440              |
| Sjuodjijaure | Terrestrial macrofossil | 231                 | 7615 ± 110                     | 8560–8130              |
| Sjuodjijaure | Terrestrial macrofossil | 244                 | 8135 ± 75                      | 9360–8730              |
| Seukokjaure  | Bulk sediment           | 62                  | 4030 ± 60                      | 4810–4354              |
| Seukokjaure  | Terrestrial macrofossil | 111                 | 7260 ± 75                      | 8160–7910              |
| Seukokjaure  | Bulk sediment           | 132                 | 9070 ± 75                      | 10280–9910             |



*vitrea* as well as different species of *Cymbella* were most common. From ca. 128 cm (ca. 3900 cal yr BP) *Achnanthes scotica* and different species of *Fragilaria* increased, whereas *Brachysira vitrea* decreased.

The chironomid composition was highly variable below 210 cm (ca. 7300 cal yr BP), with rapid changes between “cold” and “warm” taxa, e.g., *Corynocera ambigua*, *Corynocera oliveri*-type, *Chironomus anthracinus*-type, and *Procladius* spp. (Fig. 3). Between 210 and 122 cm (ca. 7300–3700 cal yr BP), the chironomid composition was more stable, with a higher frequency of “warmer” taxa such as *Psectrocladius septentrionalis*-type and *Pentaneurini*-type. From 122 cm (ca. 3700 cal yr BP), *Paratanytarsus* spp. and *Heterotrissocladius brundini* increased.

The pollen assemblage reflected partly open birch-forest vegetation below 210 cm (ca. 7300 cal yr BP), with declining frequency of *Betula* pollen and increasing frequency of *Pinus* pollen (Fig. 3). Between 210 and 133 cm (ca. 7300–4100 cal yr BP), the pollen composition reflected a transition from an initially more open vegetation, characterized by shrubby birch vegetation, into a vegetation type with a gradually increasing presence of *Pinus*. Above 133 cm (ca. 4100 cal yr BP), *Pinus* and *Alnus* pollen decreased gradually and *Picea* pollen increased in abundance. Pine most probably disappeared from the area, and the local vegetation changed into the rather open, shrubby birch community that remains today. A more detailed description of the diatom, chironomid, and pollen assemblages for Sjuodjjaure is presented in Rosén et al. (2001).

#### Seukokjaure

Below 110 cm (ca. 8000 cal yr BP), *Fragilaria* spp. dominated the diatom flora, and thereafter *Aulacoseira* spp., *Navicula minima* var. *minima*, and *Fragilaria virescens* var. *exigua* increased in frequency (Fig. 4).

During most of the Holocene, *Tanytarsus* spp., *Paratanytarsus* spp., and *Corynocera oliveri* dominated the chironomid fauna (Fig. 4). *Paratanytarsus* spp. had a lower frequency between 67 and 22 cm (ca. 4800–1600 cal yr BP). From 102 cm (ca. 7400 cal yr BP) *Zalutschia zalutschicola* and from 62 cm (ca. 4500 cal yr BP), *Heterotrissocladius brundini* became more abundant.

The pollen diagram can be divided into three main stratigraphical sections (Fig. 4). Below 132 cm (before ca. 9500 cal yr BP), *Hippophae rhamnoides* and *Salix* spp. indicated that the vegetation was open and less forested. Between 132 and 62 cm (ca. 9500–4500 cal BP), *Betula* was the most common forest tree, *Alnus* occurred, and in the upper part of the section *Pinus* increased. The first occurrence of *Picea* pollen was recorded ca. 7000 cal yr BP. Above 60 cm (ca. 4500 cal yr BP to present), *Picea* pollen were found continuously, *Alnus* and *Pinus* decreased, and Ericaceae, Graminae, and Cyperaceae pollen increased.

#### CORRESPONDENCE ANALYSIS OF DIATOM ASSEMBLAGE DATA AND MODERN ANALOGUE MATCHING

The comparison of sample scores from correspondence analysis of the four lakes, based on the diatom community composition, with sample scores from lakes in the training set shows that all fossil samples were within the range of the training set throughout the Holocene (Fig.

5). Jeknajaure (1191 m a.s.l.) and Niak (1172 m a.s.l.) had sample scores similar to those for alpine lakes throughout the Holocene, i.e., a diatom composition similar to surface sediments from lakes in the alpine zone today. For Sjuodjjaure (826 m a.s.l.) the sample scores from the early Holocene had closer analogues in modern birch-forest lakes (Rosén et al., 2001). During the mid-Holocene, the sample scores were similar to conifer and mixed conifer–birch forest lakes. Closer to the present, the sample scores fit into the range of all three vegetation types. For Seukokjaure (670 m a.s.l.), the sample scores compared best with birch forest and alpine lakes throughout the Holocene. Interestingly, all four lakes showed a similar direction and magnitude of change in sample scores, with the exception of Sjuodjjaure, which showed another direction of change during the early Holocene. Correspondence analysis was not applied to the chironomids and pollen data due to the relatively few numbers of head capsules recovered, the relatively small training set for the chironomids, and analogue problems with the pollen assemblages.

The modern analogue matches for the proxies are reported in Figure 6. The analogue situation for diatoms in Jeknajaure was poor for 6 of 13 samples (limit 5% percentile) below 63 cm (ca. 6500 cal yr BP) and good from 63 cm to the surface (present). Niak had good modern analogues for all but 3 samples. All samples from Sjuodjjaure had good analogs. For Seukokjaure the analogue situation was good below 70 cm (ca. 6000 cal yr BP) and poor for 5 of 15 samples from 70 cm to the surface (present).

The analogue situation for the chironomids in Sjuodjjaure was poor below 205 cm (ca. 7100 cal yr BP) but good for all but 4 samples from 205 cm to today. In Seukokjaure, the analogue situation was good below 77 cm (ca. 5600 cal yr BP) but poor for most samples from 77 cm to the surface (present).

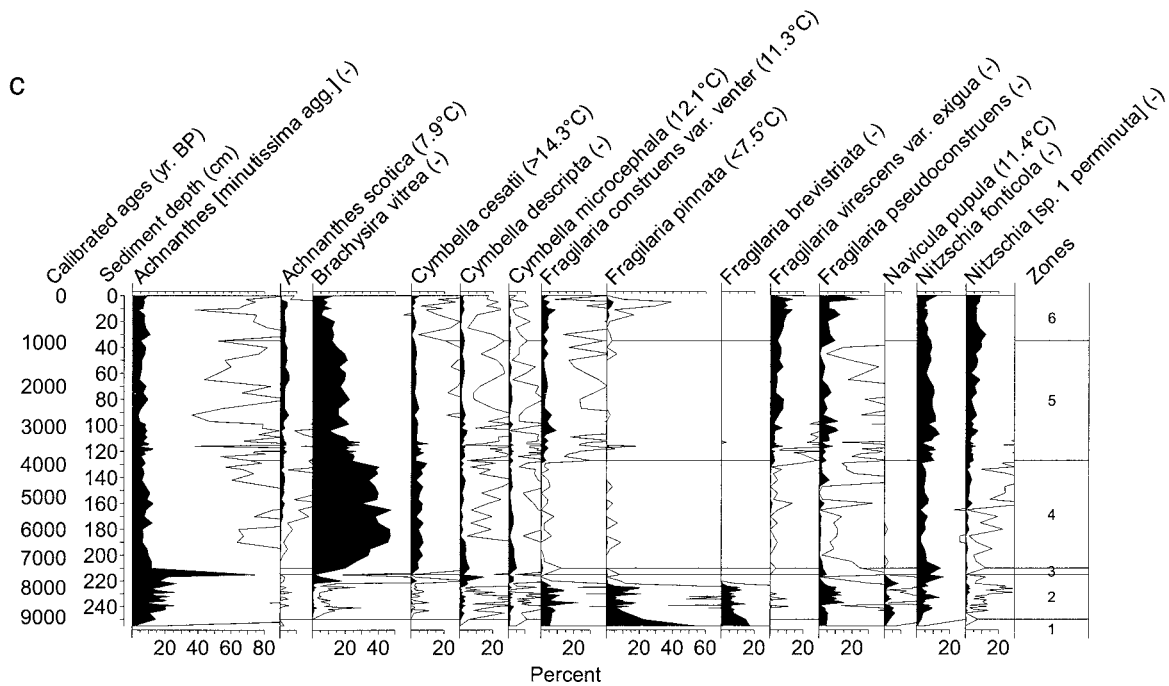
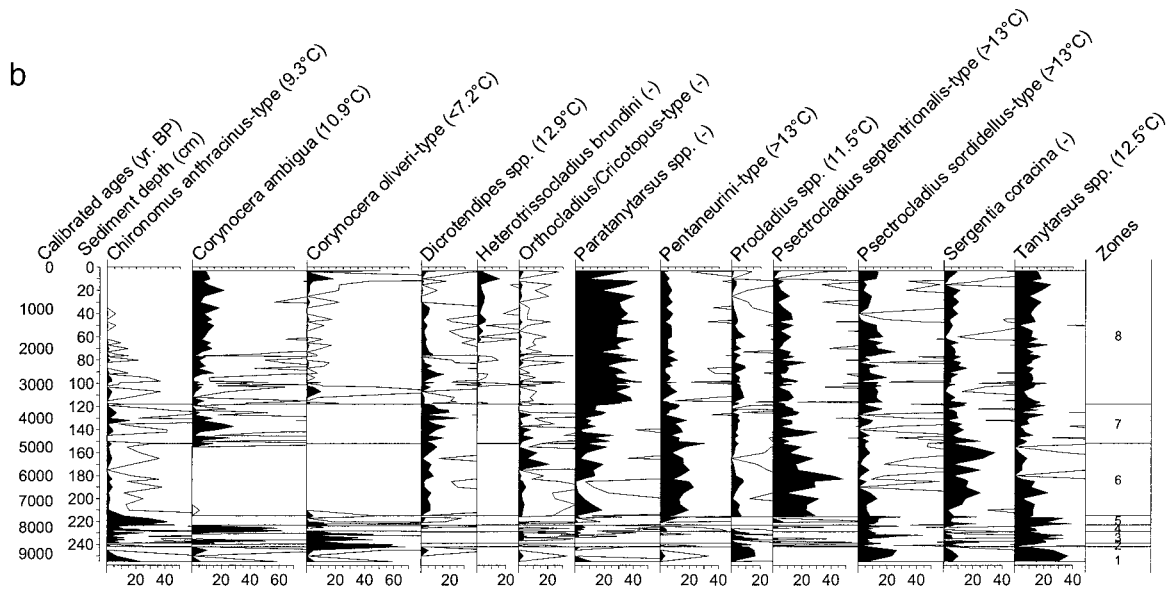
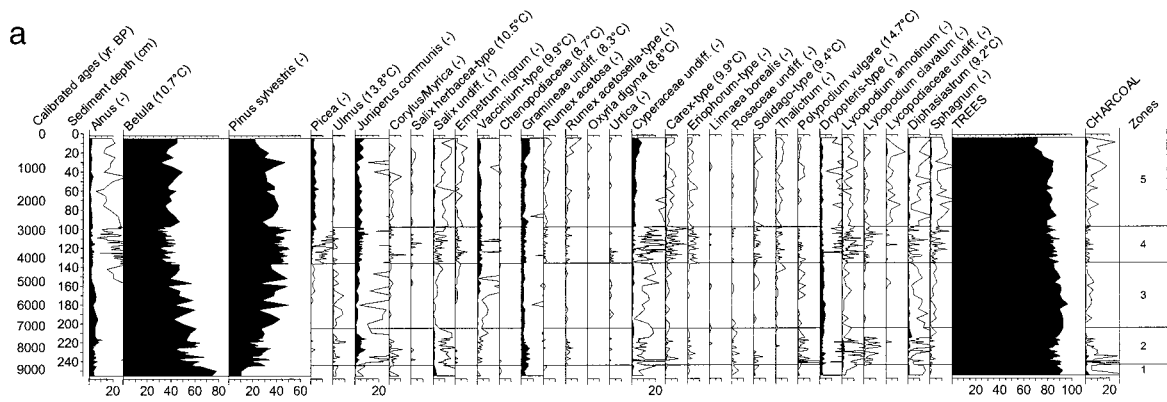
The Holocene pollen assemblages from Jeknajaure had no good modern analogues. For Sjuodjjaure, there were no good analogues below 126 cm (ca. 3900 cal yr BP), but the situation was considerably better from 126 cm to today. In Seukokjaure, there were no good analogues below 62 cm (ca. 4500 cal BP). From 52 cm to today, all samples had good analogs.

#### INFERRED JULY AIR TEMPERATURES

The diatom record from Jeknajaure implied a gradual decrease in temperature during the Holocene, with a period of higher temperatures occurring around 60 cm (ca. 6000 cal yr BP) (Fig. 6). The pollen suggested only small temperature changes and much higher temperatures than the diatom record. The diatom-inferred present-day July air temperature for Jeknajaure was 0.7°C colder (at 0 cm below the sediment surface) than the measured value but 4.4°C warmer for the pollen (1 cm). The diatom record from Niak implied a gradual decrease in temperature throughout the Holocene, and the surface sample (0 cm) suggested a temperature 0.7°C warmer than the present-day July temperature. For Sjuodjjaure the diatom, chironomid, and pollen records implied temperatures similar to today's before 210 cm (ca. 7300 cal yr BP). There was rapid increase in temperature at about 210 cm (ca. 7300 cal yr BP), and from about 200 cm (ca. 7000 cal yr BP) the temperature gradually decreased 0.7–1.0°C until the present. The diatom-inferred July air temperature for the surface sample was 0.1°C warmer (0 cm), whereas the chironomids suggested 0.9°C warmer (3 cm) and pollen

←

FIGURE 2. Pollen (a) and diatom diagrams (b) from Jeknajaure (1191 m a.s.l.) and diatom diagram from Niak (c) plotted against sediment depth. Black silhouettes represent percent and open silhouettes per mil occurrences. The first column shows calibrated ages; 0 corresponds to the coring date. Lines indicate statistically significant zones. Temperatures within parentheses are statistically significant July air temperature optima for the taxa. An optimum below the gradient in the training set is indicated by < and beyond the gradient by >; (-) indicates no statistically significant optimum. Only the most common taxa are shown.



the same (0 cm) as the measured present-day July air temperature for Sjuodjjaure. For Seukokjaure, there were large discrepancies between proxies before ca. 4000 cal yr BP. From ca. 4000 cal yr BP to the present, the diatoms and pollen suggested a decreasing trend in temperature of ca. 0.8°C. The chironomid record implied only small changes in temperature during the Holocene. The surface sample for the diatoms suggested 0.7°C warmer (0 cm), whereas the chironomids (2 cm) and pollen (1 cm) suggested the same temperature as the present-day July air temperature.

The sample-specific errors for inferred mean July air temperature varied between 0.9 and 1.2°C for diatoms, of which a minor part was caused by sample preparation and counting (SD = 0.13°C, range 10.0–10.4°C, n = 10). The sample-specific error for chironomids was 1.1–1.4 °C and for pollen 1.4–1.7°C. The interpretation of the sample-specific prediction errors was uncertain because of the strong autocorrelation and nonindependence of individual samples in stratigraphical time series (Birks, 1998). Here emphasis was placed on consistent trends within and between the different reconstructed records rather than a strict adherence to  $\pm 1.1^\circ\text{C}$  between adjacent samples.

## Discussion

For interpretation of the results, it is important to keep in mind that the uncertainties in the chronologies were large because of uncertainty inherent in the  $^{14}\text{C}$  method and bioturbation, the low sample resolution, and the large error inherent in the methods used for temperature reconstruction. Therefore, only trends should be compared between lakes.

### DIATOMS

The correspondence analysis and analogue matching showed that the diatoms had good analogues for most samples from about 6000 cal yr BP until the present. Only Seukokjaure had poor analogues for some samples. Those lakes with good analogues suggested a gradually decreasing temperature from 6000 cal yr BP until the present. The diatom record from Seukokjaure showed a decreasing trend from 4000 cal yr BP until today. Consistent with the temperature reconstructions, the correspondence analysis indicated that the lakes had developed a more alpine character through time and that the changes in species composition between lakes had been of similar magnitude during the Holocene. The surface samples for all proxies inferred the actual temperature for today fairly closely at each lake. Although most proxies consistently suggested a decreasing trend in temperature, the amplitude of change was different. This difference illustrated the problem associated with relatively high prediction errors for the models and the fact that many species lack significant temperature optima. The effect of July air temperature is not direct but can be a combination of several temperature-related variables, such as summer water temperature (Livingstone and Lotter, 1998), length of growing season, vegetation cover, ice cover, precipitation, mixing regimes, UV radiation, hypolimnion anoxia, nutrients, grazing, availability and quality of light for photosynthesis, gas exchange, and habitat availability (Walker et al., 1991a; Vinebrooke and Leavitt, 1996; Lotter et al., 1999b; Anderson, 2000; Smol and Cumming, 2000). Since these variables are not perfectly linearly related to July air temperature, vary in importance for the

different lakes, and change through time, reconstructions will inevitably vary between lakes.

Before 6000 cal yr BP, there was a large variability in the temporal patterns of inferred temperatures between lakes, and some intervals had poor analogues (e.g., those from Jeknajaure). This period should therefore be interpreted with caution in terms of climate. The period was dominated by *Fragilaria* spp., a genus common in most late glacial profiles regardless of geology, morphometry, or latitude (e.g., Haworth, 1976; Stabell, 1985; Rawlence and Senior, 1988; Bradshaw et al., 2000). It is also common in present-day alpine lakes (Laing and Smol, 2000), lakes with prolonged ice cover (Smol, 1988), and lakes with high alkalinity (Battarbee, 1986) and is probably tolerant of physical disturbance and low light conditions (Anderson, 2000). The loss-on-ignition also showed low values in the early Holocene and some rapid nonsynchronous changes in Jeknajaure, Sjuodjjaure, and Seukokjaure. Explanations for the low loss-on-ignition values may be high snow accumulation (Snowball et al., 1999) in combination with unstable soils after deglaciation and/or low production of organic material. Usually there was a good correlation between summer water and air temperatures (Livingstone and Lotter, 1998). However, periods with great accumulation of snow at high altitude may decouple the correlation due to cold water runoff. The low inferred temperatures during the early Holocene in Jeknajaure, Sjuodjjaure, and Seukokjaure may indicate more snow in the drainage area rather than lower air temperatures in the region. Niak had higher loss-on-ignition values in the early Holocene, indicating less accumulation of snow, more stable catchment conditions, or higher organic material production. The lake is surrounded by very steep slopes and has the smallest drainage area:lake area ratio of the four lakes. Hence snow accumulation is minimized, and it is therefore possible that the reconstruction for Niak was better correlated with air temperature than those for the other lakes in the early Holocene. The inferred temperatures from Niak showed a gradually decreasing trend throughout the Holocene.

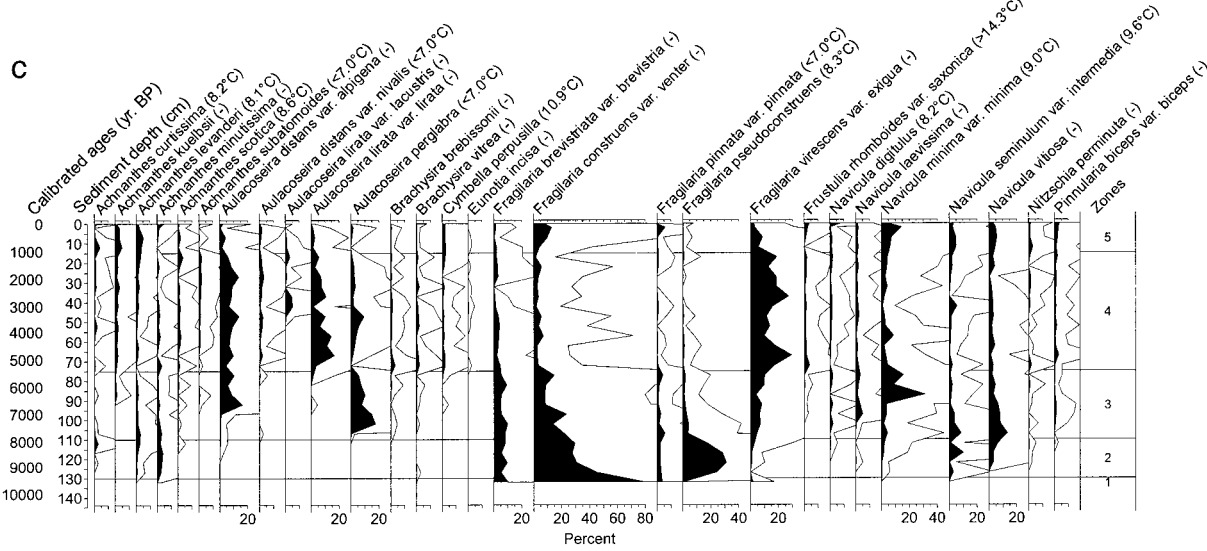
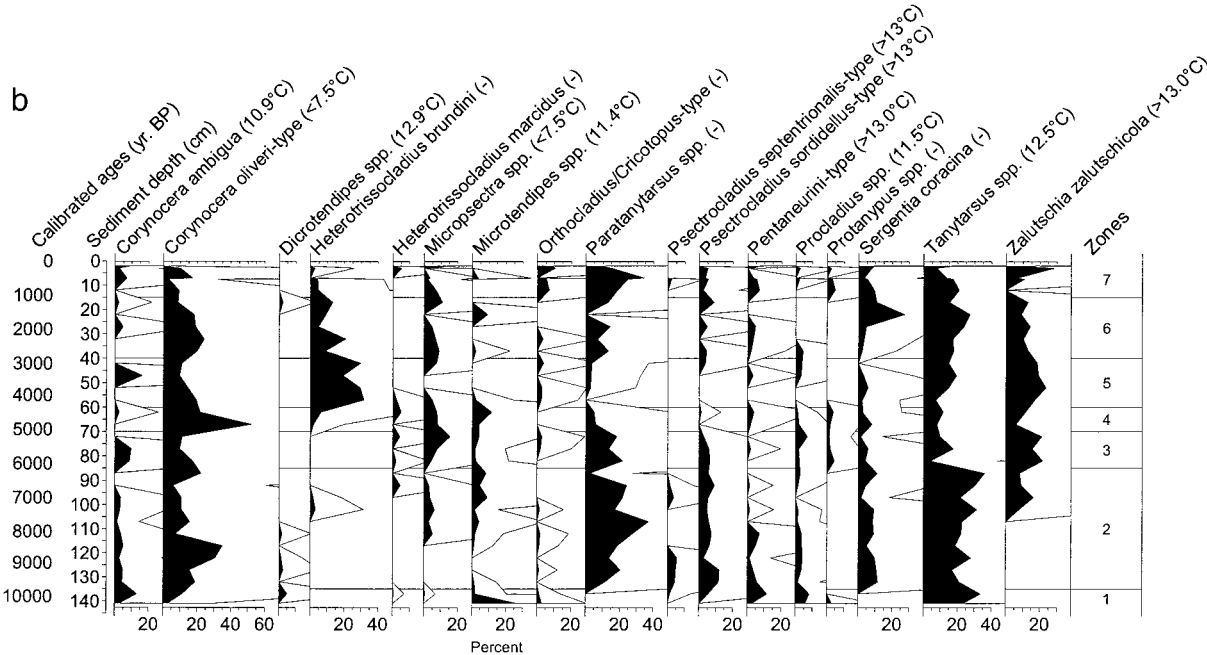
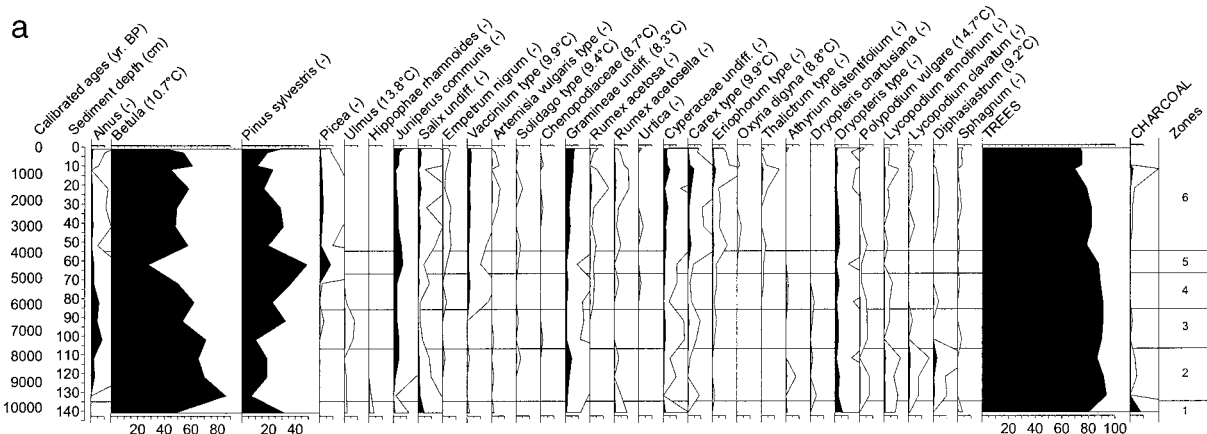
### CHIRONOMIDS

The analogue situation is poor for the chironomids in the early Holocene in Sjuodjjaure and poor from ca. 6000 cal yr BP to today in Seukokjaure. The inferred temperatures showed large discrepancies between the lakes. The chironomid record from Sjuodjjaure was similar to the diatom and pollen trends from Sjuodjjaure, with early Holocene temperatures similar to those of the present, a Holocene maximum between ca. 7000 and 5000 cal yr BP, and a decreasing trend until the present. The chironomid record from Seukokjaure suggested that only small changes occurred throughout the Holocene. The chironomid records from both lakes resembled actual present-day temperatures. The discrepancy in the temporal pattern of the temperature reconstructions could be due to the problems discussed earlier or may be due to a relatively small training set of 40 lakes and the fact that almost all levels had poor analogues based on fewer than 50 head capsules. Heiri and Lotter (2001) and Larocque (2001) found that for reliable reconstructions, more than 50–90 head capsules should be counted. Earlier studies have shown promising results using chironomids to infer past temperatures during late glacial time and suggest that chironomids are good indicators of temperature (Walker et al., 1991b; Levesque et al., 1993; Brooks and Birks, 2001). Chironomids from

←

*FIGURE 3. Pollen (a), chironomid (b), and diatom (c) diagram from Sjuodjjaure (826 m a.s.l.) plotted against sediment depth. Black silhouettes represent percent and open silhouettes per mil occurrences. The first column shows modeled, calibrated ages; 0 corresponds to the coring date. Lines indicate statistically significant zones. Temperatures within parentheses are statistically significant July air temperature optima for the taxa. An optimum below the gradient in the training set is indicated by < and beyond the gradient by >; (-) indicates no statistically significant optimum. Only the most common taxa are shown.*





Jeknajaure and Niak were not analyzed due to the low concentration of head capsules in the sediment.

## POLLEN

The analogue situation was poor throughout the Holocene in the high alpine lake Jeknajaure and before ca. 4000 cal yr BP in the lower lakes Sjuodjijaure and Seukokjaure. Despite the analogue problem, the pollen assemblages and the inferred temperatures for Sjuodjijaure and Seukokjaure showed many similarities during the Holocene as well as some similarities to other proxies. The inferred temperatures in the early Holocene from both lakes were about the same as today, but with some rapid changes occurring in the early Holocene. There was a gradual decreasing trend from ca. 7000 cal yr BP to the present. The inferred temperatures for the surface samples were the same as the actual values for today at both lakes.

Pollen-inferred temperatures from Jeknajaure were too high due to the sparse vegetation in the lake catchment and the large influence of long-range transported pollen (e.g., tree pollen). The pollen composition, and thus the temperature inferences, reflected boreal forest rather than the local situation. The pollen transfer function has a good predictive performance for lakes up to ca. 850 m a.s.l. (i.e., 150 m above treeline), as assessed by leave-one-out jackknifing, but pollen from lakes above 900 m a.s.l. overestimate the temperature by 1.5–4.5°C. Similarly, the poor analogues in Sjuodjijaure and Seukokjaure before 4000 cal yr BP may have been due to the fact that the vegetation was more open before 4000 cal yr BP than after. However, since both Sjuodjijaure and Seukokjaure are below 850 m a.s.l. and most proxy records inferred higher temperatures during the mid-Holocene than today, the poor analogues might indicate that prior to 4000 cal yr BP, a vegetation type that no longer exists dominated the region. The present vegetation communities in the region might have developed after 4000 cal yr BP. The early Holocene should be interpreted with caution in terms of climate due to the risk that the vegetation may not have been in equilibrium with climate during this successional stage.

The interpretation of pollen assemblages in terms of past vegetation communities assumed that both Sjuodjijaure and Seukokjaure were always in the zone where local influx constituted a significant proportion of the pollen influx. Both lakes reflected open or partly open birch-forest vegetation in the early Holocene. However, the recorded sequence started slightly earlier in Seukokjaure than in Sjuodjijaure, i.e., prior to the local establishment of *Alnus* at Seukokjaure. Around 7000 cal yr BP, *Betula* pollen decreased in abundance while *Pinus* pollen increased, reflecting a transition from an initially shrubby birch vegetation to a forest type with gradually increasing importance of pine. During the last ca. 5000 yr, *Pinus* and *Alnus* pollen decreased gradually, and *Picea* pollen occurred regularly. *Rumex*, *Cyperaceae*, *Graminae*, and *Ericaceae* pollen became more frequent. Tree pollen dominated the pollen assemblages in both lakes during the late Holocene, but the gradual increase of the nonarboreal pollen suggested that the local vegetation around the lakes must have become more open. The main difference between the high alpine lake Jeknajaure and the other lakes was that the pollen assemblage from Jeknajaure had high percentages of *Pinus* pollen and low percentages of *Betula* pollen compared to the lower lakes, Sjuodjijaure and Seukokjaure. The area with pine nearest to Jeknajaure is ca. 20 km

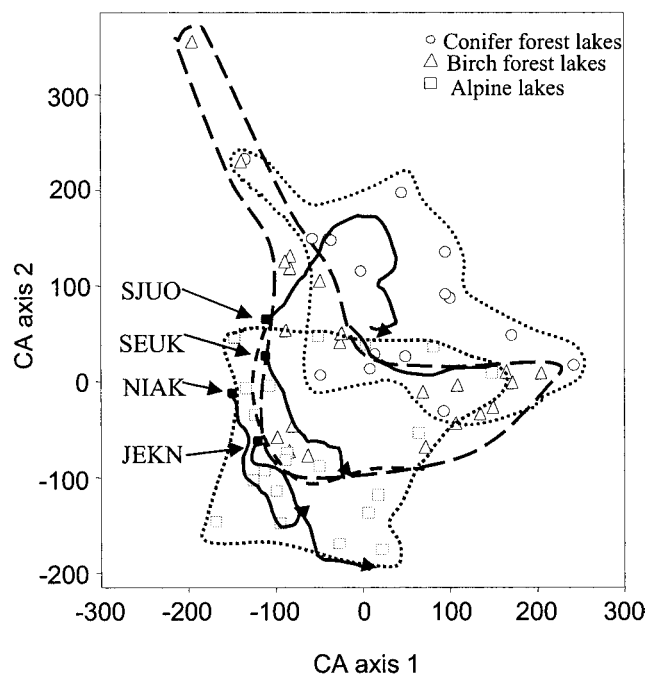


FIGURE 5. Sample scores from correspondence analysis (CA) of downcore diatom assemblages from Jeknajaure (JEKN), Niak, Sjuodjijaure (SJUO), and Seukokjaure (SEUK) compared to sample scores of diatom assemblages of surface sediments from the training-set lakes. The training-set lakes are classified as conifer forest, birch forest, or alpine lakes. Sample scores from downcore assemblages are based on 5-sample-running-mean values.  $\circ$  indicate the oldest sample in each lake and  $\triangle$  indicate the present. The CA shows both similar direction and magnitude of change in the diatom composition and suggests that the lakes have become more alpine through time.

away. The same effect could be seen in the training set, where the highest values of *Pinus* pollen occurred in the conifer forest and the high alpine area. Pollen from Niak was not analyzed due to problems with pollen studies in open areas.

## Conclusions

This study demonstrates that diatom, chironomid, and pollen assemblages contain climate information. The present temperatures at each lake can be inferred with reasonable confidence for most proxies. From ca. 6000 cal yr BP until today, most proxy records suggest a gradual decrease in temperature. However, large discrepancies, especially before 7000 cal yr BP, are probably due to differences in the development of the drainage area for each lake during the early Holocene (e.g., influence of snowfields, soil-forming processes), indicated by nonsynchronous loss-on-ignition curves. The discrepancy in the chironomid-inferred temperature records might be due to a small training set or too few head capsules for some samples, resulting in poor analogues. The poor pollen analogue situation from Jeknajaure clearly illustrates the difficulties with pollen studies in open areas such as this high alpine site with hardly any vegetation around the lake.

FIGURE 4. Pollen (a), chironomid (b), and diatom (c) diagrams from Seukokjaure (670 m a.s.l.) plotted against sediment depth. Black silhouettes represent percent and open silhouettes per mil occurrences. The first column shows calibrated ages; 0 corresponds to the coring date. Lines indicate statistically significant zones. Temperatures within parentheses are statistically significant July air temperature optima for the taxa. An optimum below the gradient in the training set is indicated by < and beyond the gradient by >; (-) indicates no statistically significant optimum. Only the most common taxa are shown.

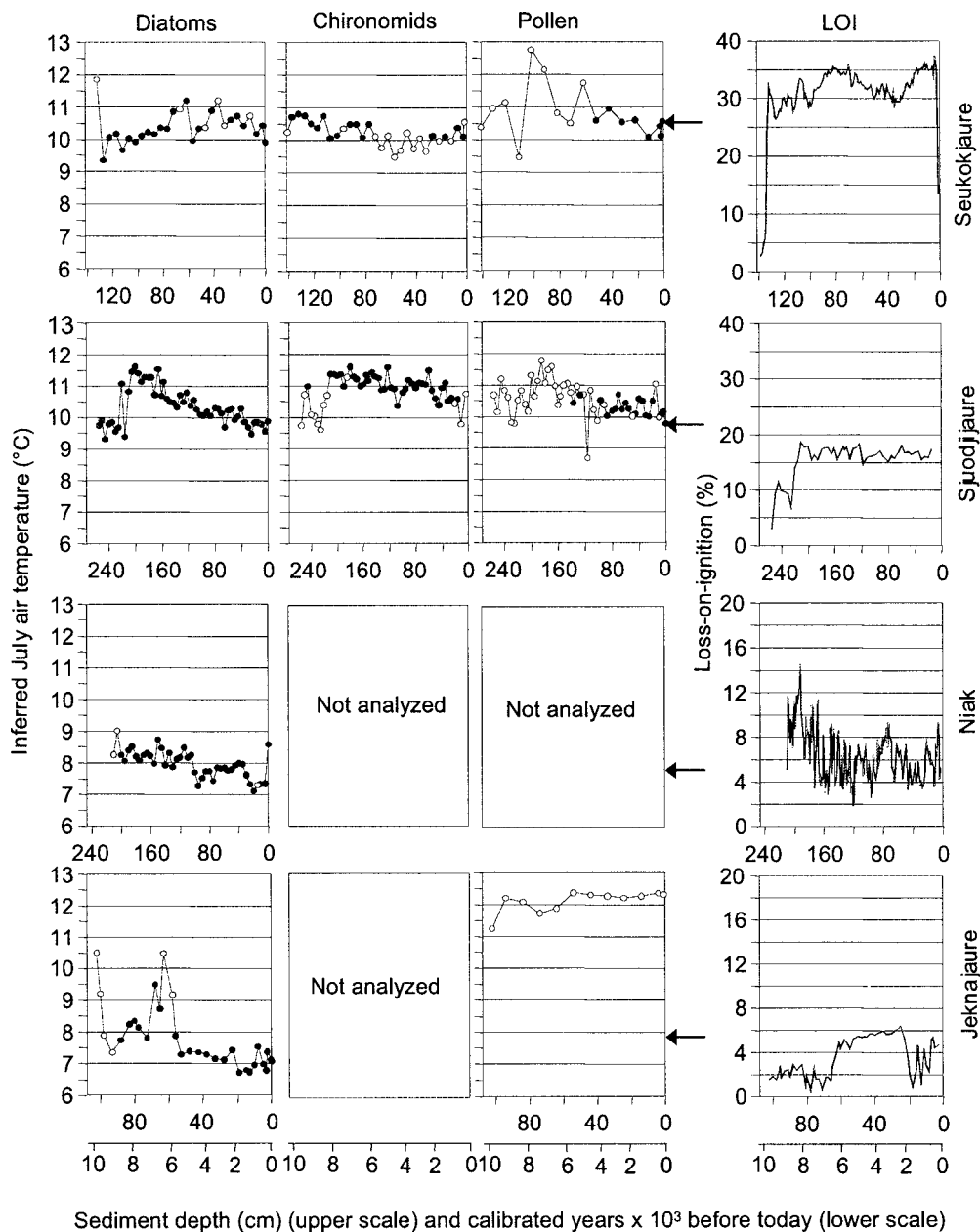


FIGURE 6. July air temperatures inferred from diatoms, chironomids, and pollen, and results of loss-on-ignition (LOI) measurements, in Holocene sediment cores from Jeknajaure (1191 m a.s.l.), Niak (1172 m a.s.l.), Sjuodjijaure (826 m a.s.l.), and Seukokjaure (670 m a.s.l.). Sample specific errors are for diatoms 0.9–1.2°C, chironomids 1.1–1.4°C, and pollen 1.4–1.7°C. Arrows show the present temperature at each lake. Open circles in the reconstructions indicate poor analogues and filled circles good analogues in the training set.

Pollen from the lower lakes, Sjuodjijaure and Seukokjaure, have poor analogue situations before ca. 4000 cal yr BP. This might indicate either that the vegetation was more open before 4000 cal yr BP or that prior to 4000 cal yr BP a vegetation type that no longer exists predominated in the region, and the present vegetation type developed after that period. Despite the analogue problem, the pollen-inferred temperatures from Sjuodjijaure and Seukokjaure show some similarities, and the pollen assemblages from all three lakes show similar trends during the Holocene. Due to large uncertainties inherent in the methods, only long-term trends in climate can be interpreted when using both multiproxy and multilake approaches. High-resolution studies using diatoms, chironomids, and pollen for climate reconstructions are probably not meaningful during periods with small changes in climate ( $<1^{\circ}\text{C}$ ). Future research should concentrate on low-resolution,

multiproxy, and multilake studies to further understand the relationship between the proxies and climate.

## Acknowledgments

This research was supported by the EC Environment and Climate Research Programme (contract ENV4-CT97-0642, Climate and Natural Hazards), the Nordic Council of Ministers (Grant FS/HFj-X-96005), and the Swedish Council for Forestry and Agricultural Sciences (SJFR). We thank Christian Bigler for sharing diatom data from eight lakes; Anders Hedefalk, Anders Eriksson, Evastina Grahn, Ann-Britt Lindström, and Mattias Karlsson for field and laboratory assistance; Arvid Odland (Telemark College) for estimating the modern temperature values for the study lakes; Einar Heegaard

(University of Bergen) for the age-depth modeling; Karin Aune for the map; and Christian Bigler and Markus Heinrichs for valuable comments on the manuscript. The manuscript was written while P. Rosén was supported by the Climate Impacts Research Centre (CIRC) via funds from the Environment and Space Research Institute (MRI) in Kiruna, Sweden. This is CHILL-10,000 contribution No. 52.

## References Cited

- Anderson, N. J., 2000: Diatoms, temperature and climatic change. *European Journal of Phycology*, 35: 307–314.
- Anderson, P. M., Bartlein, P. J., Brubaker, L. B., Gajewski, K., and Ritchie, J. C., 1991: Vegetation-pollen-climate relationships for the arcto-boreal region of North America and Greenland. *Journal of Biogeography*, 18: 565–582.
- Battarbee, R. W., 1986: Diatom analysis. In Berglund, B. G. (ed), *Handbook of Holocene Palaeoecology and Paleohydrology*. London: John Wiley and Sons, 527–570.
- Battarbee, R. W., 2000: Palaeolimnological approaches to climate change with special regard to the biological record. *Quaternary Science Reviews*, 19: 107–124.
- Bennett, K. D., 1996: Determination of the number of zones in a biostratigraphical sequence. *New Phytologist*, 132: 155–170.
- Bigler, C., and Hall, R. I., 2002: Diatoms as indicators of climatic and limnological change in Swedish Lapland: a 100-lake calibration set and its validation for paleoecological reconstructions. *Journal of Paleolimnology*, 27: 97–115.
- Birks, H. J. B., 1995: Quantitative palaeoenvironmental reconstructions. In Maddy, D., and Brew, J. S. (eds.), *Statistical Modelling of Quaternary Science Data. Technical Guide 5*. Cambridge: Quaternary Research Association, 161–254.
- Birks, H. J. B., 1998: D. G. Frey and E. S. Deevey Review No. 1: Numerical tools in palaeolimnology—progress, potentialities, and problems. *Journal of Paleolimnology*, 20: 307–332.
- Birks, H. J. B., and Gordon, A. D., 1985: *Numerical Methods in Quaternary Pollen Analysis*. London: Academic Press.
- Birks, H. J. B., Line, J. M., Juggins, S., Stevenson, A. C., and ter Braak, C. J. F., 1990: Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London B*, 327: 263–278.
- Bradshaw, E. G., Jones, V. J., Birks, H. J. B., and Birks, H. H., 2000: Diatom responses to late-glacial and early-Holocene environmental changes at Kråkenes, western Norway. *Journal of Paleolimnology*, 23: 21–34.
- Brooks, S. J., and Birks, H. J. B., 2000: Chironomid-inferred late-glacial and early-Holocene mean July air temperatures for Kråkenes Lake, western Norway. *Journal of Paleolimnology*, 23: 77–89.
- Brooks, S. J., and Birks, H. J. B., 2001: Chironomid-inferred air temperatures from Late glacial and Holocene sites in north-west Europe: progress and problems. *Quaternary Science Reviews*, 20: 1723–1741.
- Grimm, E., 1993: TILIA v2.0 (software). Springfield, IL: Illinois State Museum, Research and Collections Centre.
- Haworth, E. Y., 1976: Two late-Glacial (late Devensian) diatom assemblage profiles from northern Scotland. *New Phytologist*, 77: 227–256.
- Heiri, O., and Lotter, A. F., 2001: Effect of low count sums on quantitative environmental reconstructions: an example using sub-fossil chironomids. *Journal of Paleolimnology*, 26: 343–350.
- Huisman, J., Olf, H., and Fresco, L. F. M., 1993: A hierarchical set of models for species response analysis. *Journal of Vegetation Science*, 4: 37–46.
- Jackson, D. A., 1993: Stopping rules in principal component analysis: a comparison of heuristical and statistical approaches. *Ecology*, 74: 2204–2214.
- Jolliffe, I. T., 1986: *Principal Component Analysis*. New York: Springer-Verlag. 271 pp.
- Juggins, S., 1991: ZONE. Unpublished computer program, version 1.2. Newcastle-upon-Tyne, UK: Department of Geography, University of Newcastle.
- Juggins, S., and ter Braak, C. J. F., 1995: WAPLS. Unpublished computer program, version 1.0. Newcastle-upon-Tyne, UK: Department of Geography, University of Newcastle.
- Korhola, A., Weckström, J., Holmström, L., and Erästö, P., 2000: A quantitative Holocene climate record from diatoms in Northern Fennoscandia. *Quaternary Research*, 54: 284–294.
- Laaksonen, K., 1976: The dependence of mean air temperatures upon latitude and altitude in Fennoscandia (1921–1950). *Annales Academiae Scientiarum Fennicae*, 119: series A, 5–19.
- Laing, T. E., and Smol, J. P., 2000: Factors influencing diatom distribution in circumpolar treeline lakes of northern Russia. *Journal of Phycology*, 36: 1035–1048.
- Larocque, I., 2001: How many chironomid head capsules are enough? A statistical approach to determine sample size for paleoclimatic reconstructions. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 172: 133–142.
- Levesque, A. J., Francis, E. M., Walker, I. R., and Cwynar, L. C., 1993: A previously unrecognized late-glacial cold event in eastern North America. *Nature*, 361: 623–626.
- Livingstone, D., and Lotter, A. F., 1998: The relationship between air and water temperatures in lakes of the Swiss Plateau: a case study with palaeolimnological implications. *Journal of Paleolimnology*, 19: 181–198.
- Lotter, A. F., and Juggins, S., 1991: POLPROF, TRAN and ZONE. Programs for plotting, editing and zoning pollen and diatom data. INQUA Commission for the study of the Holocene, Working Group on Data Handling Methods, Newsletter 6.
- Lotter, A. F., Birks, H. J. B., Hofmann, W., and Marchetto, A., 1997: Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal of Paleolimnology*, 18: 395–420.
- Lotter, A. F., Walker, I. R., Brooks, S. J., and Hofmann, W., 1999a: An intercontinental comparison of chironomid palaeotemperature inference models: Europe vs North America. *Quaternary Science Reviews*, 18: 717–735.
- Lotter, A. F., Pienitz, R., and Schmidt, R., 1999b: Diatoms as indicators of environmental change near arctic and alpine treeline. In Stoermer E. F., and Smol J. P. (eds.), *The Diatoms: Applications for the Environmental and Earth Sciences*. Cambridge: Cambridge University Press, 205–226.
- Lotter, A. F., Birks, H. J. B., Eicher, U., Hoffmann, W., Schwander, J., and Wick, L., 2000: Younger Dryas and Allerød summer temperatures at Gerzensee (Switzerland) inferred from fossil pollen and cladoceran assemblages. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 159: 349–361.
- Olander, H., Birks, H. J. B., Korhola, A., and Blom, T., 1999: An expanded calibration model for inferring lakewater and air temperatures from fossil chironomid assemblages in northern Fennoscandia. *The Holocene*, 9: 279–294.
- Pellatt, M. G., Smith, M. J., Mathewes, R. W., Walker, I. R., and Palmer, S. L., 2000: Holocene treeline and climate change in the subalpine zone near Stoyoma Mountain, Cascade Mountains, south-western British Columbia, Canada. *Arctic, Antarctic, and Alpine Research*, 32: 73–83.
- Pienitz, R., Smol, J. P., and Birks, H. J. B., 1995: Assessment of freshwater diatoms as quantitative indicators of past climatic change in the Yukon and Northwest Territories, Canada. *Journal of Paleolimnology*, 13: 21–49.
- Rawlence, D. J., and Senior, A., 1988: A late-Glacial diatom and pigment history of Little Lake, New Brunswick with particular reference to the younger Dryas climatic oscillation. *Journal of Paleolimnology*, 1: 163–177.
- Rosén, P., Hall, R., Korsman, T., and Renberg, I., 2000: Diatom transfer-functions for quantifying past air temperature, pH and total organic carbon concentration from lakes in northern Sweden. *Journal of Paleolimnology*, 24: 109–123.
- Rosén, P., Segerström, U., Eriksson, L., Renberg, I., and Birks, H. J. B., 2001: Climate change during the Holocene as recorded by diatoms, chironomids, pollen and near-infrared spectroscopy (NIRS) in a

- sediment core from an alpine lake (Sjuodjijaure) in northern Sweden. *The Holocene*, 11: 551–562.
- Smith, M. J., Pellatt, M. G., Walker, I. R., and Mathewes, R. W., 1998: Postglacial changes in chironomid communities and inferred climate near treeline at Mount Stoyoma, Cascade Mountains, south-western British Columbia, Canada. *Journal of Paleolimnology*, 20: 227–293.
- Smol, J. P., 1988. Paleoclimate proxy data from freshwater arctic diatoms. *Verh. Internat. Verein. Limnol.*, 23: 837–844.
- Smol, J. P., and Cumming, B. F., 2000: Tracking long-term changes in climate using algal indicators in lake sediments. *Journal of Phycology*, 36: 986–1011.
- Snowball, I., Sandgren, P., and Petterson, G., 1999: The mineral magnetic properties of an annually laminated Holocene lake-sediment sequence in northern Sweden. *The Holocene*, 9: 353–362.
- Stabell, B., 1985. The development and succession of taxa within the diatom genus *Fragilaria* Lyngbye as a response to basin isolation from the sea. *Boreas*, 14: 273–286.
- Stuiver, M., and Reimer, P. J., 1993: Extended <sup>14</sup>C data base and revised CALIB 3.0 <sup>14</sup>C calibration program. *Radiocarbon*, 35: 215–230.
- ter Braak, C. J. F., 1991: CANOCO version 3.12. Agricultural Mathematics Group, Wageningen.
- ter Braak, C. J. F., and Looman, C. W. N., 1986: Weighted averaging, logistic regression and the Gaussian response model. *Vegetatio*, 65: 3–11.
- Vinebrooke, R. D., and Leavitt, P. R., 1996: Effects of ultraviolet radiation in an alpine lake. *Limnology and Oceanography*, 41, 1035–1040.
- Vyverman, W., and Sabbe, K., 1995: Diatom-temperature transfer functions based on the altitudinal zonation of diatom assemblages in Papua New Guinea: a possible tool in the reconstruction of regional palaeoclimatic changes. *Journal of Paleolimnology*, 13: 65–77.
- Walker, I. R., Smol, J. P., Engstrom, D. R., and Birks, H. J. B., 1991a: An assessment of Chironomidae as quantitative indicators of past climatic change. *Canadian Journal of Fisheries and Aquatic Sciences*, 48: 975–987.
- Walker, I. R., Mott, R. J., and Smol, J. P., 1991b: Allerød–Younger Dryas lake temperatures from midge fossils in Atlantic Canada. *Science*, 253: 1010–1012.
- Weckström, J., Korhola, A., and Blom, T., 1997: Diatoms as quantitative indicators of pH and water temperature in subarctic Fennoscandian lakes. *Hydrobiologia*, 347: 171–84.
- Wunsam, S., Schmidt R., and Klee, R., 1995: *Cyclotella*-taxa (Bacillariophyceae) in lakes of the Alpine region and their relationship to environmental variables. *Aquatic Science*, 57: 360–386.

*Ms submitted June 2001*  
*Revised ms submitted May 2002*